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The Fossil History of the Juglandaceae

Steven R. Manchester

Monographs in Systematic Botany
from the Missouri Botanical Garden

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Author's address:

Departments of Geology and Biology, Indiana University, Bloomington, Indiana 47405.

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The cover illustration: Fossil engelhardioid fruits; see Figure 30.

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Contents

Abstract	1
Description of Extant Juglandaceae	2
Systematic Relationships	4
Diagnostic Value of Different Organs	5
Early Occurrences	8
Platycaryeae	17
Engelhardieae	34
Hicoreae	63
Juglandaeae	81
General Discussion and Conclusions	120
Literature Cited	129
Taxonomic Index	136

ABSTRACT

A critical review of the fossil record of pollen, inflorescences, fruits, and foliage provides a basis for interpreting the evolutionary and biogeographic history of the walnut family (Juglandaceae). Intergrading features of pollen and floral morphology suggest that the Juglandaceae evolved from plants of the Normapolles complex with bisexual flowers and tiny bicarpellate nutlets during the latest Cretaceous or early Paleocene. The paleogeographic distribution of Normapolles pollen and of early juglandaceous taxa indicates that the family originated in the Northern Hemisphere. Although the present-day center of diversity for the family is eastern Asia, the fossil record does not support previous arguments for an Asian origin. All of the six genera present today in Asia have Tertiary records in Europe and North America. The earliest center of generic diversity appears to have been North America or Europe. The major diversification of the family is recorded in the pollen and megafossil record of the early Tertiary. Fruits from the Paleocene include representatives of the tribe Juglandae as well as genera that cannot be assigned with certainty to modern tribes. During the Eocene, all four extant tribes were present, and the family achieved its greatest generic diversity including both extinct and extant genera. As today, most of the early Tertiary genera had winged fruits; however, large, wingless fruits apparently adapted for animal dispersal were also present. Although the Engelhardiidae retains more primitive characters than other modern tribes, its evolution, as defined by the appearance of the trilobate inflorescence bract, was apparently subsequent to that of other tribes. Nearly all modern genera had broader distributions in the Tertiary than today. Some of the Paleocene and Eocene genera (such as *Polyptera*, *Paleoplatycarya*, *Paleooreomunnea*, and *Paraengelhardtia*) were never very widespread and became extinct, presumably in response to climatic fluctuation, by the end of the Eocene. During the same interval, *Cyclocarya* and *Platycarya* became extinct in North America but survived in Eurasia. In the early Tertiary, the major route of intercontinental migration appears to have been across the North Atlantic between North America and western Europe. During the Neogene, exchange of taxa occurred between North America and Asia and between Europe and Asia, resulting in broad Miocene distributions of *Pterocarya*, *Juglans* (sect. *Cardiocaryon*), *Carya*, and *Cyclocarya*. Extreme range reductions occurred during the Pliocene and Pleistocene, resulting in the elimination of *Pterocarya*, *Juglans* sect. *Cardiocaryon*, and *Carya* from western North America and western Europe, and the restriction of *Platycarya*, *Cyclocarya*, and *Engelhardtia* to eastern Asia.

There have been various attempts to describe the evolution and diversification of extant angiosperm families based on the fossil record. However, most studies have been restricted to one or two organ types (e.g., leaves or pollen), one locality or geographic region, one stratigraphic interval or age, or rely uncritically on previously published identifications. Although there is a rich and well-sampled fossil record for many Northern Hemisphere angiosperm families, few have been singled out for comprehensive study. The Juglandaceae is ideally suited for such analysis and is the subject of this work.

The Juglandaceae is a well-defined family with eight living genera and about 60 modern species. With the exception of *Juglans*, which ranges well into South America, and *Engelhardtia*, which extends into Sumatra, Java, and New Guinea, the family is restricted to the Northern Hemisphere. The Juglandaceae has been the subject of numerous anatomical, morphological, and taxonomic studies (reviewed in Manning, 1978). Modern genera have been studied from a variety of aspects, including inflorescence morphology (Manning, 1938, 1940, 1948; Abbe, 1974), fruit type (Manning, 1940; Stone, 1973), pollen morphology (Whitehead, 1963, 1965; Stone & Broome, 1975), leaf architecture (Wolfe, 1959),

wood anatomy (Heimsch & Wetmore, 1939; Miller, 1976), chemotaxonomy (Giannasi & Niklas, 1983), and mode of germination (Conde & Stone, 1970). The relatively large amount of data thus available for extant members of the family facilitates the recognition and interpretation of juglandaceous fossils.

There are countless citations of juglandaceous taxa in the literature on Cenozoic fossil floras of the Northern Hemisphere. Various useful reviews of Juglandaceae in the fossil record have been presented, dealing with foliage (Nagel, 1914; Wolfe, 1959), wood (Müller-Stoll & Mädler, 1960; Manchester, 1983), dispersed pollen (Nichols & Ott, 1978; Frederiksen & Christopher, 1978), staminate inflorescences (Crepet et al., 1980), and fruits (Dilcher et al., 1976; Vaudois-Miéja, 1978; Manchester & Dilcher, 1982). The fossil record of the Juglandaceae is now sufficiently well known that it is possible to present a relatively complete "case history" for the family, characterizing various extinct genera and tracing the history of modern genera. The purpose of this paper is to integrate new data from the fossil record with a critical review of previous literature as a basis for interpreting the patterns of evolution, migration, and extinction that have shaped the history of the walnut family.

TABLE 1. Classification of extant and fossil fruit genera in the Juglandaceae.

PLATYCARYOIDEAE		JUGLANDOIDEAE	
Platycaryeae	Engelhardieae	Hicoreae	Juglandeae
<i>Platycarya</i>	<i>Engelhardia</i>	<i>Carya</i>	<i>Pterocarya</i>
<i>Paleoplatycarya</i> ^a	<i>Oreomunnea</i>		<i>Cyclocarya</i>
<i>Hooleya</i> ^a	<i>Alfaroa</i>		<i>Juglans</i>
	<i>Paraengelhardtia</i> ^a		<i>Polyptera</i> ^a
	<i>Paleooreomunnea</i> ^a		<i>Sphaerocarya</i> ^a
	<i>Palaeocarya</i> ^b		

^a Extinct genus.^b Fossil genus for various fruits of the *Engelhardia*-*Oreomunnea* type.

The intrafamilial classification of the Juglandaceae shown in Table 1 seems to accurately represent the natural relationships between modern genera and is useful for application to the fossil record. The family is divided into two subfamilies, the Platycaryoideae and the Juglandoideae. The Platycaryoideae consists of the Platycaryeae with one modern genus and species, and the Engelhardieae with three modern genera. The Juglandoideae is divided into two tribes: the Hicoreae with one modern genus and the Juglandeae with three modern genera. This classification scheme is essentially that of Manning (1978), modified to include the Engelhardieae within the Platycaryoideae, as suggested by Wing and Hickey (1984) and includes *Cyclocarya* as a genus separate from *Pterocarya*, as suggested by Manchester and Dilcher (1982).

DESCRIPTION OF EXTANT JUGLANDACEAE

Identification and interpretation of the fossils upon which this study is based relies heavily on detailed comparisons with extant Juglandaceae. The following synopsis is based on extant genera and indicates various features characteristic of the family. Figure 1 summarizes, in diagrammatic form, selected morphological and anatomical features useful for segregating the genera into tribes. More complete descriptions of individual tribes and genera will be provided in the appropriate sections prefacing the discussion of fossil remains.

Juglandaceae A. Rich. ex Kunth.

Deciduous¹ trees, unisexual, usually monoecious. Leaves alternate, except in *Oreomunnea* and *Alfaroa* in which they are opposite; astipu-

late, pinnately compound, parapinnate and imparipinnate. Leaflets characteristically serrate but entire-margined in some species of *Engelhardia*, *Oreomunnea*, *Alfaroa*, *Juglans*, and *Carya*; venation semicraspedodromous to eucamptodromous with typically percurrent tertiaries and orthogonal higher order venation; teeth small, simple, usually about 1 mm, acute to obtuse, and supplied by veins of tertiary order arising from marginal loops or branches of the secondaries. Stomata anomocytic, confined to lower surface; unicellular and uniseriate hairs solitary or in tufts of two to seven, small capitate glands present in *Juglans*; rounded glandular peltate scales 50–250 μ m in diameter common.

Wood diffuse-porous to, less commonly, semi-ring-porous, with vessels often distributed in an oblique pattern. Vessels medium-sized, solitary, and in radial multiples of two to four with simple and scalariform (Engelhardieae) or exclusively simple perforation plates and alternate intervacular pits. Tyloses common. Tracheids present only in *Platycarya*. Reticulate thickening in vessels of some *Juglans* species; spiral thickening in smaller vessels and tracheids of *Platycarya*. Axial parenchyma distributed in the cross section as tangential, one to three seriate wavy or straight lines. Rays two to seven, usually two to three seriate, heterogeneous to homogeneous, procumbent cells mostly round to mostly vertically elongate in tangential section. Fibers and vessels with especially thick walls in *Carya*. Crystals in solitary idioblasts of the axial parenchyma (*Carya*), in chains of idioblasts of axial parenchyma (*Juglans*), or in solitary idioblasts within the rays (*Platycarya*). Pith chambered in *Juglans*, *Pterocarya*, and *Cyclocarya*; solid in all other genera.

Staminate catkins comprised of helically ar-

¹ Possibly evergreen in some examples of *Cyclocarya* and *Engelhardia* (Manning, pers. comm.).

FIGURE 1. Distribution of selected characters among modern tribes and genera of the Juglandaceae.—A. Characteristic fruit types.—B. Pistillate floral diagrams (from Manning, 1978, except the diagram for *Cyclocarya*).—C. Characteristic pollen types.—D. Condition of pith: chambered in the Juglandaceae, solid in all other genera.—E. Tracheary elements of secondary xylem.

ranged floral envelopes (flowers?) with basically seven parts: a bract (primary bract), two bracteoles (secondary bracts), and four sepals (tepals). Deviating from the basic plan are *Carya*, in which all of the sepals are usually missing, and *Platycarya*, in which the bracteoles as well as the sepals are generally absent. Bract trilobate in the Engelhardieae, unlobed in others. Anthers nearly sessile, 0.5–1.5 mm long; number of stamens two to 105, widely variable even within one genus (Manning, 1948, 1978).

Pollen normally triporate in Platycaryeae, Engelhardieae, and Hicoreae, four- to many-pored in the Juglandaceae, pores circular to meridionally elongate, isopolar to heteropolar; pore region often protruding. Grains oblate to spheroidal, 10–31 μm polar diameter by 10–68 μm equatorial diameter. Exine 0.3–2.5 μm thick consisting of a spinulose tectum 0.25–0.55 μm thick, a granular interstidium 0.11–1.3 μm thick and a footlayer one-half to one-tenth as thick as the tectum. A thin endexine layer that does not thicken in the apertural region is usually present. Tectal ornamentation consists of small (0.1–0.4 μm diameter) evenly distributed sharply pointed spinules (con) of approximately equal height. *Platycarya* distinguished by the presence of two pseudocolpi on each hemisphere; *Carya* slightly heteropolar with a thin area of exine at the proximal pole (Whitehead, 1963, 1965; Stachurska, 1961; Stone & Broome, 1975).

Pistillate inflorescences characterized by the same basic floral plan as the staminate ones: each floral envelope is comprised of a bract, two bracteoles, and four sepals subtending a pistil. The bract, bracteoles, and sepals, when present, adnate to the base of the ovary or to the entire ovary. Sepals typically absent in *Platycarya* and *Carya*. Bract trilobate in the Engelhardieae, entire in other tribes. Pistil one, ovary inferior, normally bicarpellate, with one unitegmic erect orthotropous ovule. Carpels median (= anterior-posterior; aligned with the bract and catkin axis) in most genera, transverse (aligned perpendicular to the bract and catkin axis) in *Platycarya* and *Carya*. Style short or absent with two divergent stigmatic arms. Styler orientation carinal (arms diverging along the center line of the carpels) in most genera, commissural (in the plane of carpel suture and of the primary septum) in *Carya*, *Cyclocarya* (see p. 91), and *Engelhardia* sect. *Engelhardia*. Ovary unilocular with a single erect orthotropous ovule. Fruit unilocular but with a

primary septum dividing the base of the seed into two primary lobes; incomplete secondary and sometimes tertiary septa present in some genera resulting in a fruit with two, four, or eight compartments ("cells") and a seed with a corresponding number of basal lobes. Fruit is a nut, enclosed by an adherent dehiscent (*Carya*) or indehiscent (*Alfaroa* and *Juglans*) husk, or a winged nutlet (*Platycarya*, *Engelhardia*, *Oreomunnea*, *Pterocarya*, *Cyclocarya*) (Manning, 1940, 1978). Germination epigeal (*Pterocarya*, *Platycarya*, *Engelhardia*) or hypogeal (*Carya*, *Juglans*, *Alfaroa*, *Oreomunnea*) (Conde & Stone, 1970).

Chromosome number, $n = 16$, except in some species of *Carya* where $n = 32$ (Stone, 1961).

SYSTEMATIC RELATIONSHIPS

The Juglandaceae is usually placed together with the extant monotypic Rhoipteleaceae in the order Juglandales (Hutchinson, 1959; Takhtajan, 1969; Manning, 1974; Cronquist, 1981). Both families have pinnately compound foliage and a bicarpellate ovary with a single seed. *Rhoiptelea* differs from the Juglandaceae in various features thought to be more primitive such as: exclusively scalariform vessel perforations; the presence of stipules; frequently perfect, bisexual flowers; superior completely bilocular ovary; and bitegmic, hemitropous ovules. Manning (1978) considers that the flowers of *Rhoiptelea* match the hypothetical inflorescence prototype for the Juglandaceae. Withner (1941) called attention to similarities in wood anatomy between the two families, such as the presence of thin-walled tyloses, alternate intervacular pitting, and size of the vessels, and he noted that the pattern of tangential lines of axial parenchyma characteristic of Juglandaceae is approached by the connecting bands of confluent parenchyma (one to two cells wide) seen in *Rhoiptelea*. Pollen of *Rhoiptelea* (Stone & Broome, 1971) is triporate with fine, evenly distributed con, and has a similar wall structure to that of the Juglandaceae, consisting of a tectum traversed by fine channels, a granular infratectal layer, and a footlayer of approximately the same thickness as the granular layer. The pollen differs from that of the Juglandaceae and more closely resembles that of the Myricaceae in the greater degree of thickening of the footlayer and endexine near the pores.

The Juglandales are set apart from other

"Amentiferae" (sensu Hjelmqvist, 1948) or Hamamelidae (sensu Cronquist, 1981) by their compound leaves. In this respect, and in some aspects of foliar venation, the order resembles some taxa of the Rosidae (e.g., Anacardiaceae). Wolfe (1973), Thorne (1973), and Hickey and Wolfe (1975) suggest that the order should be included in the Rosidae; however, Cronquist (1981) cites numerous lines of evidence—including pollen morphology, wood anatomy, and chemistry—supporting its retention in the Hamamelidae. Of the simple-leaved Hamamelidae, the Juglandaceae is most similar to the Myricaceae. The flowers of Myricaceae are usually unisexual (bisexual in *Canacomyrca*) and have a bicarpellate ovary with a unitegmic orthotropous ovule. The venation of myricaceous leaves differs in numerous respects from that of juglandaceous leaflets; however, both families are characterized by peltate scales comprised of radially fused cells. In the Myricaceae, these scales arise from a bicellular base, whereas in Juglandaceae there is a single basal cell (Ferguson, 1971; Chourey, 1974).

DIAGNOSTIC VALUE OF DIFFERENT ORGANS

The fossil record of the Juglandaceae includes various parts of the plant body—principally wood, leaves, fruits, pollen, and inflorescences. However, the usual detachment of organs from

one another prior to fossilization limits our understanding of extinct species to what we can determine from isolated plant parts. Since the taxonomic value of a particular organ or tissue type varies with the family or genus being investigated, it is important to understand the limitations, as well as the utility, of each organ for careful interpretation of the fossil record.

FRUITS

In the Juglandaceae the most important structure for generic level determinations is the fruit. Each modern genus is defined such that it can be recognized on the basis of its fruit, with or without information from other organs. This invites analysis of the fossil fruit record to determine the timing of appearance and evolution of modern genera, and facilitates the recognition of extinct genera.

A key to the identification of modern and fossil genera based on fruits is provided below. Features important in the identification of juglandaceous fruits include configuration of the wings and/or husk, septation within the nutlet, vasculature, styler configuration, and seed morphology. When a fossil juglandaceous fruit is not well enough preserved or understood to ascertain its intrafamilial affinities, the organ generic designation *Juglandicarya* Reid & Chandler (1933) is applied.

GENERIC KEY TO EXTANT AND FOSSIL JUGLANDACEOUS FRUITS

- 1a. Fruits borne in a cone-like infructescence; bract persisting on axis (not dispersed with fruit); fruits with a pair of lateral wings oriented parallel to the nutlet axis (Platycaryeae).
 - 2a. Sepals present, wings relatively large, with veins *Paleoplatycarya*², *Hooleya*²
 - 2b. Sepals absent, wings small, with few or no veins *Platycarya*³
- 1b. Fruits not borne in a cone-like infructescence; bract attached to and dispersed with the fruit. Fruits without a pair of lateral wings or with pair of lateral wings oriented oblique to nutlet axis.
 - 3a. Bracteoles united into a prophyllum, or not participating in fruit development.
 - 4a. Fruit winged due to enlargement of bract. Prophyllum present.
 - 5a. Bract-wing entire, forming a single lobe *Casholdia*²
 - 5b. Bract-wing trilobate (Engelhardieae).
 - 6a. Wing with shallow sinuses *Paraengelhardtia*², *Paleooreomunnea*²
 - 6b. Wing with deep sinuses *Palaeocarya*², *Oreomunnea*, *Engelhardtia*
 - 4b. Fruit wingless, trilobate bract retained as a tiny scale at the base of a large nut. Prophyllum absent *Alfaroa*
 - 3b. Bracteoles participating in wing or husk formation but not forming a prophyllum.
 - 7a. Fruits winged.
 - 8a. Nutlet encircled by a disk-like wing oriented perpendicular to the nutlet axis.
 - 9a. Disk-wing margin entire or slightly undulatory *Cyclocarya*³
 - 9b. Disk petaloid, divided into 8 to 10 lobes *Polyptera*²

² Genera established for fossils.

³ Modern genera with acceptable Paleogene fruit records discussed herein.

- 8b. Nutlet adjoined by a pair of lateral bracteolar wings oriented in a plane oblique to the nutlet axis *Pterocarya*³
- 7b. Fruits not winged.
- 10a. Nut small and spheroidal, with a low primary septum *Sphaerocarya*²
- 10b. Nut large, spheroidal to oblong, with a high primary septum.
- 11a. Husk indehiscent (partially dehiscent in *J. regia*); dorsal bundles extrorse; carpels median *Juglans*³
- 11b. Husk dehiscent; dorsal bundles introrse, carpels transverse *Carya*³

POLLEN

Pollen morphology in the Juglandaceae is generally diagnostic at the subfamilial and tribal levels but is of more limited value in distinguishing genera. For example, it is easy to distinguish pollen of extant Juglandaceae from that of the Engelhardiaceae but difficult or impossible to separate some grains of *Pterocarya* from *Juglans* (both in Juglandaceae) or *Oreomunnea* from *Alfaroa* (both in Engelhardiaceae). *Carya* and *Platycarya*, being the sole living representatives of the tribes Hicoreae and Platycaryeae, respectively, can be identified to the generic level with ease. However, it cannot be assumed that matching fossil grains represent only these modern genera because extinct genera of these tribes might have borne identical types of pollen. It is therefore advisable to use organ generic names, such as *Caryapollenites* Raatz ex Potonie and *Platycaryapollenites* Nagy for dispersed pollen, especially in the early Tertiary. *Platycaryapollenites* co-occurs in the same strata as the extinct platycaryoid fruit genera *Paleoplatycarya* and *Hooleya*, in the Early and Middle Eocene.

Pollen of the Juglandaceae is relatively uniform in wall structure and ornamentation. Intrafamilial classification is therefore accomplished mainly on the basis of pore number and distribution, specialized patterns of exine thinning, and size, and usually does not require electron microscopy. However, the relatively unspecialized triplicate pollen characteristic of extant Engelhardiaceae is rather similar to that of other amentiferous families such as Rhoipteleaceae, Myricaceae, and Betulaceae. While extant pollen of these families can usually be separated with light microscopy on the basis of subtle differences in wall thickening in the aperture regions, the identification of similar grains from the early Tertiary and Cretaceous may be more susceptible to error. Electron microscopy can help to resolve the affinities of such material. In extant Juglandaceae the ornamentation consists of evenly spaced coni on an otherwise smooth tectum. In other families the coni are on tiny bumps (Myricaceae) or ridges (Betulaceae) and are not as evenly distributed.

Analyses of fossil pollen are most meaningful when they can be linked with a particular taxon also known from megafossils. Recent analyses of fossil staminate catkins and the pollen within their anthers provide an excellent opportunity to examine relative advancement of different organs and the variation present in pollen known to be from a single plant or anther (Crepet et al., 1975, 1980; Wing & Hickey, 1984).

Although juglandaceous pollen by itself provides limited taxonomic resolution, it does provide excellent stratigraphic resolution and is thus important in the interpretation of family history. Since pollen is commonly present in, and easily sampled from, sediments for which megafossils are not available, it is useful in establishing the timing of first and last occurrences of selected taxa in different parts of the world. Also, since juglandaceous pollen is produced in large quantities and is wind dispersed it is likely to be preserved and its absence in palynological preparations can be significant.

WOOD

The taxonomic utility of fossil juglandaceous wood is similar to that of pollen. While it is usually easy to separate the genera of one tribe from those of another, it is not always possible to distinguish the woods of two genera belonging to the same tribe. To resolve this situation, organ genera have been established for fossil secondary xylem. *Pterocaryoxylon* Müller-Stoll & Mädél corresponds to the Juglandaceae (*Pterocarya*, *Cyclocarya*, and *Juglans*); *Eucaryoxylon* Müller-Stoll & Mädél accommodates woods of the Hicoreae; and *Engelhardioxylon* Manchester includes woods of the Engelhardiaceae. As yet, no fossil woods of the Platycaryeae have been described. A key to the separation of modern and fossil genera of the Juglandaceae based on wood anatomy is provided by Manchester (1983).

FOLIAGE

Foliage in the Juglandaceae is difficult to stereotype according to its taxonomic utility. Wolfe (1959) indicates that there is a more or less typ-

ical type of leaflet for each genus and section in the Juglandaceae that differs from the typical leaflets of other taxa. On this basis, he and most other paleobotanists have applied modern generic names to fossil leaf impressions. However, some architectural patterns are shared by more than one modern genus, leading to problems in the identification of fossils. There are numerous instances of synonymies generated by disagreement among authors as to the correct generic identity of Tertiary leaflets of the *Carya-Juglans-Pterocarya* type. In the early Tertiary, such problems are compounded by the presence of extinct genera (diagnosed from fruits) with foliage similar to modern genera. For example, Paleocene leaflets reasonably assigned to *Pterocarya* on the basis of leaf architecture (Brown, 1962) are correlated with fruits of *Polyptera* Manchester & Dilcher. I therefore advocate the use of organ genera such as *Oreoroa* Dilcher & Manchester for fossil leaflets whose modern generic affinities cannot be determined with certainty.

It is particularly difficult to identify entire-margined juglandaceous leaflets because they are similar in architecture to those in many different families. As a result, it is likely that some fossil species of *Carya*, *Juglans*, *Engelhardia*, *Oreomunnea*, and *Alfaroa* could be overlooked or misidentified. Cuticular information, when available, can help in the determination of such remains. Nagel (1914) documented cuticular features of taxonomic importance in the family.

Nevertheless, there are several characteristic patterns of leaf architecture among extant Juglandaceae and the fossil record provides a good opportunity to document their evolution (Wolfe, 1959). A complete revision of the taxonomy of fossil juglandaceous leaflets is beyond the scope of this paper.

SCOPE AND ORGANIZATION

In this paper I do not attempt to provide an exhaustive list and synonymy for all known fossil occurrences attributed to the family, but rather to highlight reliable records of various organs documenting the earliest occurrences and duration of taxa in specified geographic regions. The intent of this approach is to provide a factual basis for interpretations of the patterns of evolution, migration, and extinction in the history of the family. Because of the importance accorded fruits in the taxonomy of extant Juglandaceae, fossil fruits receive special attention in this paper. However, consideration of one type of organ to

the exclusion of all others would lead to an incomplete and perhaps misleading concept of family history. Selected occurrences of fossil leaflets, wood, and pollen are included to permit consideration of relative rates of evolution and extent of specialization in different plant parts. These organs are often more abundant in the fossil record than fruits and are therefore important because they help to pinpoint the earliest and latest appearances of taxa in various geographic regions.

The contents of this paper are organized according to the tribal classification of the family. The first section concerns Cretaceous and Paleocene fossils of juglandaceous affinity that cannot be placed in extant tribes. Subsequent sections deal with the fossil history of each tribe in the order presented in Table 1. The record of each tribe is considered in the sequence: pollen, wood, foliage, and then fruits. A synthesis of evolutionary, systematic, and biogeographic implications is presented at the end of each section. The final section presents a more complete synthesis dealing with origin of the family, diversification, phylogeny, paleobiogeography, extinctions, and the patterns of evolution in different organs.

MATERIALS AND METHODS

Species considered in this investigation represent collections from diverse sources in the Northern Hemisphere. Although some specimens were derived from my own field work in the western United States, a study of the present scope could not be completed without reference to collections from other parts of the world. A great deal of information was obtained directly from the literature. When possible, type specimens were borrowed from other institutions for analysis. Perusal of large paleobotanical collections, including those of the Smithsonian Institution (courtesy L. Hickey, J. Ferrigno), Harvard University (E. Barghoorn), Indiana University (D. Dilcher), Brigham Young University (W. D. Tidwell), University of Connecticut (W. Crepet), the Field Museum (P. Crane), University of Idaho (C. J. Smiley, W. Rember), University of Washington (W. Wehr), the United States Geological Survey (J. Wolfe), the University of California at Berkeley (H. Schorn, H. Meyer), and the British Museum (Natural History) (C. Hill) and the Muséum National d'Histoire Naturelle, Paris (C. Blanc) provided material important to the study.

Preparatory techniques varied with the plant

parts investigated and the nature of preservation. Fruits and foliage were usually examined at the "macro" level with dissecting microscopes, and important features of compression fossils not exposed in the initial fracture of a specimen, such as styles and sepals, were revealed by grinding with a diamond drill tip (hard matrix) or by probing with fine needles (soft matrix). Cuticles were prepared and examined according to techniques of Dilcher (1974). In some instances, pieces of the matrix of important megafossil specimens were removed and macerated to assess the types of dispersed pollen deposited contemporaneously with the megafossil.

Stereo-pair photographs (e.g., Fig. 39G–J) were taken with a Nikon FE camera mounted on a Nikon SMZ-10 stereomicroscope. These may be viewed with stereoscopic glasses or by training one's eyes simultaneously on both photos of the pair to obtain a three-dimensional image of the actual specimen.

Extensive comparisons were made with specimens of extant species in order to interpret the fossil specimens. Modern fruits and foliage were borrowed from major United States herbaria. Extant woods were observed in thin sections at the United States Forest Products Laboratory, Madison, Wisconsin courtesy of Regis Miller. Reference slides of pollen of modern species were made available by D. Whitehead, Indiana University.

Terminology used here follows recommendations of the International Association of Wood Anatomists (IAWA, 1964) for wood anatomy, Hickey (1973) for foliar architecture, Dilcher (1974) for cuticular anatomy, Manning (1940, 1978) for inflorescence and fruit morphology, and Erdtman (1966) and Faegri and Iversen (1964) for pollen morphology.

Individual fossil specimens and locality numbers cited in the text are prefixed by abbreviations representing the following institutions: BM [British Museum (Natural History), London, England], FM (Field Museum of Natural History, Department of Geology, Chicago, Illinois), HU (Harvard University, Biology Laboratories, Cambridge, Massachusetts), IU (Indiana University, Department of Geology, Bloomington, Indiana), MNHNP (Muséum National d'Histoire Naturelle de Paris, Laboratoire de Paléobotanique, Paris, France), NDGS (North Dakota Geological Survey, Grand Forks, North Dakota), OMSI (Oregon Museum of Science and Industry, Earth Science Collection, Portland, Oregon),

UCM (University of Colorado Museum, Boulder, Colorado), UCMP (University of California Museum of Paleontology, Berkeley, California), UCONN (University of Connecticut, Biological Sciences Group, Storrs, Connecticut), UI (University of Idaho, Department of Geology, Moscow, Idaho), USGS (United States Geological Survey, Branch of Paleontology and Stratigraphy, Denver, Colorado), USNM (United States National Museum, Smithsonian Institution, Division of Paleobotany, Washington, D.C.), UWA (Burke Memorial Washington State Museum, University of Washington, Seattle, Washington). The sources of extant comparative material in the Indiana University modern reference collection are indicated by standard herbarium abbreviations: A (Arnold Arboretum Herbarium, Harvard University, Cambridge, Massachusetts), F (Field Museum of Natural History, Chicago, Illinois), G (Gray Herbarium, Harvard University, Cambridge, Massachusetts), and MO (Missouri Botanical Garden, St. Louis, Missouri).

EARLY OCCURRENCES

The Juglandaceae can be traced with confidence back to the Paleocene on the basis of fruits, foliage, and pollen, and it appears that the main diversification of the family occurred at that time. The Upper Cretaceous and Paleocene record includes taxa that are possible precursors of the family, as well as taxa assignable to the family but too generalized to be placed within a modern tribe. A few middle and late Paleocene genera have obvious modern tribal affinities and will be dealt with later in this paper. This section considers taxa of juglandaceous affinity that cannot be assigned modern tribes (Table 2).

POSSIBLE PRECURSORS OF THE JUGLANDACEAE

Comparative analyses of pollen (Wolfe, 1973, 1976) and floral structure (Friis, 1983) suggest that the Juglandaceae probably originated from part of the Normapolles complex. The name Normapolles (Pflug, 1953) is applied to dispersed fossil pollen taxa characterized by triplicate grains with complex, typically thick-walled and protruding, pore regions. Such pollen is first observed in the Middle Cenomanian, becomes diverse and common in the Upper Cretaceous, and wanes during the Early Tertiary through extinction and intergradation with modern taxa (review by Batten, 1981). More than 85 genera have been recognized (Batten & Christopher, 1981)

TABLE 2. Important Upper Cretaceous and Paleocene occurrences.

Taxon	Age and Location	Comment
POLLEN		
Normapolles Complex	Cenomanian-Eocene; Europe, eastern North America	A diverse complex defined on the basis of pollen that probably included precursors of the Juglandaceae.
<i>Plicapollis</i> Pflug	Santonian-Eocene; Europe, eastern North America	Genus of Normapolles pollen with wall structure and ornamentation very similar to that of the Juglandaceae; associated with <i>Caryanthus</i> fruits.
<i>Momipites</i> Wodehouse	Campanian-Tertiary; North America, Europe, Asia	Organ genus for triporate isopolar pollen like that of extant Engelhardieae; a primitive type possibly predating the origin of the family and associated with various extinct fruit genera.
FOLIAGE		
" <i>Carya</i> " <i>antiquorum</i> Newberry	Paleocene; North America	Leaflets with an extinct architecture bearing similarities with Hicoreae and Juglandaceae, but of uncertain modern generic relationships.
" <i>Pterocarya</i> " <i>hispida</i> Brown	Paleocene; Montana	Leaflets very similar to those of " <i>Carya</i> " <i>antiquorum</i> but with abundant trichome impressions; associated with fruits of <i>Cyclocarya brownii</i> Manchester & Dilcher.
" <i>Pterocarya</i> " <i>glabra</i> Brown	Paleocene; Wyoming	Leaflets with long petiolules and without prominent trichome impressions; associated with fruits of <i>Polyptera manningii</i> Manchester & Dilcher.
FRUITS		
<i>Manningia</i> Friis	Upper Santonian or Lower Campanian; Sweden	Tiny fruits of juglandalean-myricalean affinity associated with Normapolles (<i>Trudopollis</i> -type) pollen, tricarpellate, bisexual.
<i>Antiquocarya</i> Friis	Upper Santonian or Lower Campanian; Sweden	Tiny fruits of juglandalean-myricalean affinity associated with Normapolles pollen, tricarpellate, bisexual.
<i>Caryanthus</i> Friis	Upper Santonian or Lower Campanian; Sweden	Tiny fruits remarkably similar to Juglandaceae, associated with Normapolles (<i>Plicapollis</i>) pollen, bicarpellate, bisexual, subtended by a bract and two bracteoles.
<i>Juglandicarya simplicarpa</i> Manchester	Paleocene; Wyoming	Locule casts of a large wingless juglandaceous nut, perhaps primitive within the Hicoreae.
<i>Casholdia microptera</i> Crane & Manchester	Upper Paleocene; England, France	Juglandaceous winged fruit sharing characters with the Engelhardieae but lacking the trilobate bract diagnostic of that tribe; associated with <i>Momipites</i> pollen.
<i>Cyclocarya</i> Iljinskaya spp.	Paleocene; North Dakota, Montana, Wyoming	Three species of this modern genus are known from the Paleocene of North America and are treated with the Juglandaceae (p. 93).
<i>Polyptera</i> Manchester & Dilcher	Paleocene; Wyoming	An extinct genus related to <i>Cyclocarya</i> , treated with the Juglandaceae (p. 99).

and their restricted individual stratigraphic ranges have proven extremely useful in biostratigraphy of the Late Cretaceous and Early Tertiary. The Normapolles group is also useful in paleophytogeography. The geographic distribution of such pollen defines a "Normapolles Province" extending across Europe and eastern North America. The rarity of Normapolles grains outside the

province suggests that epicontinental seas constituted barriers to migration of the group. These barriers began to break down as the seas regressed in the Maastrichtian, and the group makes appearances in western North America and Asia at that time (Srivastava, 1981).

Despite its utility in biostratigraphy and paleogeography, the Normapolles complex is re-

FIGURE 2. Reconstruction and floral diagrams for flowers associated with Normapolles pollen from the Upper Santonian or Lower Campanian of Sweden.—A. Reconstruction of *Caryanthus* Friis, modified from Friis (1983).—B. Floral diagram for *Caryanthus* showing two median carpels, six stamens, four sepals in two whorls, two bracteoles, and a bract (cf. floral diagram for *Pterocarya*, Fig. 1).—C. Floral diagram for *Manningia* Friis showing three carpels, five stamens, and five sepals.—D. Floral diagram for *Antiquocarya* Friis showing three carpels, six stamens, and six sepals.

garded as a heterogeneous assemblage of taxa including genera with diverse affinities. It is also acknowledged that some of the “morphotypes such as *Nudopollis*, *Plicapollis*, and *Trudopollis* were produced by more than one genus” (Batten, 1981). Upon critical analysis, only a few of the recognized Normapolles genera appear to be of direct juglandaceous affinity.

The majority of investigations of Normapolles pollen have employed light microscopy, and supplementary data from electron microscopy (Stanley & Kedves, 1975; Kedves & Stanley, 1976) are available only for a few genera. High resolution light microscopy and scanning electron microscopy indicate that some genera have rugulate and verrucate exine ornamentation (e.g., *Basopollis*, *Krutzschipollis*) while others have a relatively smooth exine surface with fine coni (e.g., *Nudopollis*, *Plicapollis*). The even distribution of coni observed in some species, for example *Plicapollis*, is virtually indistinguishable from the ornamentation observed in modern genera of Juglandaceae.

High resolution microscopy has only rarely been carried out for Cretaceous examples of Normapolles pollen. The most complete study involving electron microscopy analysis of Normapolles pollen types was that of Stanley and Kedves (1975) and Kedves and Stanley (1976), based on selected Eocene species. From transmission electron microscopic analysis they concluded that a granular interstidium comparable to that of modern Juglandaceae, *Rhoiptelea*, and Myricaceae pollen occurs in Eocene examples of *Plicapollis*, *Nudopollis*, and *Plicatopollis* and “is characteristic for the lower Eocene Normapolles.” Additional rigorous electron microscopy

and high resolution light microscopy analysis, particularly of Cretaceous material, is needed for a better understanding of various Normapolles taxa and their relationships to modern families.

Friis (1983) has provided much-needed information on the types of floral structures produced by some of the Normapolles plants. In a detailed study of numerous organically preserved floral and fruit remains from the Upper Santonian or Lower Campanian of Scania, southern Sweden, Friis recognized three genera of floral structures intimately associated with Normapolles pollen: *Manningia*, *Antiquocarya*, and *Caryanthus*. All are small, bisexual flowers with inferior ovaries producing unilocular nuts with a basal orthotropous seed. Although clearly extinct at or above the generic level, they appear to be of myricalean and/or juglandalean alliance (Friis, 1983).

Manningia Friis (Fig. 2C) has a regular flower with an epigynous perianth of five free sepals, five antisepalous stamens, and a unilocular gynoecium with a single style and three stigmatic arms. With the aid of scanning electron microscopy, Friis observed numerous isolated pollen grains and dispersed pollen sacs containing pollen adhering to the inside of the perianth in many specimens. The pollen is of a single type conforming closely to the Normapolles genus *Trudopollis*. The floral structures of *Antiquocarya* Friis (Fig. 2D) are similar to those of *Manningia* but have six sepals and six stamens and a gynoecium with three distinct styles. A few pollen grains of Normapolles type were found adhering to the apical parts of the fruits, which may or may not have been produced by the same species (Friis, 1983). From the scanning electron micrographs provided, these grains appear similar to

those associated with *Manningia* but have less pronounced verrucae.

Although the general morphology of *Manningia* and *Antiquocarya* flowers suggests juglandean affinity, they are easily distinguished from modern families of the Juglandales. They differ most notably from the Juglandaceae in their tricarpellate (rather than bicarpellate) pistils, which lack septae, and in their bisexuality. However, aberrant tricarpellate flowers and stamen-bearing pistillate flowers are occasionally seen in modern juglandaceous genera and are thought to be indicative of the ancestral condition (Manning, 1940, 1978). *Rhoiptelea* produces perfect flowers with six stamens; however, there are only four sepals, and the pistil is bicarpellate with a septum and superior with an anatropous ovule that is not basal.

The *Trudopollis*-type pollen recovered from *Manningia* and figured by Friis (1983) differs significantly from that of all Juglandaceae. In addition to having the thickened protruding aperture regions typical of many Normapolles taxa, the exine ornamentation consists of large verrucate processes that are, in turn, covered by more or less evenly spaced fine coni. Juglandean pollen has coni of similar size and distribution but lacks verrucae.

The third genus described by Friis (1983), *Caryanthus*, seems to be the most closely allied with the Juglandaceae in fruit and flower morphology as well as the morphology of associated pollen. *Caryanthus* flowers (Fig. 2A, B) are bisexual and bisymmetrical with a single small bract and two lateral bracteoles united with the base of the ovary, an epigynous perianth of four sepals, six to eight stamens opposite the lateral sepals, and a gynoeceium of two median carpels. The fruit is a laterally compressed nut 0.6–1.55 mm long, 0.6–1.31 mm wide, and 0.3–0.9 mm thick, with the apical part flattened into a short wing, and is unilocular with a single orthotropous seed arising from a raised placental area. Friis recognized two species of *Caryanthus* from the Swedish deposit, *C. knoblochii* and *C. elongatus*, and a third species from the Senonian of South Bohemia, Czechoslovakia, *C. deltoides* (Knobloch) Friis. Although anthers were not found attached to the stamen filaments,⁴ pollen grains of a single type, attributable to *Plicapollis* Pflug, were found in-

side the perianth of many specimens of *C. knoblochii* and in the apical part of many fruits of *C. elongatus*. The grains are described as 13 μ m in equatorial diameter, peroblate, triangular with slightly convex sides, protruding rounded angles, meridionally elongate apertures, usually showing a triradiate fold over the polar area, and having a surface with evenly and closely spaced coni.

Caryanthus shares numerous features with the Juglandaceae and is apparently quite closely related. In addition to certain characters seen in *Manningia* and *Antiquocarya* (inferior ovary, basal orthotropous seed), the one-bract, two-bracteole, four-tepal, two-carpel plan observed in the many specimens of *Caryanthus* is also characteristic of the Juglandaceae. Friis observed simple uniseriate hairs on the specimens of *C. knoblochii* and *C. deltoides* and small peltate hairs on *C. elongatus*. The occurrence of peltate hairs provides additional evidence of juglandaceous affinity. As noted by Friis, the details of flower and fruit structure in *Caryanthus* closely parallel those seen today in *Pterocarya*. "Both have bracteoles fused with the ovary for some of its length, four tepals in two sets united with the ovary to its apex, median carpels and one-loculed ovary with a single basal and orthotropous ovule."

The associated *Plicapollis* pollen, as figured in scanning electron micrographs by Friis (1983), is remarkably similar to juglandaceous pollen. The exine ornamentation, comprising small coni evenly distributed on an otherwise smooth surface, is identical to that of all extant Juglandaceae and is readily distinguished from modern Myricaceae (in which the coni are not evenly distributed and are often clustered) and Betulaceae (coni aligned in rows and on slight ridges). Kedves and Stanley (1976) have shown Eocene examples of *Plicapollis* to resemble Juglandaceae in wall structure as seen in transmission electron microscopy. Similar triporate isopolar pollen of small size and with meridionally elongate pores occurs today in tribes Engelhardieae (*Engelhardia roxburghiana*) and Platycaryeae (*Platycarya strobilacea*). Although modern genera lack the triradiate polar thickening, distinctive patterns also due to variations in exine thickness occur in *Carya* and *Platycarya*.

Aside from the triradiate fold in the pollen, the only other known characters that preclude

⁴ Friis (1983) has now recovered a *Caryanthus* flower from Aachen, Germany with attached anthers containing *Plicapollis* pollen.

placement of *Caryanthus* in the Juglandaceae are the regular occurrence of bisexual flowers, already mentioned, and the lack of a prominent septum within the fruit. A diagnostic feature of juglandaceous fruits is the presence of a primary septum arising from the base of the locule, dividing the locule into two compartments interconnected by an apical foramen. In some cases there are secondary and/or tertiary septa effectively dividing the locule into four or eight compartments. The raised placental area seen in *Caryanthus* results in a locule that is slightly bilobed basally, suggestive of an incipient primary septum. The small size of the fruits, only 0.6–1.55 mm in longest dimension (assuming they are indeed mature), contrasts with even the smallest extant Juglandaceae (*Platycarya* fruits are about 5 mm long). However, none of these differences are as great, for example, as those separating extant *Rhoiptelea* or Myricaceae from the Juglandaceae. It would, of course, be of interest to know if the leaves were compound, as in *Rhoiptelea* and Juglandaceae, or simple, as in all other extant "Amentiferae." Nevertheless, the large suite of available characters suggests that Nor-mapolles plants yielding fruits of the *Caryanthus* type and pollen of the *Plicapollis* type may have been ancestral to extant Juglandaceae.

EARLY JUGLANDACEOUS POLLEN

Dispersed triporate pollen apparently indistinguishable from that of the Juglandaceae can be traced to the Upper Cretaceous; for example, *Myricipites cavilloratus* Drugg and *Momipites tenuipolus* Anderson in the Maastrichtian of California (Drugg, 1967; Chmura, 1973), and *Momipites fragilis* from the lower Campanian of the southeast United States (Frederiksen & Christopher, 1978). While these reports are based only upon light microscopy, scanning electron microscopy work on similar Paleocene material suggests that at least some of the grains could have been identical to those encountered in the Juglandaceae. However, attainment of juglandaceous pollen characters may have preceeded the occurrence of juglandaceous morphology in other organs. The Late Cretaceous pollen of *Plicapollis* described above could, on pollen-morphological grounds, probably be placed in the Juglandaceae, yet the associated fruits of *Caryanthus* Friis (and hence the plant as a whole) had not achieved juglandaceous status. In the absence of corroborative evidence from other

plant organs, identifications of Cretaceous pollen to the Juglandaceae should be regarded as tentative.

EARLY JUGLANDACEOUS FOLIAGE

The earliest confirmed megafossil remains of the Juglandaceae include foliage and fruits from the Paleocene of North America and southern England. Paleocene fossil woods have seldom been studied, and it is not surprising that the earliest known juglandaceous woods are Eocene (Manchester, 1983).

Acceptable reports of juglandaceous foliage from the Paleocene include "*Carya*" *antiquorum* Newberry, "*Pterocarya*" *hispida* Brown, and "*Pterocarya*" *glabra* Brown from the Rocky Mountain and adjacent Great Plains regions of North America, and one or two unnamed species from the Reading Beds of southern England (Crane & Manchester, 1982, figs. 10–12). Although not precisely similar to foliage of modern genera, the leaflets are architecturally most similar to taxa of modern Juglandaceae and Hicoreae. No specimens closely comparable in foliar architecture to extant Engelhardieae or *Platycaryae* have been confirmed prior to the Eocene. *Juglandiphyllum denticulatum* (Heer) Koch from the Paleocene of northwest Greenland was placed in the family on the basis of its compound leaves and serrate leaflets (Koch, 1963); however, the fine details of venation are not clear from the illustrations or description. Reports of *Juglans* foliage from the middle and late Cretaceous by pioneering paleobotanists near the turn of the century are now rejected because they were based upon impressions of entire-margined laminae lacking features diagnostic of the Juglandaceae.

Juglandaceous foliage has been identified from numerous localities in the Paleocene Fort Union and adjacent formations in Wyoming, Montana, Colorado, and North Dakota (Brown, 1962), and it is likely that at least several different species are present. Two of the taxa, "*Pterocarya*" *hispida* and "*P.*" *glabra*, appear to represent the Juglandaceae and are treated later in the discussion of that tribe. The generic affinities of "*Carya*" *antiquorum* Newberry have long been questioned and it seems appropriate to consider this species in more detail here.

"*Carya*" *antiquorum* Newberry, Ann. Lyceum Nat. Hist. New York 9: 72. 1868; Monogr. U.S. Geol. Surv. 35: 35. pl. 31: figs. 1–4. 1898. Figure 3A–D.

FIGURE 3. Original specimens of "*Carya*" *antiquorum* Newberry, from the "Mouth of the Yellowstone" locality, Paleocene Fort Union Formation, eastern Montana.—A. Specimen with impressions of two leaflets. The larger one was figured diagrammatically by Newberry (1898). Note the basal asymmetry and high angle of the secondary veins (USNM 567), $\times 1$.—B. Lectotype showing the steeply arched secondary veins, evenly spaced teeth, and percurrent tertiary veins (USNM 568), $\times 1$.—C. Enlargement of specimen in B, showing marginal details. Veins of tertiary order enter the teeth submedially, $\times 2$.—D. Marginal details of the larger leaflet figured in A, $\times 4$.

Description. Leaflets obovate to elliptical, 4.5–7.5 cm wide, 6–16 cm long, length-to-width ratio 1.5 to 2.1, apex attenuate, base acute, slightly to markedly asymmetrical; petiolule 1–3 mm long; midvein medium thickness, straight to slightly curved; secondary veins semicraspedodromous to craspedodromous, arising from the midvein at 75° (basally) to 45° (apical secondaries), arched upward with their extremities prolonged parallel to the margin, eventually terminating in a tooth and/or sending a branch to the

supra-adjacent secondary; intersecondary veins occasionally present but uncommon; tertiary veins percurrent, usually opposite, strongly impressed, regularly spaced, 1.5–3 mm apart; marginal tertiary veins arising at regular intervals from the secondaries, extending perpendicular to the secondary for one-third of the length, then flexed upward next to the outer margin of the tooth, entering the tooth submedially; teeth small, acute to right-angled; basal flank convex to straight, 1.5–2 mm long; apical flank concave to

straight, 0.5–1 mm long; ultimate venation and cuticular features unknown.

Specimens. The lectotype is USNM 568 (Fig. 3B, C; Newberry, 1898, pl. 31: fig. 2) and the syntype is USNM 567 (Fig. 3A, D; Newberry, 1898, pl. 31: fig. 1). Both specimens are housed at the United States National Museum.

Discussion. The above description is based primarily upon the type specimens of Newberry (1868, 1898), but also applies to specimens attributed to the species by Lesquereux (1878) and Brown (1962). Newberry's material came from the "Mouth of the Yellowstone River" in eastern Montana and subsequent collections were reported from Wyoming, Colorado, Montana (Brown, 1962), and Alaska (Wolfe, 1966). It has not been reported from post-Paleocene rocks.

The type specimens are figured and redescribed here because the original figures (line drawings) and description omitted some important characters, particularly those of the higher order marginal venation. There has been a tendency to use the name in a broad sense to include various presumed juglandaceous leaflets of the American Paleocene. The specimens attributed to "*Carya*" *antiquorum* from the Golden Valley Formation of North Dakota (Hickey, 1977) appear to represent a distinct taxon, having acute, symmetrical bases, weakly impressed tertiaries, and secondaries arising at broader and more consistent angles than in "*C.*" *antiquorum*. Hickey also recognizes "*C.*" *antiquorum* in the Maastichtian of Clark's Fork Basin, Montana (Hickey, 1980) and as early as the Campanian in high arctic Canada (Hickey et al., 1983), but the material from these localities has not been described or figured and its relationship to the type material is not clear from the literature.

The affinity of "*Carya*" *antiquorum* with Juglandaceae is assured by the combination of compound leaves, basal asymmetry of the leaflets, semicraspedodromous secondary venation, well organized percurrent tertiaries, and small, evenly spaced teeth. In the prominent percurrent tertiaries and general lack of intersecondaries, the leaflets are closest to those in the tribes Juglandae and Hicoreae. Ever since the first specimens were described, there has been question as to the actual generic identity of these leaflets. Both Newberry (1898) and Lesquereux (1878) expressed concern that the leaflets named *Carya antiquorum* might instead be *Juglans* and suggested that fruits would be useful in the distinc-

tion. Brown (1962) noted that the species was difficult to separate from those that he named *Pterocarya hispida* (leaflets associated with *Cyclocarya* fruits) and *P. glabra* (leaflets associated with *Polyptera* fruits). However, *Pterocarya glabra* can be distinguished by its long petiolules. The distinction of *Carya antiquorum* from *Pterocarya hispida* rests primarily on the lack of trichome impressions on the lamina surface, a feature that might be attributed to differential preservation. A relation of "*C.*" *antiquorum* with the Hicoreae is supported by the peculiar submedial venation of the teeth that is similar to patterns seen in some specimens of *Carya*. However, the successive branching of secondaries near the margin, common in modern *Carya*, does not seem to occur in the fossil specimens. In addition, the steeply rising secondary veins of the fossil are unlike those of extant *Carya*.

"*Carya*" *antiquorum* does not appear to represent the extant genus *Carya*, though it may be closely related. I place the originally suggested generic name in quotation marks but refrain from coining a new organ generic name until further information can be obtained through relocation and intensive collection of the type locality. More intensive collecting might reveal the associated type(s) of juglandaceous fruits.

EARLY JUGLANDACEOUS FRUITS

Four genera of juglandaceous fruits have been recognized in the Paleocene: *Cyclocarya*, *Polyptera*, *Juglandicarya*, and *Casholdia*. *Cyclocarya*, with three species known from the Paleocene, and *Polyptera* represent the Juglandae and are considered later in the treatment of that tribe. *Juglandicarya simplicarpa* and *Casholdia microptera* cannot be placed in modern tribes and are therefore considered here.

Juglandicarya simplicarpa Manchester, sp. nov. Figure 4A–D.

Juglandicarya spp. Brown, Profess. Pap. U.S. Geol. Surv. 375: 56. pl. 19: figs. 5, 8–11 (not 7). 1962.

Diagnosis. Locule casts 12–15 mm wide, 13–17 mm high; imprint of surrounding nutshell indicating an outer diam. 14–20 mm wide and 22–40 mm high; wall thickness 1.5–2 mm; two primary lobes of seed well developed, entire or slightly emarginate at base indicating absence or weak development of secondary septum; shoulder region straight or slightly convex; contours

FIGURE 4. Fruits of *Juglandicarya* from the Paleocene Fort Union Formation of Wyoming and Early Eocene London Clay Formation of England. A–D. *Juglandicarya simpliciarpa* Manchester, sp. nov.—A. Stereo-pair of the holotype, a locule cast showing the smooth contours, from Hells Half Acre, Wyoming, IU locality 15740 (IU 4860), $\times 1.5$.—B. Stereo-pair of specimen from USGS locality 9112 (USNM 313747), $\times 1$.—C. Stereo-pair of a locule cast preserved at right angles to the plane of dehiscence, with only a slight suggestion of a secondary septum. Note the thickness of the shell wall impression, USGS locality 9112 (USNM 312920), $\times 1$.—D. Exterior mold of nut showing smooth surface, USGS locality 9112 (USNM 387384), $\times 1$. E, F. *Juglandicarya cantia* Reid & Chandler from Sheppey, England, holotype (BM-V 22121), $\times 1.5$.—E. Front view of pyrite cast showing smooth contour of the locule and thickness of the nutshell, $\times 1.5$.—F. Side view showing smooth surface of nut shell and locule cast with straight shoulder region and no secondary septum, $\times 1.5$.

of locule cast smooth; nutshell mold rounded and smooth, suggesting little or no ribbing.

Specimens. The holotype is IU 4860 (Fig. 4A) from Hells Half Acre, Wyoming (IU loc. 15740). Paratypes are USNM 313747 (Fig. 4B), USNM 312920 (Fig. 4C), and USNM 387384 (Fig. 4D).

Discussion. *Juglandicarya simpliciarpa* occurs in the Paleocene Fort Union Formation and is known from eight localities in Wyoming, six reported by Brown (1962) and two recently discovered in central Wyoming (IU loc. 15740, 15757). Seven of the localities are considered Lower Fort Union, while one (USGS loc. 9198) was labeled Upper Fort Union by Brown (1962). Brown (1962) designated this material, together with specimens from another Fort Union locality in Montana, "*Juglandicarya* spp." The specimen from Montana (Brown, 1962, pl. 19: fig. 7) is only about half as large as the others and has a high secondary septum indicating that it is probably a locule cast of *Cyclocarya brownii* (complete fruits of which occur at the same site).

Juglandicarya simpliciarpa is the earliest wingless juglandaceous fruit known. In the relatively large size and lack of wings it resembles fruits of *Carya*, *Juglans*, and *Alfaroa*. However, the sim-

plicity of the locule rules out placement in any of these modern genera. *Juglans* locule casts have concave shoulder regions (Scott, 1954) whereas the fossil displays convex, rounded shoulders. *Carya* locules are intruded by longitudinal inner ribs, which are lacking in the fossil. *Alfaroa* fruits have well-developed tertiary, as well as primary and secondary, septa, dividing the base of the locule into eight compartments, whereas the fossil fruits have only a primary septum and a weakly developed secondary septum. Since the fossil species is known only from casts and molds, characters that would be helpful in resolving tribal affinities, such as the presence or absence of lacunae and the nature of vasculature, cannot be determined. It is therefore retained in the organ genus *Juglandicarya* Reid & Chandler. *Juglandicarya simpliciarpa* is virtually indistinguishable in size and morphology from *J. cantia* (Fig. 4E, F) from the Early Eocene London Clay of southern England and it is possible that the two were in fact conspecific. However, the American species is known only from siltstone casts and molds, and direct anatomical comparison with the pyritized British species is not possible.

Evidence from other plant organs associated in the same stratum provides a suggestion of hircoreoid affinity for *Juglandicarya simpliciarpa*

FIGURE 5. Fruits of *Casholdia microptera* Crane & Manchester and associated pollen of the Upper Paleocene of southern England and France.—A. Holotype, showing the typical unlobed bract with three strong more or less parallel ascending veins and the orthogonal meshwork and marginal loops formed by tertiary veins; from Cold Ash Quarry site C in the Reading Beds (Crane, 1981) of England (BM-V 59868), $\times 5$.—B. Similar specimen from Menat, France, showing remains of prophyllum (arrows) (MNHNP-Men 31), $\times 5$.—C. Specimen from Menat showing two divergent style arms (MNHNP-Men 32), $\times 5$.—D. Scanning electron micrograph of pollen grain from a dispersed anther from the same locality as A. Note the meridionally elongate pores, $\times 2,000$.—E. Enlargement of same grain showing evenly distributed coni typical of Juglandaceae, $\times 4,000$.—F. Additional grain from same anther viewed under light microscopy showing relatively uniform thickness of wall near pores, $\times 1,000$. D–F from photographs provided by M. Collinson.

and *J. cantia*. *Carya*-like pollen is common in the Fort Union (Nichols & Ott, 1978) and London Clay (Gruas-Cavagnetto, 1976) Formations where the fruits occur, yet no pollen of obvious affinity with modern *Juglans* has been recovered.

***Casholdia microptera* Crane & Manchester, Bot. J. Linn. Soc. 85: 91. figs. 1–9. 1982. Figure 5A–C.**

Description (after Crane & Manchester, 1982). Fruit a nutlet subtended and dorsiventrally sandwiched between two leaf-like wings: one larger and presumably representing the bract; the other smaller and apparently representing the prophyllum; bract ovate to elliptic with a rounded to retuse apex, 9–12.5 mm long, 4–6 mm wide, with three more or less parallel main veins: a

median primary and a pair of prominent ascending lateral secondaries; tertiary veins forming marginal loops and delimiting more or less rectangular areas between the main veins; prophyllum broadly ovate to elliptic, almost circular, 4–6 mm long, 3–4 mm wide, extending 1–2 mm beyond the nutlet apex, and supplied with more or less parallel, radiating venation; nutlet non-pedicellate, 2.25–3 mm long, 1.25 mm wide, with a septum at 90° to the plane of the wings; two relatively long style arms 1–1.25 mm, arising from the nutlet apex, diverging in a plane parallel to that of the wings; no perianth evident.

Discussion. *Casholdia* is the oldest known juglandaceous fruit species in the Eurasian fossil record. It is known from the single species described above and was originally described on

the basis of six specimens from the Upper Paleocene Reading Beds of southern England (Crane & Manchester, 1982). The same species is now known from sediments of similar age from Menat, in the Paris Basin of France (Fig. 5B, C).

Casholdia shows features indicative of juglandaceous affinity such as the bipartite nutlet, subtending bracts developed into wings, *Oreomunnea*-like venation and two style arms but cannot be placed in a modern tribe (Crane & Manchester, 1982). In its small size, median septum, stylar orientation, entire margined bract, and apparent absence of perianth parts, *Casholdia* resembles fruits of the Platycaryeae. However, it cannot be accommodated in the Platycaryeae because the bract is developed as part of the dispersed fruit rather than persisting on the axis, and the bracteoles do not form lateral wings. As pointed out by Crane and Manchester (1982), the enlarged bract and apparent fusion of bracteoles into a prophyllum suggest that *Casholdia* is most closely related to the Engelhardieae. Extant *Engelhardia* and *Oreomunnea* fruits, although larger, exhibit the same basic arrangement of parts. The unlobed bract of *Casholdia* precludes placement in the Engelhardieae. The bract is trilobate in all extant Engelhardieae and this condition is considered to be diagnostic for the tribe. *Casholdia* apparently predates the evolution of trilobate bracts. Fruit with "incipiently" trilobate bracts occur in the Middle Eocene (Fig. 28).

Dispersed pollen sacs bearing *Momipites* pollen (Fig. 4D–F) were recovered through maceration of sediment from the same clay lenses of the Reading Beds that produced *Casholdia* fruits (Collinson, pers. comm.; Crane, pers. comm.). Although not physically connected, the stratigraphic proximity and juglandaceous affinity of both fruits and pollen suggests that the organs might be parts of the same species. Associated juglandaceous foliage in the Reading Beds resembles that of tribe Juglandae ("Pterocarya-like"; Crane & Manchester, 1982, figs. 10–12) but has long petiolules—a feature of some modern En-

gelhardieae and fossil Platycaryeae (Wing & Hickey, 1984).

PLATYCARYEAE⁵

The tribe Platycaryeae is represented today by the single genus *Platycarya*. The single extant species, *Platycarya strobilacea* Sieb. & Zucc., is confined to the sclerophyllous broad-leaved and mesophytic forests of eastern China and Japan.⁶ During the Tertiary, the tribe was widespread across Europe and North America, as well as Asia. The rich fossil record of the tribe is reviewed by Manchester (1981b) and Wing and Hickey (1984) and includes pollen, foliage, and fruiting structures (Table 3).

Platycarya is distinct in various aspects of anatomy and morphology from the other modern genera of the family and therefore is placed in its own tribe (Manning, 1978). The wood is unique in the family because of the presence of tracheids, spiral thickening (both in smaller vessels and in tracheids), and rhomboidal crystals in idioblasts of the rays (Heimsch & Wetmore, 1939; Metcalfe & Chalk, 1950; Manchester, unpubl. data). Unlike all other extant genera of the family, *Platycarya* bears its fruits in cone-like catkins. The inflorescence bracts persist on the catkin instead of becoming incorporated into the dispersal unit as in other extant genera (Manning, 1978). The small triporate pollen is easily distinguished from the other extant genera of the family by the presence of crease-like thinnings of the exine known as pseudocolpi (Whitehead, 1965; Stone & Broome, 1975).

POLLEN

Pollen of *Platycarya strobilacea* is small, averaging 15–16 μm in diameter, triporate, usually isopolar, and has meridionally elongate pores. In these features it resembles *Engelhardia roxburghiana* of the Engelhardieae. However, *Platycarya* pollen is distinguished by the presence of pseudocolpi. There are typically two pairs of pseudocolpi, one pair on each polar surface.

⁵ As this paper went to press, an important contribution was published by Endress (1986), who has observed pollination of *P. strobilacea* by syrphids and other diptera. He describes an entomophilous syndrome in the extant species, including strongly scented inflorescences, staminate and pistillate flowers on the same spike, small stigmas, anthers and pollen, and flowering in July when the trees are in full foliage. Endress interprets this as an example of secondarily evolved entomophily in a family that has long been regarded as exclusively anemophilous. The fossil record of the Platycaryeae should be re-examined in light of this discovery.

⁶ A second species, *Platycarya longipes* Wu, is reported from Kwantung, Kwangsi, and Kweichow Provinces in China (Kuang et al., 1979), but Manning (pers. comm.) considers this to be a form of *P. strobilacea* with short infructescences and leaves.

TABLE 3. Important fossil occurrences of Platycaryeae.

Taxon	Age and Location	Comment
POLLEN		
<i>Platycaryapollenites</i> Nagy emend. Frederiksen & Christopher	Late Paleocene to Neogene; North America, Europe	Pseudocolpate triporate isopolar pollen; associated with fruits of <i>Hooleya</i> and <i>Paleoplatycarya</i> as well as <i>Platycarya</i> .
WOOD		
There are no accounts of fossil secondary xylem attributed to Platycaryeae.		
FOLIAGE		
<i>Platycarya americana</i> Hickey	Early Eocene; North Dakota	Leaflets associated with fruits and in- fructescences of <i>Platycarya ameri-</i> <i>cana</i> ; distinct in many features from modern <i>Platycarya</i> foliage but shar- ing some features with Engelhardieae, including basilaminar auricles.
" <i>Platycarya</i> " <i>castaneopsis</i> Wing & Hickey	Early Eocene; Wyoming	Leaflets associated with <i>Paleoplatycarya</i> <i>wingii</i> ; similar to those of <i>P. ameri-</i> <i>cana</i> but lacking the basilaminar au- riculae.
<i>Vinea Wolfe</i> spp.	Middle Eocene; northwestern North America	Leaflets bearing a close resemblance to modern <i>Platycarya strobilacea</i> but not firmly associated with platycar- yoid fruits.
FRUITING MATERIAL		
<i>Platycarya richardsoni</i> Reid & Chandler	Early Eocene; southern England	Infructescences remarkably similar to those of extant <i>Platycarya strobila-</i> <i>cea</i> .
<i>Pterocaryopsis</i> Chandler spp.	Early Eocene; southern England	Organ genus for dispersed biwinged fruits of the type produced by <i>Platy-</i> <i>carya richardsoni</i> .
<i>Platycarya americana</i> Hickey	Early Eocene; North Dakota	Infructescences and dispersed fruits much like modern <i>Platycarya</i> ; associ- ated with distinctive foliage.
<i>Paleoplatycarya wingii</i> Manchester	Early Eocene; Wyoming	Infructescences and attached fruits; fruits with free median sepals and lateral sepals fused along the upper wing margins.
<i>Hooleya</i> Reid & Chandler	Middle Eocene to Early Oligocene; southern England, Oregon	Platycaryoid fruits with large wings, free median sepals, and partially free lateral sepals.

This distinctive pollen is easily recognized and has been confirmed in Paleogene sediments of Europe and North America with both electron (Leopold & MacGinitie, 1972; Kedves & Stanley, 1976; Chateauneuf, 1980) and light microscopy. Various names have been applied to fossil platycaryoid pollen in the literature, including *Triatriopollenites*, *Platycaryapollenites*, *Momipites*, and *Platycarya*. Although such pollen is encountered only in *Platycarya* today, the Paleogene occurrences are associated with a variety of platycaryoid fruit types.

The earliest well-documented platycaryoid pollen occurs in the late Paleocene of western Europe where it is abundant at some localities of the Woolwich and Reading Beds in southern England (Gruas-Cavagnetto, 1976) and the Thanetian strata of the Menat (Kedves, 1982) and Paris (Chateauneuf, 1980) Basins. Platycaryoid pollen has been found intact within dispersed anthers in the Woolwich Beds (Allen, 1982). Occurrences of similar pollen in the Miocene of southwest Poland (Macko, 1957, pl. 42: fig. 16) and Hungary (Nagy, 1969) suggest that

the *Platycaryeae* persisted to the late Tertiary in Europe.

In North America, *Platycaryapollenites* is first observed as rare grains in the late Paleocene of the southeastern United States (Frederiksen & Christopher, 1978). Although rare in the Paleocene, it becomes common in the early and middle Eocene across much of North America, including the Mississippi Embayment region (Nichols, 1973; Elsik, 1974; Frederiksen & Christopher, 1978), the Rocky Mountain and adjacent Great Plains region (Rouse et al., 1971; Leopold & MacGinitie, 1972; Nichols & Ott, 1978; Leopold in Hickey, 1977), and the Pacific Northwest (Elsik, 1974; Leopold & MacGinitie, 1972; Newman, 1981). These fossils, placed together under the name *Platycaryapollenites platycaryoides* (Roche) Frederiksen & Christopher, are morphologically indistinguishable from extant *Platycarya*, but may be slightly larger (Leopold & MacGinitie, 1972; Frederiksen & Christopher, 1978). Although abundant in the early and middle Eocene, *Platycarya*-like pollen is unknown in North America beyond the Early Oligocene.

The platycaryoid identity of the early Tertiary dispersed grains is corroborated by studies of in situ pollen. Collections from the Lower Eocene Camels Butte Member of the Golden Valley Formation in North Dakota include compressed catkins with anthers containing masses of *Platycaryapollenites* pollen (Fig. 6B–G). Formerly attributed to *Cyperacites* sp. (Hickey, 1977: 173. pl. 8: figs. 4, 5), the catkins are fully described by Wing and Hickey (1984) who consider them to be conspecific with *Platycarya americana* Hickey fruiting material recovered from the same collection sites. The catkins are structurally similar to those of extant *Platycarya* (Fig. 6A), differing only in the shorter, more rounded bracts. The stamens, like those of the extant *P. strobilacea*, are small (average 0.5 mm), contrasting with the larger stamens (1–1.5 mm) characteristic of other Juglandaceae. Pollen from the anthers has been studied with both light (Fig. 6D) and scanning electron microscopy (Fig. 5E, F) and is similar to that of the extant species.

"*Platycarya*" pollen is regarded as an Eocene indicator in palynological studies of the early Tertiary in Asia (Bratzeva, 1966). While *Platycarya* is reported in numerous floral lists for the Asian Tertiary in the Soviet literature, most accounts do not include descriptions or figures, and the criteria for identifications are not presented.

Although the genus is native to China and Japan today, it is interesting that platycaryoid pollen has not been observed in any of the Tertiary floras of Japan nor in the Miocene of Korea (survey of literature; K. Takahashi, pers. comm.). In Japan, such pollen first appears in the Quaternary (Tsukada, pers. comm.).

WOOD

Platycarya is the only extant genus of the Juglandaceae with tracheids in the secondary xylem. The tracheids and smaller vessels exhibit spiral thickening, another feature unique for the Juglandaceae. The distribution of crystal-bearing idioblasts within the xylem is often overlooked but provides another diagnostic character. Whereas the idioblasts of *Juglans* and *Carya* are restricted to the axial parenchyma, those of *Platycarya* occur only in the ray parenchyma.

There are no reports of platycaryoid wood from the fossil record. However, in their description of pyritized *Platycarya richardsoni* infructescences from the Eocene of southern England, Reid and Chandler (1933) reported spirally thickened "fibers" in the infructescence axes, suggesting that spiral thickening was present in xylem of the genus at that time.

FOLIAGE

Leaflets of *Platycarya strobilacea* (Fig. 7) are characterized by strictly craspedodromous secondary veins that frequently branch once or twice before entering the teeth. Marginal looping of the secondaries occurs only in the uppermost portion of the lamina. Intersecondary veins, when present, rarely extend farther than one-fourth of the distance to the margin, and tertiary veins are weakly percurrent and rarely straight in their course between secondaries. Leaflets are ovate to elliptical (only rarely obovate) with broad, rounded bases, and with the exception of terminal leaflets (which have long petiolules), are virtually sessile. Teeth are typically narrow and falcate with medial to slightly supramedial vein entry and are sometimes compound. The uniformity of leaf architecture in extant *Platycarya* contrasts with the more variable architecture of other modern genera such as *Pterocarya* and *Juglans*. However, prior to the extinction of fossil species, *Platycarya* evidently exhibited a broader range in foliar architecture. Two basic types of platycaryoid foliage have been recognized in the

FIGURE 6. Staminate inflorescences and pollen of Platycaryeae.—A. *Platycarya strobilacea* Sieb. & Zucc. Modern catkin from western Hupeh, China, *Wilson* 495 (MO 809955), $\times 2$. B–F. *Platycarya americana* Hickey from Early Eocene of western North Dakota, USNM locality 14048.—B. Catkin (IU 15731-4770), $\times 2$.—C. Higher magnification of same specimen showing rounded bracts and small stamens, $\times 5$.—D. Pollen mass from an anther of the same specimen, transmitted light microscopy, $\times 500$.—E. Scanning electron micrograph of a pollen mass from another anther of the same catkin showing triplicate, isopolar morphology, $\times 1,000$.—F. Scanning electron micrograph of a single grain in same mass showing two prominent pseudocolpi, three equatorial pores, and numerous regularly distributed small coni, $\times 3,500$.

Tertiary, the “*Lamanonia*” type and the *Vinea* type.

Leaflets formerly described as *Lamanonia borealis* (Hickey, 1977) from the early Eocene Camels Butte Member of the Golden Valley Formation of North Dakota are now considered to be the foliage corresponding to *Platycarya americana* reproductive material (Wing & Hickey,

1984). It is the dominant type of foliage, and only type of juglandaceous foliage, in the low diversity assemblages where *P. americana* infructescences and fruits occur, and is hence placed in the same species by Wing and Hickey (1984).

Platycarya americana leaflets (Fig. 8) are symmetrical to slightly asymmetrical, narrow ovate to elliptic in shape, and have a length/width ratio

FIGURE 7. Foliage of modern *Platycarya strobilacea* Sieb. & Zucc. —A. Leaflets showing typical architecture with craspedodromous secondaries sometimes forking near the margin and relatively thin tertiaries, Durallon, 1868 (IU mod. ref. coll. 4039; from MO), $\times 1.5$. —B. Cleared leaflet (USNH 1757053), $\times 1$.

ranging from 2.6 to 10.2. The apex is attenuate and the base is decurrent. The teeth are regularly spaced, variable in size, and acute to obtuse with a rounded apex, a convex to straight apical flank, and a convex to concave, often “reverse acuminate” (concave below, convex above; Wing & Hickey, 1984) basal flank. The secondaries are variable from craspedodromous to semicraspedodromous, ranging from gently curved in some specimens to abruptly up-curved near the margin in others. Intersecondary veins are well developed. Tertiary veins are percurrent and the higher order veins (fourth, fifth, sixth order) form a mesh of small areoles (up to 3 mm) with few or no freely ending veinlets. The leaflets have long petiolules. A most peculiar feature of these leaflets is the occurrence of basilar auricles—a pair of small tongue-like foliar extensions recurved against the adaxial surface of the leaflet adjacent to the midrib (Fig. 9A). A similar type of foliage, “*Platycarya*” *castaneopsis* (Lesq.) Wing & Hickey, occurs repeatedly in association with the fruits and fruiting axes treated herein as *Paleoplatycarya* in the Lower Eocene of Wyoming and is described by Wing and Hickey (1984). The foliage of this species is remarkably similar to that of *P. americana*, differing primarily in its lack of

basilar auricles. Whereas the leaflet base of *P. americana* is terminated abruptly in the basilar auricles, that of *P. castaneopsis* is decurrent, gradually merging with the petiolule. However, in some specimens there is a slight widening of the lamina near the base (Fig. 15B) prior to its decurrence along the petiolule.

The fossil leaflets of *Platycarya americana* and *P. castaneopsis* differ from those of *P. strobilacea* in various architectural features, including the long petiolules, the acute, almost symmetrical bases, the course of the secondary veins, the presence of well-developed intersecondaries, and the closed areolation. These features, although retained in some living species of Engelhardieae, are apparently primitive for the Platycaryeae (Wing & Hickey, 1984). In addition, both of the Eocene species display greater intraspecific variation in features such as length/width ratios, semicraspedodromous versus craspedodromous venation, and tooth configuration than the modern species. In view of these differences, the platycaryoid identity of the fossil foliage would probably have remained unknown were it not for the consistent and repeated association with platycaryoid fruits and pollen at many different localities as demonstrated by Wing and Hickey

FIGURE 8. Leaflets of *Platycarya americana* Hickey emend. Wing & Hickey from the Lower Eocene Camels Butte Member of the Golden Valley Formation, North Dakota, all $\times 1$.—A. Typical specimen showing long petiolule, basilaminar auriculae (arrows) and intersecondaries (USNM 43028A).—B. Specimen with well-pre-

FIGURE 9. Comparison of basal auriculae of *Platycarya americana* Hickey with those of *Oreomunnea mexicana* (Standl.) Leroy.—A. Stereo pair of the base of the *P. americana* leaflet shown in Figure 7E, $\times 8$.—B. Base of a typical *O. mexicana* leaflet, Williams & Molina 42789 (IU mod. ref. coll. 4034; from F-1807787), $\times 5$.

(1984). In my opinion, a special organ generic name should be created for this extinct type of platycaryoid foliage; however, Wing and Hickey (1984) have emended the generic diagnosis of *Platycarya* to accommodate the fossil material.

The second type of platycaryoid foliage from the early Tertiary occurs in the Pacific Northwest of North America and includes *Vinea pugetensis* Wolfe from the Eocene of Washington (Wolfe, 1968) and *Platycarya pseudobrauni* (Hollick) Wolfe from the Eocene of Alaska. The leaflets have craspedodromous venation and are basally rounded, asymmetrical, short-petiolulate or sessile, and lack the basal auricles. Hence they are much more similar to extant *Platycarya* than to the Eocene platycaryoid leaflets from Wyoming and North Dakota. No fruiting material is available to substantiate the identification of this foliage to *Platycarya*, however, platycaryoid pollen occurs in the same strata as *V. pugetensis* (Newman, 1981).

No unequivocal records of *Platycarya* foliage are yet known from the Tertiary of Asia. In their description of leaflets from the Miocene of Shantung Province, China, as *Platycarya miocenica*, Hu and Chaney (1940: 27) comment "we have found it difficult to distinguish the leaflets of *Platycarya* from those of *Pterocarya*," but did

not formally recognize the presence of *Pterocarya*. Palynological preparations from the same leaf-bearing shale (UCMP collection) yield pollen of *Carya* and *Pterocarya* but not *Platycarya* (Manchester, unpubl.) and therefore cast further doubt on the determination of the leaflets of *Platycarya*. Similar leaflets described as *Platycarya hokkaidoensis* Tanai (1970) from the Oligocene of Japan warrant further study (Tanai, pers. comm.). As mentioned previously, the distinctive pollen of *Platycarya* is not known in the Tertiary of Japan.

INFRUCTESCENCES AND FRUITS

Fruits of extant *Platycarya* are borne spirally along the axis of compact woody catkins (Fig. 10A–C) 2–3.5 cm long and 1.5–2.5 cm wide. Each fruit is subtended by a bract that persists on the axis of the infructescence rather than being dispersed along with the fruit. The fruits themselves (Fig. 10D–F) are tiny biwinged nutlets, 5–6 mm wide (wing tip to wing tip) and about 5 mm long. The wings are borne laterally in a plane parallel to the long axis of the nutlet. They are narrow, about 1 mm wide, and thin with few or no major veins. The nutlet is provided with a primary and sometimes a secondary septum so

← served venation showing thin tertiaries (IU 4772).—C. Specimen with more prominent teeth and craspedodromous secondaries, typical long petiolule (IU 4774).—D. Smaller leaflet with camptodromous secondaries (IU 4773).—E. Two leaflets on the same specimen. The one on the left shows full length of the petiolule (IU 4771).

FIGURE 10. Modern and fossil *Platycarya* fruiting material. A–F. *Platycarya strobilacea* Sieb. & Zucc. from Hunan Province, China, Fan & Li 692 (IU mod. ref. coll. 4018; from A).—A. Infructescence showing spiral organization, pointed bracts, and scars on peduncle from the abscission of lateral staminate catkins, $\times 1.5$.—B. Longitudinal section through same catkin showing spirally arranged fruits in cross-section, $\times 2$.—C. Higher magnification. Note the dorsiventrally flattened fruits, the lateral wings, and the subtending bracts, $\times 5$.—D. Isolated fruit, proximal surface. Note style arms and absence of sepals, $\times 5$.—E, F. Stereo-pair of an isolated fruit showing the prominent basal scar and divergence of style arms in the same plane as the wings, $\times 5$. G–I. *Platycarya richardsoni* (Bowerbank) Chandler from the Lower Eocene London Clay Flora, England.—G. Infructescence with surface abraded showing spirally arranged fruits and subtending bracts from Herne Bay, Kent (BM-V 29803), $\times 1.5$.—H. Longitudinal section of a specimen showing bilobed nutlets subtended by bracts. Reproduced from Reid and Chandler (1933) with permission for comparison with C (BM-V 22097), $\times 5$.—I. Higher magnification of specimen in G showing the lateral wings, septation of nut, and the subtending woody

that the seed may be either two- or four-lobed at the base. Two stigmatic arms emerge from the apex of the nutlet and diverge in the plane of the wings (carinal). Sepals are generally absent. The base of the nutlet is dominated by a deeply recessed attachment scar that extends about one-third of the nutlet height along the abaxial side, representing the site of abscission from the bract.

On the basis of fruits and infructescences, I recognize two fossil species of the extant genus, *Platycarya richardsoni* and *P. americana*, and two extinct genera, *Paleoplatycarya* and *Hoo-leya*.

Platycarya richardsoni (Bowerbank) Chandler, Lower Tert. Fl. of Southern England 4: 110–111. 1964. *Petrophiloides richardsoni* Bowerbank, Hist. Fruits London Clay 44. pl. 9: figs. 9–15. 1840; Reid & Chandler, London Clay Fl. 133. pl. 2: figs. 7–20. fig. 1. 1933. Chandler, Lower Tert. Fl. Southern England 1: 136. pl. 14: figs. 11–14. 1961. Figure 10G–L.

Description. Infructescences robust, ovoid to oblong, up to 22 mm wide, 11–33 mm long; ovoid to ovately cylindrical; consisting of a stout axis, with numerous spirally arranged bracts and fruits, axis consisting of a core of parenchyma tissue surrounded by a cylinder of fibers; vascular bundles that pass into the bracts and fruits contain spirally thickened elements (Reid & Chandler, 1933); bracts arising at right angles from the axis, thick and fibrous, usually eroded distally by beach abrasion of the fossils; less eroded specimens (rare) showing imbrication of the bracts (Reid & Chandler, 1933); bracts up to 4 mm wide and more than 6 mm long; fruits borne singly in the axils of bracts; fruits 3.5 mm long, 5.75 mm wide, 1.5 mm thick, consisting of tiny nutlets compressed dorsiventrally and winged laterally; wings about 2 mm wide and 3 mm high, rounded, basal side of endocarp marked by a recessed attachment scar; seeds 1.5–2 mm diam., two- to faintly four-lobed basally.

Discussion. Specimens of this species are relatively common among the pyritized fossils of the Lower Eocene London Clay flora. They were described as a new genus, *Petrophiloides*, by Bowerbank (1840) because of their superficial resemblance to the proteaceous genus, *Petrophila*. Reid and Chandler (1933) were the first to suggest the affinity with *Platycarya*. They concluded, on the basis of a detailed study of the fossil material, that the London Clay species and *Platycarya strobilacea* were congeneric. In keeping with the nomenclatural rule of priority, Reid and Chandler indicated that the living species, *P. strobilacea*, should be transferred to the older generic name, *Petrophiloides*. Presenting this case as an example, the Botanical Congress subsequently ruled that names for fossils may not be given priority over names for extant plants (Botanical Congress, 1966) and the fossils were reassigned to *Platycarya* by Chandler (1964).

Reid and Chandler (1933) obtained much of their information about the internal morphology of the catkins through the use of ground serial sections of the pyrite petrifications (Fig. 10H). In the present investigation, similar sections of the modern *Platycarya strobilacea* were prepared by embedding a catkin in polystyrene casting resin and sectioning with a hacksaw. These sections (Fig. 10B, C) reveal internal structure almost identical to that observed in the fossils. Each fruit is subtended by a thick, woody bract. Sections through the fruits reveal single seeds that are basally two-lobed. The dimensions are strikingly similar between the fossil and extant species. The close agreement in morphology between the modern and fossil catkins supports the recognition of the Eocene fossil as a member of the modern genus *Platycarya*.

The fruits borne by *Platycarya richardsoni* differ from those of the extant *P. strobilacea* in having markedly broader wings. Cross sections of fruits within the strobili reveal wings 1.5–2 mm wide, whereas those of the extant species are only 0.5–1 mm wide. This difference was apparently

←
bract, ×6. J–L. Probable fruits of *P. richardsoni*, “*Pterocaryopsis*,” ×5.—J. “*Pterocaryopsis bagnorensis*” Chandler (1961). Note the recessed basal attachment scar and rounded wings (BM-V 30585).—K. Reverse side of same specimen.—L. “*Pterocaryopsis elliptica*” Chandler (1978). Specimen with abraded wings from Warden Point, Sheppey (Margaret Collinson coll.). M–R. *Platycarya americana* Hickey from Lower Eocene of western North Dakota.—M. Catkin showing spirally arranged bracts and stout axis, holotype (USNM 356368), ×1.5.—N. Specimen showing acuminate tipped bracts (USNM 43171), ×1.5.—O, P. Stereo-pair of dispersed fruit showing wings with only a few veins and the recessed basal attachment scar (IU 15731-4766), ×5.—Q, R. Stereo-pair of a smaller fruit with style arms intact (IU 15731-4767), ×7.5.

overlooked by Reid and Chandler because their ground sections intercepted the fruits basally, below the widest portion of the wing. Dispersed pyritized winged fruit specimens, probably representing *P. richardsoni* (Fig. 10J–L), have been assigned to *Pterocaryopsis* by Chandler (1961, 1978) and to *Platycarya bognoensis* (Chandler) Wing & Hickey by Wing and Hickey (1984). Although Chandler considered them a separate, extinct genus, they correspond in size and morphology to those embedded in the catkins. These fruits differ from those of extant *Platycarya strobilacea* (Fig. 10D–F) in at least two respects: 1) the basal attachment scar is rounded and less prominent and 2) the wings are proportionately larger. These differences support recognition of the London Clay catkins and dispersed fruits as an extinct species of *Platycarya*.

Platycarya pollen is also reported from the London Clay flora (Chandler, 1964; Gruas-Cavagnetto, 1976), but corresponding foliage has not been described from this marine deposit. It would be desirable to determine whether the leaflets were more similar to those of the extant Asian species or to the remarkably different foliage of the early Eocene species of Wyoming and North Dakota.

Platycarya americana Hickey, Mem. Geol. Soc. Amer. 150: 118–119, pl. 4–8; pl. 15: figs. 2–4, 7, 1977; Wing & Hickey, Amer. J. Bot. 71: 393–396, figs. 3–5, 7, 8 (fruits and infructescences), 1984. Figure 10M–R.

Description. Infructescences 15–40 mm long, 8–13 mm wide, ovoid to oblong, consisting of a stout axis surrounded by spirally arranged fibrous acuminate-tipped bracts averaging 5–7 mm long by 2–3 mm wide, peduncle stout, up to 30 mm long, bearing scars of possible staminate catkin abscission at intervals of several millimeters, fruits not detected in catkins, apparently dispersed prior to deposition; associated dispersed fruits are winged nutlets with two lateral auriculate wings; nutlets dorsiventrally flattened, 2–3.5 mm long and containing a rounded recessed scar, 0.4–1 mm high, at the base; lobing condition of seed not apparent from the compressed specimens; axial vascular bundles evident as impressions on surface of nutlet; fruit width including wings 3–5 mm; each wing 1.3–1.8 mm wide; two stigmas diverging from the apex of the nutlet in same plane as wings each about 0.3 mm long; perianth usually absent, but sometimes with slight development of median sepal.

Discussion. *Platycarya americana* is based upon impression-compression fossils in clay from the Early Eocene Camels Butte Member of the Golden Valley Formation in western North Dakota. These are the only fruiting remains of *Platycarya* sensu stricto known from the Tertiary of North America. Hickey (1977) placed the catkins and isolated fruits in the same species, although they have not been found attached. This treatment appears to be justified by the platycaryoid affinities of each structure combined with the fact that they are found together in the same strata.

Platycarya americana is distinguished from the previously discussed British fossil of about the same age, *P. richardsoni*, on the basis of catkin dimensions and shape of the fruit wings. The catkins of *P. americana* (Fig. 10M, N; reaching a maximum width of 13 mm) are less robust than those of *P. richardsoni* (Fig. 10G; frequently wider than 20 mm). The fruit wings of *P. americana* are auriculate (i.e., more narrowed basally than apically), whereas those of *P. richardsoni* appear to have been more evenly rounded (compare Fig. 10O–R with 10J–L). Both fossil species differ from the extant *Platycarya strobilacea* (Fig. 10D–F) in having broader fruit wings. The wings on the fossils are 1.5–2 mm wide in contrast to those of the modern species that are 0.5–1 mm wide. Also, the fruits are shorter from base to apex (2–3.5 mm versus 4–5.5 mm or more). The basal attachment scar is much smaller than the conspicuous scar of *P. strobilacea*. The impression of *P. americana* fruits in fine sediment permits observation of details of the stigma and perianth that are not observable in the water-worn pyritized specimens of *P. richardsoni*. Some specimens clearly show the impression of two tiny fringed stigmas diverging from the nutlet apex in a plane parallel to that of the wings (Fig. 10R). Their small size, 0.3–0.5 mm, contrasts with that of the stigmas in extant *Platycarya strobilacea*, which are 0.8–1 mm long. Although preservation of the fossils is sufficient to reveal the tiny and presumably fragile stigmatic arms, I have not seen any sepals (although they are mentioned by Wing & Hickey, 1984) and it is likely that they were usually absent from this species just as they are in extant *P. strobilacea*.

Wing and Hickey (1984) call attention to the co-occurrence of staminate inflorescences (Fig. 6B), pollen (Fig. 6D–F), and leaflets (Fig. 8) at localities yielding *Platycarya americana* fruits and provide an emended diagnosis for the species, including all of the associated organs as a single

species. Reconstructed as such, *P. americana* is the most completely known fossil taxon in the Juglandaceae. As a whole plant, *P. americana* compares favorably with extant *P. strobilacea* in staminate inflorescences and pollen (discussed, p. 19) as well as in fruit and infructescence morphology. However, the wood anatomy is unknown, and the foliage (discussed, pp. 20–21) is markedly different in several architectural features from that of *P. strobilacea*.

Paleoplatycarya Manchester, gen. nov.

Paleoplatycarya wingii Manchester, sp. nov. Figure 11A–K.

Platycarya castaneopsis (Lesq.) Wing & Hickey, Amer. J. Bot. 71: 396–398, figs. 17–22 (fruits and pistillate catkins only). 1984.

Diagnosis. Elongate, relatively slender infructescences, 5–13 mm wide, 15–45 mm long, borne on long pedicels bearing lateral scars (probably from staminate inflorescence abscission) at intervals of 5–10 mm; bracts fibrous, 2–5 mm long and 2–4 mm wide, wide ovate in shape, rounded to acuminate tipped, spirally arranged about the axis, subtending individual fruits; fruits preserved both within the catkins and as dispersed specimens, biwinged nutlets 3–9 mm wide; wings arising laterally, relatively large, 2–3 mm wide and 2.25–5.5 mm long, supplied with sub-parallel venation; nutlets with five to seven longitudinally oriented vascular bundles present on dorsal and ventral surfaces; base of nutlet marked by a prominent, rounded recessed attachment scar; two tiny stigmatic style arms arising directly from the top of the nutlet or sometimes from a pedestal-like style, oriented carinally; perianth represented by two free median sepals 1–2 mm wide at their base and 2.5–3.5 mm long, and two lateral sepals 3–4 mm long, one fused along the upper margin of each fruit wing in a trough-like manner.

Specimens. Six catkins and 41 dispersed fruits from the Early Eocene Wind River Formation of Wyoming (USGS loc. 8912 = UCMP loc. PA 114) were examined in this study. The holotype is USNM 356409 (Fig. 11E), and the paratypes are UCMP 9003 (Fig. 11A, B), UCMP 9004 (Fig. 11B), USNM 387390 (Fig. 11F), USNM 387391 (Fig. 11G–I), and USNM 387392 (Fig. 11J, K). Additional specimens from other localities in Wyoming were investigated by Wing and Hickey (1984).

Source of name. This species is named after

Dr. Scott Wing. This new epithet for fruiting material is required because the holotype of *Platycarya castaneopsis* is a leaflet from the Green River Formation without closely associated or attached fruits. Due to the probability of mosaic evolution, it cannot be assumed that a particular leaflet morphospecies is indicative of the fruit borne by the parent plant. The epithet *castaneopsis* has priority only for foliage.

Discussion. This extinct type of fruit is clearly attributable to the Platycaryeae (Manchester, 1981b; Wing & Hickey, 1984). As in *Platycarya*, the bracts are retained on the axis of the infructescence, rather than becoming part of the dispersal unit. Abscission from the bract results in a prominent abaxial scar at the base of the nutlet. In addition, the nutlets bear longitudinal veins, are sessile on the axis and dorsiventrally compressed, and the style arms are oriented carinally. The compound structure of the wings appears to be homologous with that inferred for *Platycarya*.

The catkins (Fig. 11A–C) are less robust, with smaller and more loosely packed bracts than fossil and modern *Platycarya*. The bracts are more rounded and only about half as long as those of *Platycarya*. The fruits themselves are preserved both within the catkins (Fig. 11C, D) and dispersed (Fig. 11E–K) and differ from those of *Platycarya* in the larger size and prominent venation of the wings and in the presence of sepals. Sepals are normally absent in *Platycarya* and, when observed (in aberrant specimens, Manning, 1948; Wing & Hickey, 1984), are minute. Those of *Paleoplatycarya* are relatively large, suggesting elongation after fertilization. The median sepals are free; however, the lateral sepals, equally well developed, are united along the top of each wing in a trough-like configuration.

Figure 14C is a reconstruction of the dispersed *Paleoplatycarya wingii* fruit. The two flaps behind and in front of the stigmas represent posterior and anterior median sepals. Because of the opaque matrix in which the fossils are preserved, it is not usually possible to see both of the sepals in a single specimen. Figure 11H, I shows a specimen in which part of the anterior sepal has been carefully excavated away to reveal the posterior sepal. Some specimens split between the sepals, revealing the stigmas that diverge in the same plane as the wings (e.g., Fig. 11E, F, J). Also depicted in the reconstruction are the lateral sepals that are fused along the upper margins of the wings. The junction formed by the union of the lateral sepals and the bracteoles is evident as

FIGURE 11. Infructescences and fruits of *Paleoplatycarya wingii* Manchester from the early Eocene Wind River Formation, Wyoming. All specimens from USGS locality 8912 = UCMP locality PA114. —A. Typical elongate catkin with spirally arranged bracts and fruits (UCMP 9003), $\times 1.5$. —B. Catkin showing stout peduncle with scars of probable staminate catkin abscission (UCMP 9004), $\times 1.5$. —C. Catkin showing short, rounded bracts and a single remaining fruit (arrow), $\times 1.5$. —D. Detail of catkin depicted in A, showing intact immature fruits. Fruit on the left shows the nutlet and distinctive wing seen in dispersed specimens, $\times 5$. —E. Holotype, a dispersed fruit showing prominent venation of wings and nutlet surface, basal attachment scar, and pronounced crease along upper margin of the wings (USNM 356409), $\times 5$. —F. Fruit with intact bilobed stigmatic region (USNM 387390), $\times 4$. —G. Specimen showing prominent median sepal typical of the species (USNM 387391A), $\times 4$. —H. Counterpart of previous specimen (USNM 387391B), $\times 4$. —I. Enlargement of same specimen in which the anterior median sepal (a) has been partially excavated away to reveal the posterior sepal (p). Note also the crease near the top of the wing formed by the right lateral sepal (l), $\times 10$. —J. Specimen with prominent bilobed stigma and typical sutures along the upper margin of each wing. The right side of the specimen was ground down to reveal the longitudinal section of the wing shown in K (USNM 387392), $\times 5$. —K. Same specimen viewed laterally to show the "Y" configuration resulting from the fusion of a folded lateral sepal (arrows) to the top of the wing, $\times 10$.

a sharp line in a face view of the wing (e.g., Fig. 11I, J) and as a Y-shaped cross section (Fig. 11K).

Wing and Hickey (1984) provide a convincing argument for the correlation of these fruits with

dispersed platycaryoid pollen and with leaflets formerly called *Quercus castaneopsis* Lesq. They observe that these different organs occur in the same strata at several different localities in the

FIGURE 12. Fruits of *Hooleya lata* Wing & Hickey and an associated infructescence from the Eocene Clarno Formation of Oregon.—A. Specimen showing the two lateral wings with subparallel venation and four perianth parts: two lateral sepals fused basally to the wings, and two free median sepals, OMSI locality 230 (IU 5298), $\times 4$.—B. Specimen with perianth parts apparently lacking, showing bipartite stigmatic region, OMSI locality 230 (IU 4859), $\times 4$.—C. Specimen showing wings with undulatory margins and small median and lateral tepals, OMSI locality 230 (IU 4780), $\times 4$.—D. Specimen showing unusual elaboration of perianth, OMSI locality 230 (IU 5299), $\times 4$.—E. Enlargement of C, showing the small rounded attachment scar at the base of the nutlet and dots on the face of the nutlet representing peltate scales. Note the bipartite nature of nutlet, suggesting presence of a median septum, $\times 10$.—F. Associated infructescence showing spirally arranged bracts persisting on an axis subsequent to fruit dispersal, OMSI locality 230 (IU 4856), $\times 1$.—G. Large specimen with well-preserved venation. Only one of the lateral sepals is developed, OMSI locality 229c (IU 5300), $\times 4$.—H. Enlargement of B, showing two short style arms diverging in the same plane as the wings, $\times 10$.

Early Eocene of Wyoming. As discussed previously (p. 21), the foliage is similar to that attributed to *Platycarya americana* from the early Eocene of North Dakota but is distinct from that of extant *P. strobilacea*. Suggesting that the unique features of these fruits and associated foliage are

merely primitive traits within the lineage that includes modern *P. strobilacea*, Wing and Hickey (1984) assign this material to the modern genus, emending the generic diagnosis to include fossil as well as modern species. I prefer to maintain *Platycarya* sensu stricto for species in which

the fruits lack elaborate wings and sepals and emphasize the archaic nature of the fossil fruits by placing them in *Paleoplatycarya*, gen. nov. The trough configuration of the lateral sepals is interpreted as a unique advancement distinguishing this fossil genus from *Platycarya*.

Hooleya lata Wing & Hickey, Amer. J. Bot. 71: 402–403. figs. 30–32, 35. 1984. Figure 12A–E, G, H.

Description. Fruits are biwinged nutlets, wings arising laterally, relatively large, 4–7 mm long, 2.5–6 mm wide, with subparallel venation, margin entire or undulate to irregularly toothed; nutlet 2–3 mm high, 2–3.5 mm wide and bipartite, apparently with a primary septum oriented perpendicular to the plane of the wings; recessed attachment scar at base of nutlet rounded, about 0.3 mm wide. Nutlet surface covered with tiny circular dots interpreted as peltate scales; perianth usually consisting of four sepals; 0.5–3 mm long, usually in two pairs, with two free median sepals, and two lateral sepals fused by their bases along the upper margin of both wings, free apically. Sometimes one or more sepals not developed, occasionally with highly divided perianth. Style arms 0.5–1 mm, diverging transversely in the plane of the wings.

Specimens. Eight fruits in the collection of Indiana University (IU 4779, 4780, 4857–4859, 5298–5300) and seven specimens in the United States National Museum (Wing & Hickey, 1984) are known. All are from the Middle (?) Eocene West Branch Creek Locality (Hergert, 1961) of the Clarno Formation, Wheeler County, Oregon.

Discussion. This species resembles the isolated fruits of *Paleoplatycarya* but differs in its generally broader wings, the less prominent attachment scar, and in the perianth development. Whereas the lateral sepals of *Paleoplatycarya wingii* are united along their entire length to the top of the wing, those of this species are free apically and fused only basally to the wing. The Oregon fossil more closely resembles the British Oligocene species *Hooleya hermis* Reid & Chandler, and it seems reasonable to place it in the same genus. Similarities between the two include wing shape, size and venation, peltate glands on the nutlet surface, and small size of the attachment scar. Wing and Hickey (1984) provide an emended generic diagnosis for *Hooleya*, incorporating characters of both the American and

British material. It is important to note that there does not appear to be a perianth in *H. hermis*, whereas that of *H. lata* is usually well developed.

It is possible that *Hooleya lata* fruits are related to platycaryoid pollen recovered from various localities in the Clarno Formation (Leopold & MacGinitie, 1972; Manchester, unpubl. palynological survey of Nut Beds deposit). Infructescences (Fig. 12F) that might represent the same taxon have been recovered from the same locality (*Platycarya manchesteri* Wing & Hickey, 1984) but do not contain intact fruits and require further study.

Hooleya hermis (Unger) Reid & Chandler, Bembridge Fl. 93–95. pl. 6: figs. 7–9. 1926; Raschy, Fölldt. Közl. 86: 170–171. pl. 26: figs. 5–8, 1956. *Hiraea hermis* Unger, Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 2: 176. pl. 1: figs. 11, 12. 1851. Figure 13A–D.

Description (after Reid & Chandler, 1926). Fruit a nutlet with two large lateral wings; wings rounded, 3.5–6 mm wide, situated in same plane as the nutlet axis, provided with fan-like venation, bifurcating about halfway and occasionally anastomosing near the margin; nutlet subpentagonal and flattened, 3–4 mm diam., slightly concave basally, with an ellipsoidal attachment scar, surface marked with three or five symmetrically placed longitudinal vascular bundles; two style arms arising from the apex of the nutlet, each giving rise to two stigmas, length of style and stigmas 1.25–1.5 mm; sepals absent; surface of nutlet, and of the wings close to the nutlet, dotted with circular peltate scales, with radiating striae; width of fruit including wings 10–16.5 mm.

Discussion. Well-preserved examples of this species from the Lower Oligocene Bembridge flora of southern England were compared with *Pterocarya* and *Platycarya* by Reid and Chandler (1926) and concluded to represent an extinct genus of the Juglandaceae, which they named *Hooleya*. In size, shape, and venation of the two wings, *Hooleya* converges closely with *Pterocarya*, particularly the Eocene species *P. macginitii*, but the divergence of the style arms in the same plane as the wings differs from the condition in *Pterocarya* and is diagnostic of the Platycaryeae.

The relationship of *Hooleya hermis* with the Platycaryeae is not immediately obvious if comparison is limited to the single extant genus. However, it shares important characteristics, such as the large wing size, with extinct North Amer-

FIGURE 13. *Hooleyia hermis* (Unger) Reid & Chandler fruits from the Oligocene Bembridge flora, southern England.—A. Specimen showing general morphology, including wing size, shape, and venation and stylar configuration (BM-V 17571), $\times 4$.—B. Additional specimen of larger size (BM-V 17014), $\times 4$.—C. Greater magnification of specimen in A, a pair of style arms rising transversely from the nutlet apex and splitting into four stigmas (arrows), $\times 8$.—D. Higher magnification of specimen in B. Note lines of vasculature and fine black dots of the peltate glands on the nutlet. Style arms diverging as in C, $\times 8$.

ican species of well-documented platycaryoid affinity, especially *Hooleyia lata*. The relatively inconspicuous basal attachment scar on the nutlet, the large wing size, and the presence of peltate scales on the nutlet support a close relationship with *H. lata*.

A peculiar feature of *Hooleyia hermis* is the presence of four stigmas, two arising from each style arm (Fig. 13C). This condition has not been observed in any of the other Paleogene platycaryoid fossils, which appear to have only a single stigma along each style arm; however, it is a feature that might easily escape preservation and detection in fossils. Only one specimen of the 22 mentioned by Reid and Chandler (1926) was noted to exhibit this detail. A similar condition exists today in *Engelhardia spicata*.

Hooleyia hermis is also known from the Late Eocene to Early Oligocene of Hungary (Unger, 1851; Rásky, 1956). No catkins of platycaryoid affinity have been reported from the deposits yielding *Hooleyia*. The pollen assemblage from the Bembridge locality includes grains identical to *Engelhardia* (abundant) and *Platycarya* (rare);

however, *Pterocarya*-type pollen has not been observed (Pallot, 1971).

GENERAL SUMMARY AND DISCUSSION, PLATYCARYEAE

The Platycaryeae apparently evolved in the Late Paleocene, as suggested by occurrences of pollen in the uppermost Paleocene and well-documented megafossils in the Lower Eocene. Features diagnostic of the tribe, including pollen with pseudocolpi, cone-like infructescences with persistent bracts, and bi-winged fruits with transverse-style arms, were all present by the early Eocene.

Figure 14 compares fruits of modern and fossil Platycaryeae. Whereas *Platycarya* (Fig. 14A) normally lacks a perianth, comparison with other modern tribes suggests that the primitive condition for the Platycareae would have included a perianth of four free sepals. The middle Eocene *Hooleyia lata* (Fig. 14D) comes closest to this configuration, with two free median sepals and a pair of lateral sepals united basally with the

FIGURE 14. Illustrations of modern and fossil platycaryoid fruits, $\times 4$.—A. Modern *Platycarya strobilacea* from China.—B. *Platycarya americana* Hickey, early Eocene of North Dakota.—C. *Paleoplatycarya wingii* Manchester, early Eocene of Wyoming.—D. *Hooleyia lata* Wing & Hickey, middle Eocene of Oregon.—E. *Hooleyia hermis* (Unger) Reid & Chandler, early Oligocene, Isle of Wight, England.

wings but free apically. *Paleoplatycarya wingii* also exhibits free median sepals, but the two lateral sepals are fused along their entire length to the upper margin of the wings in a trough-like fashion. The observed fusion of lateral sepals with the wings in *Hooleyia lata* and *Paleoplatycarya* supports earlier conclusions based on vasculature of modern fruits (Manning, 1948; illustrated in cleared modern immature fruits by Wing & Hickey, 1984) that the wings of *Platycarya* are compound structures derived from the union of lateral sepals and bracteoles. The absence of obvious sepals in the early Eocene *P. americana* (Fig. 14B) indicates that the modern perianth condition was present contemporaneously with that of the more archaic genera. Although median sepals are occasionally observed in aberrant specimens of modern (Manning, 1948) and fossil *Platycarya* (*P. americana*; Wing & Hickey, 1984), they are usually quite small. The sepals of *Hooleyia lata* and *Paleoplatycarya wingii* are large, suggesting that enlargement occurred during fruit formation subsequent to fertilization as in some modern *Engelhardia* species.

The wings of platycaryoid fruits range from elaborate to very reduced. Whereas the fruit wings of *Paleoplatycarya* (Fig. 14C) and *Hooleyia* (Fig. 14D) are large and supplied with pterocaryoid venation, those of *Platycarya* (both fossil and modern species) are small with few or no veins. Within *Platycarya* there is a trend from fruits with relatively large wings (*P. americana*, Fig. 14B, and *P. richardsoni*) in the Eocene to those

with smaller wings and relatively large nutlets in the present-day species (*P. strobilacea*, Fig. 14A).

Two distinct types of platycaryoid foliage have been recognized in the Eocene. That ascribed to *Vinea*, from Pacific northwestern North America exhibits a close similarity to modern *Platycarya strobilacea*, although the teeth are typically broader in the fossil. Platycaryoid foliage from Wyoming and North Dakota is markedly distinct from that of modern *Platycarya* and *Vinea*. Figure 15A–D illustrates some of the more obvious differences. Both the Wyoming and North Dakota species exhibit long petiolules, nearly symmetrical, acute leaflet bases, and basilaminar tissue specialization. The last feature is most pronounced in *P. americana*, in which there is an enrolled basilaminar tongue-like extension of the leaflet on either side of the midvein, as in extant *Oreomunnea mexicana*. In *P. castaneopsis*, there is only a faint broadening of the lamina near the base and, in *Vinea* and *Platycarya* there is no detectable basilaminar extension of tissue. Calling attention to these and other notable differences between the foliage of fossil and modern taxa and the similarities within modern Engelhardieae, Wing and Hickey (1984) state “all of these features are primitive for the Platycaryeae, and therefore do not provide a basis for placing the fossils in a separate genus.” Using this philosophy, they attribute the fossil species with archaic foliage to extant *Platycarya*. In my opinion a fossil organ generic name is needed for such leaves and leaflets. However, regardless of how

FIGURE 15. Illustrations comparing leaflet bases of Eocene and modern Platycaryeae, $\times 1$.—A. *Platycarya americana* Hickey, note long pedicel and basilaminar auriculae.—B. "*Platycarya*" *castaneopsis* (Lesq.) Wing & Hickey, showing long pedicel and basal decurrence of lamina.—C. *Vinea pugetensis* Wolfe, showing rounded leaflet base and very short petiolule.—D. Modern *Platycarya strobilacea* showing rounded base and very short petiolule.

the fossils are treated taxonomically, it is clear that the limited architectural variation in modern *P. strobilacea* represents only a small portion of the range that was present during the initial radiation of the tribe.

Wing and Hickey (1984) have reconstructed two early Eocene platycaryoid species from multiple organs on the basis of repeated field associations. The *Platycarya americana* plant, from the Camels Butte Member of the Golden Valley Formation in North Dakota, is known from infructescences (including the holotype), staminate catkins with in situ pollen, and leaflets. The other example, referred to as *P. castaneopsis* (Lesqueux) by Wing and Hickey (1984), occurs in the Willwood and Wind River Basins of Wyoming and is known from leaflets (including the holotype), infructescences, fruits (here placed in the separate organ genus *Paleoplatycarya*), and dispersed pollen. Comparison of these reconstructed plants with one another and with modern *P. strobilacea* illustrates the effects of mosaic evolution. The leaflets of both fossil species are well removed architecturally from those of the extant species, yet the pollen of all three species overlaps considerably. Whereas fruits and infructescences of *P. americana* closely approach those of *P. strobilacea*, those of *Paleoplatycarya wingii* are quite distinctive. Hence, the taxonomic positioning of the fossils depends on the relative weight given to the various similarities and differences.

The interrelationships between the two reconstructed Eocene platycaryoid taxa and modern *Platycarya* are similar to those between extant genera of the Englerhardieae (Fig. 16). While foliar characters unite the American taxa and distin-

guish them from Asian counterparts, features of the fruits separate the American taxa and indicate a relationship for one of them with the Asian taxon. Whether this reflects similar histories or is purely coincidental is open to speculation. However, since the level of morphological separation between the platycaryoid taxa is comparable to that between the engelhardioid taxa, it would be reasonable to accord similar taxonomic status. Rather than assigning both of the fossil taxa to the modern *Platycarya*, as Wing and Hickey (1984) have done, it might be appropriate to recognize them separately at the generic level. I do not, however, make a formal proposal for such treatment at this time.

The modern and fossil distributions of Platycaryeae are indicated in the map (Fig. 17). Although diverse and well represented in North America during the Eocene, the Platycaryeae did not withstand the climatic changes of the late Paleogene. The latest indications of the tribe in North America are rare pollen grains in the early Oligocene. In Europe, the pollen record indicates that the tribe maintained its presence through the Miocene. Although referred to simply as "*Platycarya*," the pollen is associated with fruits of extinct *Hooleya* in the Oligocene, and it is possible that Neogene pollen records in Europe do not represent the modern genus. Despite the well-studied European Tertiary fruit record, no post-Eocene *Platycarya* fruits have been recovered. The history of *Platycarya* in the area where it grows today is poorly known. Despite the occurrence of *Platycarya* in Japan today, the distinctive pollen and fruits of this genus appear to be absent from the well-studied Japanese Tertiary deposits.

*Fruits here referred to Paleoplatycarya wingii

FIGURE 16. Comparison of relationships between platycaryoid and engelhardioid taxa as suggested by characters of leaves and fruits. In each tribe, the two American taxa share foliar features that easily distinguish them from the single Asian taxon. The American taxa are most easily distinguished from each other on the basis of fruit morphology, one of them being much more similar to the Asian representative. Although the platycaryoid taxa have been attributed to a single genus (Wing & Hickey, 1984), the magnitude of difference between them is comparable to that between taxa recognized as different genera in the Engelhardieae (Stone, 1972).

ENGELHARDIEAE

The Engelhardieae comprises three extant genera, all of tropical distribution: *Engelhardia*,⁷ with five species from Asia to Sumatra; *Oreomunnea*, with two species in Central America; and *Alfaroa*, with seven species in Central America. Most species occur in the upper canopy of mountainous rain and cloud forests, although *Engelhardia* may also occur in savannas.

The trilobed bract, present in both staminate and pistillate inflorescences, is diagnostic of the Engelhardieae. The trilobed condition is preserved in the mature fruit, where the bract forms a wing with three lobes (*Engelhardia* and *Oreomunnea*) or persists as a tiny trilobed scale at the base of a wingless nut (*Alfaroa*). Leaves are usually even-pinnate. Vessels with scalariform perforations in secondary xylem are also diagnostic of extant Engelhardieae. The pollen is generally triplicate, isopolar, relatively small (13–19 μm), and does not usually exhibit marked exine specializations such as pseudocolpi. Considerations of wood anatomy (Heimsch & Wetmore, 1939) and pollen morphology (Whitehead, 1965) have led to the consensus that modern genera of the Engelhardieae are perhaps the most primitive in the Juglandaceae.

There is little question that the Engelhardieae,

as proposed by Manning (1978), is a natural group of closely related taxa. *Oreomunnea* was formerly treated as a subgenus of *Engelhardia*, with which it shares obvious similarity in external fruit morphology (Fig. 23). However, Stone (1972) called attention to the even greater similarity between *Oreomunnea* and the other New World genus, *Alfaroa*, citing congruences in internal fruit morphology, leaf phyllotaxy, leaflet architecture and anatomy as well as pollen morphology, and emphasized that the three taxa should be given equivalent status, either at the generic or subgeneric level. In my opinion *Engelhardia* and *Oreomunnea* are clearly distinct genera, but the recognition of *Alfaroa* as distinct from *Oreomunnea* should be questioned. The only characters separating *Alfaroa* from *Oreomunnea* are its lack of fruit wings and prophyllum and its somewhat larger nut.

The fossil record of the Engelhardieae is extensive in the Tertiary of the Northern Hemisphere and is known from dispersed pollen, pollen-bearing catkins, wood, foliage, and fruits (Table 4).

POLLEN

Pollen of extant genera of the Engelhardieae, reviewed by Whitehead (1965) and Stone and

⁷ *Engelhardia* is the correct original spelling, having precedence over "*Engelhardtia*" (Manning, 1966).

FIGURE 17. Map showing modern and fossil distribution of *Platycarya* and related genera. Modern distribution of *Platycarya strobilacea* indicated by shading. Undarkened triangles indicate fossil occurrences documented by pollen. Darkened triangles indicate fossil occurrences documented by fruits. — 1. *Hooletya lata* Wing & Hickey, middle Eocene. — 2. *Paleoplatycarya wingii* Manchester, Early Eocene. — 3. *Platycarya americana* Hickey, Early Eocene. — 4. *Platycarya* sp. fruits from lowermost Eocene of Tennessee (Manchester & Dilcher, in prep.). — 5. *Platycarya richardsoni* (Bowerbank) Chandler, early Eocene. — 6. *Hooletya hermis* (Unger) Reid & Chandler, early Oligocene. Distribution of platycaryoid pollen based upon reports by Frederiksen and Christopher (1978), Frederiksen (1979, 1980), Kedves (1982), Nichols & Ott (1978), Elsik (1978), Chateaufneuf (1980), Macko (1957, pl. 42: fig. 16), Nagy (1969), Gruas-Cavagnetto (1976).

TABLE 4. Important fossil occurrences of Engelhardieae.

Taxon	Age and Location	Comment
POLLEN		
<i>Momipites</i> Wodehouse	Maastrichtian-Neogene; Northern Hemisphere	Organ genus for triporate isopolar pollen resembling that of modern Engelhardieae; probably predates evolution of the Engelhardieae and may also have been produced by primitive members of the other tribes.
STAMINATE INFLORESCENCES		
<i>Eokachyra</i> Crepet, Potter & Dilcher	Middle Eocene; Tennessee	Staminate catkin from Kentucky and Tennessee, showing trilobate bracts characteristic of Engelhardieae and anthers with <i>Momipites</i> pollen; associated with <i>Oreoroa</i> foliage and <i>Palaeocarya puryearensis</i> fruits.
<i>Eoengelhardia</i> Crepet, Daghlia & Zavada	Middle Eocene; Tennessee	Staminate catkin from Tennessee, distinguished from <i>Eokachyra</i> by its smaller florets, bracts, and pollen; pollen is of the <i>Momipites</i> type and is less variable in morphology than that of <i>Eokachyra</i> .
WOOD		
<i>Engelhardioxylon</i> Manchester	Middle Eocene; Oregon, Texas	Organ genus for secondary xylem conforming in anatomy to that of extant Engelhardieae; species are reported associated with <i>Palaeocarya</i> fruits.
FOLIAGE		
<i>Oreoroa</i> Dilcher & Manchester	Middle Eocene to late Miocene; Europe, southeastern North America	Organ genus for leaflets with the architecture and cuticular features of extant <i>Oreomunnea</i> and <i>Alfaroa</i> .
<i>O. claibornensis</i> Dilcher & Manchester	Middle Eocene; Kentucky, Tennessee	Leaflets associated with the fruits of <i>Palaeocarya</i> and <i>Paleooreomunnea</i> , in the Claiborne Formation of Kentucky, Tennessee, and Mississippi.
<i>O. orsbergensis</i> (Wessel & Weber) Dilcher & Manchester	Middle Eocene to late Miocene; Europe	Species associated with fruits of <i>Palaeocarya macroptera</i> .
FRUITS		
<i>Palaeocarya</i> Saporta emend. Manchester	Middle Eocene to Neogene; North America, Europe, Asia	Organ genus for fruits with trilobate bract-wings, similar to those of extant <i>Engelhardia</i> and <i>Oreomunnea</i> .
<i>P. sect. Palaeocarya</i> emend. Manchester	Middle Eocene to Neogene; North America, Europe, Asia	<i>Palaeocarya</i> species with three major veins in each lobe, similar to modern <i>Oreomunnea</i> , but often distinct in features of the nutlet and style.
<i>P. macroptera</i> (Brongniart) Jähni-chen, Friederick & Takáč	Middle Eocene to Pliocene; Europe	Species associated with <i>Oreoroa orsbergensis</i> foliage.
<i>P. puryearensis</i> (Berry) Manchester	Middle Eocene; Kentucky, Tennessee, Mississippi, Texas	Species with wing venation of <i>Oreomunnea</i> but long style arms (like <i>Engelhardia</i>) and a bilobate prophyllum similar in general morphology to <i>Palaeocarya macroptera</i> .
<i>P. nevadensis</i> (MacGinitie) Manchester	Early or Middle Eocene; California	Species similar to <i>Palaeocarya puryearensis</i> but with a large, entire (unlobed) prophyllum.
<i>P. clarnensis</i> Manchester	Middle Eocene; Oregon, Wyoming	A species from central Oregon combining wing venation similar to <i>Oreomunnea</i> with various features of <i>Engelhardia</i> including pubescence of nutlet, two-compartmented locule, a small prophyllum, and a long style.

TABLE 4. (Continued).

Taxon	Age and Location	Comment
<i>P. wolfei</i> Manchester	Late Eocene; Washington	Species similar to <i>Oreomunnea</i> but with hairy nutlet.
<i>P. willamettensis</i> Manchester	Oligocene; western Oregon	Species with short pedicel and apparently lacking a prophyllum.
<i>P. olsoni</i> (Brown) Manchester	Late Oligocene(?) to Miocene; Alaska, Idaho, Oregon	The youngest representative of <i>Palaeocarya</i> known in the Tertiary of North America. Characterized by strong median septum and large peltate scales on nutlet.
<i>P. koreanica</i> (Oishi) Manchester	Late Oligocene to early Miocene; eastern Soviet Union, Korea, Japan	Species with very reduced prophyllum and exceptionally long pedicel related to extant <i>Engelhardia roxburghiana</i> ; the only record of the genus in the Asian Tertiary.
<i>P. sect. Monocosta</i> Manchester	Middle Eocene to Neogene; North America, Europe	<i>Palaeocarya</i> species characterized by wing lobes having a single mid-vein and simple pinnate secondary venation, like that of extant <i>Engelhardia</i> .
<i>P. mississippiensis</i> (Berry) Manchester	Middle Eocene; northern Mississippi	Species known from a single specimen easily distinguished from sympatric <i>Palaeocarya puryearensis</i> by its large size and <i>Engelhardia</i> -like venation.
<i>P. uintaensis</i> (MacGinitie) Manchester	Middle Eocene; Utah	Species from the Green River Formation distinguished from <i>Palaeocarya clarnensis</i> by wing venation.
<i>P. oxyptera</i> (Saporta) Manchester	Late Oligocene; Armissan, France	Species from France characterized by high-angled secondary veins of the wing lobes.
<i>Paraengelhardtia</i> Berry	Middle Eocene; Puryear, Tennessee	Fruits with shallow sinuses between lobes of the wing; nutlet small and globose.
<i>Paleooreomunnea</i> Dilcher, Potter & Crepet	Middle Eocene; Kentucky, Tennessee	Fruits with a trilobate wing with shallow sinuses, distinguished from <i>Paraengelhardtia</i> by its large bilobed nut.

Broome (1975), is generally triporate (less commonly 2–8-porate) and isopolar (rarely heteropolar), oblate, and finely scabrate. The lack of exine modifications, such as pseudocolpi (cf. *Platycaryeae*) or pronounced polar thin areas (cf. *Hicoreae*), along with the small size and number of pores, has been used to infer that pollen of this tribe is the most primitive in the family. Relatively similar triporate pollen appears in *Rhoiptelea* (Stone & Broome, 1975) and in other amentiferous families; for example, the *Myricaceae* and *Betulaceae*.

Triporate pollen resembling that of the *Engelhardieae* is abundant in the fossil record of the Northern Hemisphere and has gone under various names, including *Engelhardia*, *Momipites*, *Triatriopollenites*, *Triporopollenites*, and *Myricipites*. According to W. Krutzsch (pers. comm.), the type material of *Triatriopollenites*, *Triporopollenites*, and ?*Myricipollenites* bear no relation to *Engelhardia*, and it is unfortunate that these names have been used subsequently for engelhardioid pollen. The preferable generic name for dispersed juglandaceous pollen that is tri-

porate and isopolar like that of extant *Engelhardieae* is *Momipites* Wodehouse. The “coryloides-group” of *Momipites* (Nichols, 1973) includes grains identical to recent *Engelhardia* pollen and is reportedly present as early as the Maastrichtian in North America (Nichols in Muller, 1981) and common in the Paleocene of North America and western Europe. However, I consider it unlikely that the Cretaceous and Paleocene grains were produced by plants that had differentiated to the level of *Engelhardieae*. Fruits with the characteristic trilobed bract, though common in the Eocene and later Tertiary, are unknown prior to the Eocene. A probable pre-engelhardioid fruit, *Casholdia*, from the Late Paleocene displays an unlobed bract (Crane & Manchester, 1982) and occurs in sediment that yields abundant *Momipites coryloides*-type (sensu Nichols, 1973) pollen (Fig. 5E–G; Collinson, pers. comm.). In addition, similar pollen is abundant in the matrix of *Cyclocarya brownii* fruits from the Paleocene Fort Union Formation of North America (Fig. 37H, I). Even in extant *Cyclocarya paliurus* there are occasional triporate

grains (rather than the typical tetraporate type) (Iljinskaya, 1953). If triporate, isopolar pollen is indeed primitive for the Juglandaceae, it would not be surprising to find such pollen occurring in the record prior to the divergence of modern tribes and genera. Thus, despite the fact that certain Paleocene grains are virtually identical to *Engelhardia* or *Oreomunnea* and *Alfaroa*, they cannot be accepted as an indication of the status achieved by other organs of the plant. Accordingly, the use of modern generic names should be avoided for dispersed fossil grains.

By the Middle Eocene, it is likely that much of the dispersed pollen of *Momipites* was being produced by members of the Engelhardieae. This conclusion is supported not only by the abundance of confirmed engelhardioid fruits, but by the occurrence of *Momipites* pollen in situ within the anthers of inflorescences with trilobed bracts. Two types of staminate engelhardioid catkins are recognized from the Middle Eocene Claiborne Formation of Tennessee: *Eokachyra* (Crepet et al., 1975) and *Eoengelhardia* (Crepet et al., 1980). A third type is known from the Oligocene of Texas (Daghlian, pers. comm.).

Inflorescences of *Eokachyra aeolius* Crepet, Dilcher & Potter (Fig. 18C, D) consist of catkins 6 cm or more in length, with spirally arranged staminate flowers of ten to 15 stamens with anthers about 1 mm long. Each floret is subtended by a trilobed bract measuring 3–3.5 mm long, broadening from 0.4 mm wide at the basal attachment to 2 mm wide distally, with subangular sinuses between lobes 0.4–0.8 mm deep, and surrounded by a floral envelope of three conspicuous, obovate floral parts up to 2 mm wide dotted with large peltate scales (250 μ m diam.). Pollen from the anthers of this species is triporate, occasionally tetraporate, isopolar, triangular to subtriangular in polar view, 18–20 μ m, and has a finely scabrate exine. The exopore is generally meridionally elongate. The exine is relatively uniform in thickness, about 1 μ m. Crepet et al. (1980) note three distinct types of grains on the basis of polar exine structures: "those with no modifications at the poles; those with one fold at each pole; and those with thinnings or thinnings and folds of the exine in the polar region." Dispersed grains of this type are classified as *Momipites*. The meridionally elongate pore is comparable to that of extant *Engelhardia roxburghiana* and contrasts with the rounded pores of other modern species of the tribe. All of the features described for *Eokachyra* occur in extant

Engelhardieae; however, the precise combination of a three-parted floral envelope, obovate perianth parts, bilateral symmetry, and pollen size and morphology is unknown in any single modern genus.

Eokachyra was described on the basis of three specimens, all from Warman Clay Pit in Weakly County, Tennessee. The same locality has yielded two types of engelhardioid fruits, *Palaeocarya puryearensis* with a deeply lobed bract-wing comparable in configuration to the staminate bracts described here, and *Paleooreomunnea stoneana*, with shallowly lobed bract-wings. Four additional specimens of *Eokachyra* have recently been observed in the collections of the Field Museum (FM-PP 10879, 10880, 12328, 14695) from Somerville, Tennessee, associated with the same two types of fruits.

Inflorescences of *Eoengelhardia puryearensis* Crepet, Daghlian & Zavada are staminate catkins 7 cm or longer, with alternate florets, each subtended by a trilobed bract 2.1 mm long, broadening from 0.8 mm at the basal attachment to 2 mm wide distally, with sharp, deeply incised (ca. 1 mm) sinuses and bearing large peltate scales. There are nine to 12 stamens per floret, with anthers 1 mm by 0.3 mm surrounded by at least three (possibly more) rounded ovate perianth parts. Pollen from the anthers is small, (13.2–) 14.8(–16.8) μ m, straight-sided triangular in polar view, rarely rounded triangular, triporate, rarely tetraporate, isopolar, and finely scabrate with rounded-meridionally elongate exopores.

Eoengelhardia is distinguished from *Eokachyra* by its smaller florets, bracts, and pollen. In addition, the bracts are relatively wider and more deeply and sharply divided. The pollen is more similar in size and morphology to extant *Engelhardia roxburghiana* than to *Eokachyra* or any other modern engelhardioid taxon and does not exhibit the polar thinnings and/or creases reportedly common in *Eokachyra*. This species is known from six specimens, all from Puryear Clay Pit in Henry County, Tennessee. The same locality yields the engelhardioid fruits *Palaeocarya puryearensis* (Fig. 24E–H) and *Paraengelhardtia eocenica* (Fig. 28A–D).

Considering their Eocene age, *Eokachyra* and *Eoengelhardia* are surprisingly similar in most aspects of morphology to extant Engelhardieae. The magnitude of difference between these fossils and extant genera is comparable to that between the two extant sections of *Engelhardia*, or between *Oreomunnea* and *Alfaroa*. Recent in-

FIGURE 18. Staminate inflorescences of modern and fossil Engelhardieae.—A. *Oreomunnea mexicana* (Stanley) Leroy from Oaxaca, Mexico (IU mod. ref. coll. 4089), $\times 1.5$.—B. Enlargement showing trilobed (arrows) bracts and perianth parts (p), $\times 5$.—C. *Eokachyra aeolius* Crepet, Dilcher & Potter from the Middle Eocene of Tennessee (IU 2225), $\times 1.5$.—D. Enlargement showing the trilobate bract and perianth part. Pollen figured by Crepet et al. (1975), $\times 5$.—E. Undescribed engelhardioid catkin from the Oligocene Catahoula Formation of Texas, $\times 3$.—F. Pollen from an anther of the inflorescence in E. Note the three depressions typical for grains of this species, $\times 1,000$. E, F courtesy of Dr. C. P. Daghljan.

vestigations have yielded another fossil engelhardioid staminate catkin (Fig. 18E) from the Oligocene that differs more strikingly from the extant genera (Daghljan, pers. comm.). These catkins, from the Oligocene Catahoula Formation of southeastern Texas (Daghljan et al., 1980), resemble those of *Eokachyra*, *Euengelhardia*, and the modern genera in general catkin morphology and bract configuration, but contain a distinct type of pollen (Fig. 18F). The grains are triporate, isopolar, about $18\ \mu\text{m}$, and ornamented with fine evenly spaced coni and are unusual in the presence of three symmetrically placed oval thin areas in the exine of each hemisphere. Such pollen is distinct from that known in living species of Engelhardieae but is frequently encountered in the early Tertiary dispersed pollen record. Nichols (1973) established the *Momipites triorbicularis* group for such grains, which are known as early as late Paleocene. The occurrence of these grains in quantity within anthers supports recognition of similar dispersed pollen as a valid biological entity, although Crepet et al. (1980) suggest that some might be extreme variant grains of the type observed in *Eokachyra*. The subtending trilobed bracts confirm the engelhardioid status of this

material; however, the affinity of similar grains from the Paleocene remains to be determined.

Dispersed pollen data suggest that the migration of Engelhardieae to Middle America occurred during or prior to the Oligocene. *Engelhardia* sensu lato pollen is reported as abundant in Oligocene and Miocene deposits of Chiapas, Mexico (Langenheim et al., 1967) and in Oligocene strata of Puerto Rico (Graham & Jarzen, 1969). The northern extension of the American range, spanning from Oregon to Maryland during the Paleogene, persisted until the late Miocene. Engelhardioid pollen persists in the European record until the Pliocene.

WOOD

Secondary xylem of the Engelhardieae is like that of other extant Juglandaceae but is distinguished by the presence of scalariform vessel perforation plates. A full description is given by Manchester (1983). The wood anatomy of extant Engelhardieae has been suggested to be most primitive in the family on the basis of its longer vessel elements and scalariform plates (Heimsch & Wetmore, 1939). In addition, the wood lacks

specialized features characteristic of other tribes, such as crystals in idioblasts (Juglandaceae, Hicoreae, Platycaryaceae), spiral thickening (Platycaryaceae), and associated septate pith (Juglandaceae).

The organ genus *Engelhardioxylon* is applied to fossil woods conforming in anatomy to extant Engelhardieae (Manchester, 1983). Two species have been identified, *E. nutbedensis* and *E. texana* from the Middle Eocene of eastern Oregon and northeastern Texas, respectively. The anatomical uniformity between the Eocene species and the extant genera of Engelhardieae supports the conclusion that *Engelhardia*, *Oreomunnea*, and *Alfaroa* share a type of anatomy that was already established in the early Tertiary. Whether engelhardioid anatomy occurred in the family prior to the late Paleocene or early Eocene appearance of trilobed inflorescence bracts is a question that must await analysis of Paleocene woods.

FOLIAGE

Leaves of the extant Engelhardieae differ from others in the Juglandaceae by their typically even-pinnate organization (other tribes are typically, but not always, odd-pinnate) and are characterized by well-developed intersecondary veins and abundant peltate scales up to 150 μm on the lower epidermal surface. Leaflets of the tribe are most commonly entire-margined. However, serrate leaflets occur in two of five species of *Engelhardia*, one of two species of *Oreomunnea*, and two of six species of *Alfaroa*. In *O. mexicana*, *A. costaricensis*, and *A. williamsoni*, Stone (1972) notes that foliage is mostly entire-margined except in young shoots, stump sprouts, and seedlings. Stone (1972) also pointed out that seedlings often bear odd-pinnate leaves for a short interval before the even-pinnate condition prevails.

Based upon foliar criteria, extant Engelhardieae fall naturally into two groups, *Engelhardia* and *Oreomunnea-Alfaroa*. Characters important in this distinction include phyllotaxy, tooth configuration, venation, and presence or absence of papillae on the lower epidermis.

The opposite leaf arrangement of *Alfaroa* and *Oreomunnea* contrasts with the alternate phyllotaxy encountered in *Engelhardia* and the rest of the Juglandaceae. Stone (1972) observed that alternate to whorled leaves occur in young rapidly growing shoots of *A. costaricensis*. Leaflet bases are usually revolute in *Alfaroa* and *Oreomunnea* but flat in *Engelhardia*. When teeth are

present on the leaflets, they provide taxonomically useful information. Those of *Engelhardia* are rounded with convex apical and basal flanks (e.g., Fig. 19E), whereas those of *Oreomunnea* and *Alfaroa* are usually sharp with a straight or concave apical flank and a convex basal flank (e.g., Fig. 19F). In *Engelhardia* the main vein entering the tooth is approximately medial in course, whereas in the other two genera the vein enters the tooth supramedially, often contacting the sinus and paralleling the apical flank of the tooth.

Wolfe (1959) noted that *Engelhardia* can be separated from the New World genera on the basis of ultimate venation. The areolation of *Alfaroa* and *Oreomunnea* is typically closed, with almost no free-ending veinlets (Fig. 19G, H), whereas *Engelhardia* and other members of the Juglandaceae usually have open areolation with many freely ending veinlets (Fig. 19I, J). The closed nature of the ultimate venation also results in smaller areoles in *Oreomunnea* and *Alfaroa* than are commonly encountered in *Engelhardia*. There is some haziness to this distinction, however, as some specimens of *Alfaroa* have more freely ending veinlets than expected and some specimens of *Engelhardia* exhibit fewer freely ending veinlets than is usual. However, the typical ultimate venation for each genus supports the recognition of *Alfaroa* and *Oreomunnea* as being more closely related to each other than to *Engelhardia*.

Leaflets of *Engelhardia* have a smooth, non-papillate lower epidermis (Fig. 20A), often with hairs, as well as peltate scales. Those of *Oreomunnea* and *Alfaroa* have a papillate lower epidermis (Fig. 20B, C), with papillae especially concentrated around the stomata, and are frequently devoid of trichomes except for the prominent circular scales.

In most of the foliar characters considered above, including phyllotaxy, ultimate venation, and cuticle, *Oreomunnea* and *Alfaroa* appear to be relatively specialized while *Engelhardia* is more generalized and similar to the foliage of other tribes. Within the *Oreomunnea-Alfaroa* group, *O. mexicana* is easily recognized by the presence of one or two small tongue-like foliar extensions recurved against the lower surface of the leaflet base adjacent to the petiolule (Figs. 9B, 19A, 21A). As yet, well-developed auriculae are unknown in the fossil record of the Engelhardieae. However, they do occur in the extinct *Platycarya americana* foliage (Fig. 9A).

FIGURE 19. Cleared leaflets of extant Engelhardieae.—A. *Oreomunnea mexicana*, Stone 2807 (IU mod. ref. col. 1927), showing basilar auriculae and intersecondary veins, $\times 1$.—B. *Alfaroa costaricensis* ssp. *costaricensis*, with regularly spaced teeth and intersecondary veins, Keith 371 (USGS 957), $\times 1$.—C. *Engelhardia roxburghiana*, Twang 1312 (USGS 1312), $\times 1$.—D. *Engelhardia apoensis* showing toothed margin, Elmer 11744 (USGS 893), $\times 1$.—E. Enlargement of D, showing rounded tooth apices and medial entry of veins into teeth, $\times 2.5$.—F. Enlargement of B, showing sharp tooth apices and supramedial venation of the teeth, $\times 2.5$. G–J. Higher order venation in modern Engelhardieae, $\times 15$.—G. *Oreomunnea mexicana* showing closed areolation with relatively few freely ending veinlets (IU mod. ref. coll. 1308).—H. *Alfaroa manningii* showing areolation similar to that of *Oreomunnea*, Stone 2170 (IU mod. ref. coll. 1313).—I. *Engelhardia roxburghiana*, with relatively open areolation (IU mod. ref. coll. 517).—J. *E. spicata* showing areolation similar to that of *E. roxburghiana* (IU mod. ref. coll. 434).

FIGURE 20. Scanning electron micrographs of the lower epidermis of leaflets of extant Engelhardieae, $\times 150$.—A. *Engelhardia chrysolepis*, showing peltate scales and relatively smooth, non-papillate surface characteristic of *Engelhardia*, Law 195 (IU mod. ref. coll. 1921).—B. *Oreomunnea mexicana* showing peltate scales and papillate epidermis, Stone 2807 (IU mod. ref. coll. 1927).—C. *Alfaroa costaricensis* showing papillate epidermis and a large peltate scale, Standley 33501 (IU mod. ref. coll. 4027).

Leaflets of the *Oreomunnea-Alfaroa* type are common in the Tertiary of Europe (Kvaček, 1972; Jähnichen et al., 1977, 1984) and southeastern North America (Dilcher & Manchester, 1986). Observing that leaflets of *Oreomunnea* and *Alfaroa* are often indistinguishable, and that the same kind of foliage is also associated with extinct engelhardioid fruit types, Dilcher and Manchester (1986) erected the organ genus *Oreoroa* for fossil foliage. *Oreoroa* leaflets (Figs. 21C–G, 22A–F) are characterized by slender shape, basal asymmetry, abundant intersecondary veins, closed areolation, and papillate lower epidermis with large circular peltate scales. In all of these characters they resemble extant *Oreomunnea* and *Alfaroa*. Teeth, when present, are usually acute and are similar to those of both modern genera. Two species of *Oreoroa* have been recognized (Dilcher & Manchester, 1986) and are reviewed here.

Oreoroa orsbergensis (Wessel & Weber) Dilcher & Manchester (Fig. 21C, D) ranges from the Middle Eocene to the Upper Miocene of France, West Germany, East Germany, Austria, Switzerland, Czechoslovakia, Poland, Rumania, Bulgaria, and Yugoslavia and is correlated with *Palaeocarya macroptera* fruits (Jähnichen et al., 1984). As noted by Jähnichen et al. (1977, 1984), these leaflets are very similar to those of extant *Oreomunnea mexicana*, however the basal auriculae characteristic of this modern species are absent in the fossil material.

Oreoroa claibornensis Manchester & Dilcher leaflets (Figs. 21E–G, 22A–F) occur in the Mid-

dle Eocene Claiborne Formation in Tennessee and Kentucky. The American species is distinguished from *O. orsbergensis* in the more markedly asymmetrical leaflet bases and in the tendency for larger size. Although the type material of *O. claibornensis* came from localities where *Paleooreomunnea stoneana* fruits were abundant, association evidence suggests that other types of fruits, including *Palaeocarya puryearensis*, and *Paraengelhardtia eocenica* may have borne similar foliage.

A portion of a complete leaf of *Oreoroa claibornensis* with at least seven lateral leaflets and a small terminal one is shown in Figure 21G. Another specimen figured by Dilcher and Manchester (1986) also shows a terminal leaflet. Terminal leaflets are unusual in foliage of extant Engelhardieae, which ordinarily is even-pinnate. Odd-pinnate foliage characterizes all other extant tribes of the Juglandaceae and is usually confined to early stages of seedling development in the Engelhardieae (Stone, 1972). More data is needed on the nature of early Tertiary engelhardioid leaves, but it appears likely that the odd-pinnate condition was more prevalent in early representatives of the tribe than it is today.

FRUITS

The three modern genera of Engelhardieae are easily distinguished on the basis of fruit morphology (Fig. 23). *Engelhardia* and *Oreomunnea* both have trilobed wings, but differ in features such as wing venation, styler configuration, and

FIGURE 21. Modern *Oreomunnea* and fossil *Oreoroa* Dilcher & Manchester foliage.—A. *Oreomunnea mexicana* leaflet, showing basal auricle and scattered teeth (cf. Fig. 19A) (IU mod. ref. coll. 1308), $\times 1$.—B. Higher magnification of the same leaflet showing intersecondary veins, lack of percurrent tertiaries, closed areoles, and a tooth with supramedial vein entry, $\times 5$.—C. *Oreoroa orsbergensis* (Wessel & Weber) Dilcher & Manchester from the Miocene of Wackersdorf, Germany (IU 4764), $\times 1$.—D. Detail of the same leaflet for comparison with B, $\times 5$.—E. *Oreoroa claibornensis* Dilcher & Manchester, holotype from the Middle Eocene Warman Clay Pit, Tennessee (IU 15826-2278), $\times 1$.—F. Higher magnification of the same leaflet showing venation and teeth. Main vein enters tooth supramedially (arrow), $\times 5$.—G. Compound leaf of *Oreoroa claibornensis* from Middle Eocene of Somerville, Tennessee. Note presence of terminal leaflet (FM-PP 9423), $\times 0.8$.

nutlet septation. *Alfaroa* has a relatively large nut, without wings. Before considering the extensive fossil record of engelhardioid fruits, it is appropriate to consider in more detail the fruit morphology of these extant genera.

Engelhardia

The fruit of *Engelhardia* is a nutlet subtended by a prominent abaxial bract forming a trilobed wing, the lobes of which have pinnate venation

FIGURE 22. *Oreoroa* leaflets from the Middle Eocene of Kentucky and Tennessee. — A. Large, entire-margined leaflet of *Oreoroa claibornensis* Dilcher & Manchester showing markedly asymmetrical base and frequent intersecondary veins, Warman Clay Pit, Tennessee (IU 15826-4478), $\times 1$. — B. *O. claibornensis* leaflet with asymmetrical base and overall shape similar to A and D but with prominent teeth, Somerville, Tennessee (FM-PP

(Fig. 23A, C, D). The inflorescence bracteoles are usually united into an adaxial appendage, which is addressed to the base of the nutlet (Manning, 1978). This appendage has been variously called the basal lobe, forth lobe, front bract, etc. Since it is a compound structure formed by the union of two bracteoles, it cannot properly be referred to as a bract. The terms fourth lobe and basal lobe imply that the structure is simply another lobe of the abaxial bract, and are therefore undesirable. I prefer the term "prophyllum," a contraction of "mesoprophyllum" (Hjelmqvist, 1948). The nutlet may be partitioned into two or four basal compartments ("cells" in earlier literature), depending on development of the secondary septum and is bipartite in equatorial section (Fig. 23B). When present, the secondary septum is low, not extending more than one-third of the distance to the top of the locule (Fig. 23G). Germination is epigeal (Conde & Stone, 1970).

The two extant sections of *Engelhardia* may be distinguished from one another on the basis of stylar configuration and nutlet indument. *Engelhardia* sect. *Engelhardia*, with four species, has a deeply bifurcate style with elongate stigmas extending well beyond the sepals, and a hairy nutlet. *Engelhardia* sect. *Psilocarpeae*, with the single species *E. roxburghiana*, is characterized by a short style with globose stigmatic areas and nutlets that lack hairs but are densely covered with peltate scales. The prophyllum is reduced or absent in *E. roxburghiana*, but relatively well developed in sect. *Engelhardia*.

Oreomunnea

Fruits of *Oreomunnea*, like those of *Engelhardia*, are trilobed-winged nutlets. This and other similarities led some taxonomists (e.g., Manning, 1959, 1960) to consider *Oreomunnea* a section within *Engelhardia*. However, differences in foliage, germination, and fruit morphology are used by Stone (1972) to support its separate generic status. The venation of the wing lobes is not pinnate, as in *Engelhardia*, but "tri-veined" (Fig. 23H, J), consisting of a midvein

and a pair of prominent, ascending lateral veins. The lobes are oblong, rather than obovate in shape. The prophyllum of *Oreomunnea* is larger than that of *Engelhardia*, extending well beyond the sepals, and is generally rounded and unlobed. The stigmatic areas are globose, as in *Engelhardia* sect. *Psilocarpeae*, rather than elongate as in *Engelhardia* sect. *Engelhardia*. Unlike most species of *Engelhardia*, the nutlet is devoid of hairs. The nutlet is partitioned by thin septa into eight compartments (Fig. 23I) rather than two or four. Four major compartments are formed by the intersection of a high secondary septum with the primary septum; each of these compartments is subdivided basally by a septum of tertiary rank resulting in the "eight-cell" condition. Germination is hypogeal, rather than epigeal. The two extant species of *Oreomunnea* are easily distinguished. *Oreomunnea mexicana* has fruits comparable in size to those of *Engelhardia* (central lobe of wing ca. 40 mm long; nutlet ca. 7 mm diam.), whereas *O. pterocarpa* has very large fruits (central lobe of wing ca. 120 mm long; nutlet ca. 12 mm diam.).

Alfaroa

Except for its lack of wings and generally larger endocarp, *Alfaroa* (Fig. 23K–O) is very similar, in fruit morphology as well as other characteristics, to *Oreomunnea* (Stone, 1977). In this genus, the trilobed bract of the inflorescence is retained as a tiny scale at the base of the nut (Fig. 23O), rather than expanding into a wing as in other genera (both extinct and extant) of the tribe. The bracteoles, which form the prophyllum in *Engelhardia* and *Oreomunnea*, apparently do not contribute to fruit formation in *Alfaroa*. As in *Oreomunnea*, the styles are short, the stigmas are globose, and the nutlet is partitioned into eight compartments with the contribution of a high secondary septum and two parallel tertiary septa (Fig. 23M); germination is likewise hypogeal. The nuts range up to 6.5 cm long and 3 cm wide. The indehiscent husk ranges from thick to thin. *Alfaroa* is not known from the fossil record.

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14342), $\times 1$.—C. Leaflet of *Oreoroa* sp. showing evenly distributed peltate scales, Puryear Clay Pit, Tennessee (IU 15820-3559), $\times 7.5$.—D. *O. claibornensis* compression with intact cuticle, Lamkin Clay Pit, Kentucky (IU 15815-2568), $\times 1$.—E. Lower cuticle showing the typical peltate scales, New Puryear Clay Pit, Tennessee (IU 15819-3408), light microscopy, $\times 150$.—F. Scanning electron micrograph of lower cuticle of leaflet shown in D, showing the papillae characteristic of *Oreoroa* and the prominent peltate scales, $\times 150$.

FIGURE 23. Modern fruits of Engelhardieae. A–G. *Engelhardia* spp. from eastern Asia.—A. *E. spicata* Bl. showing the prominent trilobate bract with pinnately veined lobes, and the small prophyllum (p), *Rock 2728* (IU mod. ref. coll. 1322; from UC-264639), $\times 1$.—B. *E. spicata* nutlet sectioned equatorially showing the primary septum dividing the locule into two compartments. Note the lack of secondary and tertiary septa, *McClure 20043* (IU mod. ref. coll. 1934; from MO-1099363), $\times 4$.—C. *E. apoenis* Elmer ex Nagel showing relatively elongate, hairy nutlet, loboate prophyllum (p), exserted style arms, and the large trilobed bract-wing with pinnate venation, *Elmer 11744* (IU mod. ref. coll. 4037; from F-291237), $\times 1$.—D. *E. roxburghiana* Wall. showing very small prophyllum (p) and short globose stigmas (s) characteristic of *E. sect. psilocarpeae*, *Chuang & Kao 3352* (IU mod. ref. coll. 1324; from UC-1364403), $\times 1$.—E. Nutlet of *E. apoensis* split along the plane of dehiscence showing the high primary septum and lack of a secondary septum (IU mod. ref. coll. 4037), $\times 3$.—F. Nutlet of *E. roxburghiana* split along the primary septum (IU mod. ref. coll. 1324), $\times 5$.—G. Same nutlet split along line of dehiscence, $\times 5$. H–J. *Oreomunnea* spp. from Central America.—H. *O. mexicana* (Standl.) Leroy fruit showing the large rounded prophyllum (p) and trilobate bract with tri-veined pattern of lobe venation, *Williams & Molina*

FOSSIL FRUITS

Fossil fruits of the Engelhardieae are placed here in three genera: *Palaeocarya* (sect. *Palaeocarya* and *Monocosta*), *Paraengelhardtia*, and *Paleooreomunnea*. Features important in distinguishing these taxa are indicated in the key below. Percent sinus depth is computed as the distance between the fruit base and the sinus subtracted from the distance between the fruit base and the central lobe apex divided by the distance between the fruit base and the central lobe apex, multiplied by 100.

- 1a. Fruit with a deeply 3-lobed wing, sinus depth 65–85%.
 - 2a. Each lobe of wing with 3 ascending main veins *Palaeocarya* sect. *Palaeocarya*
 - 2b. Each lobe of wing with pinnate venation *Palaeocarya* sect. *Monocosta*
- 1b. Fruit with a shallowly lobed wing, sinus depth 12–20%.
 - 3a. Wing large (20–43 mm high) with a large bilobed and transversely flattened nut 15–22 mm wide *Paleooreomunnea*
 - 3b. Wing small (16–23 mm high) with a small spheroidal nutlet 4–5 mm diam. *Paraengelhardtia*

Palaeocarya Saporta, Ann. Sci. Nat. Bot. Sér. 5, 18: 99. TYPE: *Palaeocarya atavia* Saporta [= *P. macroptera* (Brongniart) Jähnichen, Friederick & Takáč].

Emended diagnosis. Fossil fruits consisting of a nutlet subtended by a large trilobed wing; sinuses between lobes deep, extending almost to the nutlet; lobes oblong to oblanceolate, 20–70 mm long, 4–14 mm wide; middle lobe usually longer than the laterals; venation of lobes variable, from simple pinnate to “tri-veined” (consisting of a midvein and prominent ascending lateral veins); prophyllum, when preserved, large or small, lobed or entire; nutlet rounded, sub-

divided by septa into two or more compartments as seen in equatorial section.

Discussion. The genus *Palaeocarya* Saporta (1873) is hereby emended to include engelhardioid fossils not only with the tri-veined pattern specified by Saporta (1873) in his original diagnosis, but those with a single main vein and pinnate secondaries, as well. Traditionally, fossils fitting this description have been placed in the extant genus *Engelhardia* (see, for example, Jähnichen et al., 1977). This procedure was acceptable under the older concept of the modern genus. However, with the recognition of *Oreomunnea* as a separate genus from *Engelhardia* (Stone, 1973; Manning, 1978), the range of morphological diversity within *Engelhardia* is accordingly reduced. As a result the range of variability expressed in fossil engelhardioid fruits greatly exceeds that in the extant genus as now defined. During the Tertiary, there seems to have been a complex of species in the Northern Hemisphere ranging continuously in fruit morphology between types similar to modern *Engelhardia* and modern *Oreomunnea*. In the middle of this range were species such as *Palaeocarya clarnensis*, sp. nov. and *P. olsoni* (Brown), comb. nov. that had venation like that of extant *Oreomunnea* but nutlet and styler features corresponding to extant *Engelhardia*. The organ genus *Palaeocarya* is resurrected to accommodate all fossil fruits of the *Engelhardia*-*Oreomunnea* complex because it would be difficult and excessively arbitrary to try to sort the intermediate forms according to modern generic boundaries.

The emended generic diagnosis provided above excludes leaflets and applies to fruits only. In his original description of the genus, Saporta (1873) figured a foliage fragment as well as a fruit. Re-examination of the leaf specimen at the Paris Museum shows that it is not a juglandaceous

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42789 (IU mod. ref. coll. 4034; from F-1807787), ×1.—I. *O. mexicana* nut sectioned equatorially to show the eight compartments formed by the intersection of primary, secondary and tertiary septa (compare with B, M), Stone 2141 (IU mod. ref. coll. 1306; from DUKE), ×2.—J. *O. pterocarpa* Oerst. fruit. The large size is characteristic of this species. The large rounded prophyllum and venation of the wing lobes contrast with the features of *Engelhardia* (A–G), Stone 1346 (IU mod. ref. coll. 1602; from DUKE), ×1. K–O. *Alfaroa* spp. from Central America.—K. *A. manningii* Leon. Note the large size and lack of wings, Stone 2170 (IU mod. ref. coll. 1313; from DUKE), ×1.—L. *A. costaricensis* fruit showing persistent perianth and weaker ribs than *A. manningii*, Utley 2196 (IU mod. ref. coll. 4036), ×1.—M. Same nut sectioned transversely to show the eight compartments of the locule; compare with *Oreomunnea* (I) and contrast with *Engelhardia* (B), ×1.—N. *A. williamsii* nut split along line of dehiscence; note the high secondary septum (contrast with that of *Engelhardia*, G) Stone 2210, ×1.—O. Base of nut in M showing the persistent bract with three lobes (arrows) adjacent to the pedicel scar (s), ×5.

leaflet. Jähnichen et al. (1984) placed genuine engelhardioid foliage together with the same type of fruits under the name *Palaeocarya*. I suggest that leaflets should be placed in a separate genus.

Two sections of *Palaeocarya* are proposed: sect. *Palaeocarya*, for fruits with tri-veined lobes, and sect. *Monocosta*, for those with a single main vein in each lobe. Although these sections are convenient, a more natural division would include features of nutlet septation and stylar configuration, and of other organs. However, since details of the style and nutlet are seldom preserved and other organs have not been found attached to the fruits, such features have not been utilized in this classification.

Sect. *Palaeocarya* emend. Manchester. TYPE: *Palaeocarya atavia* Saporta [= *P. macroptera* (Brongniart) Jähnichen, Friederick & Takáč].

Emended diagnosis. Fruits of *Palaeocarya* in which the lobes are tri-veined, with a midvein flanked by two prominent, ascending lateral veins.

Discussion. This taxon was originally proposed as a genus by Saporta (1873). Knobloch and Kvaček (1976) reduced it to sectional rank within *Engelhardia*, a move accepted by Jähnichen et al. (1977). Here it treated as a section within the organ genus bearing the same name. Fossil fruits referable to this section are relatively common in the Tertiary of North America and Europe.

***Palaeocarya macroptera* (Brongniart) Jähnichen, Friederick & Takáč,** Tertiary Res. 6: 109–134. pl. 1: figs. 7, 8; pl. 4: figs. 5, 6; pl. 5: fig. 8. 1984. *Carpinus macroptera* Brongniart, Prodr. Hist. Vég. Foss. 48. pl. 3: fig. 6. 1828. *Engelhardtia macroptera* (Brongniart) Unger, Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 25: 52. pl. 16: figs. 9–11. 1866; Reid & Chandler, Bembridge Fl. 87–93. pl. 6: figs. 1–6. fig. 5. 1926; Jähnichen, Mai & Walther, Feddes Repert. 88: 343–352. pl. 54–56. 1977. Figure 24A–D.

Palaeocarya atavia Saporta, Ann. Sci. Nat. Bot., Sér. 5, 18: 99–102. pl. 15: figs. 36–38. 1873.

Discussion. This species ranges from the Middle Eocene (Messel near Darmstadt, West Germany) through the Pliocene (Berga, near Sangerhausen, East Germany) in Europe. Although given various specific epithets in the past, Jähn-

ichen et al. (1977, 1984) attribute the various occurrences to a single species. The former assignment to *Engelhardia* sensu lato is misleading in view of the narrow concept of *Engelhardia* currently used by taxonomists. The tri-veined pattern of lobe venation and large prophyllum characterizing this fossil species occur today only in *Oreomunnea*. Because of the close similarity of the fruits to *Oreomunnea*, and their correlation with *Oreomunnea*-type foliage (Kvaček, 1972; Jähnichen et al., 1977), *Oreoroa orsbergensis*, it might seem reasonable to place these fruits in the extant genus *Oreomunnea*. However, the base of the locule appears to have been partitioned into two compartments, as in *Engelhardia*, rather than eight, as in *Oreomunnea* (Jähnichen et al., 1977). In addition, the lobes of the wing are sometimes obovate as in *Engelhardia* (Fig. 24C; Reid & Chandler, 1926). This suggests a morphology intermediate between the two extant genera, as implied previously by Reid and Chandler (1926) and Jähnichen et al. (1977). An organ generic name is therefore warranted for this species and the combination proposed by Jähnichen et al. (1984) appears to be correct. It would be desirable to determine the stylar condition of this species; material was not available to me for dissection.

The earliest organ generic name applied to this species was *Palaeocarya* (Saporta, 1873). The oldest specific epithet, *macroptera* (Brongniart, 1828), has priority over the epithet *atavia* proposed by Saporta (1873), so that the valid combination for the species is *Palaeocarya macroptera* (Brongniart) Jähnichen, Friederick & Takáč. The holotype for *P. atavia* is illustrated in Figure 24A.

***Palaeocarya puryearensis* (Berry) Manchester,** comb. nov. *Engelhardtia puryearensis* Berry, Profess. Pap. U.S. Geol. Surv. 91: 185. pl. 17: figs. 6, 7. 1916. *Paraoreomunnea puryearensis* (Berry) Dilcher, Potter & Crepet, Amer. J. Bot. 63: 536–537. figs. 7–15. 1976. Figure 24E–K.

Discussion. *Palaeocarya puryearensis* occurs in the Middle Eocene clays of the Claiborne Formation in Kentucky and Tennessee and is known from about 12 specimens. Berry (1916) placed the fruits in *Engelhardia*. However, the wing lobes are prominently tri-veined and the prophyllum is especially large, as in *Oreomunnea*. Dilcher et al. (1976) recognized the close affinity of the fruits with *Oreomunnea* and proposed the new generic

FIGURE 24. European and American species of *Palaeocarya*. A–D. *Palaeocarya macroptera* (Brongniart) Jähniichen, Friederick & Takáč. —A. Type specimen for the genus *Palaeocarya* “*atavia*” Saporta from the Upper Oligocene of Aix-en-Provence, France, $\times 1$. —B. Specimen from the Lower Oligocene Bembridge flora of southern England showing a large rounded prophyllum (p) and the three lobes of the wing (BM-V 17012), $\times 1$. —C. Another specimen from the same locality showing oblanceolate middle lobe of wing (BM-V 17588), $\times 1$. —D. Enlargement of same specimen showing the nutlet and sepals (se), $\times 3$. E–H. *Palaeocarya puryearensis* (Berry) Manchester from the Middle Eocene of Puryear, Tennessee, $\times 1$. —E. Holotype, showing the three main veins of the central lobe of the wing and the two long divergent style arms (st) (USNM 35527A), $\times 1$. —F. Smaller specimen showing a two-lobed prophyllum, (UConn-P 410), $\times 1$. —G. Additional specimen showing a deeply cleft bilobed prophyllum (arrows) (IU 4863), $\times 1$. —H. Specimen showing typical venation (IU 1950), $\times 1$. —I, K. Cf. *Palaeocarya puryearensis* showing large nutlets from Eocene of Somerville, Tennessee (FM-PP 6374), $\times 1$. —J. Specimen from the Oligocene of Huntsville, Texas (Dr. C. P. Daghljan, coll.), $\times 1$.

name *Paraoreomunnea* for the fossil material. However, the older generic name, *Palaeocarya* Saporta (1873) has priority for the assignment of *Oreomunnea*-like fruit fossils.

Although in venation and morphology of the wing and prophyllum *Palaeocarya puryearensis* resembles extant *Oreomunnea mexicana*, there

is a significant difference in stylar morphology. The style arms visible in the type specimen of *P. puryearensis* have previously been overlooked. As shown in Figure 24E, there are two long, curving stigmatic arms apparently diverging in a plane parallel to that of the bract. This type of style occurs in extant *Engelhardia apoensis*

FIGURE 25. *Palaeocarya* sect. *Palaeocarya* species from the Eocene of western North America. A–C. *Palaeocarya nevadensis* (MacGinitie) Manchester from the Lower or Middle Eocene Chalk Bluffs flora of California. —

but contrasts with the short globose styles of *Oreomunnea*. Dilcher et al. (1976) reported short styles for the fossil species; however, re-examination of the material suggests that the structure formerly interpreted as the style is a median sepal.

The frequent absence of the prophyllum ("fourth lobe") mentioned by Dilcher et al. (1976) for specimens of *Palaeocarya puryearensis* is apparently due to the fact that most specimens break along the surface of the trilobed bract, leaving the prophyllum buried in the clay matrix. Three specimens are now available which show that the prophyllum was large as in *Oreomunnea*. In two of these, the prophyllum is distinctly cleft into two lobes (Fig. 24F, G). In extant species of *Oreomunnea*, this feature occurs only in aberrant specimens. Although not enough samples of the fossil species are preserved with intact prophylla to determine whether this was a common occurrence, the bilobed condition supports the concept that the prophyllum is derived from the fusion of the two inflorescence bracteoles, as indicated by Manning (1978).

The differences between *Palaeocarya puryearensis* and the similar European species, *P. macroptera*, are subtle and poorly understood. While the locule was apparently bi-compartmented in *P. macroptera* it seems to have been divided into four or more compartments in *P. puryearensis*. The prophylla of *P. macroptera* were entire, whereas at least some in *P. puryearensis* were bilobate.

The morphological and geographic proximity of this species with the extant species of *Oreo-*

munnea suggests that the latter may be a southern isolate of the North American Tertiary *Palaeocarya* complex. *Palaeocarya* appears to have been common in the Mississippi Embayment region during the Paleogene. An Oligocene locality from Huntsville, Texas has yielded specimens very similar to and perhaps conspecific with *P. puryearensis* (Fig. 24J; Daghljan et al., 1980).

***Palaeocarya nevadensis* (MacGinitie) Manchester, comb. nov.** *Engelhardtia nevadensis* MacGinitie, Publ. Carnegie Inst. Wash. 534: 102–103. pl. 13: figs. 5–7, 9, 10. 1941. Figure 25A–C.

Description. Trilobed winged fruits; lobes of wing lanceolate-obovate; central lobe 30–60 mm long, 6–12 mm wide; lateral lobes arising at about 50°, 20–30 mm long, 3–6 mm wide; venation of lobes consisting of a strong midrib flanked by a pair of weaker laterals connected with the midrib by a series of branching secondaries; weak secondaries branching from the primaries and looping along the margin; tertiary veins reticulate; areolation a fine straggling reticulate web; prophyllum rounded, up to 13 mm high with venation consisting of a series of five to seven or more short primaries branching and looping at the margin, a strong median primary often present; nutlet 4–8 mm long; wings and prophyllum dotted with peltate trichomes; styler condition unknown; fruits borne spirally on a stem with scars about 2 mm apart.

Discussion. This species is from the Middle (MacGinitie, 1941) or Lower (MacGinitie, pers.

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A. Fruit showing the large rounded prophyllum with radiating subparallel venation and the three lobes of the bract-wing (UCMP 2158), $\times 1$.—B. Specimen showing typical *Oreomunnea*-type venation of wing lobes and attachment of nutlet to the axis (UCMP 2156), $\times 1$.—C. Same specimen partially dissected to reveal prophyllum. Note also the short pedicel and attachment with the axis, $\times 4$. D–H. *Palaeocarya clarnensis* Manchester from the Middle Eocene Clarno Formation.—D. Specimen showing the trilobate bract with lobes having a tri-veined pattern consisting of a midvein and a pair of strong ascending secondaries merging apically into tertiary loops; also showing stout pedicel persistently attached to nutlet, West Branch Creek locality (USNM 387385), $\times 1$.—E. Holotype showing prophyllum (p), persistent pedicel and bract with typical venation (USNM 326827), $\times 1$.—F. Same specimen, enlarged to show bilobed stigmatic arms (st), fine hairs (h) surrounding the nutlet, venation and undulate margin of the prophyllum, $\times 4$.—G. Specimen of same species from Gosner Road, OMSI locality 238, showing rounded nutlet with persistent pedicel and perianth (IU 4792), $\times 1$.—H. Another specimen from same locality dissected to show style and stigmatic arms diverging in same plane as wings (IU 4793), $\times 4$.—I. Juglandaceous locule cast with only two lobes at the base from the Clarno Nut Beds deposit, OMSI locality 225 possibly representing *P. clarnensis* (IU 15768-4871), $\times 10$.—J. Nutlet of modern *Engelhardtia spicata*, showing surface hairs, perianth, and style for comparison with F, H, McClure 20043 (IU mod. ref. coll. 1934), $\times 5$.—K. Cf. *Palaeocarya clarnensis* specimen from Middle Eocene Green River Formation, Wyoming (UCMP-PA 10589), $\times 1$.—L. *Palaeocarya wolfei* Manchester from USGS locality 9731, Upper Eocene of the Puget Group, western Washington. Note the prophyllum (p) (USNM 387388), $\times 1$.—M. Same specimen under greater magnification showing hairs (h) arising from the base of the nutlet and pedicel, $\times 5$.

comm.) Eocene Chalk Bluffs flora in the Sierra Nevada Mountains of California. It is known from several specimens, all of which show the prominently tri-veined lobes. In addition, they show a large rounded prophyllum resembling that of *Oreomunnea*. An exceptional specimen (Fig. 25B, C) shows a fruit still attached to an axis bearing helically arranged scars indicative of a spicate inflorescence. Peltate glands may be seen in freshly collected material, as brown dots, but disappear with oxidation in older specimens. Unfortunately, the condition of septation within the nutlets cannot be observed. If the nutlets were divided into eight compartments, they could perhaps be regarded as *Oreomunnea*.

***Palaeocarya clarnensis* Manchester, sp. nov.** Figure 25D–H.

Diagnosis. Trilobed winged fruits; lobes of wing lanceolate-obovate; central lobe 30–45 mm long, 4–10 mm wide; lateral lobes departing at 30–50° from the median lobe, 20–32 mm long, 3–7 mm wide; venation of lobes dominated by the midrib and a pair of strong lateral veins just inside the margin, resulting in a tri-veined aspect; in the upper one-third of the wing lobes, the lateral veins bowed outward between intercepting secondary veins resulting in a weakly looped appearance, adjoined exmedially by a series of smaller tertiary arches; ultimate venation fourth order, with freely ending veinlets common; prophyllum 6–8 mm high with a faintly crenulate margin; nutlet 3–5 mm wide, 3–5 mm high, usually retaining the pedicel, which is 1.5–3 mm long; nutlet base densely pubescent (as seen in one well-preserved specimen); sepals united into a tube 1.5–2 mm long with four free tips surrounding the style, style stout and at least 2–3 mm long, exserted 2 mm beyond prophyllum, then splitting into two stigmatic arms, each about 1 mm long, stigmatic arms diverging in a plane parallel to the wing, no septum or parting is seen in the dorsiventrally compressed nutlets, suggesting that the primary septum is parallel to the bract and that the carpels are median.

Specimens. The holotype is USNM 326827 (Fig. 25E, F), and the paratypes are USNM 387385 (Fig. 25D), IU 4792 (Fig. 25G), and IU 4793 (Fig. 25H). Sixteen specimens (mostly uncatalogued in the OMSI collection) were available for study—11 from the West Branch Creek localities (Hergert, 1961; USGS loc. 8637; OMSI

loc. 226, 229, 230), and five from the Gonser Road locality (OMSI loc. 238).

Discussion. *Palaeocarya clarnensis* occurs at Middle Eocene localities in the Clarno Formation of Oregon. Although it has tri-veined wing lobes, the ascending lateral veins are weak and grade into coalesced secondary loops apically. Thus, the ascending laterals are stronger than those of extant *Engelhardia* but not as pronounced as those of modern *Oreomunnea*. Taken alone, the tri-veined lobes of *P. clarnensis* might indicate closer affinity to *Oreomunnea* than to *Engelhardia*. However, the totality of characters indicates closer affinity with *Engelhardia*. The nutlet, as seen in the holotype (Fig. 25E, F), is covered with tiny hairs. Among modern members of the Engelhardieae, pubescent nuts/nutlets occur only in *Engelhardia* and some *Alfaroa*. Apparently the hairs were deciduous or easily abraded away, as in extant species of *Engelhardia*, because most specimens, although well preserved, do not show the hairs. The prophyllum of *P. clarnensis* is well developed but relatively small, shorter than those seen in *P. nevadensis*, *P. macroptera*, and *Oreomunnea* and is most similar to that seen today in *Engelhardia* sect. *Engelhardia*. The exserted, deeply bifurcate style (Fig. 25F, H) is like that of *Engelhardia* sect. *Engelhardia* (Fig. 25J) and unlike the stubby styles of other modern engelhardioid taxa, which usually do not extend beyond the sepals. The fact that fruits compressed in the plane of the wings do not show a median septum suggests that the primary septum was oriented in a plane parallel to the wing, as in extant Engelhardieae, and that there was not a prominent secondary septum. The seed was therefore probably bilobed, as seen in locule casts from the same formation (Fig. 25I), like that of extant *Engelhardia* rather than eight-lobed as in *Oreomunnea*. Although most of the fruit characters suggest a close relationship with extant *Engelhardia*, it would be interesting to know the type of foliage produced by this species. It is likely that these fruits were from the same taxon that produced wood of *Engelhardioxylon nutbedensis* (Manchester, 1983).

MacGinitie (1969) described three fruits from the Middle Eocene Green River Formation under the name *Engelhardia uintaensis*. Of the three specimens figured by him, only the one from northeastern Utah exhibits venation characteristic of *Engelhardia*. It is here referred to *Palaeocarya* sect. *Monocosta* under the new com-

bination *P. uintaensis* (MacGinitie) Manchester (p. 57). The other two specimens (including Fig. 26A), both from Little Mountain, Wyoming, are very similar to, and perhaps conspecific with, *P. clarnensis*, suggesting that this species had a broad range in western North America during the Middle Eocene.

***Palaeocarya wolfei* Manchester, sp. nov.** Figure 25L, M.

Diagnosis. Trilobed winged fruits; central lobe of wing slightly obovate, 40 mm long, 7 mm wide; lateral lobes diverging from central lobe at 35–65°, oblong, 18–20 mm long, 5–6 mm wide; venation of lobes consisting of a midvein paralleled by two pairs of ascending lateral veins, outer pair of ascending laterals thinner than the inner pair and enclosed by elongate tertiary loops, ascending laterals strong in lower two-thirds of lobe, weakening apically and giving rise to pinnate secondary venation in the upper one-third; prophyllum 8 mm high, rounded; nutlet 4.5 mm high, 4.5 mm wide with three longitudinal creases preserved in plane of compression; adherent pedicel 1.5 mm long; pedicel and base of nutlet with fine hairs up to 1.3 mm long.

Specimens. The holotype is USNM 387388 (Fig. 25L, M). One additional specimen is uncatalogued in the USGS collection, Denver. Both specimens are from USGS locality 9731 (Wolfe, 1968).

Source of name. After Dr. Jack A. Wolfe, who brought my attention to the material upon which this species is based.

Discussion. This species occurs in the Upper Eocene of the Puget Group in northwestern Washington. Although based upon only two specimens, it appears to be distinct from the other species of *Palaeocarya* that have been recognized. It has a well-developed prophyllum as in *P. nevadensis*, *P. puryearensis*, *P. macroptera*, and extant *Oreomunnea* but differs from them in having a hairy nutlet. Similar hairs occur on *P. clarnensis* but that species has a smaller prophyllum and venation more similar to *Engelhardtia*. The three longitudinal creases on the compressed nutlet suggest a median secondary septum plus two tertiary septa—the configuration found in extant *Oreomunnea* and *Alfaroa*. The venation of the wing, the presence of a large prophyllum, and the inferred septation of the nutlet suggest that *P. wolfei* was very similar to

extant *Oreomunnea*, although hairs do not occur on the nutlets of the two extant species.

***Palaeocarya willamettensis* Manchester, sp. nov.** Figure 26A–D.

Engelhardtia sp. Brown, J. Paleontol. 33: 125–129, pl. 24: fig. 8. 1959.

Diagnosis. Trilobed winged fruits; central lobe of wing 20–40, avg. 34 mm long, 5–9, avg. 7 mm wide, lateral lobes diverging from central lobe at 30–50°, 20–32, avg. 32 mm long, 4–7, avg. 5 mm wide; venation of lobes consisting of a midvein paralleled by two intramarginal veins formed by the coalescence of secondary loops; nutlets broader than high, 3–3.8 mm wide and about 2–2.8 mm high, pedicel adhering to nutlet only 0.3–0.5 mm long or apparently absent in most specimens; prophyllum not evident.

Specimens. The holotype is USNM 387386 (Fig. 26A, D) and the paratypes are UCMP 9244 (Fig. 26B) and UCMP 9243 (Fig. 26C). Sixteen specimens were available for study, including uncatalogued UCMP and USGS material.

Discussion. This species was reported by Brown (1959) from the Oligocene Willamette flora of western Oregon. It resembles *Palaeocarya nevadensis* and *P. clarnensis* in venation of the wing but can be distinguished from them by the very short pedicel and by the apparent lack of a prophyllum. Although preserved in shale similar to that in which *P. clarnensis* is preserved, none of the *P. willamettensis* specimens show any trace of a prophyllum. This species is similar in some respects to *P. olsoni* (discussed below) but does not have the arching tertiary veins between the midvein and ascending lateral veins.

***Palaeocarya olsoni* (Brown) Manchester, comb. nov.** *Engelhardtia olsoni* Brown, J. Wash. Acad. Sci. 30: 349, fig. 10. 1940. Figure 26E–J.

Description. Small trilobed winged fruit with a spheroidal nutlet at base; central lobe of wing about 25–30 mm long, 6–8 mm wide, side lobes 18–22 mm long, 4 mm wide; venation of each lobe consisting of a midvein paralleled by two or four prominent ascending lateral veins; midvein and laterals connected by arching tertiary veins; prophyllum not observed; nutlet 3 mm high, 2.5 mm wide, apparently at least bilobed

FIGURE 26. *Palaeocarya* sect. *Palaeocarya* species from the Tertiary of western North America. A–D. *Palaeocarya willamettensis* Manchester from the Oligocene Willamette flora, western Oregon. Note lack of a persistent pedicel at base of nutlet. —A. USNM 387386, $\times 1$. —B. UCMP 9244, $\times 1$. —C. UCMP 9243, $\times 1$. —D. Same as A, enlarged to show detail of venation and nutlet, $\times 3$. E–G. *Palaeocarya olsoni* (Brown) Manchester, Miocene of Idaho. —E. Holotype of Brown (1940) showing tri-veined central and lateral lobes of wing (USNM 42335A), $\times 1$. —F. Same specimen, enlarged to show nutlet and perianth. Note the median cleavage of the nutlet, $\times 3$. —G. Specimen from near Clarkia, Idaho, showing typical venation (UI-TO 213), $\times 1$. —H. Cf. *Palaeocarya olsoni* from Oligocene John Day Formation, Oregon (USNM 39178), $\times 1$. —I. *P. olsoni* specimen from the uppermost Oligocene of the Central Alaska Range, Alaska, USGS locality 9928 (USNM 387387), $\times 1$. —J. Same specimen, enlarged to show median septum of nutlet and perianth. Note the circular impressions on the nutlet representing peltate scales, $\times 8$.

with a prominent septum perpendicular to the plane of the wing, four sepals, about 1 mm long; style cleft into two distinct stigmatic arms exerted well beyond the sepals, about 2.5 mm long, fruit without noticeable adherent pedicle.

Discussion. *Palaeocarya olsoni* is the latest known occurrence of fossil engelhardioid fruits

in North America. It was first described by Brown (1940) on the basis of a single specimen (Fig. 26F) from the Miocene Latah Formation near Orofino in northern Idaho. A second specimen from the same locality (USGS loc. 8443) shows a single complete lobe of the wing but is missing the nutlet and lateral wings. Another specimen, showing the style arms (UI-TO 213, Fig. 26G),

has been recovered more recently from strata of similar age near Clarkia (Smiley & Rember, 1979) in northern Idaho and is housed in the Paleobotanical Collection in the Department of Geology, University of Idaho, Moscow.

As noted by Brown (1940), these fruits resemble, and are possibly conspecific with, those described as "*Carpinus grandis* Unger" by Chaney (1927) from the Oligocene John Day Formation of Oregon (Fig. 25H). The original European specimens of *Carpinus grandis* Unger have been placed in synonymy with *Palaeocarya macrop-tera* (Brongniart) Jähnichen, Friederick & Takáč and are not conspecific with the American material. A specimen from the central Alaska Range, in Alaska (USNM 387387, Fig. 26I, J; Wolfe, 1972: 219) also appears to represent *P. olsoni*. The specimen was collected from USGS locality 9928 (cited in Wahrhaftig et al., 1969), which lies stratigraphically below the confirmed Miocene Seldovian strata and is inferred to be latest Oligocene (Late Angoonian) in age (Wolfe, pers. comm.). It shows a strong median septum like that of the holotype. In addition, the nutlet cast shows circular impressions (Fig. 26J) that appear to be from large peltate trichomes. By analogy with extant engelhardioid fruits, the median orientation of the septum suggests that it is a secondary septum. Such a well-developed secondary septum differentiates this species from *P. clarnensis* (and from *Engelhardia*) and suggests closer affinity with *Oreomunnea*.

Palaeocarya koreanica (Oishi) Manchester, comb. nov. *Engelhardia koreanica* Oishi, J. Geol. Soc. Japan 43: 58. figs. 1–3. 1936; Huzioka, J. Mining Coll. Akita Univ., Ser. A, 5: 43. pl. 2: figs. 9, 10a. 1972; emend. Akhmetiev & Bratzeva, Rev. Palaeobot. Palynol. 16: 130–131. pl. 1: figs. 2–6, 8–11. 1973; Tanai & Uemura, J. Fac. Sci. Hokkaido Imp. Univ., Ser. 4, Geol. 20: 251–254. pl. 1: figs. 1–7; pl. 2: figs. 1, 7; pl. 3: figs. 1, 2. fig. 2. 1983. Figure 30.

Description. Winged fruit comprising a nutlet at the base of a deeply incised, trilobed wing, the central lobe oblanceolate; 30–50 mm long, 6–8 mm wide, lateral lobes oblanceolate to narrow oblong, 13–22 mm long, 4–8 mm wide, diverging from the central lobe at 35–80°; major venation of each lobe consisting of a midvein with pinnate secondary veins and a pair of finer, lateral veins located on either side of the mid-

vein, ascending along the margin about one-third of the lobe height and then merging into coalesced secondary loops; midvein unbranched all the way to the distal tip; prophyllum very small, almost absent, nutlet 2.5–5 mm diam., subglobose; pedicel persisting on the nutlet and relatively long, up to 10 mm, styler condition undetermined.

Discussion. *Paleocarya koreanica* occurs in the Miocene of Korea (Oishi, 1936; Huzioka, 1972), in the late Oligocene further north along the east coast of the Soviet Union in Sikhote-Alin and southern Primorye (Akhmetiev & Bratzeva, 1973), and in the Miocene of Hokkaido and western Honshu, Japan (Tanai & Uemura, 1983). This species differs from the Tertiary species of *Palaeocarya* in Europe and North America in having a longer pedicel persistently attached to the nutlet and by having a very small prophyllum.

Akhmetiev and Bratzeva (1973) figure and describe a single detached entire-margined leaflet that they believe to be the same species based on field associations; however, the features described are not diagnostic for the Engelhardieae, and the affinity of the leaflet is in my opinion uncertain. The pollen associated with *Palaeocarya koreanica* is triporate, isopolar, and small (11–15 μm), resembling that of modern *Engelhardia roxburghiana* (Akhmetiev & Bratzeva, 1973).

Tanai and Uemura (1983) noted that *Palaeocarya koreanica* is more similar to *Engelhardia* than to *Oreomunnea* because the ascending lateral veins of the wing lobes are weak and the prophyllum ("fourth lobe") is lacking. As observed by Tanai and Uemura, *P. koreanica* resembles extant *Engelhardia roxburghiana* in its long pedicel and reduced prophyllum. Some of the fruits illustrated (e.g., Tanai & Uemura, 1983, figs. 1, 6) show a well-preserved wing with the nutlet missing. A small circular scar indicates the spot where the nutlet detached. The nutlet also tends to detach from the wings of modern *E. roxburghiana* fruits because the prophyllum is too small to hold it firmly in place. Tanai and Uemura (1983) concluded that *P. koreanica* represents the same section of *Engelhardia* (*E. sect. Psilocarpeae*) as *E. roxburghiana*, but noted that it differs in venation from the modern species. In *E. roxburghiana*, the midvein of each lobe ends before reaching the apex by dividing to form marginal loops. However, in *P. koreanica* the

FIGURE 27. American and European species of *Palaeocarya* sect. *Monocosta*.—A. *Palaeocarya mississippiensis* (Berry) Manchester, holotype showing large size and vertical cleavage in nutlet area, possibly representing a septum, from the Eocene of Early Grove, Mississippi (USNM 35524), $\times 1$.—B. Enlargement of the above, showing strong midvein and pinnate secondary venation of bract lobe, $\times 2$.—C. *Palaeocarya uintaensis* (MacGinitie) Manchester. Note the single main vein in each lobe of wing. From the Eocene Green River Formation of northeastern Utah (UCMP-PA 20674), $\times 1$.—D. *Palaeocarya oxyptera* (Saporta) Manchester from the Upper Oligocene of Armissan, France (MNHP 12742), $\times 1$.

midvein extends directly to the lobe apex without forking, as in other species of *Engelhardia* and *Palaeocarya*.

Tanai and Uemura (1983) placed this fossil species in extant *Engelhardia* sect. *Psilocarpeae*. However, it also fits the diagnosis for the fossil genus *Palaeocarya* sect. *Palaeocarya*. I include it here to emphasize that, unlike *Engelhardia*, it displays ascending (though weak) lateral veins; and some of the characters necessary to diagnose extant *Engelhardia*, such as septation of the nutlet, stylar configuration, and, perhaps most importantly, foliar features, are unknown for the fossil species.

***Palaeocarya* sect. *Monocosta* Manchester, sect. nov. TYPE: *Engelhardtia mississippiensis* Berry, *P. mississippiensis* (Berry) Manchester, comb. nov.**

Diagnosis. Fruits of *Palaeocarya* with bract lobes displaying pinnate venation characterized by a midrib and looping secondary veins.

Discussion. This new section is established to accommodate *Palaeocarya* species with the type of venation found in extant *Engelhardia*. Such fossils are rare in the Tertiary, relative to those of *Palaeocarya* sect. *Palaeocarya*. Described below are the three species known to me.

***Palaeocarya mississippiensis* (Berry) Manchester, comb. nov. *Engelhardtia* (*Oreomunnea*) *mississippiensis* Berry, Profess. Pap. U.S. Geol. Surv. 91: 183–184. pl. 17: fig. 1. 1916. Figure 27A, B.**

Discussion. This species, from the Eocene of Early Grove, Marshall County, Mississippi (USGS loc. 3460), is the earliest occurrence of a fruit with the pattern of venation found in extant *Engelhardia*. The species is based upon a single well-preserved specimen described in excellent detail by Berry (1916). The fruit is large, measuring at least 65 mm in length, with a correspondingly large nutlet, about 7 mm in width. Each lobe of the bract displays simple pinnate

venation. The secondary veins branch from the midvein at relatively wide angles (Fig. 27B), which decrease upward on each lobe of the bract. As noted by Berry (1916: 183), "no subordinate primaries or discordantly directed secondaries are present." The lack of such veins is the primary feature setting this species apart from the species classified as *Palaeocarya* sect. *Palaeocarya* earlier in this paper.

The holotype of *Palaeocarya mississippiensis*, originally illustrated with a line drawing (Berry, 1916, pl. 17: fig. 1), is photographically reproduced here (Fig. 27A, B). The specimen is preserved with its ventral surface pressed into the clay matrix, so that without destroying a portion of the specimen, it is not possible to determine the condition of the nutlet, style, and prophyllum. If the style was exerted and deeply cleft and if the prophyllum was relatively small, and, finally, if the nutlet were known to be bi-compartmented, the species could reasonably be placed in the extant genus *Engelhardia*. From the bulge and longitudinal cleavage at the base of the fruit, it may be inferred that the nutlet was large and partitioned in the plane perpendicular to the wing.

Palaeocarya uintaensis (MacGinitie) Manchester, comb. nov. *Engelhardtia uintaensis* MacGinitie, Univ. Calif. Publ. Geol. Sci. 83: 94–95. pl. 8: fig. 5. 1969. Figure 27C.

Description. Trilobate-winged fruits; central lobe of wing 2.5 cm long, 7–10 mm wide; venation pinnate but with weak ascending lateral veins intermeshing with the secondary vein loops in the lower one-third of each lobe; nutlet oblong, 3 mm wide, 5 mm high; condition of style and prophyllum unknown.

Discussion. This species was initially described based upon specimens from two different localities of the Middle Eocene Green River Formation: Rainbow, Utah, and Little Mountain, Wyoming. However, only the specimen illustrated from Rainbow has the venation characteristic of *Engelhardia*. It is therefore placed in sect. *Monocosta* of *Palaeocarya*, while the other two specimens are provisionally placed in *P. clarnensis* (pp. 52–53).

Palaeocarya oxyptera (Saporta) Manchester, comb. nov. *Engelhardtia oxyptera* Saporta, Ann. Sci. Nat. Bot., Sér. 5, 4: 200–201. pl. 12: fig. 2. 1865; Jähnichen, Mai & Walther, Feddes Repert. 88: 349. pl. 54: figs. 3, 5. fig. 8 (17–19). 1977. Figure 27D.

Discussion. This species from the upper Oligocene of Armissan, France, exhibits a simple pinnate pattern of lobe venation, like that of *Engelhardia*, without prominent ascending laterals. The fruits are distinctive in the steepness of secondary veins. A photograph of the type, which was originally illustrated with a line drawing (Saporta, 1865), is presented in Figure 27D. The fact that none of the three figured specimens shows a prophyllum suggests that it was absent or small, as in extant *Engelhardia*.

Paraengelhardtia eocenica Berry, Profess. Pap. U.S. Geol. Surv. 92: 186–187. pl. 17: figs. 2–5. 1916. Figure 28A–D.

Description. Winged nutlet with a small trilobed wing; sinuses between lobes of wing shallow to poorly developed; central lobe 16–23 mm long; lateral lobes diverging from central lobe at 25–40°, 14–19 mm long; width of fruit measured from outer margins of the two lateral lobes 19–31 mm; each lobe supplied with a midrib and two slightly less prominent lateral veins, one on each side of the midvein; laterals giving rise to marginal tertiary loops and joined by secondary veins with the primaries; areoles supplied with numerous freely ending veinlets; prophyllum relatively large, rounded, 15–17 mm high, extending from the base of the nutlet two-thirds to four-fifths the length of the wing, six or more major veins fan out from the base of the prophyllum, looping within the margin; nutlet spheroidal, 4–5 mm diam., styler configuration unknown; pedicel not observed to be persistent on fruit.

Discussion. The extinct genus *Paraengelhardtia* was established and correctly placed within the Juglandaceae by Berry (1916). It resembles modern *Engelhardia* and *Oreomunnea* in nutlet size, the trilobed wing, and the presence of a prophyllum and is certainly attributable to the same tribe. However, the shallow sinuses and short lobes clearly differentiate the species from any living genus. The only known species is *P. eocenica*.

Paraengelhardtia eocenica is known only from one locality, Puryear clay pit in the Middle Eocene Claiborne Formation of Henry County, Tennessee. Collections of fruits from Puryear pit include samples acquired in the early 1900s by E. W. Berry at the United States National Museum and more recently collected specimens in the collections of the Field Museum and Indiana University, Bloomington. Despite massive collecting, other clay mines in northwestern Ten-

FIGURE 28. Extinct Middle Eocene engelhardtioid fruits with weakly trilobed bracts. A–D. *Paraengelhardtia eocenica* Berry from Puryear, Tennessee, all $\times 1$.—A. Typical specimen showing small circular nutlet cavity (n) filled with clay, large rounded prophyllum (p), and a trilobate bract-wing with shallow sinuses (FM-PP 7966).—B. Specimen with organic stain remaining in the nutlet cavity (IU 4853).—C. Relatively small specimen with the prophyllum (p) extending almost to the tips of the abaxial bract lobes (IU 4854).—D. Lectotype (USNM 35618). E–K. *Paleooreomunnea stoneana* Dilcher, Potter & Crepet, from localities in Kentucky and Tennessee, all $\times 1$.—E. Specimen with wing similar in size to *P. eocenica*, above, but with a much larger nutlet, from Miller Clay Pit, Tennessee (IU 4855).—F. Specimen showing shallow sinuses of bract, the bipartite nature of the nut and sepals at the nut apex from Lamkin Clay Pit, Kentucky (IU 1880).—G. Specimen with nut absent, showing radiating veins of the bract, from Somerville, Tennessee (FM-PP 11141).—H. Holotype showing intact sepals (se), prophyllum (p), and a large bract with well preserved venation from Warman Clay Pit, Tennessee (IU 1879).—I. Specimen described as *Paraengelhardtia eocenica* by Berry (1930) from Cottage Grove, Tennessee (USNM 39743).—J. Specimen showing a prominent septum dividing the nut impression into two parts from Lamkin Clay Pit, Kentucky (IU 2218).—K. Specimen with deeper sinuses between bract lobes, showing three main veins in the central lobe, from Somerville, Tennessee (FM-PP 6424).—L. Immature infructescence of *Paleooreomunnea stoneana* showing apparently spiral arrangement of small fruits. Note that the bracts are shallowly lobed even in early ontogeny, from same locality as G and K (FM-PP 14680), $\times 4$.

nessee have not yielded this species. It is interesting that the ranges of *Paraengelhardtia* and *Paleooreomunnea* appear to be mutually exclusive. The Puryear locality has also yielded fruits of *Palaeocarya puryearensis*, the staminate inflorescence *Engelhardia*, and a few leaflets of *Oreoroa* (e.g., Fig. 22C).

Paleooreomunnea stoneana Dilcher, Potter & Crepet, Amer. J. Bot. 63: 532–544. figs. 26–32. 1976. Figure 28E–L.

Paraengelhardtia eocenica Berry, Profess. Pap. U.S. Geol. Surv. 156: 60. pl. 46: figs. 11, 12. 1930.

Description. Winged nut with a large trilobed wing; sinuses between lobes shallow to nearly absent; central lobe 20–43 mm long; lateral lobes diverging from central lobe at 35–45°, 18–33 mm long; width of fruit measured from outer margins of the two lateral lobes 30–40 mm; each lobe with a primary vein and two slightly less conspicuous lateral veins, one on each side of the midvein; a few additional secondary veins extending into each lobe; primaries branching freely to form numerous secondary and tertiary veins that branch and anastomose further and form loops at the margin; areoles supplied with numerous freely ending veinlets; prophyllum large and rounded, 13–30 mm high covering the adaxial side of the nutlet and extending from the base to about two-thirds the length of the wing, six to ten major veins fanning out through the prophyllum, producing numerous secondaries and forming marginal loops; nut large, 15–22 mm wide, 10–14 mm high, constricted to 7.5–12 mm high along the axis; sepals persistent, 1 mm high; peltate scales common on the surface of the bract and prophyllum.

Discussion. *Paleooreomunnea* is an extinct genus known only from a single species in the Middle Eocene Claiborne Formation of Kentucky and Tennessee. Since the initial description of this species (Dilcher et al., 1976), additional specimens have been recovered and are included in the above description. The only significant modification from the original diagnosis concerns the recognition of freely ending veinlets in both the type material and new specimens. This feature is of limited diagnostic importance, however, because among the living genera of the Engelhardieae, both *Oreomunnea* and *Engelhardia* have fruit wings with numerous freely ending veinlets.

Specimens of this taxon were first figured by Berry (1930) as examples of his previously described species, *Paraengelhardtia eocenica*. However, the specimens differ from the type specimens of *P. eocenica* in their larger overall fruit size, and in shape and size of the endocarp. The nut of *Paleooreomunnea* is about twice as wide as it is high and is about four to five times wider than the spheroidal nutlet of *Paraengelhardtia*. Although both genera occur in the Middle Eocene Claiborne Formation of Tennessee, they are not known to have been sympatric; they have been recovered from different localities. *Paleooreomunnea* is now known from several localities in Kentucky and Tennessee, including the Lampkin, Miller, and Warman clay pits (localities in Potter, 1976) as well as the locality near Somerville, Tennessee (Berry, 1930). Most of these localities also yield fruits of *Palaeocarya puryearensis* but not *Paraengelhardtia eocenica*.

A pistillate inflorescence (FM-PP 14680, Fig. 28L) from the Somerville locality appears to represent the same species and shows sessile immature fruits subtended by bracts that are entire or only faintly trilobate. Staminate inflorescences of *Eokachyra* also occur at the same locality. Associated leaflets of *Oreoroa claibornensis* Dilcher & Manchester (e.g., Figs. 21G, 22B) may have been produced by the same plant.

Nuts of *Paleooreomunnea* are parted down the middle, suggesting the presence of a well-developed median septum. The orientation of the septum at right angles to the plane of the wing suggests that it is a secondary septum. In extant Engelhardieae, the primary septum is situated parallel to the plane of the wing and would not be detectable in the usual compressed state. Well-developed secondary septa like that inferred for the fossil occur today in *Oreomunnea* and *Alfaroa* but not in *Engelhardia*. Tertiary septa may have been present in the fossil, as in extant *Oreomunnea* and *Alfaroa*; however, they are not apparent from the compressions. The large size of *Paleooreomunnea* nuts suggests a shift toward fruits better adapted for animal dispersal. Dilcher et al. (1976) suggest that such a trend may have culminated in the large wingless fruits of extant *Alfaroa*.

GENERAL SUMMARY AND DISCUSSION, ENGELHARDIEAE

The extant genera of the Engelhardieae retain various features considered primitive for the

FIGURE 29. Map showing modern and fossil distribution of the Engelhardiaceae. Hatched areas indicate modern distribution of *Engelhardia* (NE-SW hatching) and *Alfaroa* and *Oreomunnea* (NW-SE hatching). Stippled areas indicate fossil distribution of *Oreocarya* foliage. Generic symbols: circle = *Palaeocarya* fruits; triangle = *Paraengelhardtia* fruits; diamond = *Palaeoreomunnea* fruits. — 1. *Palaeocarya olsoni*, Oligocene. — 2. *P. wolfei*, Oligocene. — 3. *P. willamettensis*, Oligocene. — 4. *P. nevadensis*, Lower Eocene. — 5. *P. olsoni*, Miocene. — 6, 7. *P. clarnensis*, Middle Eocene. — 8. *P. puryearensis*, *P. mississippiensis*, *Paraengelhardtia eocenica*, *Palaeoreomunnea stoneana*, Middle Eocene. — 9–12. *Palaeocarya macroptera*; individual localities indicated by Jähnichen et al. (1977, 1984), Middle Eocene to Miocene. — 13. *P. koreanica*, Upper Oligocene to Miocene.

Juglandaceae, such as triporate, very small, relatively unspecialized pollen, four free sepals, terminal inflorescences, and scalariform vessel perforations in secondary xylem. The fossil record demonstrates that these characteristics occur early in the history of the Juglandaceae. For example, the Engelhardieae type of pollen (*Momipites*) is common in the Paleocene and may extend back to the Late Cretaceous, and wood virtually indistinguishable from that of *Engelhardia*, *Oreomunnea*, and *Alfaroa* occurs in the Middle Eocene.

The occurrence of pollen resembling that of extant Engelhardieae in the Paleocene, and perhaps even the Late Cretaceous, does not demonstrate that the tribe was already established at that time. Such pollen, being unspecialized, could have been produced by plants whose other organs had not achieved the level of Engelhardieae and could also have been retained by the earliest and most primitive representatives of other modern tribes. For example, such pollen is associated with the Paleocene fruits of *Casholdia* in southern England and *Cyclocarya* and *Polyptera* in North America.

Fortunately, the trilobate inflorescence bract diagnostic of the Engelhardieae is easily observed in fossil reproductive material, including fruits as well as staminate and pistillate catkins, and is well represented in the fossil record. Based on the absence of trilobate bracts in the Paleocene (even at megafossil sites where *Momipites* pollen is abundant), and the occurrence of genera with "incipient" lobing (*Paraengelhardtia* and *Paleooreomunnea*) in the Middle Eocene, I conclude that the Engelhardieae evolved in the Lower Eocene. *Casholdia* fruits, from the Upper Paleocene of Europe, resemble those of *Oreomunnea* in venation of the bract and presence of a prophyllum but are excluded from the Engelhardieae by the unlobed bract. In addition, mature fruits of *Casholdia* are only one-third as large as the smallest known engelhardioid fruits. Fruits of this type are envisaged as representative of a phase in evolution just prior to the divergence of Engelhardieae.

The map (Fig. 29) illustrates the distribution of modern and fossil Engelhardieae on the basis of fruits. More detailed maps of European and Asian occurrences have been presented previously by Jähnichen et al. (1977), Jähnichen et al. (1984), and Tanai and Uemura (1983). The place of origin of the tribe, while certainly in the Northern Hemisphere, is not presently known. How-

ever, the diversity of Engelhardieae in the Middle Eocene of North America that included *Paleooreomunnea*, *Paraengelhardtia*, and several species of *Palaeocarya*, suggests that a primary radiation occurred in the New World during a period of warm, subtropical climate.

Although even-pinnate foliage is characteristic of modern Engelhardieae, seedlings pass through a brief interval during which odd-pinnate leaves are produced. The few available complete leaves of early Tertiary Engelhardieae have terminal leaflets, suggesting that the even-pinnate condition was not as well established in the tribe then as it is now. Of the two basic types of modern engelhardioid foliage, only the *Oreomunnea-Alfaroa* type has a well-documented fossil record. The *Engelhardia* type, presently restricted to Asia, has an uncertain history but is less specialized and presumably more primitive in features such as alternate phyllotaxy, medial vein entry of teeth, open areolation, and non-papillate cuticle. This type of foliage was probably present in the early Tertiary as indicated by Wolfe (1977) but is more difficult to identify with certainty because of convergences with the foliage of other families. The occurrence of *Oreoroa* in the Middle Eocene of North America demonstrates that the more specialized *Oreomunnea-Alfaroa* type of foliage was present early in the radiation of Engelhardieae. The presence of *Oreoroa* in Europe indicates that this type of foliage was widely distributed in the Tertiary, compared to its present day restriction to Middle America. *Oreoroa* foliage appears to be absent in the Tertiary of Asia and western North America. I consider it likely that two engelhardioid provinces were present in the Tertiary: a European-eastern American province, of which extant *Oreomunnea* and *Alfaroa* are remnants, and an Asian (-western North American?) province from which extant species of *Engelhardia* are derived. Late Tertiary extinctions resulted in the present day disjunct distribution of the Engelhardieae. Isolation of these provinces from one another through much of the Tertiary would explain the differences in pollen morphology and fruit morphology between the living New and Old World populations. It is important to recognize, however, that a fruit resembling modern *Engelhardia* (i.e., *Palaeocarya mississippiensis*) occurs in the Eocene of eastern North America.

In the Eocene there was a greater and more continuous spectrum of winged fruit diversity in the Engelhardieae than there is today (Fig. 30).

FIGURE 30. Diagrammatic ($\times 1$) and schematic illustrations of selected fossil engelhardtioid fruits showing shapes and venation of bracts, size of prophyllum, and orientation of septa and style arms. Septa indicated by solid lines are well documented in the fossils. Septa indicated by dotted lines are inferred but remain unproven.—A. *Palaeocarya puryearensis* showing long style arms and bilobed prophyllum. Nutlet septation inferred from Dilcher et al. (1976).—B. *P. nevadensis* and *P. macroptera* showing large rounded prophyllum; condition of septa and styler region undetermined.—C. *P. clarnensis*, showing short prophyllum, exserted style arms and hairy nutlet.—D. *P. olsoni*, showing strong median septum and reduced or absent prophyllum.—E. *P. koreanica*, with reduced prophyllum; orientation of septa and styler configuration unknown.—F. *P. mississippiensis* showing pinnate secondary venation of bract lobes.—G. *Paleooreomunnea stoneana* showing shallowly trilobed bract and large elliptical nutlet with prominent median septum and rounded prophyllum.—H. *Paraengelhardtia eocenica* with shallowly trilobed bract, large rounded prophyllum, and small globose nutlet; condition of styles and septa unknown.

The extinct genera *Paraengelhardtia* and *Paleooreomunnea* differ from extant *Engelhardia* and *Oreomunnea* by the shallow sinuses between lobes of the wing and from each other by the size and configuration of the nutlet. *Paleooreomunnea* seems more closely allied to *Oreomunnea* than to *Engelhardia* because of the high, prominent secondary septum in the nut, the large, entire-margined prophyllum, venation of the wing, and the association with *Oreoroa* leaflets. Occasional aberrant fruits of modern *Oreomunnea mexicana* exhibit shallow sinuses and appear similar to *Paraengelhardtia*. The nutlet of *Paraengelhardtia*, though rounded like that of *Oreomunnea*, is of unknown internal structure.

The organ genus *Palaeocarya*, as emended here, includes all fossil engelhardioid fruits having trilobate bracts with deep sinuses. Fruits of modern *Oreomunnea* and *Engelhardia*, if preserved as fossils, would be accommodated by this organ genus. The *Palaeocarya* complex combines in various ways characters that today are segregated into *Engelhardia* and *Oreomunnea*. Many of the early Tertiary species show the venation of *Oreomunnea* (classified as *Palaeocarya* sect. *Palaeocarya*) but have other features that occur today only in *Engelhardia*. For example, *Palaeocarya puryearensis* has long styles, and *P. macroptera* has nutlets with two, rather than eight, compartments. *Palaeocarya clarnensis* resembles *Engelhardia* in most features (long style arms, short prophyllum, hairy nutlet, bilobed seeds) but also has the tri-veined lobe venation more similar to *Oreomunnea*.

Although both monocostate and tricostate lobe venation occurs early in the radiation of engelhardioid fruits, I consider the more prevalent tricostate pattern to be primitive. Such a pattern seems more easily derived from the type of parallel venation present in the bracts before they expand. Some species, for example *Palaeocarya clarnensis* and *P. koreanica*, exhibit a more or less intermediate condition in which the ascending lateral veins are weak and join apically into a series of loops formed by pinnate secondary veins. Although the more primitive venation is retained in *Oreomunnea* today, other probable primitive features are retained instead by *Engelhardia*, such as the bi-compartmented nut and the long styles. Both of these features appear to have been prevalent in early Tertiary representatives of *Palaeocarya*.

Alfaroa is not known from the fossil record but appears to be a relatively recent derivative

of the *Palaeocarya* complex. *Alfaroa* is so similar to *Oreomunnea* in internal endocarp morphology, styler configuration, leaf morphology and anatomy, wood anatomy, pollen morphology, and other features (Stone, 1977) that its recognition as a distinct genus is more a matter of tradition and convenience than a useful indication of genetic divergence. Although the large, wingless fruits of *Alfaroa* are easily distinguished from the winged fruits of *Oreomunnea mexicana*, fruits such as those of *Alfaroa costaricensis* and *A. williamsii* could be derived from the relatively large fruits of *Oreomunnea pterocarpa* simply by suppression of ontogenetic bract enlargement. Manning (1966) notes a form of extant *Engelhardia roxburghiana* in which "the wings of the mature fruit are essentially undeveloped, as short as or hardly longer than the body of the fruit." Hence, the genetic divergence between *Oreomunnea* and some species of *Alfaroa* is probably only slight.

HICOREAE

The Hicoreae has a single living genus, *Carya*, with 18 recognized species ranging in habitat from temperate mixed mesophytic forest to montane rain forest. Although disjunct between southeastern North America and southeast Asia today, *Carya* was distributed widely across the Northern Hemisphere during the Tertiary. Table 5 summarizes the Hicoreae occurrences considered here.

Carya exhibits various specializations that support placement in its own tribe (Manning, 1978). The triporate pollen is distinguished by the position of the pores slightly offset from the equator and the thin spot in the exine at the proximal pole. The wood has especially thick vessel and fiber walls and has solitary crystal-bearing idioblasts in axial parenchyma. The flowers lack sepals and the pistillate ones often have a four-lobed stigmatic disk below the stigmas. The carpels are transverse and the stigmas commissural. *Carya* is the only genus of the family known to include tetraploid species.

Carya is divided into four sections: *Rhamphocarya*, *Apocarya*, *Sinocarya*, and *Carya* (*Eucarya*). Section *Rhamphocarya*, which is considered a separate genus by some authors (*Annamocarya*), has a single species (*C. sinensis*) in China that is relatively distinct from the other sections in locule morphology, fruit vasculature (Leroy, 1955), entire-margined leaflets, and oth-

TABLE 5. Important fossil occurrences of Hicoreae.

Taxon	Age and Location	Comment
POLLEN		
<i>Caryapollenites</i> Raatz	Paleocene to Neogene; North America, Europe, Asia	Organ genus for pollen resembling that of extant <i>Carya</i> ; a trend of increasing size is seen through the early Tertiary.
WOOD		
<i>Eucaryoxylon</i> Müller-Stoll & Mädel	Miocene to Pliocene; Europe, North America, Japan	Organ genus for wood resembling extant <i>Carya</i> .
FOLIAGE		
<i>Carya</i> Nutt.	Eocene to Recent; Europe, North America, Asia	There are numerous reports of fossil <i>Carya</i> foliage in the literature; these are not reviewed here.
FRUITS		
<i>Juglandicarya simplicarpa</i> Manchester	Paleocene; Wyoming	This species is known only from locule casts but may be an early representative of the tribe; discussed earlier in this paper (p. 14).
<i>Juglandicarya lubbocki</i> Reid & Chandler	Early Eocene; England	This species from England lacks the inner nutshell ribs diagnostic of <i>Carya</i> but has introrse dorsal bundles like <i>Carya</i> .
<i>Carya lacrymabunda</i> (Koenig) Leroy	Late Eocene to middle Oligocene; eastern Europe	The earliest known species with well-developed inner ribs diagnostic of <i>Carya</i> .
<i>C. quadrangula</i> (Kirchheimer) Leroy	Middle Oligocene; East and West Germany	Earliest European species with quadrangular nut.
<i>C. ventricosa</i> (Sternberg) Unger	Late Oligocene to early Pliocene; eastern Europe	The longest ranging and most widespread species in Europe; relatively thin-walled, generally not four-angled, secondary septum weak or absent, large lacunae present.
<i>C. rostrata</i> (Schlotheim) Schimper	Late Oligocene to Miocene; West and East Germany	Similar to <i>Carya ventricosa</i> but with a more protruding four-angled apex.
<i>C. caryoides</i> (Kirchheimer) Leroy	Middle Miocene; West Germany	A single specimen distinguished by extremely large lacunae.
<i>C. costata</i> (Presl) Unger	Oligocene; Czechoslovakia	Species used for locule casts of <i>Carya</i> .
<i>C. strychnina</i> (Sternberg) Mai	Upper Oligocene to middle Miocene; Germany	Species similar to modern <i>Carya poilanei</i> and differentiated from the other European fossils by its triangular secondary septum.
<i>C. pusilla</i> Unger	Miocene; eastern Europe	Nuts distinguished from <i>Carya ventricosa</i> by smaller size and thinner shell.
<i>C. paludis-naabi</i> Gregor	Middle Miocene; West Germany	Species with very large, thick-walled nuts not four-angled.
<i>C. globosa</i> (Ludwig) Mädlar	Miocene to Lower Pliocene; Germany, Poland	Species with very rough surface texture and well-developed secondary septum.
<i>C. bohémica</i> Brabenec	Miocene; Czechoslovakia, Poland	Similar to <i>Carya globosa</i> but with wider mesh network of ridges and depressions.
<i>C. angulata</i> Reid	Lower Pliocene; Netherlands, Germany, France	Smooth-walled species apparently lacking lacunae, with a well-developed secondary septum.
<i>C. rugosa</i> Zablocki	Miocene; southern Poland	Small heart-shaped nuts without lacunae.
<i>C. askenasyi</i> (Kinkel) Mai	Pliocene; West Germany	Smooth-walled species with well-developed secondary septum and small lacunae.
<i>C. kryštofovichii</i> (Gorbunov) Manchester	Oligocene; western Siberia	Rough-walled nuts similar to <i>Carya globosa</i> but without well-developed secondary septum.

TABLE 5. (Continued).

Taxon	Age and Location	Comment
<i>C. kompassica</i> (Gorbunov) Manchester	Oligocene or Miocene; western Siberia	Species similar to (perhaps conspecific with) <i>Carya ventricosa</i> .
<i>C. miocathayensis</i> Hu & Chaney	Miocene; Shantung Prov- ince, China	Siltstone cast of a nut and associated foliage.
<i>C. leiocarpa</i> Miki	Pliocene; Japan	Small, thin-walled nuts with secondary sep- tum present; nuts similar to <i>Carya ventri- cosa</i> but with well-developed secondary septum.
<i>C. nanocarpa</i> Miki	Pliocene; Japan	
<i>C. striata</i> Miki	Neogene; Japan	Fruits distinguished from <i>Carya nanocarpa</i> by more distinctly striate surface.
<i>C. ovatocarpa</i> Miki	Pliocene; Japan	Nuts with triangular secondary septum simi- lar to <i>Carya strychnina</i> .
<i>C. florissantensis</i> Manchester	Early Oligocene; Colorado	Strongly four-angled nuts with convoluted locules, associated with <i>Carya libbeyi</i> fo- liage.
<i>C. washingtonensis</i> Manches- ter	Middle Miocene; Washing- ton	Nuts faintly four-angled with well-developed secondary septa.

er features (Manning & Hjelmqvist, 1951). The other sections tend to intergrade in many characters and are sometimes difficult to separate (Stone et al., 1969). Species of sect. *Apocarya* are characterized by four to six valvate terminal bud scales, flanged sutural outgrowths of the fruit husk, typically lacunate nutshells, and a high number of leaflets (seven to 17). Section *Carya*, restricted to North America, has eight species and is typified by terminal buds with six to 12 imbricate scales, non-flanged fruit husks, nut-shell lacking distinct lacunae, and a low number of leaflets (three to nine) (Manning, 1978). Tetraploidy (Stone, 1961) occurs in six species of sect. *Carya*. Section *Apocarya* has traditionally been viewed as a disjunct taxon including both Asian and American species (e.g., Stone, 1962; Manning, 1978). However, Kuang et al. (1979) placed the Asian species in a new section, *Sinocarya*, emphasizing that the buds are naked and that the leaves have fewer leaflets (five to seven) than those of American species of sect. *Apocarya* (seven to 17).

With the exception of sect. *Rhamphocarya*, the recognized sections of *Carya* intergrade in many characters. Although readily separated on the basis of bud scale condition, there is overlap between sections in both chemical (Stone et al., 1969) and morphological (Stone, 1962) characters. Due to the intergradational nature of the modern sections, it may be difficult to determine sectional affinity of fossil nuts or leaflets.

POLLEN

Pollen of extant *Carya* (Whitehead, 1965; Stone & Broome, 1975) is characteristically triporate (but ranges from 1–6-porate in abnormal grains), suboblate, rounded-triangular to circular in polar view, heteropolar, with the pores slightly offset toward the distal pole, and with a distinct proximal area of thin exine. The size is larger than that of triporates in other tribes of the family, averaging 33–51 μm . There are no sharp palynological distinctions between the extant sections of *Carya*; however, the pollen of sects. *Rhamphocarya*, *Apocarya*, and *Sinocarya* tends to be smaller than that in sect. *Carya*, a feature that may be related to the occurrence of polyploidy in the sect. *Carya* (Stone, 1963). *Carya sinensis* and *C. tonkinensis* have relatively small, almost isopolar pollen regarded as primitive for the genus.

Pollen similar to that of extant *Carya*, with a thin spot in the exine at one pole and with one or more pores offset from the equator, appears in the upper Paleocene of western Europe (Thiergart, 1940; Thompson & Pflug, 1953; Kedves, 1969, 1982; Krutzsch, 1970) and North America (Frederiksen & Christopher, 1978; Nichols & Ott, 1978). These Paleocene grains fall in the range of 20–30 μm in diameter. Although the name *Carya* has been applied to them, the genus *Caryapollenites* Raatz is preferable because, although they are clearly similar to *Carya*, their

small size and evidence from the fruit record suggests that *Carya* sensu stricto had not yet appeared. European authors have frequently referred such grains to *Subtriporopollenites*.

A trend toward increase in size of *Caryapollenites* pollen through the Paleogene was first documented by Tschudy (1973) who, in studies of the Mississippi Embayment, noted a small species (22–28 μm) in lower Wilcox sediments, followed by a form with larger grains (29–30 μm) in the lower Claiborne. The same trend was reported by Frederiksen and Christopher (1978) in their study of a South Carolina drill core spanning from Upper Cretaceous to the Oligocene. They noted the first occurrence of the smaller type in lower to upper Sabinian (uppermost Paleocene) and the later appearance of the large species in the upper Jacksonian (late Eocene). Both types continued to the top of the core (Oligocene). Nichols and Ott (1978) experienced a similar trend in the Paleocene to Eocene strata of the Wind River Basin in Wyoming. They point out, however, that in the latter part of the sequence there is a reversal of the "pervasive tendency toward size increase." "Both *C. inelegans* and *C. veripites* are smaller than their stratigraphically older and more primitive ancestors." Since extant pollen of *Carya* is larger than the Paleocene and early Eocene species, the trend toward size increase must have been reasserted later in the Tertiary, as suggested by Nichols and Ott (1978), or perhaps continued in other areas as the Wind River species became extinct.

The earliest known staminate catkins of *Carya* are preserved in a single specimen (Fig. 3D) from the lowermost Oligocene Florissant flora of Colorado. The catkins are 25–40 mm long and 4 mm wide with at least 60 helically arranged florets. Floral detail is poorly preserved but the anthers, which are about 1 mm long, contain masses of pollen (Fig. 33). The pollen is 30–38 μm in equatorial diameter and, like that of modern *Carya*, has circular pores that are slightly offset from the equator toward one pole.

By the Oligocene, pollen indistinguishable in both size and morphology from that of extant *Carya* was common in North America (e.g., Traverse, 1955; Piel, 1971; Martin & Rouse, 1966), Europe (Thompson & Pflug, 1953), and western Siberia (Takhtajan et al., 1963). The first confirmed records of *Carya* pollen in eastern Asia and Japan appear to be Middle Miocene (Takhtajan et al., 1963; K. Takahashi, pers. comm.). Palynological data indicate that *Carya* was com-

mon in western Europe until the Late Pleistocene, at which time the genus became extinct in that area. *Carya* pollen occurs at least as late as the Pliocene in western North America but is no longer native to the region.

WOOD

Wood of *Carya* is relatively uniform in anatomy and is easily distinguished from that of other tribes of the Juglandaceae. The anatomy of sect. *Rhamphocarya*, as described by Leroy (1952), appears to match that of sects. *Apocarya* and *Eucarya* closely. *Carya* wood is usually ring-porous, but tropical species grade to semi-diffuse-porous. Fibers and vessels are thick-walled; especially thick walls occur in the region of contact of multiple vessels. Crystals usually occur in solitary swollen idioblasts of axial parenchyma. In other features the secondary xylem conforms to the general description for the Juglandaceae, page 2.

Müller-Stoll and Mädel (1960) established two organ genera applicable to fossil woods resembling *Carya*: *Caryojuglandoxylon* and *Eucaryoxylon*. *Caryojuglandoxylon* was erected to accommodate woods that might represent either *Carya* or *Juglans*. Müller-Stoll and Mädel (1960) suggested that these extant genera intergrade to the extent that they cannot be separated anatomically. However, wood of *Carya* can generally be distinguished from that of the Juglandaceae according to the diagnostic features mentioned above. The genus *Caryojuglandoxylon* remains useful for fossil woods too poorly preserved or known to determine the nature of ring porosity, wall thickness, and idioblasts. The genus *Eucaryoxylon* Müller-Stoll & Mädel accommodates fossil woods with anatomy identical to extant *Carya*. Some authors prefer to place such fossils in the extant genus.

Relatively few woods of *Carya* have been recognized in the fossil record and those described are from the Upper Tertiary. Examples include *Eucaryoxylon crystallophorum* that was described from the Miocene of the Tokaj-Eperjeser Mountains of Hungary (Müller-Stoll & Mädel, 1960), *E. moenanum* from the Upper Pliocene of Neu-Insensberg near Frankfurt, West Germany (Müller-Stoll & Mädel-Angeliowa, 1983), and *Carya protojapanica* from the Miocene of Japan (Watari, 1952). Beck (1942) mentioned, but did not name or adequately describe, *Carya* wood from the Miocene of Washington, United States.

Prakash and Barghoorn (1961a) studied material from Beck's collection and described "*Carya tertiara*." Although their description is compatible with identification as *Carya*, the figures of the type specimen do not confirm this relationship. The consistently thin-walled vessels and fibers and the occurrence of idioblasts in long chains are characteristic of the Juglandaceae (especially *Juglans* sect. *Rhysocaryon*) and unlike *Carya*. Hence, it should be reassigned to *Pterocaryoxylon* Müller-Stoll & Mädler. Confirmed *Carya* xylem from the same area is figured by Manchester (1981b, fig. 4.1).

As yet, no Paleogene woods of Hicoreae have been identified with certainty. I have re-examined type slides of *Eucaryoxylon canadensis* Roy & Stewart from the Oligocene Cypress Hills Formation of Saskatchewan, Canada. Although the wood resembles *Carya* in some of its features, the presence of spirally thickened tracheids separates it from all extant *Carya*. Roy and Stewart (1971) reported scalariform perforation plates, but the figured example appears to represent poorly preserved elongate vessel-parenchyma pitting. Although the material is possibly juglandaceous, it is not *Eucaryoxylon* and might not belong to the Hicoreae.

FOLIAGE

Carya leaflets are typically serrate with acute teeth and craspedodromous to semicraspedodromous venation (except in *C. sinensis*, which has entire-margined leaflets with camptodromous venation). Most species are characterized by a tendency of the secondary veins to branch two or more times near the margin, with each branch entering a successive tooth. In some instances the secondaries form angular marginal loops; however, the marginal tertiary veins are nearly always craspedodromous. Intercostal areas are transversed by strong, regularly spaced, percurrent tertiary veins. The higher order venation is orthogonal, with areoles having freely ending, simple (*C. aquatica*) or branched veinlets. The teeth are acute, usually closely spaced (three per secondary), but sometimes widely spaced (one per secondary in *C. aquatica*), and are usually vascularized medially or submedially (apically in *C. aquatica*). Hardin and Stone (1984) surveyed foliar surface features of extant American *Carya* species and observed six trichome types: acicular, fasciculate, multiradiate, solitary, capitate-glandular, and peltate scale.

The foliar architecture and anatomy of modern *Carya* sometimes overlaps with that of *Cyclocarya*, *Juglans*, and *Pterocarya* and may lead to problems in the identification of fossil leaflets. There are hundreds of identifications of *Carya* foliage in the literature (e.g., Nagel, 1914; LaMotte, 1952), and it is impractical to examine each report critically. Here I consider only a few examples that appear to be valid Tertiary records for the Hicoreae.

Reports of Eocene foliage attributed to *Carya* include *C. sessilis* MacGinitie (1941) from the Chalk Bluffs flora of California and *C. cashmanensis* Wolfe and *C. pugetensis* Wolfe (1968) from northwest Washington. These remains resemble *Carya* and have been placed in the modern genus although corroborative evidence from fruits is not available.

Carya libbeyi (Lesquereux) MacGinitie from the early Oligocene Florissant flora of Colorado is well documented on the basis of whole compound leaves and numerous isolated leaflets and is associated with *C. florissantensis*, sp. nov. fruits. *Carya serraefolia* (Goepp.) Kräusel leaflets from the upper Oligocene and Miocene of North Bohemia (Knobloch, 1961; Bůžek, 1971) also appear to be validly assigned to the genus.

FRUITS

Fruits of Hicoreae, which include the familiar pecan and hickory nuts, are large, husk-enclosed endocarps well adapted for animal dispersal. Although convergent in gross morphology with *Juglans*, fruits of *Carya* can be distinguished on the basis of various criteria. In *Carya*, the carpels are oriented transversely with respect to the bract, whereas in *Juglans* they have a median orientation (Manning, 1940, 1978). While the husks of *Carya* are dehiscent into four (less commonly five or six) valves, those of *Juglans* (except *J. regia*) are generally indehiscent. In addition, the nuts of most *Carya* species are quadrangular with four longitudinally oriented corners ("Längskanten" of German writers) corresponding to the lines of husk splitting (Fig. 31J, M). The utility of this feature is limited, however, because fruits of *Juglans ailantifolia* var. *cordiformis* (a horticultural variety) are also quadrangular. *Carya* nuts usually have a small rhomboid protuberance at the base of the endocarp that is generally not present in *Juglans* (Leroy, 1955). The nuts of most extant *Carya* species (except *C. aquatica*) have relatively smooth surfaces while those of

FIGURE 31. Modern *Carya* nuts, $\times 1$, except as noted.—A–C. *Carya myristicaeformis* (Michx. f.) Nutt., Damaree 53110 (A).—D, E. *C. aquatica* (Michx. f.) Nutt., IU Herb. 69985.—F–H. *C. poilanei* (Chev.) Leroy, photos courtesy D. Mai.—I, J. *C. cathayensis* Sarg., Chun. coll. (A).—K. *C. cordiformis* (Wangenh.) K. Koch, Deam 19244 (IU Herb.).—L, M. *C. tomentosa* (Poir.) Nutt., Stone 544 (A).—N. Latex locule cast of L, showing convoluted nature.—O. *C. ovata* (Mill.) K. Koch, Deam 10251 (IU Herb.).—P–R. *C. sinensis* Dode, Feng 13309 (A), $\times 1/2$.

most extant *Juglans* species (except *J. californica* and *J. hindsii*, for example) have rough exterior ornamentation. The primary lobes of the seed (and locule cast) of *Carya* are more elongate than those of *Juglans* and are grooved longitudinally with a pair of furrows corresponding to the inner ribs (Fig. 31C) of the nutshell. Inner ribs are not well developed in *Juglans*. The secondary sep-

tum, when present, is thin relative to the usual condition in *Juglans*. Leroy (1955) noted that *Carya* fruits show a pair of vascular bundles within the nutshell along the line of dehiscence and that the homologous bundles in *Juglans* (dorsal bundles of Benson & Welsford, 1909; Mai, 1981) run outside the endocarp, within the husk. The course of the placental bundles within

the primary septum provides another taxonomically useful feature. These bundles follow an axial course in *Juglans*, but in *Carya* they follow a peripheral course (sects. *Apocarya*, *Sinocarya*, and *Carya*) or are distributed evenly throughout (sect. *Rhamphocarya*).

Surface and sectional views of the nuts of various extant *Carya* species are shown in Figure 31. Others are illustrated by Stone (1962) and Mai (1981). Characters of the fruit can sometimes be useful in separating the extant sections of *Carya*. Fruits of sects. *Apocarya* and *Sinocarya* are characterized by a thin husk with flanged sutures, a thin (to thick; *C. myristiciformis*) shell containing lacunae (except *C. cathayensis*, *C. myristicaeformis*), and the absence or weak (to medium) development of the secondary septum. Fruits of sect. *Carya* have a thick (or thin; *C. texana*, *C. pallida*) husk without sutural flanges, a thick to very thick nutshell without lacunae, and a well-developed secondary septum. A single pair of inner ribs occur adjacent to the dehiscence plane in the nutshells of sects. *Apocarya*, *Sinocarya*, and *Rhamphocarya*. Nutshells of sect. *Carya* usually show an additional pair of inner ribs.

The fossil record of *Carya* fruits extends back to the early Eocene (Mai, 1981). It is also likely that some of the early Tertiary fruits ascribed to *Juglandicarya* belonged to the *Hicoreae*, although none show the well-developed inner ribs seen in the nutshells of all modern sections of *Carya*. *Juglandicarya simplicarpa*, from the Paleocene of North America, may be a representative of the *Hicoreae*, but is known only from molds and casts. Without information on the nature of vascularization, it is not possible to determine its tribal affinity.

Juglandicarya lubbocki Reid & Chandler, London Clay Fl. 140–142. pl. 3: figs. 1–4. 1933; Chandler, Lower Tert. Fl. Southern England 1: 137–138. pl. 14: figs. 16, 17. fig. 11. 1960.

Description. Nut 8 mm long, 8.5 mm wide, almost spherical with rounded apex and base; outer surface smooth; walls thick in proportion to nut dimensions, up to 1.5 mm thick, without lacunae; secondary septum thin but well developed, extending more than three-fifths of the distance to top of locule; locule smooth-surfaced, without inner ribs; strand of fibers running along margin of suture; placentary bundles forming a fibrous axis of medial course.

Discussion. This species is from the Early Eocene London Clay flora. As suggested by its placement in *Juglandicarya* (Reid & Chandler, 1933), it does not fall neatly within a modern genus. Reid and Chandler stated that these “fossils undoubtedly more nearly resemble *Juglans* than any other living genus,” but noted that the smooth globular shape, the lack of conspicuous intrawall lacunae, and extremely small size preclude placement in *Juglans*. Reinterpretation using the anatomical criteria of Leroy (1955) suggests that the species is more similar to *Carya* than to *Juglans*. The strand of fibers running along the margin of the suture noted by Reid and Chandler apparently represents the dorsal bundle. The presence of the dorsal bundle in the endocarp allies the species with *Carya* and differentiates it from living *Juglans* species in which the dorsal bundles pass through the husk. In addition, the thin secondary septum is comparable to that of *Carya*. The absence of lacunae occurs in some modern *Carya* species. It is worth noting that reports of fossil pollen from the London Clay flora include *Carya*, *Platycarya*, *Pterocarya*, and *Engelhardia*, but not *Juglans* (Gruas-Cavagnetto, 1978).

Although *Juglandicarya lubbocki* could represent the *Hicoreae*, it is distinguished from extant *Carya* by its small size and the lack of inner ribs on the locule surface. In addition, it seems to lack the basal plexus and four-cornered aspect common in extant *Carya*. I do not suggest that other species assigned to *Juglandicarya* (e.g., *J. depressa* Reid & Chandler) necessarily represent the *Hicoreae*. The specimens attributed to *Juglandicarya* from the Eocene of St. Saturnin, France (Vaudois-Miéja, 1978) are, in my opinion, questionably assigned to the Juglandaceae. The type specimens of *J. andegavensis* and *J. gruetti* (kindly loaned to me by N. Ginieis) appear to be casts of five-carpellate capsules.

EUROPEAN *CARYA* FRUIT RECORD

Although absent from Europe today, *Carya* was represented by a variety of European species in the Oligocene and throughout the Neogene. Mai (1981) provides a useful summary and key to European fossil *Carya* species, describes selected modern species for comparison, and provides a useful critical revision of the fossil species with smooth shells. The following review includes species with coarsely striate nutshells as well as those discussed by Mai (1981). Specific

FIGURE 32. *Carya* fruits from the Tertiary of Europe, $\times 1$, except as noted (collection numbers given by Mai, 1981; Gregor, 1978).—A, B. *C. lacrymabunda* (Koenig) Leroy, outer and inner view of nut valve from the Middle Oligocene of Profen-Nord.—C, D. *C. quadrangula* (Kirchh.) Leroy from the Middle Oligocene of Haselbach.—E–K. *C. ventricosa* (Sternberg) Unger from the Miocene of Wetterau.—L, M. *C. strychnina* (Sternberg) Mai from the Miocene Nentershausen/Unterwesterwald brown coal.—N, O. *C. strychnina* from Hessenbrücken/Wetterau.—P, Q. *C. paludis-naabi* Gregor from the Miocene of Oberpfalz, Germany. P. $\times 0.5$; Q. $\times 1$.—R–T. *C. bohémica* Brabenec from the Miocene of Quatitz (Orig. Mai, 1964).—U, V. *C. globosa* (Ludwig) Mädler, holotype from Dorheim (Orig. Mai, 1973). A–O, R–V. Courtesy D. Mai. P, Q. Courtesy J. Gregor.

locality and specimen repository information may be found in Mai (1981) and Kirchheimer (1957).

Carya lacrymabunda (Koenig) Leroy, Mem. Mus. Natl. Hist. Nat., Sér. B, Bot. n.s. 6: 165. 1955; Mai, Feddes Repert. 92: 357–358. pl. 26: figs. 5, 6. fig. 6. 1981. *Lampetia lacrymabunda* Koenig, Icones fossilium sectiles 2. pl. 2: fig. 23. 1825. *Juglans lacrymabunda* (Koenig) Kirchheimer, Planta 39: 39, fig. 4b. 1951. Figure 32A, B.

Description (after Mai, 1981). Nuts 25–28 mm long, 15–20 mm wide, nearly spherical to ovoid with a sharply tapered apex; base rounded with a somewhat protruding rhomboidal plexus; outer surface smooth to finely reticulate, slightly or not four-angled; shell thick, more than 2 mm, with large lacunae in the four inner ribs and in the plane of the primary septum; secondary septum present as a wide flange at the very base of the locule; dorsal vascular bundles introrse, distinct; funicular bundle present as a diffuse band in the primary septum.

Discussion. *Carya lacrymabunda* is the earliest *Carya* species known from Europe, occurring in the Upper Eocene to Lower Oligocene “Blue Earth” strata of the Prussian “Bernsteingrabereien” in the Kalingrad area of the Soviet Union and in the Middle Oligocene phosphate horizon in Profen-Nord/Weisselsterbecken, East Germany. Although the holotype is now missing, the lectotype (*Juglans schweiggeri* Kirchheimer, 1937) is at the Museum für Naturkunde in Berlin (Mai, 1981).

The identity of this species as *Carya* is indicated by the presence of a basal plexus and the introrse position of the dorsal vascular bundles. The latter are visible as fine lines just inside the margin in the plane of dehiscence. The characteristic features of this species are its thick shell, large lacunae, and weak development of the secondary septum. Placement in sect. *Apocarya* or *Sinocarya* is suggested by the lacunae, the weak development of the secondary septum, and the weak development of the four corners of husk dehiscence.

Carya quadrangula (Kirchheimer) Leroy, Rev. Int. Bot. Appl. Agric. Trop. 32: 290. 1952; Mai, Feddes Repert. 92: 360–362. pl. 27: figs. 1–8. fig. 8. 1981. *Caryojuglans quadrangula* Kirchheimer, Bot. Jahrb. Syst. 67: 82–85. pl. 12: fig. 36a–c, e. 1935. Figure 32C, D.

Description (after Mai, 1981). Nuts 22–37 mm long, 13.5–22 mm wide, ovoid to almost spherical with a short pointed apex; base rounded with a rhomboidal process; outer surface smooth to longitudinally striate with four distinct longitudinal corners; thin- to thick-walled (up to 3 mm) with large lacunae that interconnect basally; secondary septum developed only as a small flange along the base of the primary septum; dorsal bundle introrse.

Discussion. According to Mai (1981), *Carya quadrangula* is known from 14 middle Oligocene localities in East and West Germany, the type locality being Meuselwitz, Tagebau Phoenix, East Germany. It appears to represent sect. *Apocarya* and resembles *C. lacrymabunda* in its thick shell, large lacunae, and overall size but is differentiated by the strongly developed four-angled aspect and the less pronounced apical protrusion.

Carya ventricosa (Sternberg) Unger, Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 19: 40. 1861; Leroy, Mém. Mus. Natl. Hist. Nat., Sér. B, Bot. n.s. 6: 160–165. figs. 80–82. 1955; Mai, Feddes Repert. 92: 367–371. pl. 30: figs. 1–100; pl. 31: figs. 1–10. fig. 11. 1981. *Juglandites ventricosus* Sternberg, Vers. Fl. Vorwelt 4: 44. 1825. *Juglans ventricosa* (Sternberg) Brongniart, Prodr. Hist. Vég. Foss. 40. 1828; Kirchheimer, Die Laubgewächse der Braunkohlenzeit 202–203. figs. 132, 133. 1957. Figure 32E–K.

Description (after Mai, 1981). Nuts 16–32 mm long, 13–23 mm wide, nearly spherical to ovoid with a blunt or slightly apiculate apex; base broadly rounded with a rhomboid process at the base; outer surface almost smooth with weak connecting longitudinal striae; only faintly, if at all, four-angled near the apex; shell thin-walled, only 1–1.5 mm, primary septum about 1 mm thick; large lacunae in wall protruding into locule, one at either end of the primary septum, and four within the inner ribs; secondary septum virtually absent or developed as a slight basal flaring of the primary septum along the axis; dorsal vascular bundle interior, always distinct; placental bundles of the primary septum ramified, distinct.

Discussion. *Carya ventricosa* was the longest ranging and most widespread species in Europe, ranging from Upper Oligocene to Lower Pliocene. Mai (1981) cites 25 localities, including West and East Germany, Poland, Rumania, and the Soviet

Union. The type locality is Salzhausen, near Nidda/Wetterau, West Germany.

Miki (1955) attributed a nut from the Tertiary of Japan to *C. ventricosa* "due to the similar size and shape." Gregor (1978) upheld Miki's assignment in discussing the range of the species. However, the Japanese species is partitioned into four basal compartments (Miki, 1955), whereas the European species has only two basal compartments. In addition, no lacunae are noted in the Japanese material. Therefore, it seems that assignment of the Japanese species to *C. ventricosa* is unwarranted.

Carya rostrata (Schlotheim) Schimper, *Traité Paléont. Vég.* 3: 257. 1874; Mai, *Feddes Repert.* 92: 363–365. pl. 28: figs. 1–18; pl. 29: figs. 1–19. fig. 9. 1981. *Carpolithus rostratus* Schlotheim, *Petrefactenkunde* (Nachtr.) 98. pl. 21: fig. 8a, b. 1822.

Carpolithus subcordatus Sternberg, *Vers. Fl. Vorwelt* 4: pl. 53: fig. 6. 1825.

Description (after Mai, 1981). Nuts 13–27 mm long, 12–19 mm wide, ovoid to subcordate with a large protruding pointed apex that can be very slender; base rounded, somewhat exerted with a rhomboid process; outer surface finely wrinkled longitudinally; four to five corners present near the apex that disappear in the middle and lower part of the nut; thin-walled with lacunae that are often filled with parenchyma; medial lacunae often small; secondary septum small or almost missing, weakly flanged; dorsal vascular bundle introrse, often indistinct, placental bundles constituting a strand in the primary septum.

Discussion. *Carya rostrata* ranges from the Upper Oligocene to Miocene in Germany (Mai, 1981). It differs from *C. ventricosa* primarily in its distinctive protruding apex. Mai suggests that this species could have been derived from the Oligocene *C. lacrymabunda* by reduction in shell thickness.

Carya caryoides (Kirchheimer) Leroy, *Rev. Int. Bot. Appl. Agric. Trop.* 32: 290. 1952; Mai, *Feddes Repert.* 92: 355–356. pl. 26: figs. 1–3. fig. 5. 1981. *Antweilera caryoides* Kirchheimer, *Planta* 39: 535. figs. 2, 3. 1951.

Description. Nut 26 mm long, 18 mm wide, ovoid, apex pointed, but not long tapering, base rounded with a large swollen distinct quadran-

gular plexus; outer surface smooth to weakly longitudinally striate, four-cornered in the upper part; thin-walled with large lacunae that limit the locule to a small space; secondary septum developed only as a flange along the primary septum extending about half of the distance to the top of the locule; dorsal bundle introrse, distinct; placental bundle in primary septum, beneath the large lacunae.

Discussion. Based upon a single specimen from the Middle Miocene (age according to Mai, pers. comm.) Antweiler locality near Euskirchen, West Germany, this species is peculiar because of the extremely large lacunae within the inner ribs. Kirchheimer (1951) described it as a new genus, *Antweilera*, which he considered to be an extinct member of the Juglandaceae. Leroy (1955) correctly referred it to *Carya* on the basis of its basal plexus and the peripheral course of placental bundles within the primary septum.

Carya costata (Presl) Unger, *Syll. Pl. Foss.* 1: 41–42. pl. 19: fig. 16. 1861; Mai, *Feddes Repert.* 92: 356–357. 1981. *Juglandites costata* Presl in Sternberg, *Vers. Fl. Vorwelt* 2: 207. pl. 58: figs. 7–13. 1838.

Description. Nuts 25 mm long, 20 mm wide, suborbicular with a protruding but not prominent apex; base rounded with a rhomboid basal process; outer surface long-striate; shell 2.5–3 mm thick, internal structure unknown with a small, low secondary septum that extends to half of the height of the locule along the primary septum.

Discussion. The above description (from Mai, 1981) is based upon three specimens from the original collection of Sternberg (1838) from the Oligocene tuff of Pocerny near Karlovy Vary, West Bohemia in Czechoslovakia. Since the specimens are casts and molds only, details of the internal structure, such as presence or absence of lacunae and nature of vascularization, remain unknown. Mai points out that most specimens assigned to *Carya costata* subsequent to its initial description are better preserved than the topotypic specimens of *C. costata* and can be attributed to other species (*C. ventricosa* and *C. strychnina*).

Carya strychnina (Sternberg) Mai, *Feddes Repert.* 92: 305–306. pl. 32: figs. 1–6; pl. 33: figs. 1–4. fig. 10. 1981. *Carpolites strychni-*

nus Sternberg, Vers. Fl. Vorwelt 4: 44. pl. 41: fig. 4a, b. 1825. Figure 32L–O.

Description. Nuts 20–35 mm long, 18–22 mm wide, subglobose to ovoid, apex rounded without sharp apex; base rounded with rhomboidal plexus; outer surface wrinkled longitudinally, occasionally with four well-developed longitudinal angles and distinct inner ribs; thick-walled, mostly over 3 mm, even to 6 mm along the dehiscence face, with large lacunae; secondary septum represented by a wide flange, triangular, with ramified placental bundles; dorsal vascular bundles introrse, distinct.

Discussion. This species has been shown by Mai (1981) to be very similar to the extant species *Carya poilanei* (Fig. 31F–H) of Viet Nam because of the triangular configuration of the secondary septum, as viewed in the plane of dehiscence (Fig. 31N) and the thick shell with large lacunae in the lower half. The chief differences are the larger size and rougher surface of the fossil. *Carya strychnina* occurs in the Middle Miocene Hessenbrucker brown coal of Wetterau. Mai also recognizes the species in the Upper Oligocene of Seussen, near Arzerg, Fichtelgebirge, West Germany. Many specimens previously placed in *C. ventricosa* and *C. costata* are included in the extensive synonymy of Mai (1981). The morphological similarity with extant *C. poilanei* suggests that *C. strychnina* represents the extant sect. *Sinocarya*.

Carya pusilla Unger, Syll. Pl. Foss. 1: 41. pl. 18: fig. 12. 1861; Mai, Feddes Repert. 92: 359–360. pl. 31: figs. 11–20. fig. 12. 1981.

Description. Nuts small, 10–15 mm long, 9–15 mm wide, almost heart-shaped to swollen spherical; apex truncate, base somewhat recessed, but often with a raised rhomboidal process; outer surface smooth to weakly striate, without four corners developed; thin-walled with large lacunae; secondary septum developed as a small flange along the axis of the primary septum extending to the upper third of the locule, not widened at the base; dorsal vascular bundles introrse, distinct; placental bundles large, very distinct in primary septum.

Discussion. *Carya pusilla* occurs in at least six localities in the Miocene of West Germany, East Germany, Poland, and western Czechoslovakia. It is distinguished from *C. ventricosa* primarily by its smaller size and thinner shell.

Carya paludis-naabi Gregor, Palaeontographica, Abt. B., Paläophytol. 167: 19–20. pl. 1: figs. 8, 9. 1978. Figure 32P, Q.

Description. Nuts large, 40–44 mm long, 33–38 mm wide (in compressed state); long ovoid, with rounded apex and base; base with a large rhomboidal process; outer surface wrinkled to smooth, without corners; shell averaging 3 mm up to 5 mm thick apically; secondary septum absent or poorly developed; dorsal bundle introrse.

Discussion. *Carya paludis-naabi* is noteworthy because of its large size, thick walls, and thick septa. The surface is relatively smooth and, at least when compressed, lacks the four corners characteristic of sect. *Carya*. The presence or absence of lacunae is undetermined. This species is known only from sands associated with Miocene brown coal of Oberpfalz, West Germany (Gregor, 1978).

Carya globosa (Ludwig) Mädlér, Abh. Senckenberg. Naturf. Ges. 446: 65–67. pl. 6: figs. 6–8. fig. 20. 1939; Mai, Acta Palaeobot. 14: 99. pl. 4: figs. 1, 2. 1973. *Juglans globosa* Ludwig, Palaeontographica, Abt. B, Paläophytol. 5: 103. pl. 21: fig. 12. 1857. Figure 32U, V.

Juglans quadrangula Ludwig, Palaeontographica, Abt. B, Paläophytol. 5: 103. pl. 21: fig. 11. 1857.
Carya hauffei Kirchheimer, Planta 32: 425. fig. 5. 1942; Die Laubgewächse der Braunkohlenzeit 122, 504. fig. 136. 1957.

Description. Nuts 15–35 mm long, 15–28 mm wide, 16–11 mm thick; oval to almost spherical; exterior of endocarp longitudinally channeled with anastomosing grooves; four corners corresponding to lines of husk dehiscence evident; husk, when preserved, about 3 mm thick; endocarp wall 1–2.5 mm thick, with or without lacunae, septa 1–2 mm thick; secondary septum present; seed four-lobed at base.

Discussion. *Carya globosa* is characterized by prominent exterior sculpture, thick shell, and well-developed secondary septum. The holotype (Fig. 32U, V) is from the lower Pliocene of Dorheim, near Friedberg, West Germany. Mädlér (1939) provided a detailed description based on a collection from the Pliocene of Frankfurt, West Germany. Some of his specimens include intact husks which, because of their greater thickness,

are easily distinguished from the otherwise similar extant American species, *C. aquatica*.

I propose that *Carya hauffei*, described by Kirchheimer from Miocene strata (Kirchheimer, 1942), should be synonymized with *C. globosa*. Both have a thick, sculptured endocarp and thick primary and secondary septa. Kirchheimer (1957) maintained the distinction between *C. globosa* and *C. hauffei* primarily on the basis of the less well-developed lacunae in the latter. However, Czezzott and Skirgiello (1961) noted that their specimens of "*Juglans*" *globosa* from the Miocene of Poland vary from distinctly to indistinctly lacunose. The specimens that they ascribe to *C. hauffei* have large lacunae in some cases but lack them in other cases. Thus the presence of lacunae in this taxon appears to be variable, and it seems reasonable to merge *C. hauffei* with *C. globosa* despite their differences in age. Based primarily upon differences in exterior size and shape, Czezzott and Skirgiello (1961) assigned specimens from the Miocene of Turow, Poland, to several different species of *Carya* (*C. lusatica*, *C. turowensis*, *C. ventricosa*, "*Juglans*" *globosa*). Based on the descriptions and figures, these species might be interpreted as variations within *C. globosa*. However, I have not examined the type material.

Mädler (1939) proposed a new section of *Carya*, sect. *Aquatica*, to accommodate *C. globosa* and similar fossils along with the single living species *C. aquatica*. The rough surface sculpture and large lacunae encountered in these species (and in the fossil *C. kryshstofovichii* from western Siberia; discussed p. 75) permit their distinction from all other extant species of *Carya*. However, in the absence of other organs for the fossil taxa it is difficult to assess whether the distinction is a natural one. Neobotanists include *C. aquatica* in sect. *Apocarya*, although it is peculiar in having leaflets with widely spaced teeth and simple, unbranched freely ending veinlets.

Carya bohémica Brabenec, Rozpr. České Akad. Císaře Františka Josefa Vědy, Tr. 2, Vědy Math. Přír. 13: 9. pl. 1: fig. 10a, b. 1904; Czezzott & Skirgiello, Prace Mus. Ziemi 4: 60–61. pl. 18: figs. 5–12. 1961. Figure 32R–T.

Description (from Mai, pers. comm.). Nuts long ovoid, acuminate-tipped, 17–32 mm long, 15–30 mm wide; outer surface with a wide-mesh network of thickenings and depressions, occasionally also with four longitudinal ribs running

from the base to the apex; shell thin (1 mm), with two small submedial lacunae; secondary septum present but not well preserved.

Discussion. This species is similar to *Carya globosa* and apparently represents sect. *Apocarya* but differs in the prominence of surface depressions. It occurs in the Miocene of North Bohemia (Holedec near Mecholupy, Czechoslovakia; Brabenec, 1904), Lausitz (Wiesa, Quatitz; cf. *C. hauffei*, Kirchheimer, 1942; Mai, 1964) and western Poland (Turów; Czezzott & Skirgiello, 1961).

Carya angulata Reid, Meded. Rijksopsporing Delfstoffen 6: 74. pl. 4: figs. 28, 29. 1915; Mädler, Abh. Senckenberg. Naturf. Ges. 446: 68–70. pl. 6: figs. 12, 13. fig. 22. 1939; Kirchheimer, Die Laubgewächse der Braunkohlenzeit 505–506. fig. 138. 1957.

Description (after Mädler, 1939). Endocarps 13–24 mm long, 11–19 mm wide, rounded; surface smooth except for eight longitudinally oriented folds; two pairs of inner ribs developed within the nutshell; secondary septum well developed, lacunae apparently absent.

Discussion. This species occurs in the Upper Pliocene of Limburg, The Netherlands, Nieder-rad near Frankfurt, West Germany, and Souffle-neim near Hagenau, France. Despite its late Tertiary age, *Carya angulata* does not closely match the morphology of any single extant species.

Carya rugosa Zablocki, Acta Soc. Bot. Poloniae 7: 144–146. pl. 12: figs. 1–4. 1930.

Description (from Mai, pers. comm.). Nuts small, to 20 mm long, heart-shaped, rounded with a short protruding apex; surface with distinct longitudinal wrinkles and four well-developed longitudinal corners extending from apex to middle; lacunae not present.

Discussion. The type material of this species is from the Miocene Salt beds of Wieliczka, South Poland and is housed in the Botanical Institute of Krakow. Mädler (1939) considered this species to be comparable to *Carya angulata*. Mai (pers. comm.) considers both species, along with *C. askenasyi*, to be forerunners of sect. *Carya* in the Miocene and Pliocene of Europe.

Carya askenasyi (Kinkelin) Mai, Feddes Repert. 92: 375. 1981. *Prunus askenasyi* Kinkelin, Abh. Senckenberg. naturf. Ges. p. 269. pl. 34: fig. 18A–C. 1909.

Carya longicarpa Mädlér, Abh. Senckenberg. Naturf. Ges. 446: 67. pl. 6: figs. 9, 10. fig. 21. 1939.

Carya tomentosa Nuttall *fossilis* Mädlér, Abh. Senckenberg. Naturf. Ges. 446: 70–71. pl. 6: figs. 14, 15. fig. 23. 1939.

Description. Nuts 17–32 mm long, 11–15 mm wide, oval in longitudinal view, base and apex rounded; exterior almost smooth or faintly wrinkled, often but not always exhibiting four corners; walls and septa 1–2 mm thick; secondary septum present; locule intruded on each side by a pair of inner longitudinal ribs adjacent to the primary suture; small lacunae present in the primary septum and internal ridges.

Discussion. This species from the Pliocene of Germany was formerly placed in the extant species *Carya olivaeformis* and *C. tomentosa* (Mädlér, 1939). However, more thorough comparative studies with the modern taxa are necessary to determine the relationship of these fossils with extant species. The occurrence of this species, together with *C. angulata*, *C. globosa*, and *C. ventricosa* in the Pliocene of Frankfurt (Mädlér, 1939), indicates that *Carya* was diverse in western Europe as late as the Pliocene.

ASIAN RECORD

In addition to the four modern-day species of *Carya* in Asia, several Neogene occurrences are known. The following review includes three species from western Siberia, one from China, and four from Japan.

Carya kryshstofovichii (Gorbunov) Manchester, comb. nov. *Juglans kryshstofovichii* Gorbunov, Bot. Žurn. (Moscow & Leningrad) 41: 659, 661–662. pl. 1: figs. 1–12. fig. 2a, b. 1956.

Juglans tomiensis Gorbunov, Bot. Žurn. (Moscow & Leningrad) 41: 662–663. pl. 2: figs. 1–13. 1956.

Description. Nuts 25–44 mm long, 16–30 mm wide, obovate to oval to ovate, apex rounded or attenuate except for a mucronate tip about 2 mm high, base flattened to rounded, sometimes with a rhomboidal protuberance in the attachment region; exterior ornamented with prominent, longitudinal ribs extending from base to apex; nutshell 2–4 mm thick with a pair of inner ribs adjacent to the plane of dehiscence; primary septum without a conspicuous axial placental channel; secondary septum apparently absent or not well developed.

Discussion. Nuts of this species were described from two deposits of probable Oligocene age in the vicinity of Tomsk (Kozjulino) near the confluence of the Tomb and Ob Rivers in western Siberia. Although initially described as two species, the nuts from both localities overlap in size and morphology to such an extent that I believe they should be merged. Gorbunov (1956) ascribed the material to *Juglans*, calling attention to the similarity in exterior sculpture between the fossils and certain modern species of *Juglans* sect. *Rhysocaryon*. However, it is apparent from Gorbunov's excellent illustrations that the placental bundles are diffuse, as in *Carya*, rather than confined to an axial channel, as in *Juglans*. Additional features confirming its identity as *Carya* are the well-developed inner ribs in the locule adjacent to the plane of dehiscence (best seen in Gorbunov, 1956, pl. 2: fig. 3) and the basal protuberance. The most striking feature of this fossil, the prominent exterior sculpture, is uncommon in modern *Carya*, although it does occur in the extant *C. aquatica* of eastern North America and *C. globosa* of the European Tertiary. The absence of a well-developed secondary septum is a feature shared by many fossil *Carya* species and some extant species of *Carya* sect. *Apocarya*.

Carya kompassica (Gorbunov) Manchester, comb. nov. *Juglans kompassica* Gorbunov, Bot. Žurn. (Moscow & Leningrad) 41: 663–664. pl. 1: figs. 13–19. fig. 3. 1956.

Description. Nuts 15–25 mm long, 11–17 mm wide, long-globose to oval, apex briefly acuminate, base rounded; exterior longitudinally finely striate; walls 2 mm thick with well-developed inner ribs adjacent to the plane of dehiscence, with lacunae; secondary septum essentially absent, primary septum without an axial placental channel.

Discussion. *Carya kompassica* was collected from a Miocene(?) deposit on the Tym River in western Siberia. Its identity as *Carya* rather than *Juglans* is confirmed by the prominent inner ribs of the locule adjacent to the plane of dehiscence and lack of an axial placental channel within the primary septum (Gorbunov, 1956, pl. 1: figs. 17, 18). This species is differentiated from *C. kryshstofovichii* by its smaller size and lack of coarse exterior sculpture and is morphologically similar to the European Miocene species *C. ventricosa*.

***Carya* (?) sp.** Dorofeev, Tert. Fl. Western Siberia 140. pl. 18: figs. 15–18. 1963.

Description. Nuts 15–16 mm long, 8–9 mm wide, ovate to oblong with a gradually tapered apex and slightly indented base; nutshell about 1 mm thick with internal lacunae, exterior surface smooth but raised in a ridge along the dehiscence plane; locule smooth, inner ribs not detectable from figures; secondary septum apparently absent, primary septum without axial placental channel.

Discussion. This species is known from two specimens from Dunaevskij jar on the Tym River in western Siberia. The species could indeed represent *Carya*, as suggested by Dorofeev (1963), because of its relatively large size and the lack of an axial channel within the primary septum. However, the specimens appear to lack the basal protuberance and inner ribs of the locule, characteristic of the genus. The most peculiar feature is the ridge or flange along the dehiscence plane. This might be an artifact of compression during fossilization of the isolated nut valves. If the ridges constitute a primary feature unrelated to fossilization, affinities with *Carya* seem unlikely. Mai (1981) suggests that this species, with its smooth exterior and reduced secondary septum, is related to the European fossils *C. quadrangula* or *C. ventricosa*; however, it differs from them in its small size and apparent lack of inner ribs.

Carya miocathayensis Hu & Chaney, Publ. Carnegie Inst. Wash. 507: 26–27. pl. 7: figs. 5, 6. 1940.

Discussion. This species was described on the basis of both foliage and a nut specimen from the Miocene Shanwang flora of Shantung Province, China. The nut is “nearly globose, slightly pointed at the apex; 2.5 cm long, 2.2 cm broad; shell nearly 2 mm thick, showing longitudinal ribbing on the inside; kernel with two valves 1.5 cm long and 2 mm broad” (Hu & Chaney, 1940: 26).

Although the specimen figured by Hu and Chaney (1940) is only a siltstone cast, the thickness of the wall and the longitudinal elongation of the seed lobes suggest that the species is indeed *Carya*, not *Juglans*. A secondary septum is not evident in the fossil and it is not possible to determine the presence or absence of lacunae in the wall.

The associated leaves and leaflets are compared with the extant *Carya cathayensis* by Hu

and Chaney (1940). Hu and Chaney note that this fossil occurrence confirms a more northerly distribution of *Carya* during the Miocene than exists today in China.

Carya leiocarpa Miki, J. Inst. Polytechn. Osaka City Univ., Ser. D, Biol. 6: 132. pl. 1D. fig. 1E. 1955.

Description. Nut 12 mm long, 12 mm wide, approximately spherical, wall 0.3 mm thick, smooth-surfaced on the exterior, indistinctly striate on the inside; four-compartmented at base.

Discussion. This species, from the Pliocene of Japan, is identified by its thin walls and smooth surface (Miki, 1955). It is based on a single incomplete specimen from the “marine bed” in Hanasaki, Toyama Prefecture.

Carya nanocarpa Miki, Jap. J. Bot. 11: 265. pl. 6Dc. fig. 9E. 1941.

Carya ventricosa Unger sensu Miki, J. Inst. Polytechn. Osaka City Univ., Ser. D, Biol. 6: 132–133. pl. 1E. fig. d,D. 1955.

Description. Nut 15–25 mm long, 13–20 mm wide, ovate, more or less acute toward both ends; wall thick, without distinct striations, four-compartmented at base; husk thick.

Discussion. This species was described on the basis of specimens from the Pliocene “*Pinus trifolia* bed” in Central Hondo, Japan. Subsequent to describing these specimens as a new species (Miki, 1941), he transferred them to *Carya ventricosa* Unger (Miki, 1955). However, since the European fossils of *C. ventricosa* have prominent intrawall lacunae and only minor development of the secondary septum, the Japanese specimens are best retained in the separate species.

Carya striata Miki, J. Inst. Polytechn. Osaka City Univ., Ser. D, Biol. 6: 133. pl. 1: fig. A. fig. 1A. 1955.

Description. Nut oblong, 20–30 mm long, 15–20 mm wide, shell 1–2 mm thick, with many distinct striations on surface, without lacunae in upper part; four-compartmented at base; secondary septum thin, triangular in plane of dehiscence.

Discussion. This species is known from several localities in the Neogene of Japan. It differs from *Carya nanocarpa* only in the presence of distinct surface striations.

FIGURE 33. Fruits of *Carya florissantensis* Manchester and staminate inflorescences of *Carya* sp. from the Lower Oligocene Florissant Beds of Colorado. A–C. *Carya florissantensis*, $\times 1$.—A. Holotype, showing two of the four prominent angles characteristic of *Carya* (FM-PP 3174).—B. Stereo-pair of a locule cast (UCMP 3603).—C. Stereo-pair of a locule cast within the mold of a nutshell, viewed in the plane of the primary septum. Three of the longitudinal angles are visible on the lower portion of the nut. Cleavage at the base of the locule cast suggests a slight secondary septum (UCMP 3602).—D. Staminate inflorescences (UCM coll.), $\times 1.5$.—E. Scanning electron micrograph of a pollen mass from catkin in D. Note that the pores occur only on one hemisphere of the individual grains, $\times 1,000$.—F. Detail of pollen showing distribution of coni on surface, $\times 2,000$.

Carya ovatocarpa Miki, Jap. J. Bot. 11: 265. pl. 6: fig. Da. fig. 9c. 1941; J. Inst. Polytechn. Osaka City Univ., Ser. D, Biol. 6: 133. pl. 1A. fig. 3Ab. 1955.

Description. Nut 15–20 mm long, 15–20 mm wide, ovoid with striate surface; walls 1–2 mm thick; lacunae present in the upper part; locule surface striated, secondary septum thin, triangular in plane of dehiscence.

Discussion. *Carya ovatocarpa* closely resembles *C. striata* and is often found in the same deposits. However, the presence of lacunae distinguishes this species from *C. striata* and the other species of *Carya* described by Miki (1955). Mai (1981: 370) considers this species to be

closely related to the European fossil *C. strychnina* and to the extant Asian *C. poilanei*.

NORTH AMERICAN *CARYA* FRUIT RECORD

Although there are numerous reports of *Carya* pollen and foliage in the North American record, relatively few fruit occurrences are known.

***Carya florissantensis* Manchester, sp. nov.** Figure 33A–C.

Carya libbeyi (Lesquereux) MacGinitie, Publ. Carnegie Inst. Wash. 589. pl. 28: figs. 2–4. 1953. pro parte.

Diagnosis. Nuts 20–25 mm long, 18–22 mm wide, ovoid with rounded or slightly pointed apex;

FIGURE 34. *Carya washingtonensis* Manchester from the Miocene of Washington.—A. Original mass of silicified nuts as recovered from within a silicified *Platanus* log. Specimen now lost, possibly disaggregated and dispersed among various collections. Photo courtesy of Thomas J. Bones, $\times 0.33$.—B. Single nut from the mass showing line of dehiscence (IU 5343), $\times 1.5$.—C. Another specimen sectioned transversely near the equator, showing vascularized inner ribs of the nut shell (HU 60073B), $\times 1.5$.—D. Stereo-pair of the holotype (HU 60073A), $\times 1$.—E. Apical view of the holotype, $\times 1.5$.—F. Basal section of nut shown in C, showing well-developed secondary and primary septa dividing locule into four compartments, $\times 1.5$.

base of endocarp with a protruding rhomboidal complex 1.5 mm, endocarp surface almost smooth with four prominent corners corresponding to lines of husk dehiscence. Wall thickness, inferred from separation between locule cast and surrounding endocarp mold, 1–1.5 mm. Two pairs of well-developed inner ribs defining longitudinal grooves in the locule casts. Locule surface transversely striate. Presence or absence of lacunae and mode of vasculature unknown. Seed (locule cast) apparently two-lobed at base; secondary septum not present or not preserved.

Specimens. The holotype is FM-PP 3174 (Fig. 33A), and the paratypes are UCMP 3602 (Fig. 33C), UCMP 3603 (Fig. 33B), and FM-PP 22993.

Discussion. These fruits occur in the Lower Oligocene Florissant beds of Colorado. Lesqueux (1883) ascribed specimens to the European species *Carya rostrata* Goeppert and *Juglans costata* Unger. In size and the strongly four-an-

gled aspect, the fruits closely resemble *C. quadrangula* (Kirchheimer) Leroy from the Oligocene of Germany. However, because only casts are preserved, it is not possible to compare the Florissant material critically with that of European fossils or extant species. MacGinitie (1953) figured three fruits together with leaves and leaflets of *C. libbeyi* (Lesq.) MacGinitie from the Florissant flora but did not mention them in the text. Although it is possible that the fruits represent the same species as *C. libbeyi* foliage, they have not been found in physical connection and the new name *C. florissantensis* is hereby proposed for the fruits. Staminate catkins with *Carya* pollen also occur at Florissant (Fig. 33D–F).

***Carya washingtonensis* Manchester, sp. nov.** Figure 34A–F.

Diagnosis. Nuts 18–20 mm long, 14–19 mm wide, globose; surface almost smooth, but faintly

wrinkled and with four angles weakly developed apically; walls and septa about 1.5 mm thick, without lacunae; secondary septum present, locule divided into four compartments basally; inner ribs well developed, containing vascular bundles; placentary bundles of primary septum arching out peripherally.

Specimens. The holotype is HU 60073A (Fig. 34D, E), and the paratypes include IU 5343 (Fig. 34B) and HU 60073B (Fig. 34C, F).

Discussion. *Carya washingtonensis* is represented by numerous silicified nuts from the Miocene of Kittitas County, Washington. The specimens, now distributed among various institutions and private collectors, came from a single silicified mass (Fig. 34A) associated with a fossil sycamore stump discovered by Cline-smith in the 1940s. The original mass contained well over 50 nuts and is thought to represent a Miocene rodent cache. Although quality of preservation is variable, some sectioned specimens show details of locule configuration and endocarp vasculature. The lack of lacunae and presence of a good secondary septum (Fig. 34F) are particularly interesting. These features characterize some extant species of sect. *Apocarya* and all extant species of sect. *Carya*.

GENERAL DISCUSSION AND CONCLUSIONS, HICOREAE

The first hints of the Hicoreae occur in the Paleocene. *Caryapollenites* pollen appears in the late Paleocene of Europe and North America, apparently having evolved from more generalized *Momipites* pollen that occurs earlier in the record (Nichols & Ott, 1978). These early *Caryapollenites* grains differ only in smaller size from pollen typical of extant *Carya*. There are numerous reports of *Carya* foliage from the early Tertiary, but most require critical re-evaluation. Although pollen and foliage similar to extant *Carya* foliage and *Caryapollenites* occur in the Upper Paleocene and early Eocene, fruits with characters diagnostic of extant *Carya* have not been found prior to the Eocene. I suggest that some of the early Tertiary fruits attributed to *Juglandicarya* (e.g., *J. simplicarpa*, sp. nov. and *J. lubbocki* Reid & Chandler) may represent the Hicoreae and could be forerunners of *Carya*. These species lack the well-developed inner ribs diagnostic of the modern genus as well as the four-cornered aspect and basal protruberance

characteristic of most modern representatives. The evolution of hickory wood remains to be investigated. Although Miocene and modern *Carya* xylem is easily distinguished from that of other tribes, no Paleogene records are available.

The evolution of hickory nuts appears to have coincided with that of squirrels. The Sciuridae first occur in the fossil record of Europe and North America in the Oligocene (Romer, 1966), just as *Carya* fruits appear. Nut storage, a behavioral trait of temperate squirrels (Ridley, 1930), dates back at least to the Miocene as suggested by the large accumulation of *Carya washingtonensis* nuts within a silicified sycamore stump (Fig. 34A). More primitive types of rodents, and the *Juglandicarya* type of fruit, extend back to the Paleocene, thus antedating the appearance of both squirrels and *Carya*. It is likely that the evolution of rodents with jaw musculature better adapted for nut-munching brought about selection against nuts with the simple locule morphology of *Juglandicarya simplicarpa* and *J. lubbocki*. The seeds of these species could be removed relatively easily. The development of inner ribs and the secondary septum, as observed in *Carya*, probably discouraged the direct removal of seeds from immature and freshly fallen nuts. The convoluted nature of *Carya* locules effectively locks the seed within the hard nutshell. The burial of such fruits by squirrels (often at some distance from the parent tree; Ridley, 1930) may promote the decay and softening of the endocarp, making them available for subsequent eating, but also improves the likelihood of germination.

The map in Figure 35 shows present and past geographic ranges of the Hicoreae. During the Oligocene and Neogene, *Carya* became widely distributed across the Northern Hemisphere. The geographic range of the genus in the Miocene was much broader than today, with occurrences including Europe, Siberia, and western North America, where the genus is absent today. A more detailed map of European occurrences is presented by Mai (1981). The present-day disjunct distribution of *Carya* between southeast Asia and eastern North America is explained by extinctions in large parts of its former range during the uppermost Tertiary and Pleistocene.

Judging from characters of fossil fruits, sects. *Apocarya* and *Sinocarya* appear to have a longer history than sect. *Carya*. The occurrence of prominent lacunae in the shell wall and the absence or only weak development of the secondary septum suggests that most of the fruits described

FIGURE 35. Map showing modern and fossil distribution of *Carya*. Modern distribution (after Stone, 1962, modified with data from Kuang et al., 1979) indicated by shading. Fossil fruit occurrences indicated by dots.—1. *Carya washingtonensis*, Miocene.—2. *C. florissantensis*, Lower Oligocene.—3. Numerous European species reviewed and mapped in detail by Mai (1981), Middle Eocene to Pliocene.—4. *C. kompassica*, Miocene?—5. *C. kryshstofovichii*, Oligocene.—6. *C. miocathayensis*.—7, 8. *C. leiocarpa*, *C. nanocarpa*, *C. striata*, and *C. ovata*, Miocene-Pliocene.

here, including most of those from Europe, do not represent sect. *Carya*. Such fruits extend back to the early Eocene. The foliage record provides corroborative evidence for recognition of sect. *Apocarya* in the Paleogene. *Carya libbeyi* leaves from the Early Oligocene Florissant flora bore nine to 11 leaflets, a high number that is characteristic of sect. *Apocarya*. Extant species of sects. *Sinensis* and *Carya* usually have five to seven leaflets. The extent of intergradation in characters between modern sects. *Carya*, *Sinocarya*, and *Apocarya* species (Stone, 1963; Stone et al., 1969) suggests that their divergence was relatively recent, perhaps still incipient. The earliest records that appear to represent sect. *Eucarya* are Miocene and include fruits of *Carya washingtonensis*, sp. nov. and foliage of *C. egregia* LaMotte (1936) from the western United States. Mai (1981) considers the European fossil nut species *C. rugosa* (Miocene), *C. angulata*, and *C. askenasyi* (Pliocene) to be representatives of sect. *Carya* based upon their high secondary septum and lack of lacunae. These same features also occur in extant species of sect. *Sinocarya* (*C. cathayensis*, *C. tonkinensis*), however, and the sectional determination of the fossils may be subject to revision.

All but two modern species of sect. *Carya* exhibit tetraploidy—a derived feature with respect to the rest of the family. Although the section may have been present as early as the Miocene, the antiquity of tetraploidy has not been determined. Stone (1961) has noted a marked correlation between stomatal size and chromosome number in modern hickories. It would be interesting to examine the cuticle of fossil *Carya* leaflet remains of various ages to infer ploidy level.

JUGLANDEAE

The Juglandaceae consists of three modern genera: *Juglans*, the walnut, and *Cyclocarya* and *Pterocarya*, the wingnuts. These are the only juglandaceous genera with septate pith. In addition, features of floral morphology, pollen aperture number, wood anatomy, and leaf architecture attest to a close natural relationship between these genera (Manning, 1978). The fossil record of this tribe is extensive and includes both modern and extinct genera (Table 6).

Juglans has 21 living species and has the greatest geographic distribution and ecological amplitude encountered among extant Juglandaceae with representatives in North, Middle, and South America as well as in Europe and Asia. Three sections are recognized on the basis of fruit mor-

phology, wood anatomy, leaf architecture, and, to some extent, pollen morphology: *Rhysocaryon* (black walnuts), of American distribution; *Cardiocaryon* (butternuts), disjunct between eastern North America and Asia; and *Dioscaryon* (Persian walnut), of Eurasian distribution. The North American butternut, *J. cinerea*, is treated as a separate section, *Trachycaryon*, by some authors (e.g., Manning, 1978) but differs only in budscale condition from the Asian butternuts and is here considered a member of sect. *Cardiocaryon*.

Pterocarya and *Cyclocarya*, easily distinguished from *Juglans* by their smaller endocarps and winged fruits, are limited to the Old World today. *Cyclocarya* has a single living species confined to eastern China. *Pterocarya* has five species: one in the Caucasus region and the rest extending from southwest Asia to Japan. Both genera were monographed in detail by Iljinskaya (1953). Manning (1975, 1978) retains *Cyclocarya* as a subgenus of *Pterocarya*. However, in the judgement of Iljinskaya (1953), Dorofeev (1970b), Wolfe and Tanai (1980), and Manchester and Dilcher (1982), the taxa are sufficiently distinct to be recognized as separate, although closely related, genera. Both have good fossil records confirming their integrity at least back to the Eocene. New data presented herein show that the styler orientation of fossil and modern *Cyclocarya* is distinct from that of *Juglans* and *Pterocarya*.

POLLEN

The morphology of extant pollen of the Juglandaceae has been reviewed by Whitehead (1965) and Stone and Broome (1975). Pore number, usually in excess of three, differentiates extant species of this tribe from other tribes of the family. Within the tribe there is a trend of increased pollen size, pore number, and heteropolarity in the sequence: *Cyclocarya*, *Pterocarya*, *Juglans* (Table 7). *Cyclocarya* has smaller grains that are normally stephanoporate and tetraporate. *Pterocarya* usually has five to seven pores and only a small percentage of heteropolar grains. *Juglans* is typified by a greater number of pores (six to 17) and a high percentage of heteropolar grains. Stone and Broome (1975) note that pollen grains of *J.* sect. *Cardiocaryon* "grade imperceptively into *Pterocarya* on the one hand and *J.* sect. *Rhysocaryon* on the other." Likewise, there is intergradation between *Cyclocarya* and *Pterocarya*. This situation presents problems for the determination of dispersed fossil grains.

TABLE 6. Important fossil occurrences of Juglandaeae.

Taxon	Age and Location	Comment
POLLEN		
<i>Momipites</i> Wodehouse sp.	Paleocene; North Dakota	Simple triporate pollen associated with fruits of <i>Cyclocarya brownii</i> .
" <i>Polyporopollenites</i> cf. <i>stelatus</i> " (Potonié) Thompson & Pflug	Upper Eocene; France	This name given by Chateauneuf (1980) to tetraporate isopolar pollen similar to that of extant <i>Cyclocarya paliurus</i> .
<i>Pterocarya grandis</i> Stanley	Paleocene; South Dakota, Montana	Pentaporate isopolar pollen similar to extant <i>Pterocarya</i> .
<i>Polyporopollenites stellatus</i> (Potonié) Thompson & Pflug	Eocene to Miocene; Europe, North America, Asia	5- to 6-porate isopolar pollen similar to that of extant <i>Pterocarya</i> .
<i>Multiporopollenites maculosus</i>	Middle Eocene to Miocene; Europe	Heteropolar grains with six to many pores, probably equivalent to extant <i>Juglans</i> .
WOOD		
<i>Pterocaryoxylon</i> Müller-Stoll & Mädler	Middle Eocene to Miocene; Northern Hemisphere	Organ genus for fossil woods with anatomy like that of extant Juglandaeae.
FOLIAGE		
" <i>Pterocarya</i> " <i>glabra</i> Brown	Paleocene; Wyoming	Leaflets associated with fruits of <i>Polyp-tera</i> ; differentiated from extant Juglandaeae by long petiolules.
" <i>Pterocarya</i> " <i>hispida</i> Brown	Paleocene; Montana, North Dakota	Leaflets associated with fruits of <i>Cyclocarya brownii</i> . Differs from extant foliage by the high-arching secondary veins.
<i>Juglans</i> L. (?) sp.	Middle Eocene; Oregon	Leaflets associated with fruits of <i>Juglans clarnensis</i> .
FRUITS		
<i>Cyclocarya brownii</i> Manchester & Dilcher	Paleocene; North Dakota, Montana	Species from Montana and North Dakota with wing, style, and locule morphology like extant <i>Cyclocarya paliurus</i> but distinguished by its pyramidal nutlet and basal wing attachment.
<i>Cyclocarya minuta</i> Manchester	Paleocene; Wyoming	Species with fruit much smaller than <i>Cyclocarya brownii</i> and with a circular (not pyramidal) nutlet.
<i>C. coalmontensis</i> Manchester & Dilcher	Upper Paleocene or Lower Eocene; Colorado	Species with a pyramidal nutlet, distinguished from <i>Cyclocarya brownii</i> by its smaller wing and larger nutlet.
<i>Juglandicarya depressa</i> Reid & Chandler	Early Eocene; southern England	Earliest nutlet of possible relation to <i>Cyclocarya</i> known in Europe.
<i>Cyclocarya cycloptera</i> (Schlechtendal) Iljin-skaya	Oligocene to Pliocene; Europe, Asia	Fruits with large wing and round nutlet resembling modern <i>Cyclocarya paliurus</i> ; morphology of nutlets not preserved.
<i>C. tavidensis</i> Dorofeev	Oligocene; Tavda River, Soviet Union	Isolated nutlets distinguished from nutlets of the modern species by globose shape and smoother ribbing.
<i>C. tymensis</i> Dorofeev	Oligocene; western Siberia	Isolated nutlets morphologically intermediate between <i>Cyclocarya tavidensis</i> and <i>C. paliurus</i> .
<i>C. tomskiana</i> Dorofeev	Oligocene; western Asia, Europe	Isolated nutlets similar to <i>Cyclocarya tymensis</i> but larger and smoother.

TABLE 6. (Continued).

Taxon	Age and Location	Comment
<i>Sphaerocarya</i> Dorofeev	Oligocene to Pliocene; Asia, Europe	Genus with three Eurasian species accommodating nutlets with internal morphology like modern <i>Cyclocarya</i> but with a globose, smooth exterior, thought to have been wingless.
<i>Polyptera</i> Manchester & Dilcher	Paleocene; Wyoming	Extinct fruit type similar to <i>Cyclocarya coalmontensis</i> but with the wing divided into eight to ten separate petaloid lobes.
<i>Pterocarya macginitii</i> Manchester & Dilcher	Middle Eocene; Wyoming	Earliest known <i>Pterocarya</i> . Relatively small nutlet with two ovoid wings and carinal style arms.
<i>P. occidentalis</i> Manchester	Oligocene; Oregon, Washington	Species with larger nutlet. Wings similar to extant <i>Pterocarya</i> species.
<i>P. eomacroptera</i> Manchester	Miocene; Idaho	Species with exceptionally large wings resembling extant <i>Pterocarya macroptera</i> and <i>P. rhoifolia</i> .
<i>P. smileyi</i> Manchester	Miocene; Idaho	Species with relatively small wings and a tubular perianth similar to extant <i>Pterocarya stenoptera</i> and <i>P. fraxinifolia</i> .
<i>Pterocarya</i> Kunth sp.	Miocene; Idaho	Isolated nutlets with a pair of cusp-like protrusions of the secondary septum.
<i>P. raciborskii</i> Zablocki	Middle Miocene; Poland	Species for wingless <i>Pterocarya</i> nutlets.
<i>P. limburgensis</i> Reid	Lower to Upper Pliocene; central Europe	Wingless nutlets similar to extant <i>Pterocarya fraxinifolia</i> .
<i>P. castaneaefolia</i> (Goepp.) Schlechtendal	Oligocene to Neogene; Europe, western Asia	<i>Pterocarya</i> fruit impressions with intact wings probably representing two or more actual species.
<i>P. crassa</i> Dorofeev	Miocene; western Siberia	Species of wingless nutlets.
<i>P. kireevskiana</i> Dorofeev	Miocene; western Siberia	Wingless nutlets similar to extant <i>Pterocarya stenoptera</i> .
<i>P. protostenoptera</i> Tanai	Miocene; Korea, Japan	Species with wings intact, similar to extant <i>Pterocarya stenoptera</i> .
<i>P. asymmetrosa</i> Kono	Neogene; Japan	Species similar in wing configuration to extant <i>Pterocarya rhoifolia</i> .
<i>Juglans</i> sect. <i>Rhysocaryon</i> Dode	Middle Eocene to Recent; North and South America	This section comprises the black walnuts and is known only from America.
<i>Juglans clarnensis</i> Scott	Middle Eocene; Oregon	Earliest known <i>Juglans</i> fruit. Nutshell features of extant sect. <i>Rhysocaryon</i> but with a simpler locule.
<i>J. siouxensis</i> (Barbour) Berry	Lower Oligocene; Nebraska	Locule casts clearly attributable to sect. <i>Rhysocaryon</i> .
<i>J. calvertiana</i> Berry	Miocene; Maryland, Virginia	Oldest fossil occurrence of black walnuts known from the eastern United States.
<i>J. nevadensis</i> Berry	Miocene; Nevada	Fossil nut indicating former presence of black walnuts outside of their present range.
<i>J. linkii</i> Brown	Late Miocene or early Pliocene; Ecuador	Earliest record of <i>Juglans</i> in South America; sect. <i>Rhysocaryon</i> .
<i>Juglans</i> sect. <i>Cardiocaryon</i> Dode	Early Oligocene to Recent; Northern Hemisphere	This section comprises the butternuts of Asia and eastern North America and has fossil records in Europe and western North America, as well as within its modern geographic range.

TABLE 6. (Continued).

Taxon	Age and Location	Comment
<i>J. lacunosa</i> Manchester	Early to middle Oligocene; Alaska, Washington—Miocene; Idaho	Earliest known butternut and the only record of smooth-walled butternuts in North America.
<i>J. tephrodes</i> Unger	Middle or late Oligocene to Pliocene; Europe	Earliest scabrate-shelled butternut; more similar to extant North American than Asian species.
<i>J. megacinerea</i> Miki ex Chaney	Miocene to Plio-Pleistocene; Japan	Largest fruits known for the Juglandaceae. Scabrate-shelled butternut with several intra-wall lacunae as in extant Asian species.
<i>J. siberica</i> Dorofeev	Miocene; Siberia	One of three scabrate-shelled butternut species recognized from Siberia, similar to extant American <i>Juglans cinerea</i> but lacunar configuration unknown.
<i>J. eocinerea</i> Hills, Klován & Sweet	Miocene; Banks Island, arctic Canada	Scabrate-shelled butternut with several large lacunae as in extant Asian species.

Nichols (1973) has suggested that determination of fossil pollen to these genera cannot be done with certainty and advises use of organ generic names for dispersed pollen in this complex. This is especially important because similar or identical grains might have been produced by extinct genera such as *Polyptera* and *Sphaerocarya*. However, useful suggestions of modern affinity may be derived from the analysis of numerous grains in a population considered to represent a single species. If numerous heteropolar grains with high pore number are encountered, *Juglans* is probable. Similarly, numerous stephanoporate grains of four pores and five to seven pores are suggestive of *Cyclocarya* and *Pterocarya*, respectively. The most reliable determinations would come from studies of pollen from fossil stamens; however, no fossil catkins of the Juglandaceae have been described in detail.

To date, there have been no reports of *Cyclocarya* based on fossil pollen. It is likely that the characteristically tetraporate pollen has been overlooked and sometimes misidentified to convergent genera of the Myricaceae and Betulaceae. It is also likely that some of the Paleogene representatives were more commonly triporate than tetraporate, as suggested by analysis of American Paleocene pollen assemblages.

Recent maceration of matrix from *Cyclocarya brownii* fruit specimens from the Paleocene Fort Union Formation has yielded a pollen assemblage including a single type of juglandaceous pollen (*Momipites*) (Fig. 37H, I). The grains are

small (21–23 μm), isopolar, and triporate, and have the typical juglandaceous ornamentation consisting of evenly spaced coni. Since similar pollen is produced today by modern *Engelhardtia*, it is interesting that intensive collecting of various localities in the Fort Union Formation has failed to yield fruits or foliage assignable to the Engelhardieae. Triporate grains occur occasionally in extant *C. paliurus* pollen but are usually somewhat larger than the fossil grains (Iljin-skaya, 1953; Whitehead, 1965; Stone & Broome, 1975); since no tetraporate grains have been recovered, it is possible that early Tertiary representatives maintained the presumably more primitive triporate pollen in greater frequency.

Chateaufeuf (1980: 108) describes as *Polyporopollenites* cf. *stellatus* a type of grain with four, rarely five, pores observed to be very abundant in Upper Eocene deposits in the Paris Basin. She figures an example measuring 33 μm that is quite similar to pollen of extant *Cyclocarya* (Chateaufeuf, 1980, pl. 9: fig. 25). This might represent an early appearance of the genus in western Europe, although fruits are not confirmed prior to the Oligocene.

Pollen that at least superficially resembles *Pterocarya* has been reported from the Maastichtian of the central part of the Soviet Arctic (*Pterocarya* cf. *stenopteroides*, Bondarenko, 1973, fig. 21) and is common in the Maastichtian Hell Creek Formation in South Dakota (*Pterocarya levis* Stan., Stanley, 1965) and northeastern Montana [*Pterocaryapollenites stellatus* (Pot.)

TABLE 7. Pore number and size ranges for pollen of extant Juglandaceae. Data from Stone and Broome (1975).

	Pore Number	Size (μm)	Heteropolar Grains (%)
<i>Cyclocarya</i>	(3-)4(-5)	(20-)25-33(-40)	0%
<i>Pterocarya</i>	(4-)5-7(-8)	(24-)28-38(-45)	0.5-19%
<i>Juglans</i>	(2-)6-17(-37)	(20-)30-49(-59)	65-100%
<i>J. sect. Cardiocaryon</i>	(2-)6-8(-15)	(29-)34-41(-46)	65-99%
<i>J. sect. Rhysocaryon</i>	(5-)8-17(-37)	(20-)30-40(-44)	99.5%
<i>J. sect. Dioscaryon</i>	(7-)10-13(-20)	(34-)42-49(-59)	100%

Thiergart, Norton & Hall, 1969; *P. levis* (Stanley) Oltz, Oltz, 1969; *Pterocarya* cf. *levis* Stanley, Tschudy, 1970]. The grains are periporate with five to six pores but differ from extant and Tertiary *Pterocarya* grains in their very small size (15-20 μm) and apparently smooth exine surface. The pollen has not been examined by electron microscopy, and its juglandaceous affinity remains to be confirmed.

Fossil stephanoporate grains of five to six pores, conforming in morphology to extant *Pterocarya*, first appear in the early Tertiary and have been placed variously in *Pterocarya*, *Pterocaryapollenites* Potonie, *Polyporopollenites* Pflug, and *Polyatriopollenites* Pflug. To date, none of the fossil occurrences have been studied with electron microscopy. *Pterocarya*-like pollen is reported only rarely from Paleocene sediments. Stanley (1965) describes *Pterocarya grandis* as infrequent in the Paleocene Ludlow Member of the Fort Union Formation in South Dakota. The grains are pentaporate with an equatorial diameter of 25-32 μm with scabrate to psilate sculpture and meridionally elongate (2 μm by 4 μm) pores. A similar grain is figured by Penny (1969, pl. 16-3: fig. 25) from the Fort Union Formation in Montana. This appears to be a valid Paleocene record for the tribe and perhaps the genus. Such pollen has not been reported from the palynologically well-studied Paleocene strata of western Europe (e.g., Kedves, 1982) but is figured by Bratzeva (1966) from the Paleocene of the southern part of the Soviet Far East.

Pterocarya-like pollen was apparently widespread in the Eocene of the Northern Hemisphere; however, it is not reported to be especially abundant at any one site. Frederiksen (1979) describes and figures a single grain of "*Polyatriopollenites*" from the uppermost Paleocene or lowermost Eocene Marlborough Clay in northern Virginia. Leopold figures and identifies 6-7-porate *Pterocarya* pollen in the Middle Eocene Kissinger Lakes flora (Leopold & MacGinitie,

1972) and Teton area (Love et al., 1978) but does not comment on relative abundance. The validity of these Middle Eocene assignments to *Pterocarya* is supported by the occurrence of *Pterocarya macginitii* fruits in sediments of comparable age (Green River Formation) in northeastern Utah.

Thompson and Pflug (1953) indicate that in Germany *Polyporopollenites stellatus* first occurs in the Middle Eocene. Gruas-Cavagnetto records, but does not describe or figure, the same species from the Upper Eocene of the Paris Basin (1978) and southern England (1976) but does not observe its occurrence in the earlier Eocene strata of the region.

Pollen attributed to *Pterocarya* becomes more abundant in the Oligocene and Miocene throughout most of the Northern Hemisphere. Asian occurrences include several species described by Voicel (in Samoilovich, 1961) from the Oligocene of western Siberia and "*Pterocarya* aff. *ser-rata*" and "*Pterocarya* aff. *rhoifolia*" from the Paleogene (Oligocene?) of Novosibirsk Islands (Zalinskaya, 1981). Thompson and Pflug (1953) review numerous occurrences of *P. stellatus* in the Oligocene to Pliocene of Europe. In North America, *Pterocarya* pollen is recorded from the Oligocene of Florissant, Colorado (Leopold in Penny, 1969; Leopold & MacGinitie, 1972), the Brandon Lignite of Vermont (Traverse, 1955), and in British Columbia (Piel, 1971; Hopkins et al., 1972). It is recorded as late as the Miocene in Oregon, Idaho (Graham, 1965), and New Jersey (Rachele, 1976; Grellier & Rachele, 1983).

The early record of *Juglans* pollen is poorly known. A single report from the late Cretaceous and early Paleocene is questionable, and most reports from the early Tertiary are based only on a few grains that are not adequately described or figured. Electron microscopy is needed to confirm the affinity of grains from the early part of the record.

Drugg (1967) described and figured *Juglans*-

pollenites from Maastrichtian and Danian strata of central California. The grains are rare but closely resemble *Juglans*, at least as viewed with light microscopy. Since this occurrence predates by a considerable margin the Eocene appearance of *Juglans* elsewhere in North America, it should not be accepted as indicative of *Juglans* without more extensive documentation. There is a possibility that the grains are field contaminants since walnuts formerly grew in the area surrounding the sampling sites (Drugg, pers. comm.).

The earliest reports of *Juglans* pollen are from the Eocene of several localities in North America. Wodehouse (1933) described *J. nigripites* on the basis of a single grain from the Middle Eocene Green River Formation of Wyoming. The grain was described as 40 μm in diameter with a finely granular surface and 11 or 12 pores in a heteropolar arrangement with seven or eight pores situated approximately equatorially and the remainder confined to one polar surface. Frederiksen (1980) mentions and figures a single grain attributed to the same species from the Eocene of South Carolina. Leopold (in Penny, 1969) figures a grain identified as *Juglans* from the pollen assemblage of the Eocene Chalk Bluffs flora of California measuring about 34 μm .

Most European writers have assigned grains of presumed affinity with *Juglans* to the organ genus and species *Multiporopollenites maculosus*. Thompson and Pflug (1953) indicate that *M. maculosus* is unknown in the early Tertiary, uncommon in the mid-Tertiary, and common in the late Tertiary of Germany. Gruas-Cavagnetto (1978) reports, but does not describe or figure, rare grains of *M. maculosus* in the lower and Middle Eocene of the Paris Basin; but this report is inconsistent with data from other parts of western Europe. Lists of juglandaceous pollen from the Eocene of southern England (Sein in Chandler, 1961; Gruas-Cavagnetto, 1976) do not include *Juglans* (or *M. maculosus*), although Pallot (1971) figures *Juglans* pollen from the Oligocene Bembridge flora.

Juglans pollen is widespread in the Oligocene with localities including Siberia (Takhtajan et al., 1963), western Europe (Thompson & Pflug, 1953), the eastern United States (Traverse, 1955), and British Columbia (Piel, 1971; Hopkins et al., 1972) but appears to have been absent until the late Oligocene or Miocene in Central and South America. Mai (1981) refers to a paper by Kuyl et al. (1955) as evidence for the presence of *Juglans* pollen in the Eocene of Venezuela; however, the caption for the *Juglans* grain figured by

Kuyl et al. (1955) states that the pollen is from the Eocene of the southeastern United States. *Juglans* pollen was missing from the Oligocene strata of Puerto Rico studied by Graham and Jarzen (1969) but is present in Miocene assemblages of Veracruz, Mexico (Graham, 1976).

WOOD

The secondary xylem of *Pterocarya*, *Cyclocarya*, and *Juglans* is characterized by medium-sized vessels with exclusively simple perforations, uniseriate to biseriate wavy tangential lines of axial parenchyma, and one to three (to five in some *Juglans*) seriate rays. Other features follow the general pattern for the family (p. 2). *Pterocarya* and *Cyclocarya* generally cannot be differentiated from one another on the basis of wood anatomy and are difficult to discern from *Juglans* sect. *Cardiocaryon*. Miller (1976) has pointed out wood-anatomical features that permit distinction of the three modern sections of *Juglans* and the separation of north temperate and tropical species of sect. *Rhysocaryon*.

The organ genus *Pterocaryoxylon* Müller-Stoll & Mädel (1960) accommodates fossil woods with anatomy of the Juglandaceae. Four species have been assigned to this genus: *P. pannonicum* (Müller-Stoll & Mädel, 1960) from the Lower Pliocene of Hungary; *P. subpannonicum* (Prive, 1974) from the lower Pliocene of France; *P. honshouensis* (Watari) Müller-Stoll & Mädel (1960) from the Miocene of Japan; and *P. knowltoni* Wheeler, Scott, & Barghoorn (1978) from the Middle Eocene of Yellowstone National Park, United States. The oldest of these, *P. knowltoni*, is considered by Wheeler et al. (1978) to be closer to *Pterocarya* sensu lato (including *Cyclocarya*) than to *Juglans* because it exhibits diagonal pore arrangement, a pattern that is usually more pronounced in *Pterocarya* and *Cyclocarya* than in *Juglans*. Regardless of the exact generic identity, this species confirms that wood anatomy of the Juglandaceae had achieved its modern appearance by the Middle Eocene. It would be desirable to determine the pith condition for *P. knowltoni* to confirm the suspicion that chambered pith had evolved in the tribe by the Eocene. Müller-Stoll and Mädel (1960) have figured chambered pith in the silicified specimens of *P. pannonicum*.

FOLIAGE

Leaves of the Juglandaceae are alternate and usually odd-pinnately compound. Cuticular features include hairs, both simple and in tufts of four to

six, as well as the circular peltate scales characteristic of the family (Nagel, 1914). Leaflet margins are serrate (except in *Juglans regia*) with simple more-or-less regularly spaced small teeth. Venation is brochidodromous with secondaries joined to one another by marginal loops or semicraspedodromous with secondaries forking near the margin and sending one or more branches to the teeth and another to the super-adjacent secondary. Intercostal areas are occupied by percurrent, usually closely spaced tertiaries; intersecondaries are infrequent and rarely extend more than one-third of the distance to the margin. The areoles have branched, freely ending veinlets.

Leaflets of *Pterocarya* tend to be oblong-elliptical to obovate, less commonly ovate. The secondaries enter into marginal loops that are often enclosed by an additional row of smaller loops. Teeth are generally acute and non-apiculate with a concave apical flank and convex basal flank. They are uniform in size and close together (3.5 to five teeth per secondary vein), giving the appearance of a hacksaw blade. The main vein of each tooth is a tertiary arising from the marginal loops and enters the tooth directly, without contacting the sinus, following a medial to supra-medial course to the tooth apex.

Leaflets of modern *Cyclocarya* are similar in most architectural features to those of *Pterocarya*. However, the teeth are frequently apiculate and somewhat more widely spaced (2.5 to three per secondary vein) and there is no tendency for looping of marginal tertiary veins.

Juglans leaflets are ovate to oblong-elliptical, less commonly obovate and vary from campodromous to craspedodromous, sometimes even in a single leaflet. The teeth are usually less prominent than those of *Pterocarya* and more widely spaced. The teeth are nervated medially in leaflets of sect. *Cardiocaryon* and western North American species of sect. *Rhysocaryon*. Most species of sect. *Rhysocaryon*, including the eastern North American *J. nigra* and tropical American species show a distinctive type of tooth nervation in which the main vein contacts the sinus and sweeps along the upper flank of the tooth in its course to the tooth apex. This peculiar feature, first pointed out by Wolfe (1959), serves to distinguish this group from sect. *Cardiocaryon* and from *Pterocarya* and *Cyclocarya*. As yet, it has not been reported for fossil *Juglans* leaflets. A similar type of tooth venation occurs in extant *Oreomunnea* and *Alfaroa* and in *Carya aquatica*.

Numerous reports of fossil foliage of *Juglans* and *Pterocarya* are listed by Nagel (1914) and

LaMotte (1952). However, most of the literature is in need of critical re-evaluation—a project that has not been undertaken here. Instead, I will consider selected Paleogene leaflet taxa for which there are correlated fruits.

“*Pterocarya*” *glabra* Brown ex Watt, Taxon 20: 640. 1971. Figure 36A–G.

Pterocarya glabra Brown, Profess. Pap. U.S. Geol. Surv. 375: 57. pl. 18: figs. 1–3, 5–9, 13. 1962.

Description. Leaflets elliptical, ovate to obovate, 0.7–0.4 cm wide, 4–11 cm long, length-to-width ratio 2.5 to 3.2, apex acute, base acute to rounded-obtuse, slightly to markedly asymmetrical, petiolules of both terminal and lateral leaflets long (7–25 mm); secondary veins evenly spaced arising at 35–45°, uniformly curved, ascending apically along the margin, eucamptodromous to semicraspedodromous; 15 to 21 (average 18) pairs of secondaries per lamina; intersecondary veins absent; tertiaries strong, oppositely percurrent, closely spaced (0.5–1.8 mm apart), generally separated by two rows of quaternary areoles; areoles 0.3–0.5 mm, supplied with branched, freely ending veinlets; teeth minute, closely spaced usually with right-angle apices, fed medially by marginal veins of tertiary order. Impressions lack trichome markings.

Specimens. The lectotype (Watt, 1971) is USNM 167491. This and other specimens at the United States National Museum are figured by Brown (1962). Additional specimens are in the collections of Brigham Young University and Indiana University (IU 4865–4869). More than 40 specimens were examined.

Discussion. “*Pterocarya*” *glabra* occurs in the Paleocene Fort Union Formation in southern Wyoming. It has been collected from two areas: in the vicinity of Earnest Butte along Little Bitter Creek, south of Rock Springs (USGS loc. 8920, 8921; IU loc. 15746, 15747) and a site 25 miles north of Baggs (IU loc. 15758; Roth, 1975). In both locations, fruits of *Polyptera manningii* Manchester & Dilcher are closely associated and no other types of juglandaceous fruits or foliage have been recovered.

“*Pterocarya*” *glabra* leaflets are recognized by their long petiolules, the closely spaced high-arching secondaries, and prominent closely spaced tertiaries. In addition, they lack the trichome impressions characteristic of “*Pterocarya*” *hispida*. The leaflets resemble those of

FIGURE 36. "*Pterocarya*" *glabra* Brown leaflets from the Paleocene of southern Wyoming.—A. Specimen with well-preserved venation, showing characteristic long petiolule and fine teeth, IU locality 15746 (IU 4870), $\times 1$.—B. Lectotype showing closely spaced, prominent percurrent tertiaries, uniformly spaced high-angle secondary veins, and long petiolule, USGS locality 8921 (USNM 167491), $\times 1$.—C. Leaf showing at least seven petiolulate leaflets, USGS locality 8920 (USNM 167492), $\times 1$.—D. Higher magnification of B showing small areoles, $\times 5$.—E. Leaflet showing markedly asymmetrical base, IU locality 15758 (IU 5342), $\times 1$.—F, G. Additional specimens from IU locality 15747 showing typical architecture (IU 4866, 4867), $\times 1$.

extant *Pterocarya*, *Cyclocarya*, and *Juglans* in the closely spaced small teeth and in general organization of the venation. However, the ascription of this species to a modern genus seems unwarranted in view of the long petiolules and steeply arching secondaries. The closely associ-

ated fruits were placed along with the foliage in *Pterocarya glabra* by Brown (1962); however, these represent an extinct genus (*Polyptera*) more closely allied to *Cyclocarya* than to *Pterocarya* (Manchester & Dilcher, 1982). Pending more rigorous study of Paleogene juglandaceous foliage,

I refrain from designating a new generic name for this species. However, the name *Pterocarya* should be used only with quotation marks.

"Pterocarya" hispida Brown ex Watt, Taxon 20: 640. 1971. Figure 37A–G.

Pterocarya hispida Brown, Profess. Pap. U.S. Geol. Surv. 375: 57. pl. 19: fig. 1. 1962.

Description. Leaflets ovate to elliptical, less commonly obovate, 3.2–7 cm wide, 4.4–13.5 cm long, length-to-width ratio 1.5 to 2.5, apex rounded, base acute to rounded-obtuse, slightly to markedly asymmetrical, length of petiolules uncertain, lateral leaflets possibly sessile; secondary veins somewhat unevenly spaced and not always uniformly curved, arising at 40–50°, ascending apically near the margin, especially in the upper one-third of the lamina, semicraspedodromous; intersecondaries uncommon and rarely extending more than one-fourth of the distance to the margin; tertiaries percurrent, opposite and alternate, usually spaced evenly, 1.5–2.5 mm apart, alternating with weaker "intertertiary" veins formed by coalesced quaternary veins; areoles 0.3–0.5 mm wide, comprised of fifth-order veins with branched, freely ending veinlets; marginal tertiaries arise as exmedial branches of the secondaries approximately parallel to and the same distance apart as the intercostal tertiaries, flexed apically just inside the leaf margin, and entering the teeth submedially; teeth moderate in size, averaging 2.7–3.9 per secondary with right-angle apices; leaflet impressions with evenly spaced glandular dots.

Specimens. The lectotype is USNM 167492 (Watt, 1971; Brown, 1962, pl. 18: fig. 11). This and three other specimens from USGS locality 8910 are at the United States National Museum. Specimens from Almont, North Dakota, are in the collections of the Field Museum (PP 33617, Fig. 37A; PP 33615, Fig. 37B; PP 33616, Fig. 37C; and PP 33618), the North Dakota Geological Survey (two specimens), and Indiana University (4852). Ten specimens were available for study.

Discussion. The above description is based upon specimens from two localities in the Sentinel Butte Member of the Paleocene Fort Union Formation: one near Broadus, eastern Montana (USGS loc. 8910; Brown, 1962) and the other near Almont, North Dakota (IU loc. 15722; Manchester & Dilcher, 1982). At both localities

the only type of juglandaceous fruit present is *Cyclocarya brownii* Manchester & Dilcher.

"*Pterocarya*" *hispida* is distinguished from "*Pterocarya*" *glabra*, which occurs at other localities in the same formation, by the wider spacing of secondaries and tertiaries and by the tendency of apical secondary veins to sweep upward at high angles with their extremities parallel to the midvein (as in *Cornus*). In addition, all specimens from the two localities cited above share evenly spaced small dots representing the impression of glands or trichomes (Fig. 35F). As noted by Brown (1962), such markings are absent even in the best preserved specimens of "*P.*" *glabra*. On the basis of these criteria, the leaves and leaflets from USGS locality 8920 that Brown attributed to "*P.*" *hispida* (Brown, 1962, pl. 18: figs. 11, 12) are here reassigned to "*P.*" *glabra*.

Except for the high-arching apical secondaries, the architecture of these leaflets is similar to that of extant *Pterocarya* and *Cyclocarya*, and Brown's initial ascription of the species to *Pterocarya* sensu lato was reasonable. However, it is highly probable that the leaflets represent the same species as the co-occurring fruits of *Cyclocarya brownii*. Brown (1962) also recognized this apparent relationship, calling attention to the occurrence of glandular dots on the fruit wings (Fig. 37D) much like those on the leaflet impressions. *Pterocarya* sensu stricto has biwinged fruits distinct from those of *Cyclocarya*. In the absence of physical connection between fruits and foliage, the probable fruits of this species are retained in a separate organ species, *C. brownii*, and are discussed later in this treatment. The teeth of the fossil leaflets are not apiculate as in many specimens of extant *C. paliurus* foliage, but this feature is probably important only at the species level.

Juglans (?) sp. Figure 38A–E.

Description. Leaflets elliptical, oblong to obovate, 2.5–6.8 cm wide, 6–16.5 cm long; length-to-width ratio 2.1 to 2.4, apex and base acute, base slightly asymmetrical, apparently sessile, without petiolules; secondary veins uneven in course, camptodromous to semicraspedodromous, arising from the midvein at angles of 40–60°, curved upward (as in *Cornus*) near the margin; 15 to 18 pairs of secondaries per lamina; intersecondary veins uncommon; tertiaries percurrent, prominent, usually opposite, though not infrequently alternate, 1.6–2.8 mm apart, sepa-

FIGURE 37. "*Pterocarya*" *hispida* (Brown) leaflets and associated pollen from the Paleocene Fort Union Formation of eastern Montana and western North Dakota.—A. Silicified leaflet showing broader shape, and

rated by two to four areoles; areoles orthogonal, formed by quaternary veins; supplied with branched, freely ending veinlets; teeth prominent, regularly spaced with acute to right-angle apices, and straight to concave flanks; principal vein is a tertiary vein that enters the tooth medially.

Specimens. This description is based upon four specimens from the Oregon Museum of Science and Industry: OMSI-PB 609 (slab with two impressions), OMSI-PB 829, OMSI-PB 1371.

Discussion. This species occurs in the middle Eocene Nut Beds locality of the Clarno Formation of Oregon (OMSI loc. 225; Manchester, 1981a) and is of special interest because of its association with the earliest known *Juglans* fruits (*J. clarnensis*, p. 107). The same locality has also yielded engelhardioid wood (Manchester, 1983), locule casts, and platycaryoid pollen; however, the foliage described above and *J. clarnensis* nuts appear to be the only representatives of the Juglandaceae, and it is possible that they were produced by the same species.

These leaflets conform well architecturally with modern leaflets of the Juglandaceae except in the high-arching secondaries. This is a possible primitive feature also seen in the Paleocene species discussed previously. The irregular spacing and course of secondary and tertiary veins is similar to that of extant leaflets of *Juglans* sect. *Rhysocaryon*. However, the shape, size, distribution, and venation of the teeth more closely resemble extant *Pterocarya*. It is possible that the leaflets indeed represent *Pterocarya*; however, in view of the apparent absence of *Pterocarya* fruits in the entire Clarno Formation and the abundance of *J. clarnensis* fruits, my guess is that these leaflets are primitive representatives of *Juglans*.

FRUITS

The fossil fruit record of the Juglandaceae is extensive. The following treatment deals separately with the records of *Cyclocarya*, *Juglandicarya*,

Sphaerocarya, *Polyptera*, *Pterocarya*, and *Juglans*.

Cyclocarya Iljinskaya

Cyclocarya is of special interest because it is the only extant genus in the family that can be traced with confidence as far back as the Paleocene. Fruits of the single living species, *C. paliurus*, of southern China provide the basis for recognition of the fossil species of *Cyclocarya*.

The fruit of *Cyclocarya paliurus* (Fig. 39A) consists of a nutlet surrounded by a large, circular wing. The wing ranges from 2.5 to 5 cm in diameter and has a smooth to undulating margin. It lies in a plane perpendicular to the main axis of the nutlet and is attached almost equatorially. The veins of the wing fan outward in subparallel fashion, occasionally dichotomizing and anastomosing. According to Manning (1978), the wing is formed mostly from the bracteoles of the inflorescence; the bract persists only as a small, often deciduous, scale at the wing margin. The nutlet is almost lensoidal, but with a protruding apex and base, and is ribbed longitudinally. Dorofeev pointed out (1970b) that the vascular bundles are usually situated between the longitudinal ribs rather than at the crests, as in *Pterocarya*. The walls are thick and woody, without lacunae. The primary septum is thick but the foramen is large so that the septum is complete only at the base. The secondary septum is almost or completely missing, resulting in a locule that is two- or, less frequently, four-lobed at the base. Four sepals arise near the apex of the nutlet and two style arms diverge from the nutlet apex.

Floral diagrams have not previously been presented for *Cyclocarya* and it has been assumed that the carpel and stelar orientation is identical to that of *Pterocarya* and *Juglans* (Manning, 1978). In extant *Pterocarya* and *Juglans* the style arms are carinal (diverging in a plane perpendicular to the primary septum) (Fig. 1). However, in *Cyclocarya* the style arms are commissural (diverging in the same plane as the primary septum). This feature was observed in two collec-

more widely spaced secondary and tertiary veins than "*Pterocarya*" *glabra* (Fig. 36). Note apically arching secondaries, from IU locality 15722, Almont, North Dakota (FM-PP 33617), $\times 1$.—B. Smaller specimen from same locality (FM-PP 33615), $\times 1$.—C. Typical *P. hispida* leaflet adjacent to a *Cyclocarya brownii* fruit (lower left), same locality (FM-PP 33616), $\times 1$.—D. Specimen from USGS locality 8910, Broadus, Montana (USNM 364533), $\times 1$.—E. Enlargement of B, showing craspedodromous venation and regularly spaced teeth, $\times 2$.—F. Same specimen, more greatly magnified showing regularly spaced dots representing trichomes, $\times 5$.—G. Additional leaflet from IU locality 15722 (NDGS-A 2539), $\times 1$.—H, I. *Momipites* pollen from matrix of *Cyclocarya brownii* fruits from IU locality 15722, $\times 1,000$.

FIGURE 38. *Juglans* (?) sp. foliage associated with *Juglans clarnensis* Scott fruits in the Middle Eocene Clarno Formation of Oregon OMSI locality 225.—A. Specimen showing percurrent tertiaries, irregular spacing and course of secondaries. Note apically arching secondaries in upper one-third of lamina (OMSI-PB 609b), $\times 1$.—B. Specimen showing well-developed marginal arches of secondary veins (OMSI-PB 829), $\times 1$.—C. Additional

tions of *C. paliurus* (Sun 1296; Cheng 4052) (Fig. 40B) and in the holotype and paratype specimens of the Paleocene *C. brownii* (Fig. 40A). From the mature fruits studied, I was unable to determine the orientation of the carpels with respect to the bract. If the carpels are median, as in *Pterocarya* and *Juglans*, the resulting floral diagram (Fig. 40C) would resemble that for *Engelhardia* sect. *Engelhardia*. If, on the other hand, the carpels are transverse (Fig. 40D), there would be a close resemblance to *Carya*. The former interpretation is assumed to be correct (Fig. 1) but requires verification.

Cyclocarya brownii Manchester & Dilcher, Amer. J. Bot. 69: 278. figs. 1–5, 9–11, 15, 17–24, 28. 1982. Figure 39B–J.

Pterocarya hispida Brown, Profess. Pap. U.S. Geol. Surv. 375: 57. pl. 68: figs. 12, 13 (fruits only). 1962; Brown in Hickey, Mem. Geol. Soc. Amer. 150: 119. pl. 15: fig. 9. 1977.

Discussion. *Cyclocarya brownii* is the oldest species of *Cyclocarya* previously documented in the literature. It occurs in the Upper Paleocene of the Fort Union Formation in Montana, Wyoming, and North Dakota, and in the Upper Paleocene Hebron member of the Golden Valley Formation in North Dakota. Given the age of this species, it is rather surprising that it can be accommodated by a modern genus. However, such placement is supported by a detailed investigation of the internal and external fruit morphology (Manchester & Dilcher, 1982). Collections of silicified material from the Almont, North Dakota, locality include more than 60 well-preserved specimens of *C. brownii* (IU and FM collections) and suggest that the morphological variation within the population was similar to that of extant *C. paliurus*.

Cyclocarya brownii fruits are indistinguishable from those of extant *C. paliurus* in venation, shape, size, and orientation of the wing, and in the thick nutlet wall lacking lacunae, the smooth locule surface, and the commissural styler arms. A recently collected specimen shows an attached pedicel 2 cm long (Fig. 39B). Fruits of the extant species are borne sessile or on short pedicels up

to 0.5 cm long. Additional features separating this Paleocene species from the living one include nutlet shape, wing attachment, and septation (Manchester & Dilcher, 1982). The nutlet of the fossil is pyramid-shaped rather than lensoidal, and the wing attaches basally rather than subequatorially. The secondary septum appears to be present in all of the fossil specimens but is present only occasionally in the living populations.

Matrix of *Cyclocarya* fruits from the Almont, North Dakota, locality was found to contain a rich dispersed pollen assemblage. Only one type of juglandaceous pollen was observed: triporate grains assignable to the organ genus *Momipites* (Fig. 37H, I). Pollen of extant *Cyclocarya* is predominantly tetraporate with only a small proportion of triporate grains (Stone & Broome, 1975); however, it is possible that the more primitive triporate condition was more prevalent in the Paleocene species. As already discussed, foliage of "*Pterocarya*" *hispida* Brown (Fig. 37C) co-occurs with *C. brownii* and has glandular dots similar to those of the fruit wing, suggesting that they may constitute different organs of a single species.

Cyclocarya minuta Manchester, sp. nov. Figure 41C–E.

Diagnosis. Fruits consisting of a rounded nutlet surrounded by a circular, flange-like wing, 10–16 mm diam., undulating to almost smooth margin; width of wing measured from nutlet edge to wing margin, 3–8 mm; venation fanning outward from the nutlet with frequent dichotomies and occasional anastomoses toward the margin; nutlet 4–4.5 mm diam., circular in transverse view; secondary septum present but weakly developed. Styler configuration unknown.

Specimens. The holotype is USNM 364530 (Fig. 41C), and the paratype is USNM 364531 (Fig. 41D) from USGS locality 9483. Twelve additional specimens from IU locality 15757, including IU 5341 (Fig. 41E), were examined.

Discussion. Although distinct from *Cyclocarya brownii*, this new species also occurs in the

specimen showing high-angle secondary veins (OMSI-PB 609b), $\times 1$.—D. Higher magnification of same leaflet showing areolation with branched freely ending veinlets, $\times 5$.—E. Higher magnification of A, showing teeth with medial vein insertion, $\times 5$.

FIGURE 39. Modern and Paleocene *Cyclocarya* fruits.—A. *Cyclocarya paliurus* (Batalin) Iljinsk. Modern fruit from Tchen-Keou-tin, China, *Farges 1175* (IU mod. ref. coll.; from A). The nutlet in the center of the wing is circular in this transverse view, $\times 1.5$. B–J. *Cyclocarya brownii* Manchester & Dilcher from the Paleocene

FIGURE 40. Relative style and carpel orientation in fossil and modern *Cyclocarya*. —A. Paleocene *Cyclocarya brownii*. Style arms diverge in the plane of the primary septum. Dotted horizontal line represents the plane of dehiscence and secondary septum. —B. Modern *Cyclocarya paliurus* showing the same (commissural) styler orientation as *C. brownii*. —C. Floral diagram for *Cyclocarya* assuming median orientation of carpels with respect to bract. —D. Floral diagram assuming transverse orientation of carpels.

Paleocene Fort Union Formation. It is presently known only from two localities in central Wyoming, one in the Monument Hills District in Converse County (USGS loc. 9483) and the other at Signor Ridge in Fremont County (IU loc. 15757). *Cyclocarya minuta* specimens are clearly separable from all known specimens of *C. brownii* by their smaller size (10–16 mm versus 20–43 mm) and distinct nutlet configuration. The nutlet is circular as seen in transverse view, in contrast to the other North American fossil species that are square in transverse view. It appears that the three-dimensional shape of the nutlet was spheroidal or lensoidal but not pyramidal as in the other North American fossils. Spheroidal and lensoidal nutlets both occur in *Cyclocarya* fossils of the European Tertiary, but only lensoidal nutlets have been observed in the extant species.

Cyclocarya coalmontensis Manchester & Dilcher, Amer. J. Bot. 69: 279–280. figs. 25–27. 1982. Figure 41A, B.

Discussion. This species occurs in the uppermost Paleocene or early Eocene Coalmont Formation of Colorado. It resembles *Cyclocarya*

brownii in having a pyramidal nutlet and basal wing attachment but, like *C. minuta*, has a wing span only one-half to one-third as large as that of *C. brownii*. Despite the small diameter of its wing (12–13 mm), the nutlet (5–8 mm) is larger than those encountered in *C. brownii* so that the width of the wing (1–3 mm) is proportionately very small. The differences in relative nutlet and wing dimensions between this late Paleocene or early Eocene species and *C. brownii* suggest a trend toward reduction of wings and enlargement of the nutlet—possibly a shift favoring animal dispersal.

No later occurrences of *Cyclocarya* have been documented in North America. I have studied morphologically similar fruits assigned to *Cyclocarya* by Wolfe and Tanai (1980) from the Miocene (Seldovia Point, Alaska and Collawash, Oregon). These specimens represent the convergent rhamnaceous species *Paliurus hesperius* Berry (Manchester & Dilcher, 1982). Although *Cyclocarya* must have been present in Eurasia prior to its disappearance from North America, the first confirmed occurrences are Oligocene. It is possible, however, that some of the early Eocene

Fort Union Formation of North Dakota and Montana. —B. Specimen showing nutlet attached to a long pedicel (arrow) and surrounded by a circular wing from near Almont, North Dakota (IU 15722-4762), $\times 1.5$. —C. Fruit showing the typical diamond-shaped nutlet, as viewed transversely, surrounded by a large wing. Note the well-developed primary and secondary septa intersecting at the vertical axis of the nutlet from near Broadus, Montana, USGS locality 8910 (USNM 298887), $\times 1.5$. —D. Portion of wing figured in C, magnified to show circular impressions of hairs or glands typical of this species. —E. Fruit showing the venation and undulating margin of the wing (IU 15722-4038), $\times 1.5$. —F. Holotype, showing the base of the nutlet and the smooth wing margin. The reverse side of this specimen shows the two commissural style arms figured by Manchester and Dilcher (1982) (IU 15722-4031), $\times 1.5$. G–J. Stereo-pairs showing three-dimensional nature of the nutlets, $\times 4$. —G. Specimen showing pyramidal apex characteristic of this Paleocene species. The plane of dehiscence is seen as a vertical line passing through the abraded nut apex (IU 15722-4763). —H. Base of a nutlet, as seen in the holotype specimen figured in F. —I. Base of a nutlet with fruit wall removed to show lobes of the silica locule cast. A well-developed secondary septum, running horizontally in the picture, results in a nutlet divided into four basal compartments (IU 15722-4032). —J. Enlargement of the specimen in C showing the base of the nutlet with septa represented by molds, but not silicified.

FIGURE 41. Fruits of *Cyclocarya* and *Polyptera* from the Paleogene of Wyoming and Colorado. A, B. *Cyclocarya coalmontensis* Manchester & Dilcher from the Upper Paleocene or Lower Eocene Coalmont Formation, northern Colorado, $\times 1.5$.—A. Holotype, showing diamond-shaped nutlet with two prominent septa, surrounded by a narrow wing (USNM 298886).—B. Specimen showing impression of pedicel scar at base of the nutlet (USNM 298887). C–E. *Cyclocarya minuta* Manchester from the Paleocene Fort Union Formation, central Wyoming, $\times 1.5$.—C. Holotype, showing the relatively small circular nutlet with two prominent septa, surrounded by a wing with radiating venation and an undulating margin, USGS locality 9483 (USNM 364530).—D. Additional specimen, similar to C. *brownii* (Fig. 39B–J), but with smaller wing and rounded, rather than diamond-shaped, nutlet, USGS locality 9483 (USNM 364531).—E. Specimen from IU locality 15757 (IU 5341). F–H. *Polyptera manningii* Manchester & Dilcher from the Paleocene Fort Union Formation, southern Wyoming.—F. Specimen showing eight wings, and quadrangular nutlet with primary and secondary septa, IU locality 15747 (IU 4864), $\times 1.5$.—G. Specimen showing venation of the wings, IU locality 15758 (USNM 304360), $\times 1.5$.—H. Specimen compressed laterally showing filamentous strands arising basally and ensheathing the nutlet (USNM 298888B), $\times 2$.

endocarps assigned to *Juglandicarya* represent *Cyclocarya*.

Juglandicarya depressa Reid & Chandler, London Clay Fl. 143–145. pl. 3: figs. 8–13. 1933.

Discussion. *Juglandicarya depressa* from the early Eocene London Clay flora is the oldest occurrence of fruits suggesting *Cyclocarya* known in Eurasia. The species is based upon abraded pyritized nutlets averaging about 6–8 mm in diameter that are “roughly quadrangular to circular” in transverse view. Although no trace of a wing is evident in the abraded fossils, the small size of the nutlets is consistent with the suggestion that they may have originally been winged. In their quadrangular shape, these nutlets are somewhat similar to those of *C. brownii* from the Paleocene of North America. Another clue that the fossil may represent *Cyclocarya*, or a closely related form, is the occurrence of longitudinally oriented fibers on the surface of the nutlets that converge upon the equator from the base and apex. The same pattern occurs in extant *C. paliurus*, in which the fibers are directed out into the subequatorially attached circular wing.

Unfortunately, the lack of wing preservation (if a wing was indeed present) prevents a full understanding of this species and it is retained in the noncommittal organ genus *Juglandicarya*.

Cyclocarya cycloptera (Schlechtendal) Iljin-skaya, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vysš. Rast. 10: 120. 1953.

Pterocarya cycloptera Schlechtendal, Abh. Naturf. Ges. Halle 21: 102. pl. 4: figs. 1–3; pl. 5: fig. 3a; pl. 6: figs. 2, 3, 5b. 1896.

Emended diagnosis. Fruit a nutlet surrounded equatorially by a disk-like wing, 30–50 mm diam., with a rounded and smooth to undulating margin sometimes deeply cleft in one or two places; wing oriented perpendicular to the main axis of the nutlet, venation radiating outward from the nutlet in subparallel fashion with frequent dichotomies and occasional anastomoses toward the margin; nutlet round in transverse view, 5–7 mm diam.; fruits borne spirally, close together on a stout axis.

Discussion. *Cyclocarya cycloptera* is first documented in the Oligocene of Kazakhstan

(Takhtajan et al., 1963: 688, pl. 19: figs. 7, 8) and the middle or late Oligocene (age according to Kirchheimer, 1957) of Bitterfeld, Germany (Schlechtendal, 1896). Several occurrences are known in the Neogene of Europe including the Miocene of Schrotzburg (Hantke, 1954; Gregor, 1982), Schwandorf, Germany (Gregor, 1980), and Nieder Drove near Kreuzau (Kilpper, 1971), West Germany, and Maramures, Romania (Givulescus, 1978). Specimens described as *C. weylandi* (Straus, 1969) from the Pliocene of Willerhausen appear to represent the same species. In addition, specimens described as "*C. ezoana* (Tanai & Suzuki) Wolfe & Tanai"⁸ from the Miocene of southwest Hokkaido (Tanai & Suzuki, 1965) and Niroshi (Ishida, 1970), Japan, are similar to, and perhaps actually conspecific with, *C. cycloptera*.

In wing shape, orientation, size, and venation, *Cyclocarya cycloptera* is virtually identical to the living *C. paliurus*. Unfortunately, in the impressions upon which *C. cycloptera* is based, the nutlet structure is poorly preserved. However, well-preserved (but wingless) nutlets from lignites and sands of the same age provide information on *Cyclocarya* nutlet morphology during the same time interval. Dorofeev (1970b) recognizes four species from the Tertiary of Eurasia based on the morphology of denuded endocarps. This situation suggests that *C. cycloptera* could be divided into several species if known from nutlet structure as well as wing morphology.

Cyclocarya tavidensis Dorofeev, Bot. Žurn. (Moscow & Leningrad) 55: 1599. pl. 1: figs. 1-6. 1970.

Description (from Dorofeev, 1970b). Nutlets 4.2-6.2 mm high, 4-6.2 mm wide, almost spherical, broadly ovate, ellipsoidal; apex weakly pointed or barely protruding. Longitudinal ribs few in number, broad and gentle, occasionally thickened in places to the point of looking like tumors; some specimens have additional grooves or nodules on the crests of the ribs, sometimes sharp; the nodules are the largest of the thickenings and are situated on almost a single level; line of wing attachment indistinct; walls thick and without lacunae; secondary septum reaches less than one-fourth of the height of the locule.

Discussion. This species, from Oligocene clays near Niznjaja Pristan along the Tavda Riv-

er in the Soviet Union, is distinguished from extant *Cyclocarya paliurus* by its almost spherical rather than lensoidal nutlet morphology and by the broader and smoother exterior ribs on the nutlet. Dorofeev (1970b) distinguished it from younger *Cyclocarya* species "by their compactness, their greater symmetry of form and their smoother surface, which bears witness to a comparatively narrow, but uniformly thick wing situated on one level." The wing itself is not preserved. The nodules at the crests of the longitudinal ribs appear to represent the position where the wing attached. Dorofeev stated that the primary septum is somewhat thinner than in younger species, and the secondary septum is lower.

Cyclocarya tymensis Dorofeev, Bot. Žurn. (Moscow & Leningrad) 55: 1599. pl. 1: figs. 7-9. 1970.

Pterocarya crassa Dorofeev, Doklady Akad. Nauk S.S.S.R., Moscow 132: illustr. 1, figs. 7-9, 1960; Tertiary Floras of Western Siberia, Akad. Nauk S.S.S.R., Moscow 140. pl. 20: figs. 1-12, 14, 15. 1963.

Description (from Dorofeev, 1970b). Nutlets 4.2-7 mm high, 4.4-8 mm wide, spherical to ellipsoidal, somewhat drawn out in height or width, angular, clearly divided into upper and lower halves that are almost equal in size; apex apiculate; longitudinal ribs more or less uniformly thick and continuous except near the equator where they are slightly thickened; nodules representing the point of wing attachment well developed, equal in prominence everywhere, situated on one level; or smaller near the secondary septum and situated along a lower level; wall thick, without lacuna; secondary septum reaching one-fourth to one-third of the height of the locule.

Discussion. *Cyclocarya tymensis* occurs in the Oligocene sands of Dunaevskij jar on the Tym River in western Siberia and is distinguished from *C. tavidensis* by its well-developed longitudinal ribs and its oval rather than round lateral profile. Dorofeev (1970b) stated that *C. tymensis* differs from the extant species in being more drawn out in height, in its characteristically arched, bulging apex, and in the sharp sculpture of the sides. The nutlet flares out in the plane of the wing attach-

⁸ The fruit described as *C. ezoana* by Wolfe and Tanai (1980) from the Miocene of Alaska is about half the size of fruits of this species and actually represents the rhamnaceous taxon *Paliurus hesperius* Berry.

FIGURE 42. Illustrations of *Sphaerocarya* Dorofeev from the Tertiary of Siberia, all $\times 3$.—A–G. *Sphaerocarya nikitinii* (Dorofeev) Dorofeev (illustrations from Dorofeev, 1963). Note globose shape, smooth exterior, low primary septum.—H–L. *S. uralensis* Dorofeev (illustrations from Dorofeev, 1970a).

ment, whereas in *C. tavidensis* the nutlets are more rounded and the plane of wing attachment is less obvious.

Cyclocarya tomskiana Dorofeev, Doklady Acad. Nauk S.S.S.R. 123: illustr. 1, figs. 16–18. 1958; Bot. Žurn. (Moscow & Leningrad) 55: 1600. pl. 2: figs. 1–6. 1970.

Description (from Dorofeev, 1970b). Nutlets 5.2–6.7 mm high, 6–8 mm wide, oblate or ellipsoidal, broad, rather regular; apex uniformly convex; longitudinal ribs regular, all smoothed down, low, and only at the edges thickened into nodules that are situated on almost a single level; wall thick, lacking lacunae; secondary septum low, in some specimens almost absent.

Discussion. *Cyclocarya tomskiana* nutlets are similar to those of *C. tymensis* but are larger and less prominently sculptured. The type locality is in the Oligocene brown coals near the village of Rezenka on the Bol'saja Kirgizka River. Dorofeev (1970b: 1600) states that the Rezenka collection includes both *C. tymensis* and *C. tom-*

skiana, and transitional forms intermediate between the two, but adds that only the *C. tomskiana* type is present in the Miocene collection from Kireevskoe Selo.

Fruits of the *Cyclocarya tomskiana* type were widespread across Eurasia during the Oligocene. Dorofeev (1970b) pointed out that individual specimens described as *Engelhardia nucifera* (Ludwig) Mädlar from the Oligocene of Vixa in Saxony (Kirchheimer, 1942: 428–430, fig. 7) and the Oligocene of Brunsum, Holland (Zagwijn, 1959, pl. 1: fig. 5a, b) are especially similar. A specimen from the undifferentiated Tertiary of Japan, described under the name *Pterocarya paliurus* (Miki, 1955), confirms the occurrence of similar morphology in the Far East.

Dorofeev (1970b) suggested that the nutlets previously described as *Pterocarya crassa* Dorof. from the Miocene Ob River area of western Siberia belong to *Cyclocarya* and assigned them to *Cyclocarya crassa* (Dorof.) Dorof. However, the sharp sculpturing, asymmetry, and high secondary septum of the endocarp, and the lacunae observed in some specimens, suggest to me that the former assignment was correct.

Sphaerocarya Dorofeev. Figure 42A–L.

Description (after Dorofeev, 1970b). Pericarp crumbly, loose, uniformly thick, without bulges on sides, separating easily from the nutlet; four meridional grooves extending along the pericarp surface from the attachment point; nutlet 4.5–10.9 mm high, 4.5–10.9 mm wide, spherical, slightly flattened at the poles, sometimes with a small projection at the apex, surface almost smooth; walls thick, without lacunae; primary septum thick, column-shaped, internally hollow; secondary septum low (*S. uralensis*) or moderately high, reaching one-fourth to one-third of the height of the locule (*S. nikitinii*); locule smooth.

Discussion. The genus *Sphaerocarya* was created by Dorofeev (1970a, 1970b) for nutlets similar to those of extant *Cyclocarya paliurus* but distinct by virtue of greater sphericity, smoother surface, somewhat larger size, and inferred lack of wings. Dorofeev commented that the spheroidal shape and uniformly thick pericarp preserved on some specimens resemble the condition of extant *Juglans* and *Carya* but demonstrated a close affinity with *Cyclocarya* on the basis of endocarp morphology.

Dorofeev (1970b) recognized three species of *Sphaerocarya*: *S. nikitinii* (Dorof.) Dorof. (Fig. 42A–G) from the Miocene of Kireevskoe Selo in western Siberia, *S. uralensis* Dorof. (Fig. 42H–L) from the Miocene of Polevskij city of the Urals, and *S. nucifera* (Ludwig) Dorof. from the Lower Pliocene of Dorheim near Friedberg, West Germany. Despite reference to Dorofeev's transference of the German species to *Sphaerocarya*, Mai (1973) reinstated the species as *Cyclocarya nucifera* (Ludwig) Mai (1964) without discussion.

The validity of *Sphaerocarya* as a genus distinct from *Cyclocarya* depends primarily on the inferred lack of wings because all of the other described features overlap with *Cyclocarya*. The spheroidal and smooth nutlets are indeed distinct from the lensoidal, prominently ribbed nutlets of *C. paliurus*; however, Dorofeev himself has demonstrated that Oligocene and Miocene species of *Cyclocarya* were more spheroidal and less strongly ribbed than the extant species. The occurrence of smooth-surfaced, pyramid-shaped nutlets in the Paleocene *C. brownii* indicates there was a wider range in nutlet morphology within *Cyclocarya* in the Tertiary than is exhibited by the single modern species. In size, the nutlets of

Sphaerocarya (4.5–10.9 mm) overlap with the Oligocene and Miocene species of *Cyclocarya* described by Dorofeev (1970b) (4.5–8 mm).

Dorofeev's conclusion that *Sphaerocarya* was wingless is based on specimens of *S. nikitinii* showing the intact pericarp. The pericarp is described as uniformly thick and the specimen illustrated (Dorofeev, 1970b, pl. 2: figs. 11, 13) shows no indication of a wing or scar from wing detachment. I accept this as evidence favoring recognition of an extinct genus. The identity of *S. uralensis* and *S. nucifera* is less certain because they are not preserved with intact pericarps and fruits of *Pterocarya*, and *Cyclocarya* from the same deposits are denuded of their wings. Dorofeev stated "one specimen of *S. uralensis* (1970b, pl. 2: figs. 7, 8) differs from the rest with its sides compressed to the point of being cylindrical, which shows that the fruits of this genus had some thickening of the pericarps at this point or a rudimentary wing" [Dorofeev, 1970b: 1601 (translated)].

It would be interesting to compare the type of foliage and pollen borne by *Sphaerocarya* with that of *Cyclocarya* species. I consider it likely that the relationship between *Cyclocarya* and *Sphaerocarya* was comparable to the close relationship between extant *Oreomunnea* (winged fruits) and *Alfaroa* (wingless fruits) of the Engelhardieae.

Polyptera Manchester & Dilcher. Figure 41F–H.

Description (after Manchester & Dilcher, 1982). Fruits consisting of a pyramidal nutlet surrounded basally by eight to ten petaloid wings united in a flange 12–16 mm wide perpendicular to the main axis of the nutlet; wings irregular in size, 2.5–4 mm long, 1.5–4 mm wide; sinuses between wings deep, almost reaching the nutlet, or relatively shallow; venation subparallel, bifurcating toward the margin; nutlets 6–8 mm wide, 5–7 mm high, four-parted at the base due to the intersection of primary and secondary septa, square in transverse section, triangular, tapering apically, in lateral view, loosely ensheathed by eight to ten free strands each 8–12 mm long arising from the basal portion of the nutlet.

Discussion. *Polyptera* is known from one species, *P. manningii*, from two localities in the Paleocene Fort Union Formation in Wyoming (Manchester & Dilcher, 1982). It resembles the

FIGURE 43. Modern fruits of *Pterocarya*, all $\times 2$. A-C. *P. rhoifolia* Sieb. & Zucc., Suzuki s.n. (IU mod. ref. coll. 4002; from A) Iwate Prefecture, Japan.—A. Apical view showing four sepals near nutlet apex, bract (b) and the two lateral wings with typical pterocaryoid venation.—B. Basal view of fruit showing the seam of attachment of the wings to the nutlet.—C. Front view of fruit with nutlet axis vertical to illustrate oblique wing attachment characteristic of *Pterocarya*.—D. *P. stenoptera* C. DC., Chung & Sun 450 (IU mod. ref. coll. 4011;

Paleocene *Cyclocarya brownii* and late Paleocene or early Eocene *C. coalmontensis* in having a pyramidal nutlet with basal wing attachment and well-developed secondary septum but is distinguished from that genus by its eight to ten separate wings (Fig. 41E, F) and the occurrence of filamentous ensheathing strands (Fig. 41H). The unusual wing condition could have been derived by dissection of a *Cyclocarya*-type wing, but the homology of the ensheathing strands is unknown.

Leaflets of "*Pterocarya*" *glabra* Brown, already discussed here (pp. 87–88; Fig. 36), are abundant at both localities from which *Polyptera manningii* has been collected. Since the localities have not yielded other types of juglandaceous fruits or foliage, Brown (1962) was probably correct that these organs represent the same plant.

Pterocarya Kunth

The winged fruits of extant and fossil *Pterocarya* are easily separated from those of *Cyclocarya* and *Polyptera*. In *Pterocarya* there are two distinct lateral wings that diverge in planes skewed to the main axis of the nutlet, whereas in the other genera there is a single wing (or a single flange of eight to ten wings) oriented perpendicular to the main axis of the nutlet. Other differences include sculpture of the nutlet, presence of lacunae, and position of the bract on the fruit.

Examples of extant fruits of each of the modern species of *Pterocarya* are illustrated in Figure 43A–H. The wings range from 1 to 2.5 cm long and 0.5 to 2.5 cm wide and are usually rounded or ovoid but in *P. stenoptera* (Fig. 43D) are strap-shaped. The venation is subparallel, fanning outward from the nutlet in the same fashion as in *Cyclocarya*, and the margin is smooth to undulatory. The wings are joined to one another in a seam along the back side of the nutlet (Fig. 43B) and diverge from the nutlet in planes oblique to the vertical axis of the nutlet. This angle of divergence ranges from nearly 60° in *P. rhoifolia* to more nearly 30° in other species such as *P. stenoptera* and *P. fraxinifolia*. Manning (1978)

notes that the wings are derived from the two bracteoles of the inflorescence and that the bract remains as a tiny, often hirsute appendage at the base of the nutlet (Fig. 43G, H).

The nutlet ranges from ovate to obovate, from longer than wide to wider than long, and from 5 to 8 mm in diameter. The outer surface is ornamented with eight to ten sharp longitudinal ribs. The vascular bundles usually run along the crests of the longitudinal ribs, rather than between them as in *Cyclocarya* (Dorofeev, 1970b). The walls range from thick to thin and usually contain lacunae. The locule surface is smooth and the secondary septum is high, with its upper edge straight or with a pair of mammiform nodules in each half of the nutlet that stand out from the point where the primary and secondary septa intersect. The basal attachment scar is not recessed as it is in *Platycaryeae*. The perianth consists of four sepals that may be connate basally forming a tube surrounding the style, or free, originating 1–2 mm below the nutlet apex. Two style arms are carinal and diverge in a plane approximately perpendicular to that of the wings.

There are numerous occurrences of *Pterocarya* fruits in the Tertiary of the Northern Hemisphere, confirming that modern species occupy only a small fraction of the former range.

NORTH AMERICAN RECORD

Pterocarya macginitii, known from two compression specimens from the Middle Eocene Green River Formation in Wyoming (Fig. 44A, B), is the oldest known species of *Pterocarya* (Manchester & Dilcher, 1982). The specimens are small ovate nutlets 2–3 mm wide and 3–4 mm long, joined laterally by a pair of ovoid wings, 8–10 mm in diameter with typical pterocaryoid venation. The large size and carinal orientation of the style arms confirm the relationship of this species with *Pterocarya* and differentiate it from similar fruits of the extinct platycaryoid genus *Hooleyia*. The nutlets are compressed too badly to determine their morphology, but it is interesting that they are only one-half to two-thirds

←
from A) Kiangsi, China. Note strap-shaped wings, ribbed nutlet surface, and position of sepals at the extreme nutlet apex, fused by their bases into a tube surrounding the style.—E. *P. fraxinifolia* (Lam. ex Poir) Spoch., *Lindsay* 1034 (IU mod. ref. coll. 1931; from MO-1606137), Guilan Province, Iran.—F. *P. hupehensis* Skan., *Chow* 732 (IU mod. ref. coll. 4001; from A) Hupeh, China.—G. *P. macroptera* var. *forrestii* (W. W. Smith ex Hand.—Mazz.) Manning, *Handel Mazzetti* 7869 (IU mod. ref. coll. 4003; from A), Yunnan, China.—H. *P. macroptera* var. *insignis* (Rehder & Wilson) Manning, *Rock* 22716 (IU mod. ref. coll. 4013; from A), Yunnan, China.

FIGURE 44. *Pterocarya* fruits from the Tertiary of western North America.—A. *Pterocarya macginitii* Manchester & Dilcher from the Middle Eocene Green River Formation, Wyoming (UCMP 20561), $\times 2$.—B. Same specimen enlarged to show the distinct style arms, $\times 10$.—C. *Pterocarya occidentalis* Manchester, Oligocene Gumboot Mountain, western Washington, UCMP locality 3931 (UCMP 9000), $\times 2$.—D. Stereo-pair of *P. occidentalis*, holotype, Oligocene Weaverville flora, California, USGS locality 5748. Note position of wings in a plane skewed to the nutlet axis and exterior ribbing of nutlet mold (USNM 364532A), $\times 2$.—E. *P. occidentalis*, Oligocene Lyons flora of western Oregon, UCMP locality 487 (UCMP 9002), $\times 2$.—F. Another specimen from the same locality (UCMP 9001), $\times 2$.—G. Holotype, *P. eomacroptera* Manchester, Miocene, Idaho, UI locality

as large as those of later Tertiary and modern species.

MacGinitie (1969) considered these fruits conspecific with a leaflet described as *Pterocarya roanensis* MacG. Manchester and Dilcher (1982) subsequently transferred the fruits to a separate organ species noting that the leaflet was collected from a different locality. The leaflet figured and described as *P. roanensis* differs from extant *Pterocarya* in its long petiolule and acute base as well as in some aspects of venation, suggesting that its identification to this genus should be regarded as tentative. Pollen indistinguishable from that of modern *Pterocarya* has been figured from sediments of comparable age in the adjacent Absaroka province (Leopold in MacGinitie, 1974) and Teton area (Love et al., 1978).

***Pterocarya occidentalis* Manchester, sp. nov.**
Figure 44C–F.

Diagnosis. Fruit a nutlet with two lateral wings; wings oval to almost circular, 9–10 mm diam., with a smooth or slightly undulatory margin, extending outward in a plane skewed approximately 70° to the central axis of the nutlet; venation fanning outward from the nutlet in subparallel fashion with frequent forkings and occasional anastomoses toward the margin, often flared downward in the basal one-fourth of the wing; nutlet 3–5 mm diam., round in cross section with eight to ten longitudinal exterior ribs; stylar and perianth parts unknown; entire width of fruit 18–25 mm.

Specimens. The holotype is USNM 364532 (Fig. 44D), and the paratypes are UCMP 20561 (Fig. 44C), UCMP 9002 (Fig. 44E), and UCMP 9001 (Fig. 44F).

Discussion. The holotype of this species is from the Oligocene Weaverville flora of California, where it occurs with abundant foliage of *Pterocarya orientalis* (MacGinitie) Wolfe. Although no other specimens are known from the type locality, similar specimens that might be conspecific occur in the Oligocene Lyons flora of Oregon (Fig. 44E, F) associated with leaflets assigned to *P. mixta* (Knowlton) Brown (Meyer, 1973) and in the Oligocene Gumboot Mountain

flora of western Washington (Fig. 44C). They differ from the Eocene *P. macginitii* in the larger size of both the nutlet and wings and in the more nearly horizontal orientation of the wings. Although details of internal nutlet morphology are unknown, the exterior ribbing is prominent, as in extant species. The configuration of the wings, and their orientation with respect to the nutlet, suggest affinity with the modern section, *Platyptera*.

***Pterocarya eomacroptera* Manchester, sp. nov.**
Figure 44G, H.

Diagnosis. Fruit a nutlet with two lateral wings; wings large and rounded, 20 mm wide, 10–12 mm long, joined to one another and forming a seam at the union with the nutlet; wings situated in a plane oblique to the main axis of the nutlet; venation subparallel, fanning outward from the nutlet with occasional bifurcations and anastomoses; nutlet rounded in transverse view, about 8 mm diam., longitudinally ribbed; bract persistent, 1.2 mm wide and at least 1.5 mm long, protruding from the basal portion of the nutlet and aligned with the seam of wing fusion; stylar and perianth parts unknown; entire width of fruit 33 mm.

Specimens. The holotype is UI-TO 207 (Fig. 44G, H), and the paratype is UI-TO 208, both at the Department of Geology, University of Idaho, Moscow.

Discussion. This new species is based upon a complete fruit and an isolated wing from a Miocene deposit near Clarkia, Idaho (UI loc. P-37; Smiley & Rember, 1979). A single specimen from the Miocene Hidden Lake locality of western Oregon (J. A. Wolfe, pers. comm.) is similar in size and morphology and might represent the same species. The large size and wing configuration suggest affinity with living species of sect. *Platyptera*, particularly *Pterocarya macroptera* (Fig. 43G).

***Pterocarya smileyi* Manchester, sp. nov.** Figure 44I, J.

Diagnosis. Fruit a nutlet with a pair of lateral wings arising in planes slightly oblique to the

P-37, ×2.—H. Stereo-pair of same specimen, with matrix dissected to reveal bract (b). Note ribbed mold left by nut, ×2. I, J. *P. smileyi* Manchester, from Miocene of Idaho, UI locality P-33.—I. Holotype (UI-TO 209), ×2.—J. Paratype (UI-TO 201), ×2.

FIGURE 45. Fossil nutlets of *Pterocarya* sp. from the Miocene of Clarkia, Idaho (UI-TO 211).—A. Stereo-pair showing ribbed outer surface of nutlet, $\times 5$.—B. Stereo-pair of same nutlet fractured along the plane of dehiscence, showing cusp-like projections of secondary septum (arrows) protruding from the base of the locule, $\times 6$.

vertical axis of the nutlet; wings small, rounded, 5–6 mm wide, 9–12 mm long, supplied with sub-parallel venation, joining together in a seam at the base of the nutlet and diverging from one another in a V-configuration; bract persistent as a tiny appendage at the point of union of the two wings; nutlet 4–5 mm high, 4 mm wide, obovoid, longitudinally ribbed; two stigmatic arms arising from a common style and diverging in a plane approximately perpendicular to that of the wings, about 2.5 mm long; sepals connate basally, forming a tube around the style; entire width of fruit 14 mm.

Specimens. The holotype is UI-TO 209 (Fig. 44I), and the paratype is UI-TO 210 (Fig. 44J), both at the Department of Geology, University of Idaho, Moscow.

Source of name. *Pterocarya smileyi* is named in honor of Dr. C. J. Smiley in recognition of his contributions to paleobotany and in thanks for supplying the specimens for study.

Discussion. *Pterocarya smileyi* is based upon fruits from the Miocene deposit of Clarkia, Idaho (UI loc. P-33; Smiley & Rember, 1979). Similar, perhaps conspecific, fruits occur in the Miocene Collawash flora of western Oregon (USGS collection), and it is possible that the poorly preserved specimen figured as *P. nigella* (Heer) Wolfe from the Miocene of Seldovia Point, Alaska (Wolfe & Tanai, 1980) may be related.

Although the nutlet of *Pterocarya smileyi* is similar in size and exterior ribbing to that of *P. eomacroptera*, the wings differ in their smaller size and more narrowed shape. Venation within the wings is more strongly parallel rather than spreading in a fan-like fashion. The departure of the wings from one another in a V-configuration and their orientation in a plane only slightly

askew to the nutlet axis, and the origin of the two style arms from a common podium-like style indicate that *P. smileyi* belongs to the modern sect. *Diptera*. Of the three modern species of sect. *Diptera* (*P. fraxinifolia*, Fig. 43E; *P. hupehensis*, Fig. 43F; and *P. stenoptera*, Fig. 43D), the fossil is least similar to *P. hupehensis* and most similar to *P. stenoptera*. The basal fusion of sepals in a tube surrounding the style, and the tongue-shaped wings in the fossil are characteristic of *P. stenoptera*. However, the wings of the living species are two to three times longer than those of *P. smileyi*. Collections of foliage from the same locality as the fruits include *Pterocarya* leaflets that are virtually indistinguishable from those of *P. stenoptera*.

***Pterocarya* sp. Figure 45A, B.**

Isolated three-dimensionally preserved *Pterocarya* nutlets missing the wings occur in a sandy facies underlying the silty clay in which *P. smileyi* occurs at UI locality P-33 (W. Rember, pers. comm.). The nutlets are thick-walled with prominent longitudinal surface ribs and are thus distinguished from thin-walled, smooth-surfaced nutlets of extant Engelhardieae. It is probable that these nutlets represent either *P. smileyi* or *P. eomacroptera* (which occurs at UI loc. P-37, 4 mi. NW of UI loc. P-33), but in the absence of wings a definite assignment cannot be made. However, nutlet morphology is better preserved in the isolated nutlets than in the compression specimens upon which *P. smileyi* and *P. eomacroptera* are based. Halved nutlets show a weak secondary septum that forms a cusp-like projection protruding from the base of the locule on each side of the secondary septum (Fig. 45A). This feature characterizes extant *P. rhoifolia* and *P. macroptera* but is not seen in *P. fraxinifolia*.

and *P. stenoptera*, which have more well-developed septa. This character suggests that the nutlets may represent *P. eomacroptera*. If *P. smileyi* is interpreted correctly it should have nutlet morphology similar to that of *P. stenoptera* and *P. fraxinifolia*.

EUROPEAN RECORD

Although pollen of the *Pterocarya* type extends back to the late Eocene in Europe, the earliest fruits known from the region are Oligocene. The most complete review of *Pterocarya* fruits in the western European Tertiary is presented by Kirchheimer (1957). Most reports are based on denuded, wingless nutlets from lignites and sands, such as *P. raciborskii* from the Middle Miocene of Poland (Zablocki, 1928) and *P. limburgensis* from the Lower to Upper Pliocene of the Netherlands, Germany, and Poland (Kirchheimer, 1957). Kirchheimer notes that the latter species is similar to nutlets of extant *P. fraxinifolia*, which is the geographically closest modern species, and many authors have simply placed the fossils in "*P. cf. fraxinifolia*."

Most of the European *Pterocarya* fruits preserved as impressions with intact wings have been placed in *P. castaneaefolia*. However, it is clear from the literature that several species were present and that a revision is needed. Gregor (1982) figures as *Pterocarya* sp. two specimens from the Miocene of Achldorf that appear to represent different species.

ASIAN OCCURRENCES

Pterocarya fruits are known from various Tertiary localities in Asia, including Siberia, Korea, and Japan. The earliest occurrence known to me is a specimen figured by Takhtajan et al. (1963, pl. 19: fig. 9) as *P. castaneaefolia* (Goepp.) Schlegel from the Oligocene of Rezenka in western Siberia. The specimen has a nutlet approximately 6 mm wide with two lateral ovoid wings about 16 mm wide and 10 mm long. Finer details are not clear in the photograph, but the venation is pterocaryoid and the wings appear to be compressed in a plane almost horizontal with respect to the nutlet axis. A second specimen with similar wing configuration and orientation is figured by Takhtajan et al. (1963, pl. 19: fig. 10) as the same species, from the Miocene of Tym in western Siberia. Dorofeev recognizes three additional Miocene occurrences on the basis of wingless endocarps: *P. crassa* (1963: 140, pl. 20: figs. 13, 16,

17) and *P. kireevskiana* (1963: 143, pl. 21: figs. 1–15) from western Siberia, and *Pterocarya* sp. (1969: 66–67, pl. 8: figs. 14–16) from the Mammoth Mountain flora on the Aldan River. The nutlets are longitudinally ribbed and similar to those of extant *P. stenoptera*. Miki (1955) illustrates two species of denuded endocarps from the undifferentiated Tertiary of Japan as "*Pterocarya stenoptera*" and "*P. rhoifolia*."

Pterocarya protostenoptera Tanai occurs in the Upper Miocene of northeastern Hokkaido, Japan (Tanai, 1961), the Noroshi flora of Noto Peninsula, central Japan (Ishida, 1970), and the Miocene of Korea (Huzioka, 1972). The fruits have strap-shaped wings 3–4 mm wide and 15–20 mm long that diverge from each other in a V-shaped pattern with typical pterocaryoid venation. The nutlet is 3–5 mm in diameter and longitudinally ribbed. Persistent sepals, about 1 mm long, arise from the nutlet apex. The Korean material includes a well-preserved infructescence 7 cm long with a rather tight spiral of numerous sessile fruits (Huzioka, 1972, pl. 3: fig. 4). The specific epithet appropriately draws attention to the close morphological similarity between these fossils and the extant *P. stenoptera*.

Pterocarya asymmetrosa Konno was established on the basis of leaflets and has subsequently been used for fruits from the Neogene of Japan. Those described by Tanai and Suzuki (1965) from the Shanabuchi flora have nutlets 6–7 mm in diameter with eight sharp longitudinal ridges and two wings, each 1.5–2 cm high and 3.2–3.5 cm wide, situated almost perpendicular to the nutlet axis. Tanai and Suzuki consider *P. rhoifolia* of Japan to be the equivalent living species. Fruits assigned to the same fossil species by Ishida (1970) from the Miocene Noroshi flora are about half as large but are also suggested to be most similar to *P. rhoifolia*.

Juglans L.

Fruits of *Juglans* are easily distinguished from those of other members of the Juglandaceae by their lack of wings and by their larger size: features correlated with rodent dispersal. Convergence between the nuts of *Juglans* and *Carya* has resulted in problems in the identification of fossil remains. In the older literature (e.g., the review of Kirchheimer, 1957), numerous European *Carya* fruit occurrences were attributed to *Juglans*, resulting in misconceptions of the paleobiogeography and evolution of both genera. Ler-

FIGURE 46. *Juglans clarnensis* Scott from the Middle Eocene Clarno Formation, Oregon.—A. Base of a nut showing pedicel scar and longitudinal grooves (USNM 312738), $\times 1$.—B. Longitudinal view of a nut showing typical surface grooves (IU 15768-5338), $\times 1$.—C. Stereo-pair of a nut fractured along the plane of dehiscence (IU 4872), $\times 1.5$.—D. Base of nut in B, $\times 1$.—E. Typical locule cast viewed from side showing slight bilobing of the primary lobe (IU 4874), $\times 1.6$.—F. Stereo-pair of same locule cast oriented in the same position as the nut in C above, $\times 1.6$.—G. A nut sectioned transversely near the base showing four-parted base of locule cast, four lacunae, the dehiscence line along the secondary septum, and the central placental bundle (IU 4873), $\times 1.5$.—H. Transverse section of a nut sectioned higher than in D, showing only two lobes of the locule cast and two distinct placental bundles (IU 4875), $\times 1.5$.—I. Stereo-pair of the same locule cast figured in E and F viewed from the basal side, $\times 1.6$. J–M. Locule casts showing variation in development of secondary septum.—J, K. Specimen with well-developed secondary lobes reflecting presence of a secondary septum at the base of the nut (IU 5339), $\times 1$.—L, M. Specimen with secondary lobes undeveloped (IU 5340), $\times 1$.

oy (1955) was the first to call attention to fundamental differences in fruit vascularization allowing critical evaluation of fossil remains. In *Juglans*, the two placental strands of the primary septum follow a parallel course, straddling the fruit axis, whereas in *Carya* the same bundles diverge from one another at the base of the nut and follow a more peripheral course or are evenly dispersed and not recognizable as discrete bundles. In addition, the sutural strands are located within the endocarp wall in *Carya* but are confined to the husk in *Juglans*. Morphological cri-

teria useful in separating the two genera were presented with the earlier discussion of *Carya* fruits (p. 67–69).

The three extant sections of *Juglans* differ in fruit morphology. Section *Dioscaryon*, has a broadly ellipsoid to globose nut with a slightly rugose to smooth endocarp exterior. The nutshell and septa are relatively thin and non-lacunose. A thin secondary septum, together with the primary septum, divides the massive seed into four lobes at the base. Fruits matching this morphology have not been confirmed in the fossil

record. Nuts of sect. *Rhysocaryon* are globose, commonly wider equatorially than longitudinally. The nutshell surface is striated with weakly impressed (*J. major*) to deeply incised (*J. nigra*) longitudinal grooves. The nutshell and septa are thick and lacunose. A thick secondary septum results in a seed that is basally four-lobed. Fruits of sect. *Cardiocaryon* are typically more elongate than those of the other two sections. The exterior surface ranges from rugose to scabrate with a reticulum of blade-like ridges. The walls and primary septum are thick and lacunose. The secondary septum is not developed, so that the seed is only two-lobed at its base.

BLACK WALNUTS

Juglans clarnensis Scott, Paleontographica, Abt. B, Paläophytol. 96: 70–74. pl. 15: figs. 1–14. fig. 1. 1954. Figure 46A–I.

Description. Nuts globose to ellipsoidal, sometimes with a somewhat pointed apex; 1.4–2.4 cm long, 1.3–2.2 cm wide, exterior surface longitudinally grooved with eight to 12 shallow furrows roughly parallel in course sometimes anastomosing; locule smooth; wall 2–3 mm thick, each nutshell valve containing lacunae that bifurcate basally and rejoin near the apex, appearing in median section as two separate and laterally flattened wall cavities opposite the cotyledon lobes; two additional lacunae occurring near the center of the primary septum; secondary septum variable from poorly to well developed; base of locule two- or four-lobed; vascular strands of the primary septum located near the axis; shoulder regions of locule casts slightly concave; basal lobes of seed flattened, only slightly bulbous at the tips.

Discussion. *Juglans clarnensis*, from the Middle Eocene Clarno Formation of Oregon, represents the oldest confirmed species of *Juglans* and is known from more than 200 specimens, including silicified and carbonized nutshells, and chalcedony locule casts. Scott (1954) described the morphology in excellent detail, and cited several lines of evidence supporting its assignment to *Juglans*. In addition, the axial course of the placental bundles in the primary septum confirms the relationship with *Juglans* and distinguishes the fossil from *Carya*, in which the same bundles follow a peripheral course.

Although this fossil cannot be closely related

to a particular modern species, it compares most favorably with species of the extant sect. *Rhysocaryon*. Nuts of sect. *Cardiocaryon* are usually more elongate, typically have a scabrate surface, and have lacunae that are larger in proportion to wall thickness. The shallowly furrowed exterior, globose shape and the placement and size of lacunae, which are small relative to wall thickness, indicate a close relationship between these fossils and the black walnuts.

A peculiar feature of *Juglans clarnensis* is the variability in development of the secondary septum. There is a continuous range from specimens with no secondary septum at all to those with a reasonably well-developed septum. The same feature is reflected in the configuration of the locule casts that range from two-lobed to four-lobed at the base. Extant species of *Juglans* appear to be less variable in this regard. Members of sect. *Cardiocaryon* generally lack a secondary septum while those of sect. *Rhysocaryon* usually have a well-developed secondary septum.

Relative to modern black walnuts, the seed (locule cast) morphology of *Juglans clarnensis* is simple and unspecialized. Whereas seeds of extant species show markedly concave shoulder regions and well-developed, bulbous basal lobes, those of the fossil have convex to only slightly concave shoulder regions and thin basal lobes. Scott (1954) pointed out that the seed morphology of *J. clarnensis* is in closer agreement with that of sect. *Cardiocaryon*. Based upon the combination of features presented by nutshell (*Rhysocaryon*-like) and seed morphology (*Cardiocaryon*-like), he concluded that the fossil was intermediate between sects. *Rhysocaryon* and *Cardiocaryon*. Alternatively, it is possible that *J. clarnensis* is a primitive black walnut and that the simple seed morphology retained by modern species of *Cardiocaryon* was formerly possessed by black walnuts as well.

Juglans sp. Figure 47A, B.

A single locule cast from the Oligocene San Ramon Formation southwest of Walnut Creek, California, is housed in the paleobotanical collections of the University of California at Berkeley (UCMP 20771). While similar in size to locule casts of *Juglans clarnensis*, this specimen exhibits markedly concave shoulder regions and more bulbous secondary lobes. Although the morphology of the nutshell is unknown, this species is important as an early example of seed

FIGURE 47. *Juglans* sect. *Rhysocaryon* fruits from the Tertiary of America, $\times 1$.—A, B. *Juglans* sp. from the Oligocene San Ramon Formation of California. Locule cast showing concave shoulder regions and secondary lobing indicative of a well-developed secondary septum (UCMP 20771). C, D. *Juglans* (?) *sepultus* Hollick from the Oligocene Florissant Beds of Colorado.—C. Holotype, showing the rounded exterior of the nut and a broken locule cast showing the high primary septum (USNM 40768).—D. Stereo-pair of an undamaged locule cast similar to that of the holotype (UCMP 9240). E–G. *Juglans siouxensis* (Barbour) Berry from the Oligocene of Nebraska.—E. Stereo-pair of lectotype, a locule cast previously figured by Berry (1930). Note the concave shoulder regions and basal cleavage suggesting *Rhysocaryon* affinity (USNM 364461).—F. Stereo-pair of the same specimen viewed at right angles.—G. Additional specimen (USNM 326824).—H–J. *Juglans linkii* Brown nuts from the upper Miocene or lower Pliocene of Ecuador, from Brown (1946) with permission.

morphology characteristic of extant black walnuts.

Juglans* (?) *sepultus Cockerell, Bull. Amer. Mus. Nat. Hist. 24: 80. pl. 6: fig. 8. 1908. Figure 47C, D.

Discussion. This species from the lower Oligocene Florissant flora of Colorado was described on the basis of a single fragmentary locule cast (USNM 40768, Fig. 47C). A second specimen similar in size and shape (UCMP 9240, Fig. 47D) has been located that displays a locule cast comparable in configuration to that of the black walnut species described above from California. The lack of more definitive specimens prohibits a solid assignment to *Juglans*. Additional nuts from the same shales have proven to be *Carya* (*C. florissantensis* sp. nov., p. 71–78). *Juglans*

pollen (Penny, 1969) and a possible *Juglans* leaflet ("*J. coloradensis*," Wolfe, 1959) have been described from the same strata.

Juglans siouxensis (Barbour) Berry, Amer. Mus. Novit. 221: 1–8. figs. 1–6. 1926. *Archihicorea siouxensis* Barbour, Proc. & Collect. Nebraska State Hist. Soc., Ser. 2, 2: 272–274. pl. 5. fig. 3. 1898. Figure 47E–G.

Discussion. This species was described on the basis of silica locule casts from the *Titanotherium* beds of Hat Creek in Sioux County, Nebraska (Berry, 1926). Based upon seed configuration as reflected by the locule casts, Berry justified his placement of these fruits in *Juglans* rather than *Carya*. The locule casts of this species are about twice as large as those of the *Juglans* species discussed above. In addition, the concave

shoulder regions and secondary septum are more prominently developed.

Scott (1954: 72) noted an assemblage of the same species from the lower Oligocene White River Formation in Wyoming that included a specimen showing the exterior of the nut and wrote "it is nearly smooth except where marked by longitudinal furrows and closely resembles the nuts of *Juglans major* and *J. microcarpa*." Scott concluded that this fossil species was most closely related to the living western North American species.

Juglans calvertiana Berry, J. Wash. Acad. Sci. 24: 227–229. figs. 1, 2. 1934.

Discussion. This species was described on the basis of three carbonized specimens from Miocene marine sediments of Maryland and Virginia. Nuts of *Juglans calvertiana* are globose with shallow, but prominent longitudinal grooves on the exterior. Because of distortion, the specimens do not show the seed configuration. However, the general appearance of the nut is consistent with its placement in sect. *Rhysocaryon*, suggesting that black walnuts were indeed present in eastern North America by the Miocene.

Juglans nevadensis Berry, J. Wash. Acad. Sci. 18: 158–160. fig. 1. 1928.

Discussion. This species is represented by a single nut valve from the Miocene of Nevada, exhibiting features of modern black walnuts of the western United States. Since *Juglans* no longer occurs in Nevada, Berry (1928) suggested that the local population became extinct due to increasing aridity caused by the uplift of the Sierra Nevada Mountains.

Juglans linkii Brown, Amer. J. Sci. 244: 554–556. pl. 1: figs. 1–9. 1946. Figure 47H–J.

Discussion. *Juglans linkii* was described on the basis of 27 carbonized nut valves from the late Miocene or early Pliocene Punta Gorda Formation of northwestern Ecuador. The nuts are ovate-pyriform, rounded quadrangular in transverse view, cordate in longitudinal view, averaging 30 mm long by 25 mm wide. The walls and septa in this species are very thick and the exterior is rugose with deep longitudinal furrows. Details of the internal structure were not provided; however, the exterior shape and sculpture, along with the thick walls, indicate that it is allied

to extant tropical black walnuts. This fossil species is important as the only megafossil of *Juglans* known from South America and indicates that migration of *Juglans* into South America had already occurred by the early Pliocene.

BUTTERNUTS

Juglans lacunosa Manchester, sp. nov. Figure 48A–Q.

Diagnosis. Nut ellipsoid to oblong, 2.1–2.5 cm long, 1.5–1.9 cm wide, base and apex broadly rounded, with a slight point at the apex; surface smooth or with slight undulation, without ribbing; basal scar 2.5 mm by 5 mm, elongate in plane of primary septum; secondary septum absent to poorly developed; primary septum extending from base approximately half of the distance to the top of the locule, containing two large lacunae; placental strands following a parallel course adjacent to the fruit axis within the lacunae of the primary septum; secondary septum poorly developed to absent; wall with four lacunae in two pairs adjacent to the dehiscence plane; lacunae of wall and of primary septum joining apically into a large cavity on each side of the flattened hypocotyl. Locule smooth-walled with straight or convex shoulder regions, two lobed at base.

Specimens. The holotype is UWA 29512 (Fig. 48C–H) (collected by Chester Aumna, loaned for study and sectioning by Wesley Wehr). The paratypes are IU 4787 (Fig. 48A, B) and IU 4788 (Fig. 48I, J) (donated by Kirk Johnson). These specimens are from UWA locality 23, Eastgate site, Seattle, Washington.

Discussion. *Juglans lacunosa* is recognized by its smooth, unsculptured surface, relatively thin walls, and large lacunae. It is definitely a walnut, and not a hickory, because of the axial course of the placental bundles in the primary septum. It appears to be a butternut (sect. *Cardiocaryon*) because of its oblong shape, the virtual lack of a secondary septum, the straight (not concave) shoulder regions of the locule, and the lacunar condition. The two lacunae of the primary septum are large (Fig. 48G) and join together with the four intrawall lacunae to form a pair of large cavities in the upper one-third of the nut (Fig. 48E). The size of these apical cavities is considerably larger than that of the Eocene *J. clarnensis* and modern black walnuts and is more consistent with that observed in modern

FIGURE 48. *Juglans lacunosa* Manchester, a smooth-walled butternut from the Oligocene and Miocene of western North America. A–J. Specimens from the Lower Oligocene Blakely Formation, Eastgate locality, Washington. —A. Stereo-pair showing smooth exterior and oblong shape of nut, and the line of dehiscence (IU 4787), $\times 1$. —B. Stereo-pair of the same specimen broken along the plane of dehiscence showing relatively thin shell and the smooth locule with no suggestion of a secondary septum, $\times 1$. C–H. Holotype specimen Burke Memorial Washington State Museum 29512. —C. Specimen viewed laterally, prior to sectioning. Abraded, showing lobes of the locule cast, $\times 1$. —D. Stereo-pair of same specimen viewed basally showing base of the primary septum and pedicle scar in the center, and the two lobes of the locule cast, $\times 1$. —E. Transverse section above the equator showing the locule in the center and two large lateral lacunae, $\times 1$. —F. Transverse section, equatorial showing the two lobes of the locule and joining of septal and wall lacunae. Note the two placental bundles in the lacunae of the primary septum adjacent to the fruit axis, $\times 1$. —G. Portion of same nut sectioned subequatorially, $\times 2$. —H. Stereo-pair of the base of a primary lobe of the locule cast. Note that there is no secondary lobing, $\times 1$. —I, J. Specimen broken obliquely showing smooth exterior and lacunae situated within the wall and secondary septum (IU 4788), $\times 1$. K–M. Nut from the Miocene Oviatt Creek Site, Idaho, UI locality P35 (UI-TO 206). —K. Exterior of nut showing the smooth surface, $\times 1$. —L. Portion of same nut fractured along the plane of dehiscence, $\times 2$. —M. Stereo-pair of same nut reassembled and sectioned transversely, showing lacunae in wall and septum (cf. I, J), $\times 2$. —N. Nut from the Oligocene Twin River Formation, Washington, viewed from base. Surface abraded from predepositional water-wear (IU 4789), $\times 1$. —O. Same specimen sectioned transversely

and fossil butternuts. The smooth surface contrasts with that of most modern and fossil *Cardiocaryon* species that are prominently sculptured, often with blade-like ribbing. Similar smooth-walled nuts occur today only in *J. ailan-tifolia* of Japan and *J. cathayensis* var. *formosana* (Hayata) A. M. Lu & R. H. Chang (Kuang et al., 1979) of China.

Juglans lacunosa is represented by three specimens from the marginal marine strata of the early or mid-Oligocene Blakely Formation of northwestern Washington. The specimens are permineralized with calcium carbonate; details of internal morphology were obtained by fracturing along the line of dehiscence (Fig. 48B) and from cross-sections (Fig. 48E–G) cut with a thin diamond blade. Two additional specimens from marginal marine strata are known: one from the Lower Oligocene Twin River Formation of northwestern Washington (locality described by Underwood & Miller, 1980) (Fig. 48N, O) and the other from the Oligocene Poul Creek Formation of Yakataga Reef, Alaska (USGS loc. 11182, Fig. 48P, Q). They are larger than specimens from the Blakely Formation but show the relatively thin, smooth walls and large lacunae.

As an early member of sect. *Cardiocaryon*, this early or middle Oligocene species is of interest because of its North American occurrence. It predates all other known butternut occurrences with the possible exception of *Juglans tephrodes* (which dates from the middle or late Oligocene of Germany). Together with *J. clarnensis*, it lends support to the concept that the initial evolution of *Juglans*, including the divergence of sects. *Rhysocaryon* and *Cardiocaryon*, occurred in North America.

Another specimen provisionally placed in *Juglans lacunosa* (UI-TO 206, Fig. 48K–M) was collected from Miocene non-marine strata in northwestern Idaho (Oviatt Creek Site; UI loc. P-35; Smiley & Rember, 1979). The specimen was fractured along the line of dehiscence to show three-dimensional morphology of the valves (Fig. 48L), then reassembled and cross-sectioned to show the position of placentary bundles and lacunae (Fig. 48M). Although somewhat smaller than the permineralized Blakely Formation spec-

imens (perhaps due to shrinkage from dehydration after collecting) and more sharply pointed apically, it shares the smooth surface, thin walls, and placement of lacunae with the type material. Whether or not this represents the same species, it is significant as the first firm evidence of butternuts in the middle latitudes of North America as late as the Miocene.

Juglans tephrodes Unger, Gen. Spec. Plant. Foss., p. 469, 1850; Hills, Klován & Sweet, Canad. J. Bot. 82: 85–86, figs. 56, 60–63, 82, 1974. Figure 49A–E.

Juglans cinerea L. *fossilis* Bronn, Lethaea geognostica 2: 867, 1838; Mädler, Abh. Senckenberg. Naturf. Ges. 446: 59–60, pl. 6: fig. 4, 1939.

Juglans bergomensis (Balsamo-Crivelli) Massalongo 1852, Ann. Sci. Nat. Bot., Sér. 3, 6: 253, pl. 3: figs. 2–5, 1852; Kirchheimer, Die Laubgewächse der Braunkohlenzeit 195–196, 497–498, pl. 30: fig. 130, 1957.

Description (after Hills et al., 1974). Nuts oblong to oblong-ovate to obovate; 3–5.4, avg. 4.2 cm long, 2–2.7, avg. 2.3 cm wide; base rounded, truncate or more rarely pointed; apex conical, asymmetric; surface sculpture dominated by eight external ribs extending from base to apex, occasionally bifurcating into secondary ribs of shorter length and giving rise to blade-like minor ribs that form a reticulum; distal margins of ribs along primary suture flanged; hypocotyl pointed, flattened in the plane of the primary suture, maximum width of seed about the end of the primary septum; basal lobes of seed thin; outer sides of seeds, from point of maximum width to base concave; secondary septum absent; two large lacunae within the primary septum; nut wall with four lacunae visible in equatorial plane that join with those of the primary septum to form into two large cavities in the apical third of nut.

Discussion. This species was widespread and common in the Neogene of western Europe and apparently extends back to the middle or late Oligocene in Germany (Kirchheimer, 1957). Extensive synonymies are presented by Kirchheimer (1957) and Hills et al. (1974). The most informative descriptions of the species (including those

← showing four large lacunae in the wall and two in the primary septum, $\times 1$.—P. Nut from Oligocene Poul Creek Formation of Yakataga Reef, Alaska, USGS locality 11182, viewed basally, showing smooth, furrowed surface (USNM 387389), $\times 1$.—Q. Same specimen sectioned transversely, showing aberrant tripartite symmetry, $\times 1$.

FIGURE 49. Fossils of *Juglans* sect. *Cardiocaryon* from Europe and Asia, all $\times 1$. A–E. *Juglans tephrodes* Unger from the Pliocene of Tagebau Frechen, Germany (Kilpper coll.).—A, B. Outer and inner view of a valve. Note the high primary septum and lack of a secondary septum (IU 4791).—C. Specimen sectioned transversely, levels d and e corresponding to the following photos (IU 4790).—D. Section of specimen in C showing four lacunae in the wall and two large lacunae in the primary septum.—E. More apical section showing two large lacunae on either side of the locule. F, G. *Juglans megacinerea* Miki ex Chaney Pliocene of Nagai, Kawanischi-Mura, Kawanunja-Gun, Fukurhina Prefecture, Japan (Endo. coll.).—F. USNM 364534.—G. USNM 364535.

of Mädlér, 1939; Hills et al., 1974) are based upon the Pliocene specimens from Germany. The Oligocene specimens figured by Kirchheimer (1957) are similar in exterior sculpture, shape, and locule configuration and appear to be validly ascribed to the same species; however, only the Pliocene material has been sectioned (Fig. 46D, E). The placement and size of lacunae thus remains unknown for the older specimens.

The resemblance between *Juglans tephrodes* and the modern eastern North American butternut, *J. cinerea*, is so striking that the fossil was formerly given the same species name. They overlap in shape, size, and the prominent exte-

rior ribbing pattern. Both can be distinguished from the living and fossil eastern Asian butternuts by the presence of only four lacunae in the wall. Hills et al. (1974) carried out a statistical study involving 18 specimens of the fossil and 105 specimens of *J. cinerea* and concluded that the only significant differences are the smaller seeds, more shallow seed lobes, and generally more elongate shape of the fossil nuts. These differences are seemingly quite minor and it is likely that the fossil European and modern North American forms are very closely related, if not actually conspecific. A separate species name is retained for the European material primarily be-

cause of its fossil stature. It would be interesting to compare associated fossil foliage with that of modern *Cardiocaryon* species to determine if the same relationship is suggested.

Juglans megacinerea Miki ex Chaney, Nippon Kobutsu Shuminokai, Kyoto 77, 96–97. figs. 17–27. 1953. *Juglans cinerea* var. *megacinerea* Miki, J. Inst. Polytechn. Osaka City Univ., Ser. D, Biol. 6: 131–144. pl. 2: fig. A. 1955; Nirei, J. Inst. Polytechn. Osaka City Univ., Ser. G, Geosci. 19: 34–37. pl. 1: figs. 6–12. figs. 3, 4. 1975; Kimura, Yoshiyama & Ohana, Trans. & Proc. Palaeontol. Soc. Japan n.s. 122: 94–95. pl. 9: figs. 7–9. fig. 6a, b. 1981. Figure 49F, G.

Description. Nut oblong-ovate to ellipsoidal, 4–7.5 cm long, 2.7–3.6 cm wide, base rounded, apex acuminate; surface prominently sculptured with eight blade-like longitudinal ribs about 5 mm deep; distal margin of each rib broadened, forming thin denticulated wings overhanging to both sides; with a reticulum of minor ribs developed between the major ones; secondary septum absent; primary septum containing a pair of large lacunae; nut wall with seven to nine distinct lacunae; seed with pointed hypocotyl, flattened in the plane of the primary suture, basal lobes of seed undivided, thick.

Discussion. In shape and external sculpture, *Juglans megacinerea* closely resembles the extant *J. cinerea*, and it has previously been equated with that species in the literature. However, cross-sections of the nut reveal seven to nine distinct, well-developed lacunae within the shell (Miki, 1955; Nirei, 1975). This feature distinguishes it from most other fossil species, including the European *J. bergomensis* and the American *J. eocinerea*, as well as modern *J. cinerea*, which have only four such lacunae. In its possession of extra lacunae, *J. megacinerea* resembles the modern Asian species *J. mandshurica* and *J. cathayensis*. *Juglans mandshurica* is often similar in general shape but has more rounded, rather than blade-like, ribs. The nuts of *J. cathayensis* are similar in the possession of blade-like sculpture but are generally ovoid, rather than oblong, and the lacunae are smaller and less well developed.

Although the size range of *Juglans megacinerea* overlaps to some extent with the larger specimens of *J. cinerea*, most of the fossil specimens are much larger, up to 7.5 cm long. *Juglans*

megacinerea produced the largest fruits known for the Juglandaceae.

Juglans megacinerea occurs in many localities in Japan (Nirei, 1975) ranging from Miocene to Plio-Pleistocene. The reference to its occurrence in Eocene strata (Nirei, 1975: 37) is a misprint that should instead read Miocene (Nirei, pers. comm.). In addition to *J. megacinerea* (formerly "*J. cinerea* var. *megacinerea*"), four species have been recognized in the fossil record of Japan. *Juglans hanamakiensis* Nirei from the Pliocene Mitsuawagawa Formation differs from *J. megacinerea* in possessing spinier ribs. *Juglans mikii* Nirei of the Plio-Pleistocene is intermediate in size and depth of sculpture between *J. megacinerea* and the extant *J. mandshurica*. These species also had seven to nine intrawall lacunae. Nirei (1975) also reports that the ranges of the extant species *J. mandshurica* and *J. sieboldiana* extend back to the Pliocene in Japan based on fossil fruits.

Juglans siberica Dorofeev, Dorofeev, Tertiary Floras of the Omoloj River Basin, Akad. Nauk S.S.S.R., Moscow 87. 1972.

Juglans cinerea L. *fossilis* Dorofeev, Tertiary Floras of Western Siberia, Akad. Nauk S.S.S.R., Moscow 137–138. pl. 19: figs. 1–4. 1963.

Description (after Dorofeev, 1972). Nuts ellipsoidal to ovoid, 4.5–5.3 cm high, 2.5–3 cm wide; base rounded, or more rarely, narrowed; apex narrowed, slightly drawn out, but short; surface sculptured with four principal longitudinal ribs on the exterior, between which are one or two less prominent and more wavy secondary ribs; secondary ribs sometimes absent and replaced by small longitudinally oriented ridges; crest of principal ribs, and some of the secondary ribs, broadened, with their edges turned back, resembling a 'T' in cross section; fine, uneven, sharp diagonal to longitudinal minor ribs located at intervals between the primary and secondary ribs; lacunae placement, size, and number undetermined.

Discussion. *Juglans siberica* comes from the Miocene sands of Kireevskoe Selo on the Ob River, Tomkaja Region, in western Siberia. It closely resembles the Neogene *J. tephrodes* from Europe and the modern *J. cinerea* of North America.

Dorofeev (1972: 86–87) states that the endocarps from the Tertiary of Siberia and Europe can be distinguished from the modern American

species *Juglans cinerea* by the nature of their ribs. According to his observations, the fossil endocarps always have at least four strongly developed, or principal, ribs, while *J. cinerea* has only two principal ribs, those along the sutural plane, the rest being less prominent. However, in my own observations of *J. cinerea*, I have seen considerable variation in the relative prominence of the ridges. The taxonomic value of distinctions based only on this feature is questionable. The extant Oriental species, *J. mandshurica* and *J. cathayensis*, as well as the extant American species, *J. cinerea*, seem to exhibit a basic pattern of eight symmetrically placed ribs, including four well-developed ones in the planes of the primary and secondary septa and usually four additional, less prominent ones interspersed between them.

Butternuts were apparently well distributed across northern Asia in the Neogene. In addition to *Juglans siberica*, Dorofeev has recognized two similar species: *J. jacutica* from the Miocene of Mamontovaja gora on the Aldan (Dorofeev, 1969: 64–66, pl. 11: figs. 1–4) in western Siberia and *J. omoloica* from the Neogene (late Miocene?) of the Omoloj River in eastern Siberia (Dorofeev, 1972). *Juglans siberica* is distinguished from *J. jacutica* by a broader, more often rounded base, broader principal and secondary ribs, finer details of sculpture, and a more oblong locule cavity. *Juglans omoloica* is differentiated from the western Siberian forms by smaller size, more rounded form, and finer, more poorly developed secondary and principal ribs.

It would be desirable to know the number and placement of lacunae in the Siberian fossils since this is a feature differentiating extant Oriental and American butternuts. However, data from cross-sectioned nuts has not been provided for the Soviet material.

Juglans eocinerea Hills, Klován & Sweet, Canad. J. Bot. 82: 65–90, figs. 13–55, 57, 58, 80, 81, 83. 1974.

Description (after Hills et al., 1974). Nuts ovate to obovate, 2.5–6.1, avg. 4.3 cm long, 1.4–3, avg. 2.2 cm wide; base narrow, rounded in ovate specimens to pointed truncate in obovate specimens; the more elongate specimens exhibiting a progressive taper from maximum width to a very narrow base; apex asymmetrically conical, often acuminate, uniformly tapered in plane of primary suture; walls (1–)4(–7) mm thick; exterior sculpture comprised of eight major ribs

including those along the primary suture, extending from base to apex, occasionally bifurcating, giving rise to secondary ribs of shorter length, and to tertiary ribs that form a blade-like reticulum between the major ribs; four lacunae present within the walls adjacent to the secondary suture; four to six small lacunae at the base of the primary septum, two large intraseptal lacunae present in the main portion of the primary septum; seed 20–39, avg. 29 mm long, 7–20, avg. 15 mm wide; hypocotyls pointed, flattened in plane of primary suture; maximum width about the end of the major septum; basal lobes of seed shallow, narrow, sloping inwards, sides of seed from point of maximum width to base concave.

Discussion. This species, from the Miocene Beaufort Formation of southwestern Banks Island, arctic Canada, is noteworthy because of its extreme northerly occurrence and because it is the only fossil record of scabrate-shelled butternuts in America.

Hills et al. (1974) conducted a statistical analysis based upon 203 samples of *Juglans eocinerea* and 105 specimens of *J. cinerea* and concluded that the fossil may be distinguished from the living species by its smaller size, its tapered and narrow base, the depth of the divided seed, and its larger intra-wall lacunae. Lacunae within the walls of the living *J. cinerea* are usually smaller and flattened parallel to the seed lobes.

An interesting finding from the statistical study of Hills et al. (1974) was that the morphological variability in *Juglans eocinerea*, for most characters, is almost twice that observed in populations of *J. cinerea* and *J. nigra*. They concluded that this “may be indicative of low selection pressure, resulting in a variable population. The diversity in characters would enhance the potential for evolutionary radiation. In *J. cinerea*, presumably a descendant of *J. eocinerea*, the diversity of most characters is limited to a narrow range, suggestive of a well-adapted, somewhat specialized species.”

As Kirchheimer noted (1957: 301–302), there has been a continuing tendency for paleobotanists to overlook the extant Chinese and Japanese butternuts when discussing *Juglans cinerea*-like fossils. *Juglans cathayensis* and *J. mandshurica* nuts commonly exhibit a scabrate exterior sculpture similar to that of *J. cinerea*. In number and size of lacunae, the fossil described here appears to be more similar to the Chinese species than to *J. cinerea*. As in *J. eocinerea*, nuts

of *J. mandshurica* and *J. cathayensis* have more than four lacunae, some of which are quite large. In *J. cinerea*, there are usually just four lacunae in the wall, and they are tangentially flattened.

It would be desirable to conduct a statistical study of measurements from large suites of *Juglans mandshurica* and *J. cathayensis* for comparison with the data provided by Hills et al. (1974) on *J. eocinerea* and *J. cinerea*. It is possible that the Banks Island walnut represents a species ancestral not only to *J. cinerea* (as suggested by Hills et al., 1974), but to the extant Chinese and Japanese species as well.

GENERAL SUMMARY AND DISCUSSION, JUGLANDACEAE

The Juglandaceae can be traced with confidence back to the Upper Paleocene on the basis of fruits, foliage, and pollen. The absence of pollen characteristic of modern Juglandaceae from Cretaceous and Lower Paleocene strata suggests that the evolution of juglandeoid pollen occurred during the Paleocene. Pentaporate isopolar pollen similar to that of extant *Pterocarya* occurs as rare grains in the Upper Paleocene; however, multiporate, heteropolar grains like those of *Juglans* are unknown prior to the Middle Eocene. It is conceivable that small isopolar triporate pollen of the type associated with Paleocene *Cyclocarya brownii* fruits gave rise to larger tetraporate grains as seen in extant *C. paliurus* and ultimately to the more specialized multiporate isopolar and heteropolar grains characteristic of *Pterocarya* and *Juglans*.

Chambered pith, a diagnostic feature of extant Juglandaceae, was probably present prior to the divergence of modern genera of the tribe (unless it evolved separately more than once). It is therefore probable that the chambered condition evolved in the family by the Upper Paleocene, at which time *Cyclocarya* fruits first appear. Although silicified wood resembling that of the Juglandaceae is known from as early as the Middle Eocene, the condition of pith has not been reported.

The geographic distribution of modern and fossil *Cyclocarya* and related extinct genera is indicated on the map (Fig. 50). *Cyclocarya paliurus*, of southeast Asia, is the single living representative of a genus that was formerly spread across Europe, North America, and Siberia. The genus is first documented in the Paleocene of North America, where it is known from three

distinct species of fruits, and appears to be a product of the same diversification that produced the extinct genus *Polyptera*. The validity of the identification of such early fruits to an extant genus is demonstrated most clearly in the case of *C. brownii*, which is known from numerous excellently preserved fruits closely comparable to (although not conspecific with) modern *C. paliurus*. Even the foliage associated with *C. brownii* compares well with that of extant *Cyclocarya*.

Cyclocarya and *Polyptera* disappear from the American fossil record in the Eocene, but *Cyclocarya* survived in the Old World. Possible *Cyclocarya* pollen of tetraporate isopolar morphology is present in the Upper Eocene of the Paris Basin, and the Lower Eocene *Juglandicarya depressa* from the London Clay flora might be related to *Cyclocarya*, although it is incompletely known. Confirmed fruits of *Cyclocarya* occur in the Oligocene of both Europe and Asia. Although absent from Europe today, *Cyclocarya* has records as late as the Pliocene in Germany.

Although the basic *Cyclocarya* fruit plan was apparently fixed in the Upper Paleocene, subsequent evolutionary trends can be inferred from comparative morphology of modern and fossil fruits. The pyramidal nutlet shape, basal wing attachment, and well-developed secondary septum observed in Paleocene *Cyclocarya brownii* and *C. coalmontensis* are features shared with the extinct *Polyptera* that might be considered primitive. Pyramidal nutlet morphology and basal wing attachment is not known from the later Tertiary and apparently gave way to globose and lensoidal nutlets with subequatorial wing attachment. Oligocene species are thought to have had nearly equatorial wing attachment similar to that of the modern species. Based upon Siberian records, Dorofeev (1970b) suggests a Neogene trend from smooth-ribbed, globose nutlets to more prominently ribbed, lensoidal nutlets more closely approximating the modern condition. Considerable variation has occurred in wing development. While *C. brownii* and *C. paliurus* exhibit large wings, those of *C. coalmontensis* are relatively small and perhaps vestigial. *Sphaerocarya* appears to represent an extreme condition in which the wings were not developed at all. The nutlets of *Sphaerocarya* are internally similar to modern *Cyclocarya* and were smooth and globose, similar to certain Oligocene nutlets of *Cyclocarya*, but were apparently enclosed in a husk during life (Dorofeev, 1970b).

FIGURE 50. Map showing modern and fossil distribution of *Cyclocarya* and related extinct genera. Modern distribution of *Cyclocarya paliurus* shaded. Fossil occurrences based upon fruits. Generic symbols: triangle = *Polyptera*; circle = *Cyclocarya*; diamond = *Sphaerocarya*. Generic symbols darkened = Paleocene or Eocene; generic symbols not darkened = Oligocene, Miocene, or Pliocene. — 1. *Polyptera manningii*. — 2. *Cyclocarya brownii*, *C. minuta*. — 3, 4. *Cyclocarya brownii*. — 5. *Cyclocarya coalmontensis*. — 6. *Juglandicarya depressa* possibly related to *Cyclocarya*. — 7. *Cyclocarya cycloptera*. — 8. *Sphaerocarya* sp. — 9. *Sphaerocarya uralensis*. — 10. *Cyclocarya tavidensis*. — 11. *C. cycloptera*. — 12. *C. tymensis*. — 13. *S. nikitini*. — 14. *C. tomskiana*, *S. nikitini*. — 15, 16. *C. ezoana*.

Figure 51 compares fossil and modern distributions of *Pterocarya*. Occasional pentaporate isopolar grains resembling *Pterocarya* are reported from the Paleocene of the central United States and the far eastern Soviet Union and the Eocene of Europe. The earliest known fruits are from the Middle Eocene of North America. During the Oligocene, *Pterocarya* became widespread across North America, Europe, and Asia, as indicated by fruit, foliage, and pollen records. In contrast to *Cyclocarya*, which was absent in North America by the Oligocene, *Pterocarya* persisted with several species as late as the Miocene in western North America. The genus is also well represented in the Neogene of Europe and Asia. Regional extinctions of the Pliocene or Quaternary account for its present-day absence in North America and most of Europe.

Evolution of fruit morphology in *Pterocarya* is not well understood because of the paucity of early Tertiary fruiting material. No fruits are known from the Paleocene, although dispersed pollen suggests that the genus might have been present. The earliest fruits are from the Middle Eocene (*P. macginitii*). These have a small nutlet compared to that of later Tertiary and modern species, but the details of nutlets are not preserved. Oligocene species clearly display nutlets with pronounced longitudinal ribbing and oblique wing attachment and are associated with foliage indistinguishable from modern *Pterocarya*. By the Miocene, diversity in fruit morphology was comparable to that of today. Some of the Miocene species were essentially identical in fruit morphology to certain modern species. For example, *P. protostenoptera* of the Miocene of Japan and Korea is virtually indistinguishable from modern *P. stenoptera*, while *P. limburgensis* of the European Miocene closely resembles *P. fraxinifolia*. North American Miocene species included examples of both modern sections of the genus. Close similarity between Miocene western North American species and living Asian species suggests that there may have been continuity of populations across Beringia during the Miocene. *Pterocarya* leaflets and pollen, as well as a possible fruit, have been documented from the Miocene of Alaska (Wolfe, 1966; Wolfe & Tanai, 1980).

The modern and fossil distributions of *Juglans*, sects. *Rhysocaryon* and *Cardiocaryon*, are shown in the map in Figure 52. Section *Dioscaryon*, with a modern distribution covering southern Europe and Asia, is not known in the

fossil record and is therefore omitted from consideration. Sections *Rhysocaryon* and *Cardiocaryon* are treated separately because they are easily distinguished morphologically and appear to have distinct paleogeographic histories. Differences between the sections include leaflet architecture, wood anatomy, and pollen morphology as well as fruit morphology. The degree of divergence between them is greater than that observed between the sections of *Carya* (sect. *Eucarya* versus sect. *Apocarya*) and comparable to that between genera of the Engelhardieae.

The earliest confirmed fruit and pollen records of *Juglans* are from the Middle Eocene of North America. The early evolution of *Juglans*, including the divergence of sects. *Rhysocaryon* and *Cardiocaryon*, apparently occurred during the Eocene, possibly in North America. The earliest known walnut fruit, *J. clarnensis* from the Middle Eocene, is comparable in many aspects to modern black walnuts but has a simpler seed and locule morphology (more similar to that of modern butternuts) and variable development of the secondary septum, which ranges from absent, as in modern butternuts, to present and reasonably well developed, as in modern black walnuts. Fruits more clearly resolved along modern sectional lines occur in the Oligocene; for example, the black walnut *J. siouxensis* and the butternut *J. lacunosa*.

Section *Rhysocaryon* (black walnuts), which is endemic to the New World, does not have any known records in the Old World and has apparently been confined to America throughout its evolution. The Miocene distribution of black walnuts spanned from the west to east coasts of North America but apparently did not reach high latitudes. Black walnuts, with six extant species in South America and the West Indies (Manning, 1960), are the only members of the tribe Juglandae with a modern range extending well into the Southern Hemisphere. The occurrence of *Juglans linkii* fruits in the late Miocene or early Pliocene of Ecuador indicates that the southward migration of the genus took place prior to the beginning of the Pliocene. Graham (1973, 1976) noted that *Juglans* pollen occurs in Miocene sediments of Middle America but, along with other temperate arborescent genera, appears to be absent from Oligocene palynofloras of the region.

In contrast to sect. *Rhysocaryon*, which has remained American in distribution throughout its history, sect. *Cardiocaryon* (butternuts) has several extant species in Asia as well as the one

FIGURE 51. Map showing modern and fossil distribution of *Pterocarya*. Modern distribution shaded. Fossil data points based upon fruits. — 1. *Pterocarya macginittii*, Eocene. — 2, 3. *P. occidentalis*, Oligocene. — 4. *P. smileyi*, *P. eomacroptera*, Miocene. — 5. *P. limburgensis*, Lower to Upper Pliocene (Kirchheimer, 1957). — 6. *Pterocarya* sp., Miocene (Gregor, 1982). — 7. *P. castaneaefolia* (Kirchheimer, 1957). — 8. *P. raciborskii*, Middle Miocene (Zablocki, 1928). — 9. *P. limburgensis*, Lower Pliocene (Kirchheimer, 1957). — 10. *P. kireevskiana*, Miocene (Dorofeev, 1963). — 11. *P. castaneaefolia*, Oligocene (Takhtajan et al., 1963). — 12. *Pterocarya* sp. (Dorofeev, 1969). — 13. *Pterocarya* sect. *Chaenoptera* (Dorofeev, 1972). — 14–16. *P. protostenoptera*, Upper Miocene. — 17. *P. asymmetrica*, Miocene.

FIGURE 52. Map showing modern and fossil distribution of black walnuts and butternuts. Shaded areas indicate modern distribution of *Juglans* sect. *Rhysocaryon* (NE-SW hatching) and *J.* sect. *Cardiocaryon* (NW-SE hatching). Dots indicate fossil nuts of sect. *Rhysocaryon*. Diamonds indicate fossil nuts of sect. *Cardiocaryon*. — 1. *Juglans clarnensis*, Middle Eocene. — 2. *Juglans* sp., Oligocene San Ramon Formation. — 3. *J. siouxensis*, Oligocene. — 4. *J. calvertiana*, Miocene. — 5. *J. linkii*, Upper Miocene or Lower Pliocene. — 6–8. *J. lacunosa*, Early Oligocene to Miocene. — 9. *J. eocinerea*, Miocene? — 10. *J. tephrodes*, Oligocene to Pliocene. — 11. *J. siberica*, Miocene. — 12. *J. omoloica*, Miocene. — 13. *J. megacineria* (and other species reviewed by Nirei, 1975).

in eastern North America. The fossil fruit record indicates that the section was formerly distributed in Europe, Siberia, and western North America as well.

The earliest butternuts were probably smooth-walled like those of *Juglans lacunosa* from the early and middle Oligocene of Washington. Rough-ridged and scabrate butternuts similar to those of extant *J. cinerea* were present in the Oligocene of Germany (*J. tephrodes*) and became widespread in Eurasia during the Miocene. Noting the occurrence of similar forms in the Miocene of Siberia (e.g., *J. siberica*) and arctic Canada (*J. eocinerea*), Hills et al. (1974) suggested that such butternuts may have evolved and radiated from high northern latitudes.

By the late Miocene, *Juglans* had achieved a broad distribution, as indicated on the map in Figure 52. Black walnuts ranged across the United States and as far south as Ecuador. Butternuts spanned from the western United States and northern Canada across eastern and western Siberia to Europe and into Japan. This extensive range has since been drastically reduced as can be seen by contrasting the present distribution of the genus with its fossil occurrences. Butternuts are now isolated in two parts of their former extensive range: the eastern part of North America, and China and Japan. The range of black walnuts also decreased, but not as impressively as that of the butternuts. Black walnuts are no longer present in the Pacific Northwest region of North America. These regional extinctions occurred during the Pliocene or Pleistocene in response to climatic fluctuations and correspond to the extinctions observed in *Pterocarya* and *Carya* over the same interval.

GENERAL DISCUSSION AND CONCLUSIONS

The fossil record provides an improved basis for understanding the timing and patterns of origin, phylogeny, rates of evolution, biogeography, climatic tolerances, and extinction. Interpretations of the history of individual juglandaceous tribes and genera have been presented in the foregoing sections of this paper, and it is now possible to present a synthesis for the entire family.

ORIGIN OF THE FAMILY

The Juglandaceae appears to be a late Cretaceous or early Tertiary derivative of the Normapolles complex. There is a close similarity between certain Upper Cretaceous pollen grains of the Normapolles complex and triporate pollen of the Juglandaceae. In addition, some of the flowers associated with Normapolles pollen in the Upper Cretaceous of Sweden (e.g., *Caryanthus*) are remarkably similar in morphology to the Juglandaceae, differing primarily by their bisexual nature, lack of a well-developed primary septum, and small size.

As yet, no pre-Tertiary megafossil remains of the Juglandaceae have been confirmed. Dispersed pollen resembling that of extant Engelhardieae (*Momipites*) occurs as early as the Campanian in North America but has not been examined with electron microscopy. It is possible that pollen with the essential features of modern juglandaceous pollen (e.g., *Plicapollis*) appeared prior to the attainment of juglandaceous morphology in other organs. As resolution of the Lower Paleocene and Upper Cretaceous megafossil record improves, it may prove difficult to distinguish between "Protojuglandaceae" and Juglandaceae. The characters of prime importance in diagnosing the modern family are pinnately compound foliage, unisexual flowers, bicarpellate fruits with a well-developed but incomplete primary septum, and secondary xylem with fine tangential lines of axial parenchyma. The first obvious fruits and foliage of the family are seen in the mid-Paleocene. At present, the earliest reports of juglandaceous wood are Middle Eocene.

The origin of the Juglandaceae seems certain to have been in the Northern Hemisphere. The Normapolles complex, from which the family probably evolved, defines a mid- to late Cretaceous province extending from eastern North America to Europe.⁹ This information, combined with the geographic distribution of earliest known juglandaceous fossils (Table 2), favors an eastern North American or European origin for the family with high latitude intercontinental migration early in the radiation of the family. Although *Juglans* occurs in South America to-

⁹ There are occurrences of Normapolles pollen from outside the accepted province; however, these are chiefly Maastrichtian and younger. Srivastava (1981) suggests that the provincial boundaries began to break down with the Maastrichtian marine regression.

day, it is not known in the fossil record there prior to the Miocene.

The Late Cretaceous–early Paleocene origin of the Juglandaceae was approximately synchronous with that inferred for many modern dicotyledonous families. Prior to the Tertiary, very few extant angiosperm families can be recognized (Hickey & Doyle, 1977; Dilcher, 1979). Yet by the Eocene, numerous modern families and even extant genera were present. The comprehensive and critical study of the early Eocene London Clay fruit and seed flora (Reid & Chandler, 1933; Chandler, 1964) revealed more than 40 modern dicotyledonous families, many of which have been recognized in the North American Eocene as well. Included in this radiation were several families of the Amentiferae: the Fagaceae (Manchester & Crane, 1983), Ulmaceae (Zavada & Crepet, 1981), Betulaceae (Crane, 1981), as well as the Juglandaceae (Crepet, 1981).

DIVERSIFICATION

Although the Juglandaceae might have originated in the late Cretaceous, the major diversification occurred during the Paleocene. Throughout much of the Paleocene there was a wide range in types of triporate juglandaceous pollen (Nichols & Ott, 1978; Frederiksen & Christopher, 1978). In some localities the morphological range of variation is virtually continuous, making it difficult to discriminate between taxa (Frederiksen, 1979). However, by the late Paleocene, pollen appears to have been differentiating into forms characteristic of modern tribes and genera. Pseudocolpate pollen similar to that of extant *Platycarya*, relatively large, subisopolar pollen with polar thin spots resembling modern *Carya*, relatively unmodified triporate grains like those of extant Engelhardieae, and 4- to 7-porate pollen grains similar to *Pterocarya* are all evident in the Upper Paleocene.

Fossil fruits indicate that the family reached a peak of generic diversity in the Eocene. By the Middle Eocene at least ten genera were present, some modern (*Pterocarya*, *Cyclocarya*, *Juglans*, *Platycarya*) and others extinct (*Paraengelhardtia*, *Paleooreomunnea*, *Polyptera*, *Paleoplatycarya*, *Hooleya*).¹⁰ Although generic diversity is known to have been greater in the family at that time, species diversity is more difficult to assess.

Criteria differentiating modern species often cannot be assessed from fossil plant parts. However, *Cyclocarya* and *Platycarya*, both of which are monotypic today, are known to have been more diverse in the Paleogene. Each had two or more distinct species in the late Paleocene and/or early Eocene, based upon differences in fruit wing configuration. The reduced present-day diversity of the family is attributed to Paleogene and Pliocene–Pleistocene climate-related extinctions.

PHYLOGENY

The fossil record supports recognition of Manning's (1978) tribes as natural groups. Each tribe maintains its integrity back to the Paleogene, neatly accommodating various extinct and extant genera. Table 1 lists modern and fossil fruit genera according to their tribal affiliations. The systematic and phylogenetic relationships of modern tribes and genera have previously been inferred only from living representatives. New information from the fossil record supports some aspects of previously proposed phylogenetic schemes while also suggesting some areas where revision is necessary.

Figure 54 is a suggested phylogeny of the Juglandaceae including both modern and fossil representatives. The time scale now provided by the fossil record facilitates an understanding of relative antiquity of genera and of minimum ages for the divergence of related taxa. The scheme presented here depicts the modern tribes, including the Engelhardieae, as derivatives of a late Cretaceous–early Paleocene ancestral group. The diversification of modern tribes appears to have occurred at different times. The Juglandae appear first, followed successively by the Hicoreae, Platycaryeae, and Engelhardieae. However, there is no clear evidence demonstrating the derivation of one tribe directly from another. The phylogenetic relationships between tribes are inferred from comparative morphological data and agree, in part, with previous conclusions of Whitehead (1965), Manning (1978), and Wing and Hickey (1984).

On the basis of comparative studies of modern genera, previous workers have placed the Engelhardieae in a phylogenetic position ancestral to the rest of the family (Whitehead, 1965; Stone & Broome, 1975; Manning, 1978), suggesting that

¹⁰ *Palaeocarya* is an organ genus that could actually accommodate both extinct and extant genera.

it is a surviving stem group. This conclusion was supported by the numerous primitive characteristics of pollen, wood anatomy, and inflorescence position shared by modern genera of the tribe but is not compatible with data now available from the fossil record.

It now seems clear that the Engelhardieae, like other modern tribes, is a derived group. Although it retains a larger number of primitive characteristics today than other tribes, its origin, as defined by evolution of the diagnostic trilobate bract, appears to have been subsequent to that of other modern tribes. Trilobate bracts of the Engelhardieae are readily preserved in the fossil record, both in inflorescences and in dispersed fruits, but are not known in the Paleocene. Engelhardioid bracts are first observed in the Eocene. Fruits from the middle Eocene include forms with bracts that are only faintly trilobate (*Paraengelhardtia*, *Paleooreomunnea*), suggesting an incipient condition. The tiny fruits of *Casholdia* from the uppermost Paleocene have a simple, unlobed bract suggestive of a pre-engelhardioid condition (Crane & Manchester, 1982).

Among extant juglandaceous taxa, small, triporate, isopolar pollen is diagnostic of the Engelhardieae. However, in the Paleocene the same kind of unspecialized pollen (*Momipites* spp.) was widespread and appears to have been associated with *Cyclocarya brownii*, *Polyptera manningii* of the early Juglandaeae, *Juglandicarya simplicarpa* of possible hickeyoid affinity, as well as possible forerunners of the Engelhardieae (*Casholdia*). More specialized types of pollen, such as those characteristic of modern *Carya*, *Platycarya*, *Cyclocarya*, and *Pterocarya*, are unknown prior to the uppermost Paleocene.

The tribe Juglandaeae has the oldest megafossil record in the family with confirmed occurrences in the middle and upper part of the Paleocene. Remarkably, the Paleocene occurrences include fruits and foliage attributable to extant *Cyclocarya*, as well as extinct forms. An important feature uniting modern genera of the Juglandaeae is the occurrence of chambered pith; pith is solid in other tribes of the family. One would expect that this feature evolved prior to the divergence of modern genera of the Juglandaeae and that the pith of *Polyptera* and Paleocene species of *Cyclocarya* was chambered. Although pith is commonly preserved in the center of silicified juglandaceous woods, chambered pith has not yet been described for woods older than Pliocene. It would be interesting to examine the fossil stem record

to determine the actual antiquity of this feature. The divergence of *Juglans* and *Pterocarya* apparently occurred prior to the Middle Eocene when fruits of both are first observed in the fossil record. Certainly by the Eocene the main avenues of morphological diversification within the tribe were well established. The only post-Eocene genus, *Sphaerocarya*, may have been derived directly from *Cyclocarya* by suppression of wing development.

The Hickeyeae may be traced with reasonable certainty back to the Paleocene, based on the appearance of distinctive *Caryapollenites* pollen and *Carya*-like foliage. This is the same time interval during which the Juglandaeae is first recognized. Overlapping features of leaflet architecture and pollen morphology in fossils of the Paleocene Fort Union Formation suggest that the Hickeyeae was not as distinct from the Juglandaeae at that time as it is today. Accordingly, these are depicted as sister tribes in the phylogenetic diagram (Fig. 54).

While the Hickeyeae appears to have its beginnings in the Paleocene, the single modern genus *Carya* is not fully recognizable on the basis of fruits until the Eocene. Whereas leaves and pollen morphologically similar to *Carya* permit recognition of the tribe in the Paleocene, associated and presumably related fruits (e.g., *Juglandicarya simplicarpa*) lack the inner nutshell ribs and convoluted cotyledons diagnostic of the modern genus.

The Hickeyeae contrasts with other tribes of the Juglandaceae in its long history of low generic diversity. In other tribes the diversity is due in part to the evolution of various types of winged fruits. The Hickeyeae is known only from wingless fruits of the single modern genus *Carya* and its presumed precursors. The Paleocene occurrences of *Juglandicarya* and the lack of winged fruits throughout the known record of the Hickeyeae suggest that the adaptation for animal dispersal became fixed early in the evolution of the tribe.

The Platycaryeae, as defined by distinctive pseudocolpate pollen, is first observed in the uppermost Paleocene, and the characteristic inflorescences and fruits are known from the lowermost Eocene. Its appearance is subsequent to that of the Juglandaeae and Hickeyeae but slightly prior to the first confirmed records of Engelhardieae.

Calling attention to various unique features of *Platycarya*, Manning (1978) placed the Platy-

caryeae in its own subfamily, separate from all other tribes. However, Whitehead (1965) suggested close affinity with Engelhardieae on the basis of pollen morphology. Wing and Hickey (1984) demonstrated shared features between early Eocene platycaroid foliage and that of extant Engelhardieae and suggested that a close sister-group relationship exists between the Platycaryeae and Engelhardieae. Although the foliar similarities between extant *P. strobilacea* and Engelhardieae are not particularly striking, the early Eocene foliage associated with *P. americana* and *Paleoplatycarya wingii* exhibit several characters that are primarily confined to the Engelhardieae today such as prominent intersecondary veins, closed areolation, long petiolules, and basilaminar tissue specialization.

The fossil record suggests that the divergence of Platycaryeae and Engelhardieae was a late Paleocene–early Eocene phenomenon, subsequent to the divergence of Juglandaceae and Hicoreae. The stock from which Platycaryeae and Engelhardieae diverged remains poorly known but may have included fruits like *Casholdia*. *Casholdia microptera* from the Upper Paleocene of Britain and France is apparently juglandaceous but does not conform to a modern tribe. Crane and Manchester (1982) document characters suggestive of a close alliance with Engelhardieae but note that it lacks the trilobate bract diagnostic of that tribe. Characters in common with Platycaryeae include shape and venation of the bract, apparent absence of sepals, small fruit size, and the transverse orientation of the style arms. It is differentiated from Platycaryeae by the retention of the inflorescence bract on the fruit rather than on the axis and by the bracteoles that appear to be united into a prophyllum rather than forming lateral wings.

PALEOBIOGEOGRAPHY

Maps comparing the geographic distribution of modern and fossil members of each tribe have already been presented (Figs. 17, 29, 35, 50–52), and it is clear that each tribe was more widely distributed across the Northern Hemisphere in the Tertiary than today. By comparing the fossil records of taxa in different regions, it is possible to infer places of origin, timing, and routes of migration as well as the timing and extent of extinctions in different areas.

Figure 53 summarizes the modern occurrences and stratigraphic records of ten genera in four

major regions: North America, Europe, Asia, and Central and South America. Paleobiogeographic interpretations offered here assume completeness of the fossil record and reasonably accurate time correlations. The effect of less than complete records and less intensive study in some areas may result in underestimation of the antiquity of distributions, particularly in Asia.

As indicated in Figure 53, Asia is the center of modern generic diversity. Six genera (*Platycarya*, *Engelhardia*, *Cyclocarya*, *Pterocarya*, *Juglans*, *Carya*) are indigenous to China, including four endemics, whereas only a few genera occur today in the other regions. Classically, such a center of modern diversity might be considered evidence for an Asian center of origin (Cain, 1944). Lu (1982) suggests an Asian origin on the basis of this diversity and because the most primitive modern genera occur in China. However, it is clear from the fossil record that the region has served as a refugium rather than as a cradle for juglandaceous taxa. During the Oligocene and Miocene, all of the genera now present in Asia had broad intercontinental distributions. In addition, the well-studied fossil pollen record of Japan suggests that *Platycarya* and *Carya* did not arrive there until the late Tertiary. An Asian origin also seems unlikely because Asia lies outside of the Normapolles province from which the family probably evolved. The earliest center of juglandaceous generic diversity appears to have been North America. Since Paleocene strata are better represented and more thoroughly studied in mid-latitude North America, one cannot rule out the possibility of an Arctic or European origin.

Migration or range expansion across high northern latitudes explains occurrences of the same genera in North America and Eurasia during the Tertiary. Present climatic conditions of the arctic latitudes are too severe for juglandaceous species to become established. However, the occurrence of megafossils of the family in the Eocene to Miocene of Alaska (Wolfe, 1977; Wolfe & Tanai, 1980), the Oligocene and Miocene of Siberia (Dorofeev, 1970b), and the Miocene of Banks Island, arctic Canada (Hills et al., 1974), demonstrate that climate was favorable for the spread of juglandaceous taxa across arctic or subarctic regions through much of the Tertiary.

Migration between North America and Eurasia has probably occurred along two routes: one across the North Atlantic, leading between eastern North America and western Europe; the oth-

FIGURE 53. Stratigraphic and modern distribution of juglandaceous genera. Ranges designated by asterisks (*) are based upon fruit determinations; ranges indicated by dots (.) are inferred from pollen or other information.

FIGURE 54. Suggested phylogeny of modern and fossil Juglandaceae with time scale from the fossil record. Exemplary fruits figured. Important data points, indicated by squares, are based upon fruit determinations. Darkened square = North American occurrence. Undarkened square = Eurasian occurrence. Half darkened square = both Eurasian and North American occurrences.

er across Beringia, leading between western North America and eastern Asia. The North Atlantic connection, which was probably important in the spread of Normapolles genera during the Upper Cretaceous (Tschudy, 1981), appears to have remained open during the Paleocene and part of the Eocene (McKenna, 1983), permitting the interchange of taxa such as *Platycarya*, *Hooleya*, and *Palaeocarya* between Europe and North America prior to their appearance in Asia (Fig. 53). It is of interest in this regard that platycar-yoid fruits and pollen appear almost simultaneously in North America and Europe near the Paleocene-Eocene boundary but are apparently missing from the Asian record prior to the Miocene. It is unlikely that the distinctive pseudocolpate pollen of *Platycarya* has been overlooked in palynological research on Asian strata. Even in the Tertiary of Japan, which has been well studied palynologically, there is no record of *Platycarya* pollen prior to the Quaternary. It is probable that direct migration between Europe and Asia was limited during the initial geographic dispersal of the family due to the barrier effect of the Obik Sea and Turgai Straights (McKenna,

1983). Geophysical and paleozoological data suggest that the North Atlantic land connection was cut off by the Upper Eocene (McKenna, 1983). Effects of migration across Beringia and across the Turgai region become evident in the Oligocene with the appearance of taxa formerly restricted to Europe and/or North America (such as *Juglans* sect. *Cardiocaryon*, *Cyclocarya*, and *Pterocarya*) in Asia. Southward range expansion was in progress in North America at about the same time, as suggested by the timing of appearances of Engelhardieae and *Juglans* in Middle America.

EXTINCTIONS

The reduced modern day diversity and distribution of the Juglandaceae, as compared to that observed in the fossil record (Fig. 53), demonstrates the importance of extinction in the history of the family. Two major intervals of extinction are apparent in the fossil record: one in the Paleogene, the other in the Plio-Pleistocene.

Several well-documented Paleocene and Eocene genera disappear from the fossil record

prior to the Oligocene and are now extinct, including *Casholdia*, *Paraengelhardtia*, *Paleo-oreomunnea*, *Polyptera*, and *Paleoplatycarya*. Regional but incomplete extinctions also occurred prior to the Oligocene, as in the cases of *Cyclocarya* and *Platycarya* that became extinct in North America but survived in Europe. Climatic fluctuation, particularly the cooling at the end of the Eocene (Wolfe, 1978), may have been an important factor in Paleogene extinctions. The genera that became extinct during this interval were those that had not established large geographic ranges by the early or mid-Paleogene. Each is known from only a single species and small geographic area. Conversely, the genera that survived this period of extinction were those that had already achieved broad intercontinental distributions. *Platycarya*, *Palaeocarya*, *Cyclocarya*, *Juglans*, and *Carya* had each successfully colonized large areas of both Europe and North America by the early Oligocene.

Most of the Neogene was a time of range expansion during which no major extinctions are apparent. Disparity between Miocene and present distributions of juglandaceous genera indicates that extensive range reductions occurred at or near the end of the Neogene. Palynological evidence suggests that the range reductions were associated with climatic cooling and glaciation. Although virtually all of the genera known from the Miocene survived this episode, there were extensive regional extinctions involving numerous species. *Carya*, *Pterocarya*, *Cyclocarya*, *Palaeocarya*, and *Juglans* became extinct in western Europe. *Pterocarya* was likewise eliminated from North America, and the North American ranges of *Juglans*, *Carya*, and *Palaeocarya* were substantially reduced.

EVOLUTIONARY PATTERNS IN DIFFERENT ORGANS

Comparative morphology and anatomy of extant taxa can now be supplemented by evidence from the fossil record to suggest trends and patterns in the evolution of different organs and tissues of the Juglandaceae.

Pollen ornamentation and wall structure are remarkably uniform in modern and fossil Juglandaceae. This contrasts, for example, with the heterogeneity of these features in the Fagaceae (Crepet & Daghljan, 1980). The juglandaceous type of exine stratification and ornamentation can be traced to Upper Cretaceous pre-juglandaceous

taxa of the Normapolles complex such as *Plicapollis*. The stability of these features suggests that they represent an optimum combination for wind dispersal. More variable features of juglandaceous pollen include size, patterns of exinous thickening (including pseudocolpi), and the number and distribution of apertures. These characters are utilized in distinguishing modern genera (Whitehead, 1965; Stone & Broome, 1975).

Based upon comparative morphology, Whitehead (1965) suggested evolutionary trends to explain the present-day morphological diversity in the pollen of the Juglandaceae. Assuming simple, small, isopolar, triporate grains of the *Engelhardtia roxburghiana* type to be primitive, he derived other types through trends of pseudocolpi development (*Platycarya*), increased size (*Engelhardtia*), increased size and heteropolarity (*Carya*), increased pore number (*Pterocarya*), and increased pore number, size, and heteropolarity (*Juglans*). The sequence of appearance of increasingly specialized juglandaceous pollen in the stratigraphic record supports Whitehead's conclusions. Small triaperturate isopolar grains with meridionally elongate pores, like those of extant *E. roxburghiana*, have the most ancient record, extending back to the Upper Cretaceous; whereas the more specialized types appear in the Upper Paleocene and Eocene. Trends of increasing size and morphological complexity are observed through the early Tertiary. Nichols and Ott (1978) suggest various evolutionary trends, including one leading from *Momipites* to *Caryapollenites*, in a biostratigraphic study of a Paleocene sequence in Wyoming. By the end of the Paleocene diversification documented by Frederiksen and Christopher (1978) and Nichols and Ott (1978), nearly all of the modern pollen types were present. The heteropolar multiporate morphology characteristic of extant *Juglans* appeared later, perhaps in the middle or late Eocene. During the Neogene, there were no major innovations in pollen morphology, although trends of increasing size continued in *Carya* and *Juglans*.

Heimsch and Wetmore (1939) described the anatomy of modern woods of the Juglandaceae and suggested trends in xylem evolution for the family. They proposed that genera with longer vessel elements and scalariform perforation plates (*Engelhardtia*) are primitive, while those with shorter vessel elements and exclusively simple perforations are more advanced. *Carya*, with its ring-porosity, thick-walled late wood vessels, and

solitary idioblasts in axial parenchyma, and *Platycarya*, with its ring porosity, spiral thickening, and idioblasts in rays, are considered to be the most specialized genera. The fossil record offers an opportunity to test these generalizations, but fossil juglandaceous woods have received relatively little study. There have been no investigations of juglandaceous wood from the Paleocene and apparently no attempt to characterize woods associated with Cretaceous Normapolles pollen.

Woods representing the Engelhardieae (*Engelhardioxylon*) and Juglandaeae (*Pterocaryoxylon*) have been identified from the Middle Eocene (Wheeler et al., 1978; Manchester, 1983); however, woods of other tribes have not yet been recorded prior to the Miocene. As the Tertiary record of juglandaceous woods becomes better known, it will be interesting to determine the antiquity of various diagnostic characters such as vasicentric tracheids, spiral thickening, idioblasts in rays (*Platycarya*), thick-walled vessels and fibers, solitary idioblasts in axial parenchyma (*Carya*), associated chambered pith (Juglandaeae), idioblasts in chains within the axial parenchyma, reticulate vessel thickening (*Juglans*), and scalariform vessel perforations (Engelhardieae). One would expect the more primitive characters to occur prior to the advanced features. It is possible that scalariform vessel perforations were present in the early representations of other tribes as well as the Engelhardieae. It will also be interesting to compare the relative advancement of woods of different ages with that of fruits and other organs. Although *Platycarya* can be resolved on the basis of fruits and pollen in the Early Eocene, the foliage is not as similar to modern *Platycarya*; the condition of corresponding xylem remains to be investigated.

The compound pinnately leaf, which also occurs in *Rhoiptelea*, is an important feature separating the Juglandaceae from other amentiferous families. The antiquity of this feature, which may predate the origin of the family, is unknown; and the kind of foliage associated with Normapolles taxa remains to be determined.

The earliest confirmed juglandaceous foliage includes "*Pterocarya*" *hispida* Brown, "*Pterocarya*" *glabra* Brown, and "*Carya*" *antiquorum* Newberry from the Paleocene Fort Union Formation of North America. These species exhibit various features seen in extant Juglandaeae and Hicoreae, such as semicraspedodromous venation, strong percurrent tertiary veins, open areo-

lation with branched freely ending veinlets, and evenly spaced small teeth fed by veins of tertiary order. However, some of the characters of these Paleocene species, such as long petiolules and steeply arching secondaries, are uncommon in later Tertiary and extant Juglandaceae and possibly primitive.

Long petiolules frequently occur on the terminal leaflets in modern Juglandaceae; however, the lateral leaflets are usually sessile except for a few species of Engelhardieae in which short petiolules (1–10 mm) occur. Long petiolules (8–25 mm) characterize both terminal and lateral leaflets of "*Pterocarya*" *glabra* and at least two Early Eocene platycaryoid species (Wing & Hickey, 1984). Petiolules are also seen on leaflets of "*Pterocarya*" *hispida* and on the undescribed British Upper Paleocene leaflets figured by Crane and Manchester (1982); however, the sample size is relatively small and it is possible that only terminal leaflets were petiolulate. It seems reasonable to conclude that a trend toward shortening and loss of petiolules occurred in the early Tertiary. Despite the former presence of long petiolules in Juglandaeae and Platycaryeae, the condition is retained today only in certain Engelhardieae.

In early Tertiary juglandaceous species the course of the secondaries as they approach the margin has a strong apical component analogous to that of *Cornus*. This feature is well illustrated by "*Carya*" *antiquorum* (Fig. 3), *Cyclocarya* *hispida* (Fig. 37), "*Pterocarya*" *glabra* (Fig. 36), and is seen in the Middle Eocene foliage associated with *Juglans clarnensis* fruits (Fig. 38). Although the feature has not been observed in fossils or modern Platycaryeae and Engelhardieae, it may be a primitive feature for Juglandaeae and Hicoreae.

Alfaroa and *Oreomunnea* are the only modern genera of the family with opposite leaves. This and other novel characters, such as closed areolation and papillate epidermis, separate the New World Engelhardieae from all other extant Juglandaceae, including *Engelhardia*, suggesting that this is a specialized type of foliage that became isolated early in the evolution of the Engelhardieae. Fossil *Oreoroa* leaflets exhibit the same suite of architectural and cuticular features (but with unknown phyllotaxy) and occur as early as the Middle Eocene in North America and in the Middle Eocene to Miocene of Europe in association with *Palaeocarya* and other engelhardioid fruit taxa.

The earliest known platycaryoid foliage, early Eocene, departs in numerous architectural features from that of extant *Platycarya strobilacea* and might not have been attributed to the correct tribe were it not for its repeated association with platycaryoid fruits, inflorescences, and pollen in low diversity assemblages lacking engelhardioid fruits and pollen. As noted by Wing and Hickey (1984), the leaflets of *Platycarya americana* and *P. castaneopsis* share many features in common with extant Engelhardieae, including common intersecondary veins, closed areolation, and basilar auricles. The striking differences between this North American platycaryoid foliage and that of the extant Asian *Platycarya*, are comparable to those between American and Asian engelhardioid foliage and suggest a higher level of evolutionary plasticity of morphology in foliage than in other organs of these tribes.

The success of the Juglandaceae may be attributed in part to evolutionary plasticity in fruit morphology and the associated flexibility in dispersal strategies. A wide range of fruit morphology has developed, enabling effective dispersal in a variety of ecological settings. The Paleocene records of small, winged and large, wingless fruits indicates that both wind and animal dispersal strategies are ancient in the family. Tiny, perhaps wingless, nutlets such as those associated with Upper Cretaceous Normapolles pollen (Friis, 1983) are envisaged as the primitive condition from which fruits better adapted for wind and animal dispersal may have evolved.

Throughout the known history of the family there has been a greater diversity of winged than wingless fruit genera. During the Paleogene, there were at least nine genera with winged fruits, whereas only two with wingless fruits are known. Fruit wings have evolved along several different pathways in the family as reflected by their varied homology (Manning, 1978). They have developed from the primary bract (e.g., *Casholdia*, Engelhardieae), bract plus bracteoles (*Cyclocarya*), bracteoles plus lateral sepals (Platycaryeae), and bracteoles alone (*Pterocarya*).

Among fossil and modern winged juglandaceous fruits there is a range from tiny nutlets with well-developed wings (e.g., *Platycarya*, *Casholdia*) to large nutlets with relatively small wings (e.g., *Cyclocarya coalmontensis*, *Paleooreomunnea*). The tinier fruits are better suited for long-distance dispersal by the wind but, because of their small food reserves, can only germinate and establish seedlings in areas of good light inten-

sity. Wing and Hickey (1984) suggest that the weedy, r-selected dispersal strategy employed by modern *Platycarya* was well established by the early Eocene in the Platycaryeae. Larger fruits with less effective wings are not dispersed as widely by the wind but, because of their larger food reserves, are better equipped for seedling establishment in shaded areas. Larger, wingless fruits such as modern *Juglans*, *Carya*, and *Alfaroa*, must rely on mechanisms other than wind for dispersal.

The animal dispersal syndrome, characterized by large nut size and lack of wings, has evolved more than once in the Juglandaceae (Stone, 1973). In the Engelhardieae, *Alfaroa* appears to have evolved from *Oreomunnea* or *Palaeocarya* by suppression of ontogenetic bract enlargement. *Alfaroa* is virtually identical in vegetative and reproductive morphology to *Oreomunnea* except in its somewhat larger fruit size, lack of wings, and presence of a husk. *Alfaroa* is the only modern genus of the family with no known fossil counterpart, and it seems likely that its divergence from *Oreomunnea* or *Palaeocarya* may have occurred relatively recently. In the Juglandaceae the wingless fruits of the extinct *Sphaerocarya* could have been derived from *Cyclocarya* by analogous suppression of wing development. Stone (1973) suggests that a similar relationship exists between the animal-dispersed fruits of *Carya* and *Juglans* and the wind-dispersed winged fruits of *Pterocarya*.

The suggestion that *Carya* and *Juglans* evolved from *Pterocarya* (Stone, 1973) is intriguing but open to question. Both *Pterocarya* and *Juglans* have fruit records extending back to the Middle Eocene, and there are no hints of one having evolved from the other. An alternative model would derive both winged and large, wingless fruits from a common ancestor with small, wingless, relatively unspecialized endocarps. *Carya* is not closely related to the *Juglans*-*Pterocarya* alliance (Manning, 1978) and probably represents yet another example of convergent evolution for the animal dispersal syndrome.

Trends in the evolution of animal-dispersed juglandaceous fruits seem to reflect ongoing co-evolution with rodents. The Rodentia enter the fossil record in the Paleocene. The first large, non-winged nuts known, *Juglandicarya simplicarpa*, are also Paleocene. Early rodent-dispersed fruits are smooth-walled with simple, uncomplicated locules. The seeds within such nuts could have been relatively easily removed compared

to those of modern *Juglans* and *Carya*. As rodents became more sophisticated (squirrels are not known prior to the Late Eocene), so did the modes of seed packaging in juglandaceous fruits. In the Oligocene, various modifications appeared in the walnuts and hickories that would seem to discourage predation. *Juglans* sect. *Cardiocaryon* maintained a simple locule with easily removed seeds but evolved a scabrate endocarp consisting of a reticulum of blade-like ridges that, Miki (1955) has observed, seems to deter rodent gnawing. *Juglans* sect. *Rhysocaryon* and *Carya* evolved thicker walls and complex locule and septal configurations that effectively lock the seed within the endocarp valves. Modern squirrels are observed to store nuts by burying them in the ground, usually some distance away from the parent tree. Although some of these "planted" nuts are later eaten as the endocarp softens, others are never recovered and thus left to germinate. The familiar commercial walnut (*Juglans regia*) and pecan (*Carya illinoensis*) are exceptions to this trend that might be attributed to relatively recent selection by man; neither of these species has been confirmed in the fossil record.

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TAXONOMIC INDEX

- Alfaroa* 2-4, 7, 15, 34, 38, 40, 42-43, 45, 61, 127; Figs. 19-20, 23
Annamocarya 63
Antiquocarya 9-11; Fig. 2
Basopollis 10
Betulaceae 6, 121
Carya 2-4, 7, 14-15, 19, 23, 63-81, 108, 121, 123, 126, 128-129
 angulata 74
 antiquorum 9, 12-14, 127; Fig. 3
 askenasyi 74
 cashmanensis 67
 cathayensis 81; Fig. 31
 costata 72
 egregia 81
 florissantensis 67, 77-78; Fig. 33
 globosa 73-75; Fig. 32
 hauffei 74
 illinoensis 129
 inelegans 66
 kompasica 75
 kryshstofovichii 75
 lacrymaebunda 71; Fig. 32
 leiocarpa 76
 miocathayensis 76
 myristicaeformis 69; Fig. 31
 nanocarpa 76
 olivaeformis 75
 ovatocarpa 77
 paludis-naabi 73; Fig. 32
 poilanei 73; Fig. 31
 pugetensis 67
 pusilla 73
 quadrangula 71; Fig. 32
 rostrata 72
 rugosa 74
 serraefolia 67
 sessilis 67
 sinensis 63, 65, 67
 sp. 76
 striata 76
 strychnina 72-73; Fig. 32
 tertiara 67
 tomentosa 75
 tonkinensis 65, 81
 ventricosa 71-72; Fig. 32
 veripites 66
 washingtonensis 78-79, 81; Fig. 34
Caryanthus 9-12
Caryapollenites 65, 79, 122, 126
Caryojuglandoxylon 66
Casholdia 16-17, 61, 122-123, 126; Fig. 5
Cyclocarya 2-4, 9, 67, 81, 84, 86, 88-89, 91-99, 101, 117, 121-122, 124-126
 brownii 15, 37, 89, 93, 95, 115, 122; Figs. 39, 40
 coalmontensis 95, 115, 128; Fig. 41
 cycloptera 96-97
 minuta 93, 95; Fig. 41
 paliurus 37, 89, 93, 96-97, 115
 tavdensis 97
 tomskiana 98
 tymensis 97-98
 weylandi 97
Engelhardia 1, 3-4, 7, 17, 31, 34, 38-39, 40-47; Figs. 19-20, 23
Engelhardioxylon 40, 127
Eoengelhardia 38
Eokachyra 38-39; Fig. 18
Eucaryoxylon 67
Fagaceae 121
Hamamelidaceae 5
Hooleyia 6, 30, 121, 123, 125; Figs. 12-14
 hermis 30-31; Figs. 13-14
 lata 30-31; Figs. 12, 14
Juglandicarya 5, 69, 79
 andegavensis 69
 cantia 15-16; Fig. 4
 depressa 69, 96, 115
 gruetti 67
 lubbocki 69, 79
 simplicarpa 14-16, 122, 128; Fig. 4
Juglandiphyllum 12
Juglans 1-4, 7, 15-16, 19, 67-69, 81, 85-88, 105-120, 123, 125, 128-129
 ailantifolia 111
 bergomensis 111
 californica 68
 calvertiana 109
 cathayensis 111, 113-115
 clarnensis 91, 107, 111, 117; Fig. 46
 cinerea 112-115
 eocinerea 120
 hanamakiensis 113
 hindsii 68
 jacutica 114
 lacunosa 109-110, 117, 120; Fig. 48
 linkii 109, 117; Fig. 47
 mandsurica 113-115
 megacinerea 113; Fig. 49
 nevadensis 109
 nigra 114
 omoloica 114
 sepultus 108; Fig. 47
 siberica 113, 120
 sieboldiana 113
 siouxensis 108, 117; Fig. 47
 sp. 89-91; Fig. 38
 tephrodes 111, 113, 120; Fig. 49
Krutzschipollis 10
Lamanonia 20
Manningia 9, 11, 13; Fig. 2
Momipites 9, 17-18, 61, 79, 81, 120, 126; Figs. 5, 37
Multiporopollenites 86
Myricaceae 4-6
Normapolles group 8-9, 125, 128
Nudopollis 10
Oreomunnea 2-4, 7, 17, 34, 38, 42, 45, 47, 51, 127, 128; Figs. 9, 18, 21, 23
Oreoroa 7, 40, 42, 127; Fig. 21
Palaeocarya 42, 47-57, 125, 127, 128
 clarnensis 52; Figs. 25, 30
 koreanica 55; Fig. 30
 macroptera 48, 51, 61; Figs. 24, 30
 mississippiensis 56-57, 61; Figs. 24, 30
 nevadensis 51; Figs. 25, 30
 olsoni 53-55; Figs. 26, 30

- puryearensis* 48–51; Figs. 24, 30
uintaensis 57; Fig. 27
willamettensis 53; Fig. 26
wolfei 53; Fig. 25
Paleooreomunnea 42, 47, 59, 121, 126, 128; Figs. 28, 30
Paleoplatycarya 121, 123, 126; Figs. 11, 14
Paliurus hesperius 95
Paraengelhardtia 2, 42, 47, 57–59; Figs. 28, 30
Platycarya 2–4, 17–27, 31, 67, 121–123, 125–128
 americana 19–22, 26–30, 123, 128; Figs. 6, 8–10, 14–15
 bognorensis 26
 castaneopsis 21, 27–28; Fig. 15
 hokkaidoensis 2
 manchesteri 30
 miocenica 23
 pseudobrauni 23
 richardsoni 25, 26
 strobilacea 26–27, 29, 123, 128; Figs. 6–7, 10
Platycaryapollenites 6, 18–19
Plicapollis 9–11, 120
Plicatopollis 10
Polyatriopollenites 85
Polyporopollenites 85
Polyptera 2, 7, 9, 99, 101, 115, 121–122, 126; Fig. 41
Pterocarya 2–4, 7, 11, 19, 85, 101–105, 115, 117, 121, 123, 126, 128
 asymmetrosa 105
 castaneaefolia 105
 crassa 98, 105, 115, 120, 122
 eomacoptera 103–104, 105; Fig. 44
 fraxinifolia 104–105, 117; Fig. 43
 kireevskiana 105
 limburgensis 105, 117
 mixta 103
 nigella 104
 occidentalis 103; Fig. 44
 orientalis 103
 protostenoptera 105, 117
 raciborskii 105
 rhoifolia 105; Fig. 43
 roanensis 103
 smileyi 103–104; Fig. 44
 sp. 104; Fig. 45
 stenoptera 101, 104–105, 115; Fig. 43
 “*Pterocarya*” *glabra* 87–89; Fig. 36
 hispida 89; Fig. 37
Pterocaryopsis 26; Fig. 10
Rhoiptelea 4, 11, 67, 86, 127
Rosidae 5
Sphaerocarya 84, 91, 99, 115, 122; Fig. 42
Subtriporopollenites 66
Triatriopollenites 37
Trudopollis 11
Ulmaceae 121
Vinea 20, 23; Fig. 15