

THE CLASSIFICATION WITHIN THE JUGLANDACEAE¹

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ABSTRACT

A full description is presented of the Juglandaceae and of the two subfamilies (Platy-caryoideae, Juglandoideae), three tribes of the Juglandoideae (Juglandae, Engelhardieae, Hicorieae), seven genera, with their subgenera and sections. Figures and tables are given to illustrate the evolution of the genera, the comparative classifications within the family, and the comparative interpretations of the parts of the floral envelopes. Diagrams are presented of the position of the carpels, the orientation and type of the stigmas, and the parts of the floral envelopes. A list is given of the 59 species, with the subspecies and varieties of each, including their distribution.

This article on the Juglandaceae of the world brings together full descriptions of morphological features of the family, subfamilies, tribes, genera, subgenera, and sections, as well as a list of species. Published descriptions are scattered through the literature. Many of the family and generic descriptions are found in regional taxonomic treatments, primarily for members native to the United States, and hence are incomplete, such as Sargent (1933), Rehder (1940), Fernald (1950), and Gleason (1952); few descriptions are given of lesser categories between the ranks of family and genera and genera and species. Modern descriptions of the family applicable to world-wide members are available in works such as Koidzumi (1937), Manning (1952, 1970, 1974), Melchior (1964), Hutchinson (1959, 1967), Elias (1972), and a few others. Engler (1889), Koidzumi (1937), and Melchior (1964) give descriptions of genera, but only Hutchinson (1967) presents rather full descriptions of all (8) modern genera. Some descriptions contain scattered inaccuracies; most do not include all of the variations which occur in the taxa.

This paper describes some features not normally included, such as the nature of early scales and buds and leaves on the seedlings. New information comes from the reassessment of the cross sections of the bases of *Engelhardia* fruits, and of the timing of the appearance of the staminate catkin buds in *Pterocarya rhoifolia*.

A new classification within the family is necessary in order to show the true relationships of genera. The most complete classifications to date are given in Oersted (1870a, 1870b), Koidzumi (1937), Leroy (1955), and Melchior (1964), the taxa of the last two being invalidly published. Elias (1972) also discusses the classifications, but does not propose any formal treatment. In these publications the arrangement of genera is based primarily on fruits, their sizes, and structure of organs involved in dissemination, such as wings or husk. Stone (1973) has suggested that the obvious fruit characteristics are in large part ecological, not necessarily indicative of relationships.

Studies in type and position of inflorescences, nature of parts of floral

¹I wish to thank Dr. Donald E. Stone for his careful checking of the manuscript, and Dr. Carroll E. Wood, Jr. for his help with problems in nomenclature.

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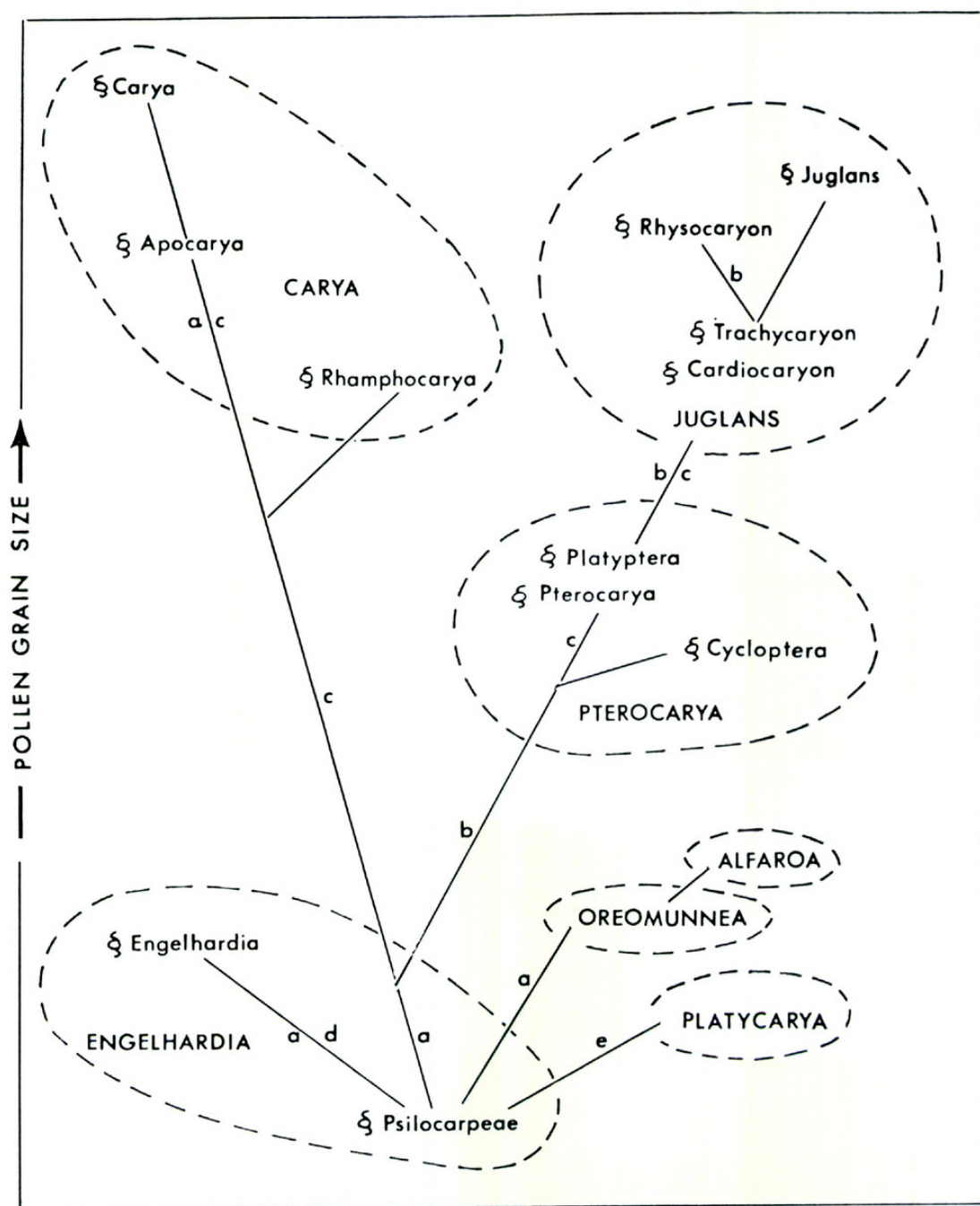


FIGURE 1. Evolution of pollen grain structure in genera and sections of the genera of the Juglandaceae, from Stone & Broome (1975: fig. 14). Letters indicating structure of the pollen grains are explained in that article. Course of evolution shown is very close to my opinion of relationships, except that *Platycarya* is more advanced judging from wood anatomy and floral structure.

envelope, wood anatomy, seedling anatomy, and pollen types of members of the family (Manning, 1938, 1940, 1948; Kribs, 1927; Heimsch & Wetmore, 1939; Whitehead, 1963, 1965; Conde & Stone, 1970; Stone, 1970; Stone & Broome, 1975) agree in general as to the relationships and relative primitiveness and

advancement of genera and even species, and the results are quite different from those of most published classifications.

I have given an outline of my suggested classification in *Encyclopedia Britannica* (Manning, 1974), but only two of the taxa below the family level have descriptions. The present paper is an amplification of that classification, with necessary descriptions, cross references, and a Latin diagnosis where necessary. Since I wrote the 1974 article I have decided not to recognize *Cyclocarya* as a genus (Manning, 1975); hence there are now seven genera. The key to genera and the descriptions of the subfamilies and tribes identify the characters of most diagnostic value. In addition, discussions of relationships of the genera are presented under *Platycarya*, *Pterocarya*, *Engelhardia*, and *Carya* as bases for the classification. Figure 1, based on fig. 14 of Stone & Broome (1975), shows how clearly the evolution of pollen grain structure parallels my opinion of the relationships of the genera and even the sections of the genera as shown in my classification. Table 1 shows the differences between the present classification and those of previous writers, especially for the location of genera.

The only complete list of species of the family is given in Manning (1948). There have been many changes in the last 30 years, and it is necessary to update the list. It seems unnecessary to give citations for the species, subspecies and varieties. The principal publications involved in the changes of names are Iljinskaya (1953), Jacobs (1960), Manning (1949, 1950, 1951, 1957, 1959, 1960, 1966, 1975), Stone (1968, 1972, 1977). Dr. Stone and I now recognize seven genera and 59 species. The species, subspecies and varieties which I recognize, and their distribution, are listed in Table 3 (p. 1083) arranged according to the classification used in this paper. Sargent (1933) and Steyermark (1963) recognize other varieties (and forms), especially for *Carya*.

TERMINOLOGY AND INTERPRETATION

There has been considerable variation among authors in terminology applied to the unit within the catkin. In this paper I am following my previous terminology (Manning, 1938, 1940, 1948); that is, the unit includes the pedicel (unless absent), floral receptacle, subtending bract, two bracteoles (unless absent), 4 or fewer sepals, stamens (in staminate flower), pistil (in pistillate flower). Of the total of 7 (or 9?) leafy organs (the floral envelope) in the most well-developed units, the flower proper consists, of course, of only the sepals (when present) with the stamens or the pistil. However, the subtending bract and bracteoles are united so intimately with the floral receptacle that these seem to be a part of the flower. Consequently, in some cases the description may include the involucre as part of the apparent flower.

A discussion of the terminology with illustrations is given in Manning (1938, 1940, 1948), Hjelmqvist (1948), Abbe (1974) and elsewhere. Abbe, however, has adopted a different terminology for all members of the Amentiferae and a comparison is in order here. In the following statement my terms are given first and Abbe's equivalent follows in parentheses. Floral unit of the catkin, the apparent flower, with its involucre, calyx or stamens or pistil (partial staminate or pistillate inflorescence); bract (bract or primary bract); bracteoles

TABLE 1. Comparative list of classifications within the Juglandaceae, subfamilies, tribes, genera; arranged to show comparisons, not in the order of the authors; numbers and letters show the latter.

OERSTED 1870 (not called tribes)	KOIZUMI 1937	LEROY 1955 (no Latin descr., no types)	MELCHIOR 1964 (no Latin descr., no types)	MANNING 1978
C. PLATYCARYEAE	I. NUCIFEROIDEAE	II. OREOMUNNOIDEAE	I. PTEROCARYOIDEAE	I. PLATYCARYOIDEAE
	A. PETROPHILOIDIEAE		A. PLATYCARYEAE	
6. <i>Platycarya</i>	1. <i>Petrophiloides</i>	8. <i>Platycarya</i>	1. <i>Platycarya</i>	1. <i>Platycarya</i>
				II. JUGLANDOIDEAE
A. ENGELHARDTIEAE	B. PTEROCARYEAE		B. PTEROCARYEAE	B. ENGELHARDIEAE
1. <i>Pterocarya</i>	2. <i>Pterocarya</i>	4. <i>Pterocarya</i>	2. <i>Pterocarya</i>	
2. <i>Engelhardtia</i>	3. <i>Engelhardtia</i>	7. <i>Engelhardtia</i>	3. <i>Engelhardtia</i>	4. <i>Engelhardtia</i>
3. <i>Oreomunnea</i>		6. <i>Oreomunnea</i>	4. <i>Oreomunnea</i>	5. <i>Oreomunnea</i>
		5. <i>Alfaroa</i>		6. <i>Alfaroa</i>
	II. DRUPOIDEAE	I. JUGLANDOIDEAE	II. JUGLANDOIDEAE	
B. JUGLANDEAE VERAЕ	C. ALFAROEAE		A. ALFAROEAE	
	4. <i>Alfaroa</i>		5. <i>Alfaroa</i>	
	B. CARYEAE		B. JUGLANDEAE	A. JUGLANDEAE
4. <i>Juglans</i>	5. <i>Juglans</i>	1. <i>Juglans</i>	6. <i>Juglans</i>	2. <i>Juglans</i>
				3. <i>Pterocarya</i>
				C. HICORIEAE
5. <i>Carya</i>	6. <i>Carya</i>	2. <i>Carya</i>	7. <i>Carya</i>	7. <i>Carya</i> (incl. <i>Annamocarya</i>)
		3. <i>Annamocarya</i>	8. <i>Annamocarya</i>	

TABLE 2. Comparison of interpretation of floral envelope by different authors. Key to abbreviations at bottom of table.

	MANNING	EICHLER	NAGEL	HJELMQVIST	HUTCHINSON
<i>Platycarya</i> :	♂: B * *	B * *	B * *	B * *	B * *
			[Bbb] *	[Bbb] *	
♀: B [b 1] [b 1] (3, 4)		B bb *	B * 4	[Bbb] 4	B * 2,3
<i>Juglans</i> :	♂: B bb (14)4-1	B bb 4-2	B * 6-4	B bb 4-1	B * 6,5
			B bb 6-4		
♀: B bb 4		B bb 4	B bb 4	B bb 4	B bb 4
				B bbb' 4	
<i>Pterocarya</i> :	♂: B bb 4-1	B bb 4-2	B * 6-4	B * 4	B * 6-3
				B bb 4-1	
♀: B bb 4		B bb 4	B bb 4	B bb 4	B bb 4
<i>Engelhardia</i> :	♂: B3 bb 4-1(0)	[Bbb] 4	[Bbb] 4-3	[Bbb] 6-4	B * 6-3
	B3 * 4-0			[Bbb] 4,3,0	
♀: B3 bb 4		[Bbb] b'b' 4	[Bbb] b'b' 4	[Bbb] b'b' 4	B3-5 * 4
		[Bbb] 4			
<i>Oreomunnea</i> :	♂: B3 bb 4-2	-	-	[Bbb] 6-3	B * 5-3
♀: B3 bb 4		-	-	[Bbb] b'b' 4	B3-5 * 4
<i>Alfaroa</i> :	♂: B3 bb 4-2	-	-	[Bbb] 5	B * 5,4
♀: B3 bb 4		-	-	[Bbb] 4	B3 * 4,5
<i>Carya</i> :	♂: B bb *(1, 2)	B bb *	B bb *	B * 2,3	B * 2,3
♀: B bb (st.d.)		B bb 1	B bb 1	Bbb' (4?)	(B) * 4
	B bbb'b'b'? *				

B, bract; b, bracteole; b', extra bracteole; B3, B3-5, 3- or 3- to 5-lobed bract; [Bbb], bract and bracteoles fused to form a 3-lobed structure; [b 1], bracteole and a sepal fused to form a lateral appendage; st. d., stigmatic disc, modified calyx?; numbers in last column of each author, numbers of sepals; *, organs absent.

(secondary bracts); extra bracteoles (tertiary bracts); flower (florete); receptacle (torus); calyx or perianth (perigon); sepals (tepals).

There is wide diversity of opinion among authors concerning the nature or interpretation of the parts of the floral envelope, that is, of the bract, unlobed or lobed, bracteoles and sepals. Manning (1940, 1948), Iljinskaya (1953), and Abbe (1974) have summarized the interpretations of various authors, especially of Eichler (1878), Nagel (1914), Hjelmqvist (1948), Leroy (1955), and Hutchinson (1967). Interpretations that differ from mine are given in parentheses: (1). STAMINATE FLOWERS. *Pterocarya* and *Juglans*: bract, 2 bracteoles, 4 or fewer sepals (bract, no bracteoles, 6 or fewer sepals); *Engelhardia*, *Oreomunnea*, *Alfaroa*: 3-lobed bract, 2 bracteoles beside the 4 or fewer sepals (bract and 2 bracteoles fused into a 3-lobed structure, no bracteoles beside the 6 or fewer sepals); *Carya*: bract, 2 bracteoles, with rarely 1 or 2 sepals (bract, no bracteoles, 2 sepals with rarely one or 2 other sepals); *Platycarya*: bract (bract, or bract and 2 bracteoles as a slightly 3-lobed structure). (2) PISTILLATE FLOWERS. *Pterocarya*: bract, 2 bracteoles separate or united, 4 sepals (bract, 2 bracteoles, 4 sepals); *Juglans*: as in *Pterocarya*, but the apices of the bracteoles often split into 3 or 4 segments (bract, 2, 3, or 4 bracteoles, 4 sepals); *Engelhardia*, *Oreomunnea*, *Alfaroa*: 3-lobed anterior bract, 2 posterior bracteoles, these often reduced, 4 sepals (bract and 2 bracteoles fused into one 3-lobed structure, 1 or 2 additional posterior bracteoles often present, 4 sepals); *Carya*: bract, 2 bracteoles whose tips are divided into 3–5 structures, or possibly bract and 3–5 bracteoles, stigmatic disc (where present) probably a modified calyx (bract, 2 bracteoles, 1 sepal, or bract, 3–4 bracteoles, 1 sepal, or low bract, 4–6 sepals, or bract, 2–4 bracteoles, and an inner circle of 2–4 “sepals”); *Platycarya*: bract, 2 lateral appendages each consisting of the fusion of a bracteole and a sepal, and sometimes 1 or 2 anterior-posterior sepals (bract, 2, 3, or 4 sepals, or bract, 2 bracteoles, no sepals, or bract and 2 bracteoles fused into a somewhat 3-lobed structure, 2–4 sepals).

The different interpretations of the floral envelopes depend primarily on whether the 2 lateral organs inside the bract in the staminate flowers are bracteoles or sepals; whether the 3-lobed anterior structure in staminate and pistillate flowers of *Engelhardia*, *Oreomunnea*, and *Alfaroa* represents a 3-lobed bract or the fusion of a bract and 2 bracteoles; whether the organs in the pistillate flower of *Carya* are, in part or entirely, sepals instead of the bract and bracteoles; whether the lateral appendages in *Platycarya* consist of the fusion of bracteoles and sepals, or are bracteoles alone, or sepals alone.

Table 2 compares my interpretation of the floral envelope with that of four other authors. The terminology used in this paper is based on a comprehensive study of all known species in the family, with special emphasis on the inflorescences, pistillate and staminate flowers, and fruits (Manning, 1926, 1938, 1940, 1948). Leroy (1955) has studied the floral anatomy of the pistillate flowers and fruit and Berquam (1975) that of the staminate flowers.

In the pistillate flowers of *Engelhardia* and its relatives, Leroy (1955) has interpreted the anterior (abaxial) structure as a bract and 2 bracteoles. However, Crepet et al. (1975) and Dilcher et al. (1976) have shown that the 3-lobed bracts

of fruits and staminate flowers of fossil relatives of *Engelhardia* in the Eocene are very similar to those of modern members; the ancestral condition of the fruiting bracts seems to have been a broad slightly 3-lobed bract (see also Manning, 1940: fig. 25) somewhat similar to the occasional, slightly 3-lobed bract in *Platycarya*. Berquam (1975) interprets the 3-lobed structure as a 3-lobed bract, thus supporting my interpretation for *Engelhardia*, *Oreomunnea*, and *Alfaroa*.

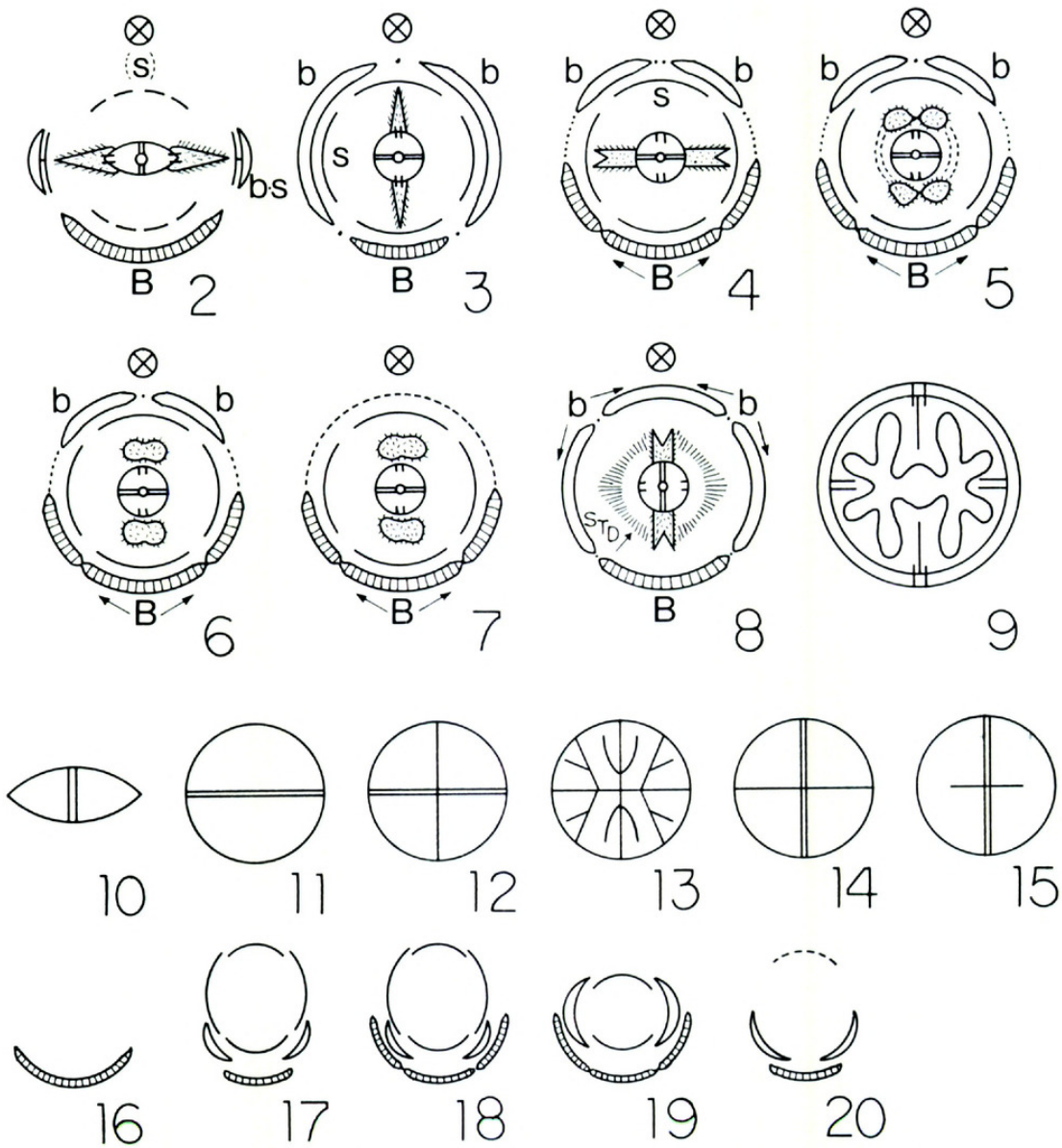
The interpretation above indicates in turn that the most fully developed staminate flowers of most genera (not including the greatly reduced flowers in *Carya* and *Platycarya*) normally have 6 organs besides the bract. Thus the number is identical to that in the pistillate flowers, where the interpretation of 2 bracteoles and 4 sepals is rather definite. Berquam (1975), on the other hand, did not find any anatomical differences between what I have called the bracteoles and the sepals, and thus interprets the 6 organs as 6 "tepals." Abbe (1974) has pointed out that the study of the development of the staminate flowers by Macdonald (1971) indicates that the outer organs (bracteoles) differ from the 4 inner ones.

The 4 foliar organs in the pistillate flowers of *Carya* sections *Carya* and *Apocarya* are clearly involucral, not calyx or in part calyx, because of their structure, arrangement, and vascular anatomy. Furthermore, Hjelmqvist (1948) has found 1-4 "sepals" inside of this involucre in a few flowers of a few species, and I have interpreted the stigmatic disc as a modified calyx. Whether the 3 structures besides the bract represent 2 bracteoles whose tips are split into 3 structures or 3 bracteoles is uncertain. In section *Rhamphocarya*, where there are 5 structures besides the bract, Leroy (1955) (using the generic name *Annamocarya*) believes that some of these are bracteoles and others (which ones uncertain) are sepals. A stigmatic disc seems absent in this section.

In the broad bract of the pistillate flowers of *Platycarya* the floral anatomy is more complex than in the narrow bract of most genera; the structure is occasionally 3-lobed, suggesting to some authors a bract and 2 bracteoles. However, the organ is probably a primitive one, and the 3-lobed structure probably represents a structure similar to that in the fossil relatives of *Engelhardia* mentioned previously. Furthermore, if the bracteoles are not present in the bract complex, each of the 2 lateral appendages, with a slightly double aspect, could represent a bracteole, in part. In addition, there is a vascular supply to the organ from the base of the flower, shown in Manning (1926) and in Leroy (1955), and also a separate vascular supply to the organ high in the flower.

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FIGURES 2-20. Diagrams of flower and fruit structure of genera and generic sections of the Juglandaceae. Orientation with reference to the bract and axis of the catkin is the same in all figures, except Fig. 9.—2-8. Diagrams of the typical structure of the pistillate flowers in all 7 genera, showing the orientation of the 2 carpels with reference to the bract and axis of the catkin (only primary partition shown), orientation and shapes of stigmas, location of lines of dehiscence of the fruits (short double line at right angles to the primary partition), and the parts of the floral envelope present.—2. *Platycarya*.—3. *Juglans*, *Pterocarya*.—4. *Engelhardia*, sect. *Engelhardia*.—5. *Engelhardia*, sect. *Psilocarpeae*.—6. *Oreomunnea*.—7. *Alfaroa*.—8. *Carya*.—9. Diagram indicating, for all genera, the location in the



fruits of the two 4-lobed cotyledons of the embryo, one cotyledon in each valve (right and left), not carpel, of the fruit; folding and enlargement of cotyledons not shown, as diagram is essentially the condition of the embryo in the upper part of the loculus of a young ovary; primary and secondary incomplete partitions and lines of dehiscence indicated, though secondary partition absent in some genera; orientation of carpels with reference to axis depends upon the genus.—10–15. Diagrams of cross sections of nuts and nutlets in all genera showing typical presence of primary (double line) and secondary (single line) incomplete partitions at base of fruit, thus indicating number of “cells” at base of fruit; lines of dehiscence, secondary and tertiary internal projections, and lacunae are not indicated, except in Fig. 13.—10. *Platycarya*.—11. *Juglans*, sections *Cardiocaryon* and *Trachycaryon*; *Pterocarya*, subgen. *Cyclocarya*.—12. *Juglans*, sections *Dioscaryon* and *Rhysocaryon*; *Pterocarya*, sections *Pterocarya* and *Platyptera*; *Engelhardia*.—13. *Oreomunnea*, *Alfaroa*; tertiary incomplete septa, with internal projections, shown at one level.—14. *Carya*, sections *Carya* and *Apocarya*; *Pterocarya*, sect. *Pterocarya*, occasional variation.—15. *Carya*, sect. *Rhamphocarya*.—16–20. Floral diagrams for the staminate flowers, showing the parts of the floral envelope present in the most fully developed flowers; variation in parts not shown; that is given in Manning (1948).—16. *Platycarya*.—17. *Juglans*, *Pterocarya*.—18. *Engelhardia*, sect. *Engelhardia*; *Oreomunnea*; *Alfaroa*.—19. *Engelhardia*, sect. *Psilocaryeae*.—20. *Carya*. B, bract, unlobed and 3-lobed, structure cross lined; b, bracteole, structure not lined; b-s, lateral appendage, bracteole and sepal fused; s, sepal, single line; st d, stigmatic disc, probably modified calyx.

This combination is similar to that of the bracteoles and sepals in *Pterocarya* and *Juglans*, so I believe that the interpretation of the lateral appendage as a fusion of a bracteole and a sepal is correct, even though there are occasional flowers with 1 or 2 additional organs, making 3 or 4 organs apparently in a ring, resembling 4 sepals.

Figures 2–8 show diagrammatically the typical structure of the pistillate flowers in all 7 genera, the orientation of the carpels with reference to the bract and the axis of the catkin (only primary partition shown), the orientation and shapes of the stigmas, the location of the lines of dehiscence of the fruit (at right angles to the primary partition), and the parts of the floral envelope present. Figures 10–15 show diagrammatically in all genera the typical presence of the primary and secondary incomplete partitions at the base of the fruit; the lines of dehiscence, the secondary and tertiary internal projections, and the lacunae are not indicated, except in Fig. 13. Figures 16–20 illustrate for the staminate flowers the parts of the floral envelope present in the most fully developed flowers; the variation in parts present is not shown; this aspect is described and illustrated in Manning (1948). Figure 9 diagrammatically shows the location of the two 4-lobed cotyledons in the fruits, one cotyledon in each valve (not carpel) of the fruit.

JUGLANDACEAE A. Rich. ex Kunth, Ann. Sci. Nat. (Paris) 2: 343. 1824, "Juglandeae," nom. cons.

Trees or rarely large shrubs, mostly with abundant tannin; buds naked or scaly; terminal buds present, the lateral often several superposed; leaf scars large, with 3 groups of vascular bundle scars; pith solid or chambered; leaves deciduous or rarely evergreen, alternate, rarely opposite or whorled, exstipulate, pinnately compound, often aromatic; leaflets (3–)5–31, entire or serrate; leaves, buds, flowers, fruits commonly resin dotted (glandular dotted, lepidote) with yellow or pale several-celled peltate glandular scales in various amounts; hairs often fascicled or glandular; flowers unisexual, wind pollinated, typically dichogamous; plants monoecious or rarely dioecious, staminate or pistillate flowers or both in elongate drooping or rarely erect catkins or spikes; staminate and pistillate inflorescences sometimes separate, sometimes combined into an androgynous panicle with the central spike wholly or partly pistillate and the lateral branches staminate; separate staminate inflorescence a cluster of 3–8 catkins or a solitary catkin; separate pistillate inflorescence a many-flowered catkin or a 2- to several-flowered spike; inflorescences terminal, or lateral on old wood, or the staminate sometimes at the base of new growth; flowers 1 to a bract, apetalous; sepals in staminate flowers 4, or reduced in number or lacking, often irregular, the entire or 3-lobed bract and 2 bracteoles (when present) fused with the floral receptacle and appearing as part of the calyx, stamens thus appearing to be on the involucre and calyx; stamens 3–105, sessile, the anthers longitudinally dehiscent; rudimentary pistil rarely present; pistillate calyx usually 4-lobed, fused with the ovary, or absent, the subtending bract and 2 (or 3 or 4?) bracteoles fused only with the pedicel and base of the ovary or with the whole ovary, a ring of minute inner bracteoles very rarely present; a few stamens present in individual flowers

of a few species of certain genera; pistil bicarpellate, or very rarely in individual flowers with 3 or 4 carpels; ovary inferior, 1-locular, with 1 true incomplete partition and often with a false secondary one or even a tertiary one, thus 2- or falsely 4- to 8-celled below, 1-celled above the middle, sometimes falsely 5-celled at the very apex due to intrusions from the wall, thus matching the 4-celled condition at the base of the ovary; lower part of the loculus in the immature ovary usually filled with packing tissue; ovule 1, erect, orthotropous, with a single integument, located at the top of the primary partial partition; placentation modified axile, but at first superficially appearing basal; style 1, rarely absent, with 2-4 stigmatic branches; fruit a nut enclosed in an adherent thin or thick fibrous indehiscent or dehiscent husk, or a nut with a thin dry skin, or a thin-skinned nutlet with 2 or 3 wings or 1 circular one; whole fruit drupelike, but the husk derived from the involucre and the calyx, and the skin from the calyx alone, neither one from the pericarp, hence fruit not a true drupe, sometimes called a tryma; nut or nutlet loculicidal in germination; seed solitary, large, 2- to 4- to 8-lobed, without endosperm, filling the cavity of the nut or nutlet; cotyledons 4-lobed, often fleshy, oily, at germination remaining in the nut or nutlet or appearing above ground as 4-lobed leaves; chromosome number $n = 16$ or rarely $n = 32$; fertilization chalazogamous.

TYPE: *Juglans* L.

Seven genera, 59 species; distribution North, Central and South America, West Indies, eastern Asia, Japan, Philippines to East Indies, Himalayas, southwestern Asia, and southeastern Europe (Caucasus Mountains).

Key to Genera of the Juglandaceae

- a. Bracteoles and sepals absent in staminate flowers; inflorescences (panicles of catkins) terminal at the tip of main shoots and also at the tips of short axillary shoots just below those panicles; staminate and pistillate catkins many-flowered, erect; pistillate and fruiting inflorescences condensed, conelike; pistillate catkins usually tipped by a staminate one; carpels transverse; fruits very small, narrowly 2-winged; leaves odd-pinnate; leaflets serrate; pith solid; buds scaly 1. *Platycarya*
- aa. Bracteoles and usually 1 or more sepals present in staminate flowers; inflorescences (panicles of catkins or solitary catkin or spike) terminal on the main shoots or lateral on old wood at the base of new growth; staminate catkins drooping; pistillate inflorescences either few-flowered and erect or if many-flowered then slender, elongate, drooping; pistillate catkins completely pistillate; carpels median or transverse; fruits small to large, either not winged or broadly winged; leaves odd- or even-pinnate; leaflets serrate or entire; pith solid or chambered; buds scaly or naked.
 - b. Definite sepals absent in pistillate flowers (only the single row of involucre organs present; carpels transverse; stigmas commissural, hence anterior-posterior; bracts not 3-lobed; staminate catkins in clusters of 3-8 at the base of new growth; leaves odd-pinnate; pith solid; fruits rather large nuts with a husk slightly to strongly dehiscent along the 4-6 ridges; buds scaly 7. *Carya*
 - bb. Definite sepals present in pistillate flowers (a row of 4 organs inside that of the involucre); carpels median (anterior-posterior); stigmas carinal or commissural; bracts sometimes 3-lobed; staminate catkins solitary or if clustered, terminal on new growth or lateral on old growth; leaves odd- or even-pinnate; pith solid or chambered; fruits winged or if with a husk this mostly indehiscent; buds scaly or naked.
 - c. Pistillate and staminate inflorescences in different locations, the pistillate terminal, the staminate lateral; bracts of all flowers narrow, unlobed; fruits

- with 2 lateral or 1 circular wing or with a thick husk; leaves alternate, mostly odd-pinnate; pith chambered; staminate catkins mostly solitary (in clusters of 3-5 in one species of *Pterocarya*); buds naked or scaly.
- d. Fruits winged nutlets; bract scalelike at the base of the fruit or at the outer margin of a circular wing; staminate inflorescences stalked solitary catkins or stalked clusters of 3-5; buds naked or scaly; germination epigeal 3. *Pterocarya*
- dd. Fruits nuts with a husk; bract fused with the ovary to its apex and involved in the husk; staminate catkins solitary, sessile, though often superposed; buds scaly; germination hypogeal 2. *Juglans*
- cc. Pistillate and staminate inflorescences in the same location in a given species, both terminal or both lateral, the two sexes often combined in an androgynous panicle; bracts of flowers 3-lobed, usually comparatively broad; fruits thin- to thick-skinned, either not winged or with an anterior large 3-lobed wing; leaves alternate, opposite or whorled, even-pinnate; pith solid; staminate catkins in clusters of 3-6; buds naked.
- e. Leaves alternate; nutlets winged, 2- to 4-celled at the very base; central lobe of wing of fruit with midrib only, not 3-nerved; stigmas (stigmatic style arms) either commissural and elongate or split-carinal, very short, without a style or style arms; trees of the Old World 4. *Engelhardia*
- ee. Leaves opposite or whorled; nuts or nutlets 8-celled at the base or middle; stigmas carinal, almost round, at the tips of elongate style arms; trees of the New World.
- f. Fruits nuts within a thin to thick skin, the bract a minute scale at the base of the fruit; adaxial bracteoles reduced to a mere rim 6. *Alfaroa*
- ff. Fruits winged nutlets with a thin skin, the bract developing into the large anterior 3-lobed wing, the central lobe of the wing trinerved; bracteoles developing into a rather prominent 2-lobed posterior flap enclosing the nutlet 5. *Oreomunnea*

SUBFAM. I. PLATYCARYOIDEAE Mann., stat. nov.

Tribe(?) Platycaryeae Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1870a: 172; 1870b: 2. TYPE: *Platycarya* Sieb. & Zucc.

Tribe Platycaryeae Nakai, Fl. Sylv. Koreana 20: 76. 1933. TYPE: *Platycarya* Sieb. & Zucc.

Tribe Petrophiloidieae Koikzumi, Acta Phytotax. Geobot. 6: 10. 1937. TYPE: *Petrophiloides* Bowerbank = *Platycarya* Sieb. & Zucc.

Pith solid; bud scales present; leaves alternate; leaflets serrate; fruiting catkin condensed, conelike, many-fruited, erect, the unmodified, rather broad, unlobed or rarely slightly 3-lobed elongate bracts woody, rigid, prominent, projecting far beyond the nutlets and hiding them; the very small narrowly 2-winged nutlets falling off the tree, separating from the fruiting bracts, the bracts persisting on the tree as cone-scale-like structures; nutlets strongly flattened anteriorly-posteriorly (lateral with regard to carpels) and with 2 narrow lateral wings; fruiting catkin and nutlets resembling those of *Betula*; inflorescences terminal on the main shoot or also on the upper, very short axillary shoots, consisting of a cluster of short-stalked staminate catkins or a central pistillate catkin surrounded by several staminate ones, all of the catkins erect; pistillate catkin many-flowered, usually tipped by a staminate one, thus the catkin androgynous; bracteoles and sepals absent in the staminate flower; the 2 bracteoles in the pistillate flower inconspicuously fused with the lateral sepals, these together called lateral appendages, the latter fused with the ovary to its apex, 1 or 2 additional median (anterior-posterior) sepals occasionally present; wings of the nutlet developed from the lateral appendages; carpels lateral (transverse), the style absent, the

stigmas elongate, carinal; ovary and nutlet 2-celled at the base; germination epigeal.

TYPE: and only genus, *Platycarya* Sieb. and Zucc.

1. *Platycarya* Sieb. & Zucc., Abh. Math.-Phys. Cl. Königl. Bayer Akad. Wiss. 3: 741. 1843.

Petrophiloides Bowerbank, Foss. Fruits London Clay: 43, tab. 9, 10. 1840, cf. Art. 58, *International Code of Botanical Nomenclature* where this is used as an example.

Fortunea Lindl., J. Hort. Soc. London 1: 150. 1846. TYPE: *F. chinensis* Lindl. = *P. strobilacea* Sieb. & Zucc.

The only genus of the subfamily; characters of the subfamily.

Deciduous tree or large shrub; terminal bud prominent; buds scaly; pith solid; leaves odd-pinnate, alternate, exstipulate, the 7–15 leaflets serrate, glandular-dotted beneath; staminate and pistillate inflorescences terminal, on the main shoot or also on the upper short lateral shoots, either combined in an androgynous panicle with the pistillate catkin central surrounded by several staminate catkins or a separate cluster of stalked staminate catkins, all catkins erect; pistillate catkin many-flowered, condensed, conelike, usually tipped by a staminate one with a short intermediate zone of abnormal perfect flowers; bracteoles and sepals absent in staminate flowers; stamens 4–15, apparently located on the surface of the unlobed elongated comparatively broad bract, an abortive pistil sometimes present; bract very rarely with 2 small lobes; anthers glabrous; unlobed bract in the pistillate flower large and stiff, becoming neither husk nor wings, essentially separate from the ovary and fruit; bracteoles minute and fused with the 2 lateral sepals, called lateral appendages, reaching to the apex of the ovary, and forming narrow lateral wings for the nutlet; median pair of sepals occasionally present; carpels transverse (lateral); common style absent; stigmas carinal, elongate, hence also transverse, the stigmatic area on the inner surface of the style arms; fruiting catkin erect, conelike, resembling the fruiting catkin of *Betula*; nutlets very small, 2-celled at the base, 4 mm in diameter including the very narrow lateral wings, strongly flattened anteriorly-posteriorly, falling off from the bracts and from the persistent fruiting catkin; germination epigeal, the cotyledons leaflike, 4-lobed; first true leaves of the seedling above the cotyledons simple, then small compound ones; cotyledonary node 1-gap 2-trace.

TYPE: and only species, *P. strobilacea* Siebold & Zuccarini (including *P. longipes* Wu).

Japan, Korea, China, and Viet Nam.

Platycarya and *Pterocarya* do not belong in the same tribe or subfamily; they are similar only in having small winged fruits, but are different in size of bracts, orientation of carpels, type and position of inflorescences; sepals are completely absent in the staminate flowers of the former genus. As indicated by wood anatomy, pollen type, and final separation of fruit and bract, *Platycarya* has evolved along a different line of development from the rest of the family. Although the size of the bract, the type and position of the inflorescences, and the separation of the fruit from the bract are of primitive types, the wood

anatomy, the complete reduction of sepals in the staminate flowers with the fusion of the flower with the axis of the catkin, and the fusion of the bracteoles and sepals in the pistillate flowers indicate a definite advancement and specialization. Stone (1970) has shown, however, that *Platycarya* and *Pterocarya* have retained similar primitive seedling anatomy.

SUBFAM. II. JUGLANDOIDEAE.

Subfam. Drupoideae Koidzumi, Acta Phytotax. Geobot. 6: 10. 1937, nom. inval.

Pith solid or chambered; buds scaly or naked; leaves exstipulate, alternate, opposite or whorled; leaflets serrate or entire; inflorescences terminal or lateral; fruiting catkin or spike not condensed or conelike, either few-fruited and erect, or many-fruited, elongated and drooping, the bracts not rigid and woody nor resembling cone-scales; fruiting bract remaining attached to the nut or nutlet and falling off the tree with it (in *Carya* the husk in some cases remaining on the tree for a short time); bract unlobed or 3-lobed, becoming modified in fruit as part of the husk, or as a wing or part of the wing, or as a minute scalelike structure at the base of the fruit; catkins or spikes many- to few-flowered, solitary or clustered, at least the staminate catkins elongate, drooping; pistillate catkin not tipped by a staminate one, thus the pistillate catkin or spike completely pistillate; bracteoles present in the staminate flowers and mostly evident in the pistillate ones; definite sepals usually present in the staminate and pistillate flowers (except in *Carya* where sepals are rarely present in individual staminate flowers and are modified in pistillate ones); stamens 3–105; bracteoles in pistillate flowers distinct, at least at the tips, from the sepals when the latter are present; carpels median or transverse, the stigmas carinal or commissural, elongate or subglobose; ovary and fruit 2- to 4- to 8-celled below the middle; fruits not flattened or only slightly so, not minute but small to large, 15 mm or more in diameter including wings or husk; germination epigeal or hypogeal.

TYPE: *Juglans* L.

TRIBE A. JUGLANDEAE.

Tribe(?) Juglandae verae Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1870a: 172; 19780b: 2. LECTOTYPE: *Juglans* L.

Tribe Juglandae Nakai, Fl. Sylv. Koreana 20: 83. 1933. TYPE: *Juglans* L.

Tribe Pterocaryae Koidzumi, Acta Phytotax. Geobot. 6: 10. 1937. TYPE: *Pterocarya* Nutt.

Pith chambered; buds scaly or naked; leaves alternate; bract unlobed, narrow, remaining small and narrow in fruit; bracteoles broad, enlarging in fruit into wings or husk; bract free or essentially so from the ovary or fused with it to its tip; bracteoles mostly fused with the ovary, at least on the posterior (adaxial) side; staminate and pistillate inflorescences in different locations, the pistillate terminal, the staminate lateral on old wood or at the base of new wood; sepals typically present in both staminate and pistillate flowers, though often reduced in number in staminate ones; carpels median; short common style present; stigmas carinal, elongate, the plumose stigmatic areas on the inner surface of the recurved style arms, hence also median; fruit a nut with a husk or a winged

nutlet; surface of nutlet rather smooth over the ridges, that of the woody nut shell (pericarp) typically rough ridged externally or rugose, very rarely smooth; nut shell typically with several lacunae in the wall, 2- to 4-celled at the base; germination epigeal or hypogeal.

TYPE: *Juglans* L.

2. *Juglans* L., Sp. Pl. 2: 997. 1753; Gen. Pl., ed. 5: 431. 1754.

Hippocarya Dochnahl, Sich. Fuhr. Obstk. 4: 22. 1860. LECTOTYPE: *H. quadrangularis* Dochnahl = *J. regia* L.

Wallia Alefeld, Bonplandia 9: 335. 1861. LECTOTYPE: *J. nigra* L.

Deciduous trees or large shrubs; pith chambered; buds with a few bud scales, the latter often accrescent in spring, the terminal bud prominent; lateral buds sessile, usually superposed; leaves alternate, odd-pinnate, large, aromatic, exstipulate; terminal leaflet rarely reduced in size; leaflets serrate or entire, glandular-dotted beneath; plants monoecious; staminate catkins lateral, solitary, on old wood, in the axils of leaf scars, sessile, drooping, the immature naked catkins first appearing in late summer in the axils of leaves and persisting over winter as small budlike structures; pistillate spike 2- to 25-flowered, terminal on new leafy growth; staminate and pistillate flowers with bract, 2 bracteoles, and 4 sepals, the sepals in the staminate flowers often reduced in number ("sepals" in some Latin American species frequently 6-14); bract small, narrow, unlobed (occasionally in *J. nigra* with "ears" beside the tip of the bract, so bract 3-lobed?); staminate flower consisting of 7-85(-105) stamens apparently on the bract, bracteoles, and sepals as these are fused with the floral receptacle; anthers glabrous but sometimes slightly pubescent in some species; apparent pistillate flower consisting of bract, 2 bracteoles, whose free tips are variously lobed, and 4 sepals, all fused to the apex with the ovary except for short free tips, so ovary inferior (5 sepals reported in a few individual flowers); carpels 2, median (anterior-posterior), rarely 3-4 in individual flowers on individual trees; style with 2 elongate recurved style branches, the stigmatic areas plumose on the inner surfaces of the style arms; stigmas carinal, hence also median; a ring of inner bracteoles very rarely present (in *J. nigra*); fruit large, drupelike, consisting of a rough-ridged or rarely rugose (or even smooth) nut enclosed in an adherent thick fibrous usually indehiscent husk, the husk derived from the involucre and calyx; wood nut shell (pericarp) usually with prominent wall cavities, 2- to 4-celled at the base; cotyledons fleshy, 4-lobed, straight, 1 cotyledon in each valve (not carpel) of the nut, the cotyledons hypogeal in germination; cotyledonary node 2- to 3- to 4-gap, 2- to 3- to 4-trace.

TYPE: *J. regia* L.

Twenty-one species, North and South America, West Indies, and from southeastern Europe to eastern Asia and Japan.

Sect. a. *Juglans*.

Juglans sect. *Dioscaryon* Dode, Bull. Soc. Dendrol. France 2: 72. 1906. LECTOTYPE: *J. regia* L.

Juglans sect. *Cinerea-Regia*, subsect. *Regia* Nagel, Bot. Jahrb. Syst. 50: 483. 1914. TYPE: *J. regia* L.

Husk usually irregularly dehiscent into 4 valves, easily separating from the nut; nut with thin partitions, externally rugose to almost smooth, with 2 winged ridges (sutures), easily splitting; leaflets 5-9(-11), entire on mature trees; staminate flowers sessile, the receptacle elongate, with 10-28(-40) stamens; pistillate spike 2- to 5-flowered; nut 4-celled at the base, falsely 5-celled at the apex; embryo and seedling with 2 rows of scales with buds, superposed above the cotyledons, then with small spirally arranged compound leaves.

TYPE: and only species, *J. regia* L.

Southeastern Europe, Iran to Himalayas, and China.

Sect. b. **Rhysocaryon** Dode, Bull. Soc. Dendrol. France 11: 165. 1909.

Juglans sect. *Nigra* Nagel, Bot. Jahrb. Syst. 50: 484. 1914. LECTOTYPE: *J. nigra* L.

Husk indehiscent, persistently attached to the nut, which is strongly rough-ridged, but the sharp ridges highly indefinite in number and arrangement, in one species almost smooth, but no winged sutures present; leaflets 9-31, serrate; staminate flowers short-stalked, with round receptacle and 7-85(-105) stamens; nut 4-celled at the base, falsely 5-celled at the apex; pistillate spike 2- to 5-(to 10-)flowered; embryo and seedling with 5 rows of scales, these merging into small spirally arranged compound leaves; top of leaf scar without hairy fringe.

TYPE: *J. nigra* L.

Sixteen species, North, Central, and South America and the West Indies.

Sect. c. **Cardiocaryon** Dode, Bull. Soc. Dendrol. France 11: 22. 1909.

Husk indehiscent, persistently attached to the nut; nut rough-ridged (though smooth in one cultivated variety), with 4 or 8 ridges, these in some cases represented by lines, with rugosities between the ridges; leaflets 9-17, serrate; staminate flowers sessile, the receptacle elongate with 7-18(-25) stamens; pistillate spike elongate with 5-10(-25) flowers; nut 2-celled at the base, 1-celled at the apex; embryo and seedling with 5 rows of scales, these merging into small alternate compound leaves; top of leaf scar notched with hairy fringe.

TYPE: *J. sieboldiana* Maxim. = *J. ailantifolia* Carr.

Three species; Japan, Manchuria, eastern China, Taiwan.

Sect. d. **Trachycaryon** Dode ex. Mann.

Juglans sect. *Trachycaryon* Dode, Bull. Soc. Dendrol. France 11: 22. 1909. nom.

Juglans sect. *Cinerea-Regia*, subsect. *Cinnerea* Nagel, Bot. Jahrb. Syst. 50: 482. 1914. LECTO-TYPE: *J. cinerea* L.

Exocarpium indehiscens; endocarpium, id est nux vere, valde et argute poratum, porcis 8 vulgo prominentibus; flores staminati sessiles, receptaculis elongatis; nux basin bilocularis; embryo et plantula sine squamis; caulis plantulae elongatus, pro maxima parte aphyllus, supra foliae compositae ferens.

Husk indehiscent; nut strongly and sharply ridged, 8 of the ridges usually prominent with sharp anastomosing cross ridges; leaflets 11-19, serrate; staminate flowers sessile, the receptacle elongate with 7-15 stamens; pistillate spike 5- to

8-flowered; nut 2-celled at the base, 1-celled at the apex; embryo and seedling without scale leaves beyond the 2 or 3 buds superposed above the cotyledons, the rather large compound leaves appearing on the seedling above a long naked area of the stem; top of leaf scar not notched, with hairy fringe.

TYPE: and only species, *J. cinerea* L.
Eastern United States.

3. **Pterocarya** Kunth, Ann. Sci. Nat. (Paris) 2: 345. 1824.

Cyclocarya Iljinsk., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vysš. Rast. 10: 115. 1953. TYPE: *P. paliurus* Batal.

Deciduous trees; pith chambered; buds stalked, the terminal bud prominent, the lateral often superposed; buds naked or, if scaly at first, naked in late autumn; leaves exstipulate, odd-pinnate, though terminal leaflet sometimes reduced; leaflets serrate, glandular-dotted beneath; plants monoecious; staminate catkins short-stalked, lateral, solitary or in clusters of 3–5, in the axils of leaf scars or of the scars of scale leaves on old wood, or in the axils of bud scale scars at the base of new growth; immature staminate catkins (naked catkin buds) present on old wood in winter, or when bud scales are present, hidden within the bud scales in late summer and appearing at the base of the immature leaves of the bud in late autumn after the bud scales have fallen off; pistillate catkins 10- to many-flowered, finally drooping, terminal on new growth; staminate and pistillate flowers with bract and 2 bracteoles and 4 sepals, the sepals in the staminate flowers often reduced in number; bract small, narrow, unlobed; staminate flowers consisting of 9–31 stamens apparently located on the bract, bracteoles, and sepals, as these are fused with the floral receptacle; anthers glabrous or rarely slightly pubescent; apparent pistillate flower consisting of the bract, 2 bracteoles and 4 sepals, the sepals fused with the ovary to its tip, thus ovary inferior, the bract almost free from the ovary at its base, and the bracteoles almost free in the abaxial region (above the bract) but fused variously with the adaxial part of the ovary; carpels typically 2, median, or sometimes in individual flowers oblique or even transverse; style with 2 elongate recurved stigmatic style branches, the stigmatic areas on the inner surfaces of the style arms (carpels occasionally 3 on individual flowers of a spike); stigmas carinal, hence also typically median; fruit a small broadly winged nutlet, the 2 lateral wings or the completely circular one derived either from the 2 bracteoles alone or from the bracteoles and also in very small part from the bract when there is only one wing; the bract either a small scale at the base of nutlet or the scalelike tip of the bract appearing at the outer margin of the circular wing, this scale often disappearing; nutlet 2- or 4-celled at the base, usually with small lacunae in the wall; cotyledons entangled in the nutlet, in germination epigeal, appearing as small 4-lobed leaves, the next leaves simple or compound; cotyledonary node 1-gap 2-trace.

TYPE: *Juglans pterocarpa* Michx. = *P. fraxinifolia* (Lam. ex Poir.) Spach.
Six species, Caucasus Mts. of USSR, Iran, Japan, China, Laos and Viet Nam.

Subgen. 1. **Pterocarya**.

Pterocarya Kunth sensu Iljinsk., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vysš. Rast. 10: 38. 1953. TYPE: *Juglans pterocarpa* Michx. [*Pterocarya pterocarpa* (Michx.) Kunth ex Iljinsk.] = *P. fraxinifolia* (Lam. ex Poir.) Spach.

Buds naked, or if scaly at first becoming naked in late autumn; wood tending to be diffuse-porous; leaflet venation with none of lateral veins going directly to the teeth; staminate catkins solitary, short-stalked, in the axils of leaf scars or scars of scale-leaves on old wood, or in the axils of bud scale scars at the base of new growth; staminate flowers sessile, with elongate receptacle, 5–17 stamens, and the bracteoles slightly different in appearance from sepals, the whole flower zygomorphic; pollen grains (4-) 5- to 6-(to 8-) porate; pistillate flowers 40 or more per inflorescence, sessile, the bract fused only with the base of the ovary, separate from the 2 bracteoles, the latter unequally fused with the ovary, abaxially fused only with the base, adaxially fused to the base, the middle, or almost to tip of the ovary; nutlet 4-celled at the base, sessile, with 2 lateral separate broad wings derived exclusively from the bracteoles; bract remaining at the base of the nutlet as a small scale.

TYPE: *P. fraxinifolia* (Lam. ex Poir.) Spach [*P. pterocarpa* (Michx.) Kunth ex Iljinsk.].

Sect. a. **Pterocarya**.

Pterocarya sect. *Diptera* Henry in Elwes & Henry, Trees Gt. Brit. Irel. 2: 437. 1907; emend. Leroy, Mém. Mus. Natl. Hist. Nat., Sér. B, Bot. 6: 86. 1955. LECTOTYPE: *P. caucasica* Meyer = *P. fraxinifolia* (Lam. ex Poir.) Spach.

Pterocarya sect. *Stenoptera* Nagel, Bot. Jahrb. Syst. 50: 479. 1914. TYPE: *P. stenoptera* C. DC.

Pterocarya sect. *Eupterocarya* Rehder & Wilson in Sarg., Pl. Wils. 3: 181. 1916, emend. Iljinsk., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vysš. Rast. 10: 40. 1953. LECTOTYPE by Iljinskaya: *P. pterocarpa* (Michx.) Kunth ex Iljinsk., but this species not mentioned by Rehder & Wilson, so lectotype *P. stenoptera* C. DC.

Buds naked; lateral buds superposed; new growth not constricted at the base, without a ring of narrow bud scale scars at its base; staminate catkins solitary on old wood, in the axils of leaf scars or the scars of scale leaves; immature staminate catkins, naked catkin buds, appearing in late summer and persisting over winter as small budlike structures; stamens 5–17; bracts of staminate flowers, pistillate flowers, and fruits short, glabrous or with a few hairs; tips of the leaflets without tufts of hairs; nutlet usually with large cavities in the wall.

TYPE: *P. fraxinifolia* (Lam. ex Poir.) Spach [*P. pterocarpa* (Michx.) Kunth ex Iljinsk.].

Three species, Caucasus Mts. of USSR; Iran; eastern China, Laos, and Viet Nam.

Sect. b. **Platyptera** Nagel, Bot. Jahrb. Syst. 50: 481. 1914; emend. Rehder, Bibl. Cult. Trees and Shrubs: 89. 1949.

Pterocarya sect. *Chlaenopterocarya* Rehder & Wilson in Sarg., Pl. Wils. 3: 183. 1916. TYPE: *P. rhoifolia* Sieb. & Zucc.

Buds long, clearly stalked, conical, beaked, covered by a few hoodlike bud scales, these falling off in late autumn and then buds naked; lateral buds not superposed; new growth constricted at its base, with a ring of narrow bud scale scars at its base; staminate catkins solitary, at the base of new growth, essentially in a ring in the axils of bud scale scars, the immature catkins formed in late summer but not evident until late autumn after the bud scales have fallen off; bracts of staminate flowers, pistillate flowers, and fruits narrow, strongly hairy; stamens 9–13; tips of the leaflets with tufts of hairs, these sometimes deciduous; nutlets without cavities in the wall.

LECTOTYPE: *P. rhoifolia* Sieb. & Zucc. in Rehder, Bibl. Cult. Trees and Shrubs: 89, 1949, indicated by synonymy of sect. *Chlaenopterocarya* Rehder & Wilson. Two species, western China, Tibet, and Japan.

Subgen. 2. **Cyclocarya** (Iljinsk.) Mann., Bull. Torrey Bot. Club 102: 165. 1975.

Pterocarya sect. *Cycloptera* Franch., J. Bot. (Morot) 12: 318. 1898. TYPE: *P. paliurus* Batal. *Cyclocarya* Iljinsk., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vysš. Rast. 10: 115. 1953. TYPE: *P. paliurus* Batal.

Buds naked; wood tending to be ring-porous; leaflet venation usually with some of the lateral veins going directly to the teeth; staminate catkins in clusters of 3–5, the clusters stalked, in the axils of leaf scars on old wood; staminate flowers short-stalked, with round receptacle, 20–31 stamens, and the 2 bracteoles similar to the usually 2 sepals, the flower appearing actinomorphic; pollen grains 3- to 4-(to 7-)porate; pistillate flowers 10–20, short-stalked, the base of the bract fused with the 2 bracteoles, the involucre in turn fused equally with the base of the ovary or the middle(?); nutlet 2-celled at the base, short-stalked, with one circular wing derived mostly from the bracteoles but also in very small part from the bract; bract not at the base of nutlet, but the tip of the bract remaining as a small often deciduous scale at the outer margin of the wing of the fruit.

TYPE: and only species, *P. paliurus* Batal.
Eastern China.

I believe that *Pterocarya* is closely related to *Juglans*, not so closely to *Platycarya* or to *Engelhardia*; the relationship to the last two genera is indicated by the classifications of various authors.

The relationship of *Pterocarya* to *Juglans* is indicated in the key to genera and the descriptions of the tribes. The pith is chambered in both genera, and there is a similar organization of the type and positions of staminate inflorescences, the parts of the floral envelope present, the orientation of carpels, and the type and orientation of stigmas. The wood anatomy, according to Kribs (1927) and Heimsch & Wetmore (1939), is extremely close; and there is a clear evolutionary development of the types of pollen grains from *Pterocarya* to *Juglans* (Whitehead, 1963, 1965; Stone & Broome, 1975); see Fig. 1. Although there is some relationship of *Pterocarya* to *Engelhardia*, as presumably the two genera had a common ancestor, the type of bracts and stigmas, and the positions

and types of inflorescences are quite different. The similarity of small-winged fruits, with the involucre at a low position on the ovary, is superficial. See Stone (1973) for a discussion of the relationships of the fruits of the family.

TRIBE B. ENGELHARDIEAE Mann., stat. nov.

Tribe(?) Engelhardtiae Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1870a: 172, 1870b: 2. LECTOTYPE: *Engelhardia* Lesch. ex Blume.

Tribe Alfaroae Koidzumi, Acta Phytotax. Geobot. 6: 10. 1937. TYPE: *Alfaroa* Standl.

Pith solid; buds naked; leaves alternate, opposite or rarely whorled, even-pinnate; leaflets serrate or entire; staminate and pistillate inflorescences in the same position (axillary or terminal) in a given species, frequently combined into an androgynous panicle; staminate catkins clustered, elongate, drooping; pistillate catkin many-flowered, elongate, finally pendulous; bract broad, 3-lobed in staminate and pistillate flowers, the lobes rarely filiform; staminate flower consisting of 3-lobed bract, 2 bracteoles (or these very rarely absent), 4 to 1 (or rarely 0) sepals, and 4–23 stamens; pistillate flower consisting of 3-lobed bract and 2 bracteoles fused with the base of the ovary, and 4 sepals fused to its tip; bract modified into a large anterior 3-lobed wing for the fruit, or in one genus reduced to a minute scale at base of the fruit; bracteoles adaxial, varying in flower from a prominent 2-lobed structure to a minute line around the base of the ovary, and in fruit from a large adaxial 2-lobed wing to apparently no structure; carpels median; style present or absent, stigmas carinal, commissural or split-carinal; fruit a small to medium winged nutlet, or a thin- to thick-skinned nut without a wing or true husk; shell of nutlet and nut cartilaginous-sublignous, rather thin; septa thin; fruit 2- to 4- to 8-celled near the base; pericarp without lacunae; cotyledons hypogeal or epigeal in germination.

TYPE: *Engelhardia* Lesch. ex Blume.

4. *Engelhardia* Lesch. ex Blume, Bijdr. 10: 528. 1825.

Pterilema Reinw., Syll. 2: 13. 1826. TYPE: *P. aceriflorum* Reinw. = *E. spicata* Lesch. ex Blume var. *aceriflora* (Reinw.) Koord. & Valet.

Deciduous or sometimes evergreen trees; pith solid; buds naked; leaves exstipulate, alternate, even-pinnate, the leaflets serrate or entire, glandular-dotted beneath; leaflet venation, intercostal mesh with free-ending veinlets; large rhombic leaflet crystals absent; trees monoecious or dioecious; staminate and pistillate inflorescences separate or combined in an androgynous panicle, the pistillate central; all catkins elongate, pendulous; staminate and pistillate inflorescences in the same location in a given species, either terminal on new growth or lateral on old wood; staminate catkins in clusters of 3–6; bract broad, 3-lobed in all flowers, sometimes much enlarged in staminate flowers; 2 bracteoles and 4 sepals present in both staminate and pistillate flowers, though sepals often reduced in number in the former or even absent; stamens 4–13; anthers pubescent or glabrous; pollen diameter averaging (13–)15–19(–25) μm ; polar view of pollen oblate to oblate-spherical; involucre fused with the lower half of the ovary and the sepals fused to the top; carpels median; stigmas either commissural, the

stigmatic areas on the edges of the elongate style arms, and the stigmatic style arms transverse (lateral), or the style absent and the stigmas short on the top of the ovary, split-carinal; fruit a small nutlet, with a large 3-lobed anterior wing derived from the development of the bract, the bracteoles present as a much reduced often 2-lobed adaxial wing; large central lobe of the wing of the bract pinnately veined; fruit with thin skin, developed from calyx; nutshell cartilaginous-subligneous, rather thin, without lacunae; septa of the fruit thin, the fruit mostly 4-celled at the base due to a primary partition and a low secondary one, possibly 2-celled in smaller fruits; cotyledons entangled in the seed, the testa loose in fruit; cotyledons epigeal in germination, first true leaves of the seedling simple or compound; cotyledonary node 1-gap, 2-trace.

LECTOTYPE: *E. spicata* Lesch. ex Blume.

Five species, northern India to eastern China, Indo-China, East Indies, and Philippines.

Sect. a. **Engelhardia**.

Engelhardia sect. *Pterilema* (Reinw.) C. DC., Ann. Sci. Nat. Bot. Sér. 4, 18: 35. 1862. TYPE: *E. aceriflora* (Reinw.) Blume = *E. spicata* Lesch. ex Blume var. *aceriflora* (Reinw.) Koord. & Valet.

Engelhardia sect. *Trichotocarpeae* Nagel, Bot. Jahrb. Syst. 50: 475. 1914. LECTOTYPE: *E. spicata* Lesch. ex Blume.

Leaves deciduous or evergreen; inflorescences lateral on old wood; staminate flower sessile, the receptacle elongate; calyx usually irregular, the sepals often reduced in number or rarely even absent; stamens 4–13, the anthers pubescent; pistillate flower essentially sessile; style present, short; stigmas elongate, commissural, stigmatic areas on the edges of each style arm, or sometimes the style arms split so there are 4 elongate filiform stigmas; fruit sessile or obscurely short-stalked, 4-celled at the base in most fruits, possibly 2-celled in smaller ones; body of fruit and lower part of bract hairy.

TYPE: *E. spicata* Lesch. ex Blume.

Four species, northern India to eastern China, Malaya, East Indies to Philippines.

Sect. b. **Psilocarpeae** Nagel, Bot. Jahrb. Syst. 50: 475. 1914, emended Leroy, Mém. Mus. Natl. Hist. Nat., Sér. B, Bot. 6: 126. 1955.

Leaves apparently evergreen; inflorescences terminal; staminate flower short-stalked, the receptacle round, the perianth cup-shaped, regular in appearance, typically of 4 similar organs (2 bracteoles and 2 sepals?); stamens 4–12; anthers glabrous; pollen diameter averaging 15(13–17) μm ; exine thick; pistillate flower and fruit clearly short-stalked to long-stalked (7 mm long); style absent, the stigmas short, on top of the ovary, split-carinal; body of fruit and bract glabrous though usually densely glandular dotted; fruit 4-celled at the base.

LECTOTYPE: (by Leroy) *E. wallichiana* Lindl. ex C. DC. = *E. roxburghiana* Wall.

East Pakistan, southern China, Taiwan, Viet Nam, Borneo, Sumatra.

Engelhardia, *Oreomunnea*, and *Alfaroa* are very closely related in having similar broad 3-lobed bracts, inflorescence position and type, floral envelopes, leaflet pinnation, buds, pith, wood anatomy, and pollen. Manning (1966) suggested that the 3 genera could essentially be considered one genus. Crepet et al. (1975) and Dilcher et al. (1976) show that an almost identical 3-lobed bract occurred in ancestral genera in the Eocene. The two American genera are quite different in arrangement of leaves, cross section of the fruit, and germination of the fruit, but the relationship otherwise is very close. *Alfaroa* clearly should not be placed in the same tribe as *Juglans* and *Carya*. The relationship of the group to *Pterocarya* is discussed under that genus. All studies indicate that the three genera as a whole are the most primitive in the family.

5. ***Oreomunnea*** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1856: 33.

Engelhardia sect. *Oreomunnea* (Oerst.) C. DC., Ann. Sci. Nat. Bot. sér. 4, 18: 32. 1862.
TYPE: *O. pterocarpa* Oerst.

Evergreen trees; pith solid; buds naked, the lateral superposed; leaves exstipulate, opposite, even-pinnate; leaflets 4–12, glandular-dotted beneath, serrate or entire on young trees, entire on mature ones; leaflet venation, intercostal mesh with closed veinlets; plants monoecious; staminate panicles of catkins separate or combined with a central pistillate spike to form an androgynous panicle; inflorescences terminal or lateral, all catkins many-flowered, drooping; bract broad, 3-lobed in staminate and pistillate flowers; 2 bracteoles and 4 sepals present in both flowers but sepals often reduced in staminate flowers; staminate flowers sessile, the receptacle round or elongate, with 3-lobed bract, 2 bracteoles, 1–4 sepals and 8–23 stamens; anthers glabrous; pollen diameter averaging 21 μm (19–23); polar view subtriangular, equatorial view sublobate; pistillate flowers short-stalked; involucre fused with the lower half of the ovary, and the 4 sepals fused to the top; 6 sepals found in one 3-carpelled fruit of *O. pterocarpa*; carpels median, the stigmatic areas short, subglobose or horseshoe shaped at the tips of the elongate style arms; fruit a short-stalked nutlet, medium in size, with a large anterior 3-lobed wing from the development of the bract, but with a smaller 2-lobed rather prominent posterior wing developed from the 2 bracteoles; fruit with subligneous rather thin wall, covered by a thin skin developed from the sepals, with thin septa, 8-celled in the middle, the primary and secondary partial partitions and tertiaries with projections into the loculus so in part more than 8-celled; lacunae absent in the walls; central lobe of the fruit wing trinerved; cotyledons separate, not entangled in the fruit, one to a valve, hypogeal in germination; first true leaves of seedling simple; cotyledonary node 1-gap, 3-trace; fruit and wings both larger than those of *Engelhardia* of Asia.

TYPE: *O. pterocarpa* Oersted.

Two species, Mexico and Central America.

6. ***Alfaroa*** Standl., J. Wash. Acad. Sci. 17: 77. 1927.

Evergreen trees; pith solid; buds naked; leaves exstipulate, opposite or

whorled, rarely in part alternate, even-pinnate; leaflets 4–12, glandular-dotted beneath, serrate on young trees, entire on mature ones; leaflet venation, intercostal mesh with closed veinlets; plants monoecious; staminate panicles of catkins separate or combined with a central pistillate spike to form an androgynous panicle; inflorescences terminal or lateral, all catkins many-flowered, drooping; bract broad, 3-lobed in staminate and pistillate flowers; 2 bracteoles and 4 sepals present in both flowers but sepals often reduced in staminate ones; staminate flowers sessile, the receptacle round or elongate, with a 3-lobed bract, 2 bracteoles, 1–4 sepals and 6–10 stamens; anthers glabrous; pollen diameter averaging 24 μ m; polar view subtriangular, equatorial view sublobate; pistillate flowers sessile, the 3-lobed bract very small, fused only with the very base of the ovary, and not enlarging into a wing for the fruit but remaining as a minute scale at the base of the fruit; sepals fused to the top of the ovary; carpels median, the stigmatic areas short, subglobose or horseshoe shaped at the tips of the elongate style arms; bract so small that the venation is not recognizable in pistillate flower or fruit; bracteoles (adaxial) so small that these are essentially absent; fruit a rather large thin- to thick-skinned nut compared with the medium size of *Oreomunnea*, not winged nor with a true husk (that is, not developed from the involucre); wall of nut thin to thick, subligneous, covered with a thin to thick skin developed from the calyx, with thin septa, 8-celled in the middle, the primary and secondary partial partitions and tertiaries with projections into the loculus so in part more than 8-celled; lacunae absent in the walls; cotyledons separate, not entangled in the fruit, 1 to a valve, hypogeal in germination; first true leaves of seedling simple or compound; cotyledonary node 1-gap, 3-trace.

TYPE: *A. costaricensis* Standl.

Seven species, Mexico, Central America, and northwestern South America (Colombia).

TRIBE C. HICORIEAE Mann., nom. nov.

Tribe Caryeae Koidzumi, Acta Phytotax. Geobot. 6: 10. 1937, excl. *Juglans* L., nom. superfl. (incl. *Juglans* Linnaeus).

Pith solid; bud scales present, sometimes accrescent in spring; leaves exstipulate, alternate, odd-pinnate; leaflets 3–17, glandular-dotted beneath, serrate or entire; unlobed bract and the bracteoles both rather broad in the pistillate flower, developing in the fruit into a husk which is completely or partially 4- to 6-valved at maturity; bracteoles apparently 3–5, but these may represent 2 bracteoles, variously lobed and divided, though the posterior 1–3 sometimes interpreted as sepals; plants monoecious; staminate and pistillate inflorescences in different locations, the pistillate terminal and few-flowered, the staminate in clusters of 3–8, lateral at the base of new growth, drooping; bracteoles present in the staminate flower; sepals normally absent in the staminate and pistillate flowers, though 1 or 2 sepals occasionally present in individual staminate flowers, and sepals possibly represented in the pistillate ones by the 4-lobed stigmatic disk below the stigmas and apparently confluent with them; carpels transverse; common style apparently absent; stigmas commissural, thick, hence apparently

median, rather short, the stigmatic area completely covering the style branches and stigmatic disc (when present); style branches occasionally split so 4 stigmas present; fruit large, consisting of a nut enclosed in a completely or incompletely 4- to 6-valved husk; nut shell woody, externally smooth, often 4-angled, rarely somewhat wrinkled, often with lacunae present in the wall; nut 2- to 4-celled at the base; cotyledon 1 in each valve (not carpel), fleshy; germination hypogeal.

TYPE: *Carya* Nutt., the only genus.

7. *Carya* Nutt., Gen. N. Amer. Pl. 2: 220. 1818, nom. cons.

Hicorius Raf., Fl. Ludovic.: 109. 1817, nom. rejic. LECTOTYPE: *H. amara* (Michx.) Raf.

Hicoria Raf., Alsogr. Am. 65. 1838, orth. mut. TYPE: *Juglans alba* L. (fide Britton, N. Amer. Trees, 223.)

Pacania (Raf.) Dochnahl, Sich. Fuhr. Obstk. 4: 26. 1860. TYPE: *Hicoria oliveformis* Raf.

Deciduous (or rarely evergreen?) trees; pith solid (or rarely hollow?); bud scales present; terminal bud prominent, the lateral buds often superposed; leaves exstipulate, alternate, odd-pinnate; leaflets glandular-dotted beneath, serrate or entire; flowers appearing with the leaves; staminate flowers in axillary drooping catkins, these in stalked clusters of 3–8, each flower in the axil of a bract and 2 bracteoles; sepals typically absent, but 1 or 2 rarely present in individual flowers of a catkin of some species; stamens 3–15, usually 4; anthers pubescent; pistillate flowers sessile, in terminal 2- to 10-flowered spikes, consisting of a 1-celled ovary enclosed by an apparently 4- to 6-lobed involucre (bract and 3–5 bracteoles or bract and 2 bracteoles, the latter variously lobed at the apex); (a ring of 2–3 “sepals” reported as occurring occasionally inside the involucre in a few species); carpels transverse; stigmas 2, short, commissural (hence median), these frequently each 2-parted, a stigmatic disc (modified calyx?) usually beneath the stigmas; fruit a nut enclosed in an adherent husk, the whole globose to oblong, the husk separating more or less completely into 4–6 valves, and typically becoming free from the nut at maturity; nut smooth or slightly rugose, often angled. 2- to 4-celled at the base, 1-celled at the apex; cotyledons fleshy, not entangled in the nut, hypogeal at germination; cotyledonary node 3- to 6-gap, 3- to 6-trace.

LECTOTYPE: *C. tomentosa* (Lamarck) Nuttall (*Juglans alba* Linnaeus in part).

Seventeen species, eastern United States, northeastern Mexico, eastern Asia.

Sect. a. **Carya.**

Hicoria subgen. *Glycaria* Raf., Alsogr. Am. 66. 1838. TYPE: *Hicoria alba* (L.) Raf.

Hicoria subgen. *Hexacaria* Raf., Alsogr. Am. 66. 1838. TYPE: *H. tomentosa* Raf.

Hicoria sect. *Euhicoria* Dippel, Handb. Laubh. 2: 331. 1892. LECTOTYPE: *H. alba* (L.) Britt.

Carya sect. *Eucarya* C. DC., Prodr. 16, 2: 142. 1864. LECTOTYPE: *C. tomentosa* Nutt.

Hicoria sect. *Eucarya* (C. DC.) Sarg., Sylva N. Amer. 7: 135. 1895. LECTOTYPE: *C. tomentosa* Nutt.

Pith solid; bud scales 6–12, imbricated, strongly accrescent in spring; leaflets 3–9, serrate, not falcate; staminate catkins essentially in a ring around the stem, in the axils of early deciduous bud scales (or rarely also in the axils of 1 or 2 leaves above the bud scale zone) at the base of elongate leafy growth, in clusters of 3 (very rarely of 4, 5, 6 or 7 in individual trees); stamens 3–8(–10?), usually 4;

bracteoles in pistillate flower in addition to bract apparently 3, rarely 2 or 4; stigmatic disc present beneath the true stigmas; husk 4-valved, rarely in individual trees 3- or 5-valved, the valves not keeled nor usually winged along the margins; nut shell rather thick, without definite lacunae; secondary septa well developed, hence nut 4-celled below; secondary internal ridges (projections) present and often tertiary ones also; outer common ring of involucral and carpellary vascular bundles ascending in the outer or inner part of the primary partition; first true leaf above several spiral scale leaves of seedling usually slightly lobed, the second leaf compound with 3 leaflets; $n = 16$ or $n = 32$.

TYPE: *C. tomentosa* Nutt.

Eight species, eastern United States to northeast Mexico.

Sect. b. **Apocarya** C. DC., Prodr. 16, 2: 144. 1864.

Hicoria subgen. *Pacania* Raf., Alsogr. Am. 65. 1838. TYPE: *H. oliveformis* Raf.

Hicoria subgen. *Drimocaria* Raf., Alsogr. Am. 66. 1838. TYPE: *H. amara* Raf.

Hicoria sect. *Apohicoria* Dippel, Handb. Laubh. 2: 336. 1892. LECTOTYPE: *H. minima* Britton.

Carya sect. *Pacania* (Raf.) Rehder, J. Arnold Arbor. 28: ined. 1947, see Rehder, Bibl. Cult.

Trees and Shrubs: 91. 1949. TYPE: *Hicoria oliveformis* Raf.

Pith solid; bud scales few, 4–6, valvate, not accrescent in spring or only slightly so, the buds possibly naked in the Chinese species, *C. cathayensis*; leaflets 5–17, serrate, commonly falcate; staminate catkins in clusters of 3, essentially in a ring around the stem in the axils of early deciduous bud scales, these located at the base of long terminal leafy shoots, or in most species some or all of them usually on short special essentially leafless side branches attached to old wood in the axils of leaf scars; stamens 3–8, usually 4; in pistillate flowers bracteoles in addition to bract commonly 3, rarely 2, 4, or 5; beak of ovary absent, though nut pointed; stigmatic disc present; husk 4-, rarely 3-, 5- or 6-valved, the segments (valves) not keeled, frequently winged along the margins; nut shell thin, rarely thick; nut with lacunae present in the wall (in the internal ridges and sometimes at the ends of the primary partition) in most but not all species; secondary septa present or reduced to a pair of wings from the primary partition and appearing absent, hence nut 2- to typically 4-celled below; secondary and tertiary internal ridges usually present; outer common ring of involucral and carpellary vascular bundles ascending in outer or inner part of primary partition; first true leaves above several alternate scale leaves of seedling mostly simple, unlobed, or in *C. myristiciformis* one slightly lobed leaf followed by a compound leaf with 3 leaflets; $n = 16$.

LECTOTYPE: *C. oliveformis* (Raf.) Nutt. = *C. illinoensis* (Wang.) K. Koch.

Five species, northeastern United States to northern Mexico; 3 species eastern China to northern Viet Nam and eastern India (eastern Pakistan).

Sect. c. **Rhamphocarya** (Kuang) Mann. & Hjelmqvist, Bot. Not. 1951, 4: 330. 1951.

Annamocarya Chev., Rev. Int. Bot. Appl. Agric. Trop. 21: 504. 1941. TYPE: *A. indochinensis* Chev. = *Carya sinensis* Dode.

Rhamphocarya Kuang, Icon. Fl. Sin. 1: 1. 1941. TYPE: *R. integrifoliolata* Kuang = *C. sinensis* Dode.

Pith hollow or solid; bud scales few, unequal; leaflets 7-9, entire, not falcate; staminate catkins much elongated, in clusters of 5-8 at the base of elongate leafy shoots, apparently scattered along the base of the shoot rather than in a close ring, evidently in the axils of lower foliage leaves; stamens 5-15; pistillate flowers with 3-5 bracteoles in addition to the bract, the ovary with a beak so the stigmas not strictly sessile; stigmatic disc apparently absent; husk 4- to 6-valved, the valves typically keeled, at least above; nut apiculate; lacunae absent in the wall of the nut in the lower part but sometimes present near the apex; secondary partition weakly developed, represented by a pair of wings from the primary partition hence the nut essentially 2-celled at the very base; secondary internal ridges present but tertiary ones apparently absent; cavity in nut large at the apex; outer common ring of involucral and carpellary vascular bundles ascending in the potential nut-shell part of the ovary wall; nature of leaves of seedling unknown.

TYPE: and only species, *C. sinensis* Dode.

Southern China and northern Viet Nam.

The mature fruit of *Carya* with its thick husk is quite similar to that of *Juglans*, and the husk of *J. regia* is irregularly 4-valved much as in *Carya*. Furthermore, the general, but not the detailed, arrangement of inflorescences is similar in the two genera. The location of lacunae in the nuts of *Carya* is for the most part rather different from that of *Juglans*, but Leroy (1955) points out that *C. poilanei* shows an intermediate condition. Leroy (1955: 82) believes that there is an evolutionary series of development in arrangement of vascular bundles of the carpels in the flower and fruit from *Annamocarya* (*Carya*, sect. *Rhamphocarya*) through certain species of *Carya* to *Juglans*. Thus practically all writers have placed *Juglans* and *Carya* in the same tribe. However, the two are different in the parts of the floral envelope present in both staminate and pistillate flowers, the location of staminate inflorescences, orientation of carpels, type and orientation of stigmas, anatomy of the wood, and the type of pollen grains. Furthermore, the pith in *Carya* is solid, not chambered. With reference to the floral anatomy as discussed by Leroy, it should be pointed out that the floral anatomy of the carpels of *Juglans* is very close to that of *Pterocarya* and of *Engelhardia*, and the primitive condition, according to Leroy, of *Annamocarya* is quite different from that of the truly primitive condition of *Engelhardia* (from which presumably *Carya* probably evolved). Thus *Carya* and *Juglans* have followed a parallel evolutionary development; Stone (1973) has discussed the evolutionary development of the fruits in the family. Studies of wood anatomy and of pollen grains indicate that *Carya* is not only along a different line of evolution, but is the most advanced genus in the family. I have placed the genus in a separate tribe.

Four species of *Carya* have been reported to be tetraploid, *C. glabra*, *C. ovalis*, *C. floridana*, *C. texana*, *C. pallida*, *C. tomentosa*; $n = 32$.

TABLE 3. List of species of Juglandaceae arranged according to the classification in this paper, with general distribution of each species.

SUBFAM. I. PLATYCARYOIDEAE Mann.		
1. <i>Platycarya</i> Sieb. & Zucc.	1 sp.	
<i>P. strobilacea</i> Sieb. & Zucc.		Korea, eastern China, Viet Nam, Japan
SUBFAM. II. JUGLANDOIDEAE		
TRIBE A. JUGLANDEAE		
2. <i>Juglans</i> L.	21 spp.	
Sect. a. <i>Juglans</i>		
<i>J. regia</i> L.		southeastern Europe, Iran to Himalayas, and China
subsp. <i>turcomanica</i> Popov		
subsp. <i>fallax</i> (Dode) Popov		
Sect. b. <i>Rhysocaryon</i> Dode		
<i>J. australis</i> Griseb.		Argentina
<i>J. boliviana</i> (C. DC.) Dode		western South America
<i>J. californica</i> S. Wats.		California
<i>J. hindsii</i> (Jeps.) Rehder ³		California
<i>J. hirsuta</i> Mann.		northeastern Mexico
<i>J. jamaicensis</i> C. DC. ²		West Indies
<i>J. major</i> (Torr. ex Sitsgr.) Heller		
var. <i>major</i>		southwestern United States, northwestern Mexico
var. <i>glabrata</i> Mann. ¹		south-central Mexico
<i>J. microcarpa</i> Berl.		
var. <i>microcarpa</i>		southwestern United States, northwestern Mexico
var. <i>stewartii</i> (Johnston) Mann. ³		northern Mexico
<i>J. mollis</i> Engelm. ex Hemsl.		central Mexico
<i>J. neotropica</i> Diels		northwestern South America
<i>J. nigra</i> L.		eastern United States
<i>J. olanchana</i> Standl. & L. O. Williams ²		
var. <i>olanchana</i> ³		Guatemala
var. <i>standleyi</i> Mann. ³		southwestern Mexico
<i>J. pyriformis</i> Liebm.		southeastern Mexico
<i>J. soratensis</i> Mann. ⁴		Bolivia
<i>J. steyermarkii</i> Mann.		Guatemala
<i>J. venezuelensis</i> Mann. ²		Venezuela
Sect. c. <i>Cardiocaryon</i> Dode		
<i>J. ailantifolia</i> Carr.		
var. <i>ailantifolia</i>		Japan
var. <i>cordiformis</i> (Makino) Rehd. ³		Japan
<i>J. cathayensis</i> Dode		eastern China, Taiwan
<i>J. mandshurica</i> Maxim.		Manchuria, northeastern China, Korea
Sect. d. <i>Trachycaryon</i> Dode ex Mann.		
<i>J. cinerea</i> L.		eastern United States
3. <i>Pterocarya</i> Kunth	6 spp.	
Subgen. <i>Pterocarya</i>		

TABLE 3. Continued

Sect. a. <i>Pterocarya</i>		
<i>P. fraxinifolia</i> (Lam. ex. Poir.) Spach	USSR Caucasus, Iran	
<i>P. hupehensis</i> Skan.	eastern China	
<i>P. stenoptera</i> C. DC.		
var. <i>stenoptera</i>	eastern China, Viet Nam, Laos	
var. <i>tonkinensis</i> Franch. ³	Viet Nam	
Sect. b. <i>Platyptera</i> Nagel emend. Rehder		
<i>P. rhoifolia</i> Sieb. & Zucc.	Japan	
<i>P. macroptera</i> Batal.		
var. <i>macroptera</i> ¹	northwestern China	
var. <i>delavayi</i> (Franch.) Mann. ¹	western China	
var. <i>forrestii</i> (W. W. Smith ex Hand.-Mazz.) Mann. ¹	western China, Tibet	
var. <i>insignis</i> (Rehder & Willson) Mann. ¹	western China	
Subgen. 2. <i>Cyclocarya</i> (Iljinsk.) Mann.		
<i>P. paliurus</i> Batal.	eastern China	
TRIBE B. ENGELHARDIEAE Mann.		
4. <i>Engelhardia</i> Lesch. ex Blume	5 spp.	
Sect. a. <i>Engelhardia</i>		
<i>E. apoensis</i> Elmer ex Nagel	Malaya, Borneo, Philippines	
<i>E. rigida</i> Blume		
var. <i>rigida</i>	Java, Borneo, New Guinea	
var. <i>subsimplificifolia</i> (Merr.) Mann. ¹	Borneo, New Guinea, Philippines	
<i>E. serrata</i> Blume		
var. <i>serrata</i>	Malaya, Java, Philippines	
var. <i>cambodica</i> Mann. ³	southwestern China, Cambodia, Burma, Thailand	
var. <i>nudiflora</i> (Hook.f.) Mann. ¹	Thailand, Malaya, Sumatra, Borneo	
var. <i>parvifolia</i> (C. DC.) Mann. ¹	Sumatra, Borneo, Philippines	
<i>E. spicata</i> Lesch. ex Blume		
var. <i>spicata</i>	Nepal, western India, southern China, Malaya, East Indies, Philippines	
var. <i>aceriflora</i> (Reinw.) Koord. & Valet.	Tibet, northern India, Burma, Thailand, Java, New Guinea, Philippines	
var. <i>colebrookeana</i> (Lindl. ex Wall.) K.&V.	northern India, western China, Burma, Laos, Thailand, Philippines	
Sect. b. <i>Psilocarpeae</i> Nagel emend. Leroy		
<i>E. roxburghina</i> Wall. ²	East Pakistan, southern China, Taiwan, Viet Nam, Sumatra, Borneo	
5. <i>Oreomunnea</i> Oerst.	2 spp.	
<i>O. mexicana</i> (Standl.) Leroy ²		
subsp. <i>mexicana</i>	Mexico, Central America	
subsp. <i>costaricensis</i> Stone ³	Costa Rica	
<i>O. pterocarpa</i> Oerst. ²	Costa Rica	
6. <i>Alfaroa</i> Standl.	7 spp.	
<i>A. costaricensis</i> Standl.	Mexico to Panama	
<i>A. guanacastensis</i> Stone ³	Costa Rica	

TABLE 3. Continued

<i>A. guatemalensis</i> (Standl.) L. O. Williams ³	Guatemala
<i>A. hondurensis</i> L. O. Williams ex Mann. ⁴	Honduras
<i>A. manningii</i> León ³	Costa Rica
<i>A. mexicana</i> Stone ³	eastern Mexico
<i>A. williamsii</i> A. Molina ³ subsp. <i>williamsii</i> ³	Nicaragua
subsp. <i>tapantiensis</i> Stone ³	Costa Rica
TRIBE C. HICORIEAE Mann.	
7. <i>Carya</i> Nutt.	17 spp.
Sect. a. <i>Carya</i>	
<i>C. floridana</i> Sarg.	Florida
<i>C. glabra</i> (Mill.) Sweet var. <i>glabra</i>	eastern United States
var. <i>hirsuta</i> (Ashe) Ashe ³	eastern United States
var. <i>megacarpa</i> (Sarg.) Sarg. ³	southeastern United States
<i>C. laciniosa</i> (Michx.) Loud.	eastern United States
<i>C. ovalis</i> (Wang.) Sarg. var. <i>ovalis</i>	eastern United States
var. <i>mollis</i> Ashe ³	eastern United States
<i>C. ovata</i> (Mill.) K. Koch var. <i>ovata</i>	eastern United States
var. <i>mexicana</i> (Engelm.) Mann. ¹	northeastern Mexico
var. <i>australis</i> (Ashe) Little ³	southeastern United States
var. <i>pubescens</i> Sarg. ³	eastern United States
<i>C. pallida</i> (Ashe) Engl. & Graebn.	eastern United States
<i>C. texana</i> Buckl. var. <i>texana</i>	south-central United States
var. <i>villosa</i> (Sarg.) Little	south-central United States
<i>C. tomentosa</i> Nutt.	eastern United States
Sect. b. <i>Apocarya</i> C. DC.	
<i>C. aquatica</i> (Michx. f.) Laud.	southeastern United States
<i>C. cathayensis</i> Sarg.	southeastern China
<i>C. cordiformis</i> (Wang.) K. Koch	eastern United States
<i>C. illinoensis</i> (Wang.) K. Koch	southeastern United States
<i>C. myristiciformis</i> Nutt.	southeastern United States
<i>C. palmeri</i> Mann. ³	northeastern Mexico
<i>C. poilanei</i> (Chev.) Leroy ³	Laos, Viet Nam
<i>C. tonkinensis</i> Lecomte	northeastern India, southern China, Viet Nam
Sect. c. <i>Rhamphocarya</i> (Kuang) Mann. & Hjelmq.	
<i>C. sinensis</i> Dode ²	southeastern China, Viet Nam

Changes in names:

¹ Former species reduced to variety.
² Different specific name replacing former one or specific name removed to different genus.
³ New species, subspecies, or variety described, or different name added.
⁴ New species, but probably not a good species—hybrid?

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<https://doi.org/10.2307/2398782>.

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