ISSN 0031-0301, Paleontological Journal, 2007, Vol. 41, No. 11, pp. 1040–1053. © Pleiades Publishing, Ltd., 2007.

Fossil Wood of the Juglandaceae: Some Questions of Taxonomy, Evolution, and Phylogeny in the Family Based on Wood Anatomy

N. I. Blokhina

Institute of Biology and Soil Science, Far East Division, Russian Academy of Sciences, pr. Stoletiya Vladivostoka 159, Vladivostok, 690022 Russia

e-mail: blokhina@ibss.dvo.ru

Received December 5, 2006

Abstract—Some problems in the taxonomy of the Juglandaceae are discussed based on wood anatomy; the identification of fossil juglandaceous wood is considered. Data on fossil wood of the Juglandaceae are summarized; a key for identification of wood anatomy in modern and fossil Juglandaceae is compiled. Wood anatomical characters in members of the family are discussed in the light of major evolutionary trends in the secondary xylem of dicots, and a comparative characterization of members of the family is developed. A hypothesis is proposed that the subfamily Engelhardioideae is the most primitive member of the Juglandaceae based on wood anatomy, the tribe Juglandeae and subfamily Platycaryoideae are slightly more highly specialized, and the tribe Hicorieae is the most advanced. Evolutionary relationships between the members of the Juglandaceae are reviewed based on wood anatomy.

DOI: 10.1134/S0031030107110032

Key words: fossil Juglandaceae, wood anatomy.

INTRODUCTION

Fossil wood showing anatomical characteristics of the Juglandaceae A. Rich. ex Kunth were described as *Juglandinium* Unger, *Juglandoxylon* Kraus, *Pterocaryoxylon* Müller-Stoll et Mädel, *Caryojuglandoxylon* Müller-Stoll et Mädel, *Eucaryoxylon* Müller-Stoll et Mädel emend. Dupéron, *Engelhardioxylon* Manchester, *Rhysocaryoxylon* Dupéron, *Manchesteroxylon* Wheeler et Landon, and *Clarnoxylon* Manchester et Wheeler.

Wood remains earlier described as *Annonoxylon gümbelii* (Felix) Boureau (=*Eucaryoxylon guembelii* (Felix) Müller-Stoll et Mädel-Angeliewa), *Liquidambaroxylon speciosum* Felix (=*Pterocaryoxylon pannonocum* Müller-Stoll et Mädel), *Laurinoxylon chinense* Francini (=*Pterocaryoxylon chinense* (Francini) Müller-Stoll et Mädel) (Müller-Stoll and Mädel-Angeliewa, 1983), and *L. branneri* Knowlton (=*Engelhardioxylon texana* Manchester (Manchester, 1983) also belong to the Juglandaceae. However, *Mirbellites lesbius* Unger, *M. schuchii* Unger, *Jugloxylon hamaoanum* Stopes et Fujii, and *Caryoxylon* sp. do not belong to the Juglandaceae. *Juglandinium zuriense* (Falqui) Edwards (=*Juglansoxylon zuriensis* Falqui) are assigned to the Sterculiaceae (DC.) Bartl.; and *Juglandoxylon princes* (Ludwig) Müller-Stoll belong to the Actinidiaceae Hutch. (Dupéron, 1988). Dupéron (1988) was unable to reliably assign *Juglandinium longiradiatum* Vater, *J. mediterraneum* Unger, *J. wichmanni* (H. Hofmann) Edwards (=*Juglandoxylon wichmanni* H. Hofmann), *Juglandoxylon mediterraneum* Kraus, and *J. schadleri* E. Hofmann to the Juglandaceae due to the brevity of the anatomical descriptions and the absence of photographs.

The precise identification of fossil wood depends both on the preservation of the fossil remains and the available information about the wood anatomy of modern members of a given group, as well as the possibility of differentiating between modern members on the basis of wood anatomy. Both fossil and modern genera of Juglandaceae are often hard to differentiate by wood anatomy. The wood anatomy in members of the Juglandaceae was studied by Kribs (1927), Heimsch and Wetmore (1939), Müller-Stol and Mädel (1960), Miller (1976a, 1976b), Manchester (1983, 1987), Müller-Stoll and Mädel-Angeliewa (1983), Dupéron (1988), Manchester and Wheeler (1993), and others. Müller-Stoll and Mädel (1960), Müller-Stoll and Mädel-Angeliewa (1983), Dupéron (1988) revised fossil wood of the Juglandaceae. However, additional material has since become available (Gottwald, 1992; Wheeler and Landon, 1992; Blokhina et al., 2002; Iamandei and Iamandei, 2002, 2003; Wheeler and Manchester, 2002). The present paper summarizes data on the wood anatomy of fossil Juglandaceae and considers some aspects of the evolution and evolutionary relationships between members of the Juglandaceae on the basis of wood anatomy.

WOOD ANATOMY OF MODERN MEMBERS OF THE JUGLANDACEAE

According to Iljinskaja (1990; *Fossil*…, 1994), the Juglandaceae includes ten modern genera of three subfamilies: Platycaryoideae Mann. (*Platycarya* Siebold et Zucc.), Engelhardioideae (Mann.) Iljinskaja (*Engelhardia* Lesch. ex Blume, *Oreomunnea* Oest., *Alfaroa* Standl., and *Alfaropsis* Iljinskaja), and Juglandoideae Leroy. The latter subfamily consists of the tribes Juglandeae Nakai with the genera *Juglans* L., *Pterocarya* Kunth, and *Cyclocarya* Iljinskaja (Manning (1978) considers *Cyclocarya* as the subgenus *Cyclocarya* (Iljinskaja) Mann. of the genus *Pterocarya*) and Hicorieae Mann. with the genus *Carya* Nutt. (= *Hicoria*). The genus *Alfaropsis* was established by Iljinskaja on the basis of *Engelhardia roxburghiana* Wall. (synonyms: *E. wallichiana* Lindl. ex DC., *E. chrysolepis* Hance, *E. fenzelii* Merr., and *E. formosana* Hayata) of the monotypic section Psilocarpeae Nagel emend. Leroy.

Twelve extinct genera represented by fruit remains are assigned to the Juglandaceae: *Pterocaryopsis* Chandler, *Paleoplatycarya* Manchester, *Hooleya* Reid et Chandler, *Juglandicarya* Reid et Chandler, *Sphaerocarya* Dorofeev, *Polyptera* Manchester et Dilcher (Iljinskaja, 1990), *Paleocarya* Saporta, *Paleooreomunnea* Dilcher, Potter et Crepet, *Paraengelhardtia* Berry (Manchester, 1987; Iljinskaja, 1990; Stone, 1993), *Casholdia* Crane et Manchester (Manchester, 1987), *Cruciptera* Manchester (Manchester, 1991), and *Amurcarya* Kodrul et Krassilov (Kodrul and Krassilov, 2006).

The main diagnostic characters of juglandaceous wood are as follows: diffuse-porous to ring-porous wood; vessels are solitary or arranged in radial multiples of 2–4(6) vessels, vessel diameter is moderate (100–200 μm, in *Carya* occasionally up to 246 μm); perforation plates are simple, occasionally scalariform; intervessel pits are alternate, large (6–10(12) μm in diameter); axial parenchyma is arranged in narrow undulate or straight tangential bands 1–3(4) cells wide or, more rarely, vasicentric; ray are homocellular to indistinctly heterocellular, uni–penta(hepta)seriate, aggregate rays are lacking (Kribs, 1927; Heimsch and Wetmore, 1939; Hammerman et al., 1946; Metcalfe and Chalk, 1950; Vikhrov, 1959; Müller-Stoll and Mädel, 1960; Miller, 1976a, 1976b; Müller-Stoll and Mädel-Angeliewa, 1983; Manchester, 1983, 1987; Voroshilova and Snezhkova, 1984; Dupéron, 1988; *Atlas*…, 1992; etc.).

Main diagnostic features differentiating between subfamilies and tribes of the family are the type of the pith, perforation plates, and vessel arrangement and the presence of vasicentric (vascular) tracheids, helical thickenings, and crystals. However, Manchester and Wheeler (1993) believed that the main differentiating features are the morphology of the pith and perforation plates. Table 1 shows the main diagnostic features of the comparative wood anatomy of modern Juglandaceae.

Subfamily Platycaryoideae

The wood of the only modern member of the Platycaryoideae, the monotypic genus *Platycarya*, differs from all other members of the Juglandaceae in the presence of vascular tracheids and helical thickenings (Table 1); the thickenings are situated on the walls of both vascular tracheids and narrow vessels (Metcalfe and Chalk, 1950).

Subfamily Engelhardioideae

The main diagnostic character of the wood of modern members of the Engelhardioideae is the presence of both simple and scalariform perforation plates (Table 1). However, scalariform perforation plates are only situated in narrow vessels and usually occur much more rarely than simple perforation plates (Kribs, 1927). Manchester (1983) pointed out that it is sometimes necessary to screen several growth rings or sections to find this character. The absence of crystals is also a character of the subfamily, although Kribs (1927), Heimsch and Wetmore (1939), and Müller-Stoll and Mädel (1960) recorded occasional crystals in the axial and/or ray parenchyma.

Modern genera of the Engelhardioideae are virtually indistinguishable based on their wood anatomy, although attempts at differentiation have been made. Thus, Kribs (1927) proposed to use the ratio between simple and scalariform perforation plates, the number of bars in the scalariform perforation plates, and the presence of crystals in axial or ray parenchyma as diagnostic features. Heimsch and Wetmore (1939) considered as diagnostic features the thickness of vessel walls, solitary vessel outlines, and the ratio between solitary vessels and groups of vessels. Manchester (1983) studied nearly all species of the subfamily, but found no reliable criteria for generic differentiation. He concluded that since the above-mentioned characters all strongly vary within each genus, they cannot be diagnostic above the species level. However, he neither traced the ecological variability nor provided descriptions of the wood anatomy of the species studied; this information is still lacking.

Subfamily Juglandoideae

The wood of modern members of the tribe Juglandeae (genera *Juglans*, *Pterocarya*, and *Cyclocarya*) differs from that of the Hicorieae as well as other Juglandaceae in the presence of septate pith and in having crystals only in axial parenchyma (Table 1). However, it is very difficult to differentiate between *Juglans*, *Pterocarya*, and *Cyclocarya* based on wood anatomy. Müller-Stoll and Mädel (1960) thought that the width of rays could be used as a feature differentiating *Pterocarya* from *Juglans*. Unfortunately, so far there is not sufficient data to show that triseriate rays, so typical of *Juglans*, are completely lacking in *Pterocarya*.

Table 1. Comparative wood anatomy of modern and fossil members of the Juglandaceae by main diagnostic features

Modern taxa	Pith		Perforation plates		Porosity			Vessel walls		Helical thicken-ings	Crystals in parenchyma		Vascular tracheids
	hard	septate	scalari-form	simple	diffuse-porous wood	semi-ring-porous wood	ring-porous wood	thin	thick		axial	ray	
Platycaryoideae Mann.	+	–	–	+	–	–	+	+	–	+	–	+	+
Engelhardioideae (Mann.) Iljinskaja	+	–	+	+	+	+–	–	+	–	–	–	–	–
Juglandoideae Leroy	+–	+–	–	+	+–	+––	+–	+–	+–	–	+	+––	–
Juglandeae Nakai	–	+	–	+	+	+–	–	+	–	–	+	–	–
Hicorieae Mann.	+	–	–	+	–	+	+	–	+	–	+	+–	–
Fossil taxa													
Pterocaryoxylon Müller-Stoll et Mādel	?	?	–	+	+	+–	–	+	–	–	+	–	–
Eucaryoxylon Müller-Stoll et Mādel	?	?	–	+	+––	+–	+	–	+	–	+	–	–
Rhysocaryoxylon Dupéron	?	?	–	+	+–	+	–	–	+	–	+	–	–
Engelhardioxylon Manchester	+	–	+	+	+	+–	–	+	–	–	–	–	–
Manchesteroxylon Wheeler et Landon	?	?	+	+	–	+	+–	?	?	–	–	–	+
Clarnoxylon Manchester et Wheele	+	–	–	+	+	+–	–	?	?	–	–	+	–

Note: (+) character is present, (–) character is absent, (+–) character is occasionally present, (+––) character occurs very rarely, (?) no data.

Although the only modern member of the tribe Hicorieae, *Carya* (=*Hicoria*), is characterized by semi-ring-porous to distinctly ring-porous vessels, in some species differences between early- and latewood vessels are not very prominent, and the wood in these species appears as transitional from semi-ring-porous to diffuse-porous (Müller-Stoll and Mädel, 1960; Manchester and Wheeler, 1993).

FOSSIL WOOD OF THE JUGLANDACEAE

Fossil wood remains of the Juglandaceae are ascribed to the genera *Juglandinium*, *Juglandoxylon*, *Pterocaryoxylon*, *Caryojuglandoxylon*, *Eucaryoxylon, Engelhardioxylon*, *Rhysocaryoxylon*, *Manchesteroxylon*, and *Clarnoxylon*.

The formal genus *Juglandinium* was erected by Unger (1845) to describe fossil juglandaceaeous wood with anatomical characters of modern *Juglans*. Kraus (1882) proposed the formal genus *Juglandoxylon* for fossil wood sharing characters of *Juglans* and *Pterocarya*, because of difficulties in differentiation between these two genera. Later, both generic names were used to describe fossil wood of members of the tribe Juglandeae as well of the whole family Juglandaceae. Müller-Stoll and Mädel (1960) accomplished an analysis of wood anatomy of modern Juglandaceae and proposed to substitute *Juglandinium* and *Juglandoxylon* with three new formal genera, *Pterocaryoxylon*, *Caryojuglandoxylon*, and *Eucaryoxylon*, describing fossil juglandaceous wood.

Pterocaryoxylon was erected for fossil wood with the anatomy of modern members of the Juglandeae, in particular, *Pterocarya* (all species), *Cyclocarya* and *Juglans* (species with thin-walled vessels and libriform fibres, short strands of axial parenchyma, and prevailing uniseriate rays). The main diagnostic features of *Pterocaryoxylon* are given in Table 1. In addition, in *Pterocaryoxylon* vessels are solitary or in radial multiples of two to four, libriform fibres are thin-walled, apotracheal parenchyma is in short tangential bands one cell wide, and rays are uni–tri(tetra)seriate homocellular to slightly heterocellular (Müller-Stoll and Mädel, 1960).

Caryojuglandoxylon was proposed to describe fossil wood of the subfamily Juglandoideae with anatomical characters of *Juglans* (species with thick-walled vessels, uni-bi-(tetra)seriate rays, and long strands of constantly occurring axial parenchyma) and *Carya* (species with semi-ring-porous to diffuse-porous wood). To summarize, the diagnostic characters of *Caryojuglandoxylon* are semi-ring-porous to diffuse-porous wood, thick-walled vessels, uni–tri-(penta)seriate homocellular to slightly heterocellular rays, and crystals in axial parenchyma (Müller-Stoll and Mädel, 1960).

Eucaryoxylon was established for fossil wood of the Juglandaceae showing the anatomy of the modern genus *Carya* (most American species with distinctly ring-porous wood). The main diagnostic features of *Eucaryoxylon* are given in Table 1. In addition, *Eucaryoxylon* is characterized by uni-tri-(penta)seriate homocellular to slightly heterocellular rays (Müller-Stoll and Mädel, 1960). Dupéron (1988), who revised fossil wood of the Juglandaceae, supplemented the diagnosis of *Eucaryoxylon* with the inclusion of fossil wood showing the anatomy of species of *Carya* with semi-ring-porous to slightly diffuse-porous wood and sank the genus *Caryojuglandoxylon*.

The formal genus *Rhysocaryoxylon* was proposed by Dupéron (1988) and includes fossil wood with anatomical characteristics of modern *Juglans*. The main diagnostic characters of *Rhysocaryoxylon* are listed in Table 1. In addition, in *Rhysocaryoxylon*, vessels are solitary or in radial multiples, vessel-ray and vessel-parenchyma pits with significantly reduced borders and large apertures, apotracheal parenchyma is in bands 1–2(4) cells wide, and rays are uni-tri-(penta)seriate homocellular to slightly heterocellular (Dupéron, 1988).

Engelhardioxylon (Table 1) was proposed by Manchester (1983) for fossil wood of the Juglandaceae with the anatomy of modern members of the tribe Engelhardioideae. *Engelhardioxylon mameticum* Blokh. et Snezhk. from the Oligocene of the northwestern Kamchatka Peninsula is the first find of fossil wood of the Engelhardioideae in Russia, and the first find of fossil juglandaceous wood in the Russian Far East (Blokhina et al., 2002).

Wheeler and Landon (1992) established the formal genus *Manchesteroxylon*, which is characterized by a combination of features that is unknown in modern Juglandaceae (Table 1). It shows some wood characters of the Engelhardioideae (simple and scalariform perforation plates) and Platycaryoideae (vascular tracheids, trend to ring-porosity with diagonal arrangement of vessels); however, helical thickenings and crystals, typical of the Platycaryoideae, are lacking. Unfortunately, the pith was not preserved in specimens of *Manchesteroxylon*.

The formal genus *Clarnoxylon*, which was established by Manchester and Wheeler (1993), is characterized by the presence of exclusively simple perforation plates and hard (non-septate) pith; these anatomical features are typical of the modern genera *Platycarya* and *Carya* (Table 1). Manchester and Wheeler (1993) found no characters separating *Clarnoxylon* in an independent tribe or subfamily and proposed to place this genus either in the subfamily Platycaryoideae or in the tribe Hicorieae (Juglandoideae), pointing out a slightly greater similarity to the Platycaryoideae. It resembles *Platycarya* in the presence of crystals only in ray parenchyma; in addition, *Carya* has very thick walls of latewood vessels. However, *Clarnoxylon* lacks ring-porosity, vascular tracheids, and helical thickenings (diagnostic features of *Platycarya*), and has long vessel segments unlike short vessels of *Platycarya*. By vessel arrangement, *Clarnoxylon* differs from both *Platycarya*

Table 2. Fossil woods of the Juglandaceae

Number	Taxon	Basionym	Geological age
	Juglandinium Unger		
1	*Juglandinium tasseewii* Nastschokin (Nastschokin, 1960)		Oligocene
	Pterocaryoxylon Müller Stoll et Mädel, 1960		
2	*Pt. knowltonii* Wheeler, Scott et Barghoorn (Wheeler et al., 1978)		Middle Eocene
3	*Pt. honshouense* Müller-Stoll et Mädel (Müller-Stoll and Mädel, 1960)		Miocene
4	*Pterocaryoxylon* sp. (cited after Dupéron, 1988)		Miocene
5	*Pt. subpannonicum* Privé (Privé, 1974)		Early Pliocene
6	*Pt. pannonicum* Müller-Stoll et Mädel (Müller-Stoll and Mädel, 1960)		Early Pliocene
7	*Pt. chinense* (Francini) Müller-Stoll et Mädel (Müller-Stoll and Mädel, 1960)		Tertiary
	Eucaryoxylon Müller-Stoll et Mädel, 1960 emend. Dupéron, 1988		
8	*Eu. boureaui* Dupéron (cited after Dupéron, 1988)		Late Oligocene
9	*Eucaryoxylon* sp. 1 (cited after Dupéron, 1988)		Miocene
10	*Eu. budense* Greguss (Greguss, 1969)		Miocene
11	*Eu. crystallophorum* Müller-Stoll et Mädel (Müller-Stoll and Mädel, 1960)		Miocene
12	*Eu. protojaponicum* (Watari) Müller-Stoll et Mädel (Müller-Stoll and Mädel, 1960)		Miocene
13	*Eu. zarandense* S. Iamandei et Eu. Iamandei (S. Iamandei and Eu. Iamandei, 2002)		Middle Miocene
14	*Eucaryoxylon* sp. 2 (cited after Dupéron, 1988)		Pliocene
15	*Eu. moenanum* Müller-Stoll et Mädel-Angeliewa (Müller-Stoll and Mädel-Angeliewa, 1983)		Late Pliocene
16	*Eu. guembelii* (Felix) Müller-Stoll et Mädel-Angeliewa (Müller-Stoll and Mädel-Angeliewa, 1983)		Tertiary
	Rhysocaryoxylon Dupéron, 1988		
17	*Rh. caucasicum* (Gaivoronsky) Dupéron (Dupéron, 1988)	*Juglandinium caucasicum* Gaivoronsky, 1962	Oligocene
18	*Rh.* aff. *schenkii* (Felix) Dupéron (Dupéron, 1988)		Late Oligocene
19	*Rh. fryxellii* (Prakash et Barghoor) Dupéron (Dupéron, 1988)	*Juglans fryxellii* Prakash et Barghoor, 1961; *Caryojuglandoxylon fryxellii* (Prakash et Barghoor) Müller-Stoll et Mädel-Angeliewa, 1983 (Dupéron, 1988)	Miocene
20	*Rh. tertiarum* (Prakash et Barghoor) Dupéron (Dupéron, 1988)	*Carya tertiara* Prakash et Barghoor, 1961; *Caryojuglandoxylon tertiarum* (Prakash et Barghoor) Müller-Stoll et Mädel-Angeliewa, 1983 (Dupéron, 1988)	Miocene
21	*Rh. pilinyense* (Greguss) Dupéron (Dupéron, 1988)	*Pterocaryoxylon pilinyense* Greguss, 1969 (Dupéron, 1988)	Miocene
22	*Rhysocaryoxylon* sp. 1 (Dupéron, 1988)	*Pterocaryoxylon pannonicum* Müller-Stoll et Mädel in Greguss, 1969 (Dupéron, 1988)	Miocene

Table 2. (Contd.)

Number	Taxon	Basionym	Geological age
23	*Rhysocaryoxylon* sp. 2 (Dupéron, 1988)	*Pterocaryoxylon sf. pannonicum* Müller-Stoll et Mädel in Greguss, 1969 (Dupéron, 1988)	Miocene
24	*Rh. pravalense* S. Iamandei et Eu. Iamandei (S. Iamandei and Eu. Iamandei, 2002)		Middle Miocene
25	*Rh. ocii* S. Iamandei et Eu. Iamandei (S. Iamandei and Eu. Iamandei, 2002)		Middle Miocene
26	*Rh. transylvanicum* S. Iamandei et Eu. Iamandei (S. Iamandei, Eu. Iamandei, 2003)		Middle Miocene
27	*Rh. schenkii* (Felix) Dupéron (Dupéron, 1988)	*Juglandinium schenkii* Felix, 1884; *Caryojuglandoxylon schenkii* (Felix) Müller-Stoll et Mädel, 1960 (Dupéron, 1988)	Tertiary
28	*Rh. triebelii* (Caspary) Dupéron (Dupéron, 1988)	*Juglans triebelii* Caspary, 1887; *Caryojuglandoxylon triebelii* (Caspary) Müller-Stoll et Mädel, 1960 (Dupéron, 1988)	Tertiary
	Engelhardioxylon Manchester, 1983		
29	*E. nutbedensis* Manchester (Manchester, 1983; Wheeler and Manchester, 2002)		Middle Eocene
30	*E. texana* Manchester (Manchester, 1983)		Middle Eocene
31	*E. macrocrystallosum* Gottwald (Gottwald, 1992)		Late Eocene
32	*E. mameticum* Blokh. et Snezhk. (Blokhina et al., 2002)		Oligocene
	Manchesteroxylon Wheeler et Landon, 1992		
33	*M. intermedium* Wheeler et Landon (Wheeler and Landon, 1992)		Late Eocene
	Clarnoxylon Manchester et Wheeler, 1993		
34	*Cl. blanchardii* Manchester et Wheeler (Manchester and Wheeler, 1993; Wheeler and Manchester, 2002)		Middle Eocene

and *Carya* and resembles members of the tribe Juglandeae (Juglandoideae) and subfamily Engelhardioideae (Table 1). However, the Juglandeae has septate pith and crystals in axial parenchyma, and the Engelhardioideae is characterized by scalariform perforation plates (Table 1). *Clarnoxylon*, similarly to *Manchesteroxylon*, shows a combination of anatomical characters that is unknown in the wood of modern Juglandaceae.

To summarize, the taxonomic diversity of fossil wood of the Juglandaceae described to date, taking into account the revision by Dupéron (1988), comprises 34 species of seven formal genera: *Juglandinium*, Pterocaryoxylon, Eucaryoxylon, Engelhardioxylon, Rhysocaryoxylon, *Manchesteroxylon*, and *Clarnoxylon* (Table 2).

KEY FOR IDENTIFICATION OF MODERN AND FOSSIL MEMBERS OF THE FAMILY JUGLANDACEAE BASED ON WOOD ANATOMY

1. Only simple perforation plates present...........2

Simple and scalariform perforation plates present...7

2. Vascular tracheids present...........Platycaryoideae

Vascular tracheids lacking.............................3

3. Wood ring-porous..................................4

Wood diffuse-porous or semi-ring-porous...........5

4. Wood up to semi-ring-porous, vessels thick-walled, crystals occur in axial and ray parenchyma..Hicorieae

Wood up to semi-ring-porous, occasionally up to diffuse-porous, vessels are thick-walled, crystals occur in axial parenchyma.........................*Eucaryoxylon*

5. Crystals present only in ray parenchyma..*Clarnoxylon*

Crystals present only in axial parenchyma...........6

6. Vessels thick-walled..............*Rhysocaryoxylon*

Vessels thin-walled......Juglandeae, *Pterocaryoxylon*

7. Vascular tracheids present.........*Manchesteroxylon*

Vascular tracheids lacking...Engelhardioideae, *Engelhardioxylon*

Table 3. Main trends in specialization of anatomical characters in secondary xylem of dicots

Anatomical characters	Primitive	Advanced
Size (diameter) of vessel segments	Small	Large
Length of vessel segments	Long	Short
Transverse outlines of vessels	Angular	Rounded
Thickness of walls of vessel segments	Thin	Thick
Perforation plates	Scalariform	Simple
Inclination of the terminal wall of vessel segment	Oblique	Right
Number of bars in scalariform perforation plate	Numerous	Not numerous
Ratio between simple and scalariform perforation plates	Scalariform perforation plates prevail	Simple perforation plates prevail
Intervessel pits	Scalariform	Alternate
Growth ring boundaries	Indistinct	Distinct
Porosity	Diffuse-porous wood	Ring-porous wood
Vessel grouping	Solitary	In multiples, clusters (groups), or arranged in pattern
Ratio between solitary and grouped vessels	Solitary vessels prevail	Grouped vessels prevail
tracheids and fibres	Vascular tracheids	Libriform fibres
Thickness of walls of vascular tracheids	Thin-walled	Thick-walled
Size (diameter) of bordered pits in walls of vascular tracheids	Large	Small
Vascular tracheids	Present	Absent
Helical thickenings	Present	Absent
Rays	Heterocellular	Homocellular
Ray width	Uniseriate	Multiseriate
Multiseriate rays	Narrow	Broad

EVOLUTIONARY RELATIONSHIPS BETWEEN MEMBERS OF THE JUGLANDACEAE ON THE BASIS OF WOOD ANATOMY

The code of primitive and advanced characters in wood anatomy of angiosperms was developed by Bailey (1920, 1953, 1957) and his followers Frost (1930), Kribs (1935, 1937), and Tippo (1946) and significantly supplemented by Yatsenko-Khmelevskii (Yatsenko-Khmelevskii, 1954; Yatsenko-Khmelevskii and Gzyryan, 1954; etc.), Kedrov (1967, 1971, etc.), and other Russian scientists. The main evolutionary trends in the secondary xylem of dicots were discussed by Calquist (1988), Wheele and Baas (1991), Baas and Wheeler (1996), Herendeen (1996), Herendeen et al. (1999), etc. Some problems of the evolution of wood anatomy of the Juglandaceae were considered by Heimsch and Wetmore (1939).

As far as the specialization of water-conductive tissue is directed to more effective and reliable water conduction, during the evolution of mature secondary xylem of dicots, vessel segments increased in diameter and diminished in length, their walls thickened, and the section of vessels became more and more rounded. Scalariform perforation plates with numerous bars were moved from lateral to terminal walls of vessel segments, individual borders reduced, and the number of bars diminished up to formation of simple perforations, situated at a right angle to the vessel length (Bailey, 1920; Frost, 1930a, 1930b; Tippo, 1946; Yatsenko-Khmelevskii, 1954; Kedrov, 1967; Calquist, 1984, 1988; Chavchavadze and Sizorenko, 2002; etc.).

The evolution of vessel segments was accompanied by changes of their distribution within a growth ring: from diffuse-porous to semi-ring-porous and ring-porous types (Yatsenko-Khmelevskii, 1954; Calquist, 1984; Chavchavadze and Sizorenko, 2002; etc.). Diffuse-porous wood is most primitive; wood with vessels arranged in bands, groups, or patterns is more specialized. The ring-porous type represents a side branch of specialization (Yatsenko-Khmelevskii, 1954).

During the evolution of secondary xylem, its elements differentiated into water-conducting and mechanical. The specialization of fibre elements, namely, the appearance of fibre-tracheids and libriform fibres, was accompanied by thickening of walls of unperforated elements and diminishing of the number and size of their pits (Bailey, 1953; Yatsenko-Khmelevskii, 1954; Calquist, 1988; Chavchavadze and Sizonenko, 2002; etc.). Yatsenko-Khmelevskii (1954) considered the appear-

Table 4. Comparative-anatomical lines (morphoclines) in members of the Juglandaceae

By the diameter of vessel segments:
Alfaroa ⟶ Pterocarya ⟶ Engelhardia ⟶ Platycarya ⟶ Juglans ⟶ Carya
By the length of vessel segments:
Alfaroa ⟶ Engelhardia ⟶ Pterocarya ⟶ Juglans ⟶ Carya ⟶ Platycarya
By solitary vessel outlines:
Alfaroa ⟶ Engelhardia ⟶ Pterocarya ⟶ Juglans ⟶ Carya, Platycarya
By the thickness of walls of vessel segments:
Alfaroa ⟶ Engelhardia, Pterocarya, Juglans ⟶ Platycarya ⟶ Carya
By the inclination of the terminal wall of vessel segment:
Alfaroa ⟶ Pterocarya ⟶ Engelhardia ⟶ Juglans ⟶ Platycarya ⟶ Carya
By the type of perforation plates:
Alfaroa ⟶ Engelhardia ⟶ Platycarya, Pterocarya, Juglans, Carya
By the porosity:
Alfaroa ⟶ Engelhardia ⟶ Pterocarya, Juglans ⟶ Carya ⟶ Platycarya
By the type of fibers:
Alfaroa ⟶ Pterocarya ⟶ Engelhardia ⟶ Juglans, Platycarya ⟶ Carya
By the length of fibres:
Alfaroa ⟶ Pterocarya ⟶ Platycarya ⟶ Engelhardia ⟶ Juglans ⟶ Carya
By the presence of vascular tracheids:
Platycarya ⟶ Alfaroa, Engelhardia, Pterocarya, Juglans, Carya
By the presence of tertiary thickenings:
Platycarya, Juglans ⟶ Alfaroa, Engelhardia, Pterocarya, Carya
By the type of rays:
Alfaroa ⟶ Engelhardia ⟶ Platycarya ⟶ Juglans ⟶ Carya ⟶ Pterocarya
By the maximal width of rays:
Alfaroa ⟶ Pterocarya ⟶ Engelhardia ⟶ Juglans ⟶ Platycarya

ance of vasicentric (vascular) tracheids, which differ from segments of small vessels in the absence of perforations, as a lateral evolutionary branch. Similarly to vessels, vascular tracheids also serve for water-conduction; this function is considerably reduced or completely absent in fibre-tracheids and libriform fibres. The appearance of tertiary helical or reticulate thickenings on the surface of the secondary wall is considered as a lateral line in the specialization of water-conducting elements; however, so far the function of these thickenings has not been definitely revealed (Yatsenko-Khmelevskii, 1954; Chavchavadze and Sizonenko, 2002; etc.).

The ray parenchyma of the secondary xylem stores and transports nutrients in a radial direction. Therefore, the rays evolved from the heterocellular to the homocellular type, the latter is related to the increased radial diameter of the stem and the necessity to transport nutrients from the center to the periphery for a long distance (Kribs, 1935; Yatsenko-Khmelevskii, 1954; Kedrov, 1967; Chavchavadze and Sizonenko, 2002; etc.).

Taking into consideration the main evolutionary trends in the secondary xylem of dicots and primitive and advanced states of anatomical characters (Table 3), modern genera of the Juglandaceae are arranged in comparative-anatomical lines (morphoclines), dependent on the directed change of a given character (Table 4). Constructing the morphoclines, we used the descriptions of wood anatomy from the works cited at the beginning of the present paper. Modern juglandaceous genera are arranged in morphoclines based on the following characters: diameter of vessel segments, length of vessel segments, solitary vessel outlines, wall thickness in vessel segments, inclination of the terminal wall of vessel segment, type of porosity, type of fibre-tracheids, length of fibres, presence of vascular tracheids, presence of tertiary thickenings, type of rays, and the maximal thickness of rays.

The diameter of vessel segments (μm): *Alfaroa* (100), *Pterocarya* (140), *Engelhardia* (146), *Platycarya* (193), *Juglans* (207), and *Carya* (246).

The length of vessel segments (μm): *Alfaroa* (901), *Engelhardia* (806), *Pterocarya* (612), *Juglans* (592), *Carya* (496), and *Platycarya* (493).

Solitary vessel outlines: *Alfaroa* (predominantly angular), *Engelhardia* (angular outlines are less numerous than in *Alfaroa*), *Pterocarya* and, more rarely, *Juglans* (weakly angular in grouped vessels), and *Carya* and *Platycarya* (weakly angular in small vessels in latewood).

The walls of vessel segments: *Alfaroa* (thinnest), *Engelhardia*, *Pterocarya*, and *Juglans* (thin), *Platycarya* (thickened), and *Carya* (thick).

The inclination of the terminal wall of vessel segment: *Alfaroa* (45°), *Pterocarya* (47°), *Engelhardia* (48°), *Juglans* (58°), *Platycarya* (65°), and *Carya* (69°–90°).

Perforation plates: *Alfaroa* (the maximal percentage of scalariform perforation plates and the maximal number of bars per perforation plate), *Engelhardia* (scalariform perforation plates occur predominantly in narrow vessels), and *Platycarya, Pterocarya*, *Juglans*, and *Carya* (exclusively simple perforation plates).

Porosity: *Alfaroa* (distinctly diffuse-porous, solitary vessels prevail), *Engelhardia* (diffuse-porous to semi-ring-porous, the ratio between solitary and grouped vessels is nearly equal), *Pterocarya* and *Juglans* (diffuse-porous to semi-ring-porous), *Carya* (ring-porous), and *Platycarya* (ring porous, small vessels in flamelike pattern).

The type of fibre-tracheids: *Alfaroa* (thin-walled with relatively large bordered pits), *Pterocarya* (thin-walled with relatively large bordered pits, a band of thick-walled fibre-tracheids at the end of each growth ring), *Engelhardia* (with slightly thickened walls and small bordered pits), *Juglans* and *Platycarya* (with thin and slightly thickened walls and distinctly bordered pits, narrow bands of thick-walled elements at the end of each growth ring), and *Carya* (with thin and slightly thickened walls and very small and occasionally indistinct bordered pits).

The length of fibres (μm): *Alfaroa* (1.333), *Pterocarya* (1.339), *Platycarya* (1.479), *Engelhardia* (1.481), *Juglans* (1.503), and *Carya* (1.516).

Vascular tracheids: *Platycarya* (especially numerous in latewood, in combination with small vessels form flamelike patterns) and *Alfaroa*, *Engelhardia*, *Pterocarya, Juglans*, and *Carya* (completely lacking).

Tertiary thickenings: *Platycarya* (helical thickenings on walls of narrow vessels and vascular tracheids) and *Juglans* (reticulate thickenings on walls of narrow vessels in latewood of *J. nigra* L., *J. major* (Torr.) Heller, *J. microcarpa* Berlander, and *J. californica* S. Wats., including *J. hindsii* (Jeps.) Rehder (section *Rhrysocaryon* Dode), visible only in SEM), and *Alfaroa*, *Engelhardia*, *Pterocarya*, and *Carya* (thickenings lacking).

The type of rays: *Alfaroa* and *Engelhardia* (heterocellular), *Platycarya* (weakly heterocellular), *Juglans* (predominantly homocellular, with a trend to heterocellular, which is occasionally relatively distinct), *Carya* (predominantly homocellular with a trend to heterocellular), and *Pterocarya* (homocellular).

The maximal thickness of rays: *Alfaroa* (uniseriate rays with biseriate regions), *Pterocarya* (biseriate rays, occasionally tri- or tetraseriate rays), *Engelhardia* (tri- or tetraseriate rays), *Carya* (tri- to pentaseriate rays), *Juglans* (penta- or hexaseriate rays), and *Platycarya* (hepta- or octoseriate).

Table 5 shows the comparative characteristics of the subfamilies of the Juglandaceae by the degree of evolutionary primitiveness of the wood's anatomical characters. Summarizing the data on the evolution of wood characters within the family, I infer that the Engelhardioideae is the most primitive subfamily, with *Alfaroa* situated at the beginning of the lineage. The tribe Juglandeae is situated farther (*Juglans* is a more advanced genus in comparison with *Pterocarya*). By several characters, the subfamily Platycaryoideae occupies a more advanced position. The Hicorieae is the most evolutionary advanced tribe based on wood anatomical characters.

However, Heimsch and Wetmore (1939) believed that the Platycaryoideae is the most specialized subfamily within the Juglandaceae. The different conclusions mostly result from different evaluations of the relative evolutionary primitiveness of vascular tracheids with helical thickenings, the presence of those in *Platycarya* was considered by these authors as a highly specialized feature. Wheeler and Landon (1992) also considered vascular tracheids and helical thickenings of *Platycarya* as autapomorphic characters and supposed the secondary origin of vascular tracheids from vessel segments.

The Platycaryoideae is the most advanced subfamily in floral morphology (Manning, 1978), but the most primitive subfamily in the morphology of pollen grains (Bolotnikova, 1975). Thus, the Platycaryoideae is a striking example of heterobathmy in the Juglandaceae.

The comparative-anatomical lines demonstrate unequal rates of specialization in structural elements of secondary xylem of the Juglandaceae (Table 4). The mature xylem of some members shows both primitive and advanced characters. This feature is most distinct in *Platycarya*, in which vascular tracheids and helical thickenings are present, although the wood is relatively highly specialized. Reticulate thickenings are present in several species of *Juglans*, which are a very primitive feature, although the wood is relatively highly specialized. The Oligocene wood *Engelhardioxylon mameticum* has, in comparison with Eocene *Engelhardioxylon*, a higher number of bars (20) in the scalariform perforation plates, a character of a higher degree of primitiveness, but broader (pentaseriate) rays and semi-ring-porous wood, more evolutionary advanced characters (Blokhina et al., 2002; Blokhina and Snezhkova, 2003).

According to Chavchavadze and Sizorenko (2002), the heterochrony of characters increases the ecological flexibility of plants and allows them to occupy various ecological niches. On the other hand, these authors

Table 5. Comparative characteristics of the subfamilies of the Juglandaceae by the degree of primitiveness of their wood anatomical characters

Wood anatomical characters		Platycaryoideae	Engelhardioideae	Juglandoideae	
				Juglandeae	Hicorieae
Primitive	Small diameter of vessel segments	–	+	–	–
	Long vessel segments	–	+	–	–
	Angular solitary vessel outlines	+––	+	+–	+––
	Thin walls of vessel segments	–	+	+	–
	Small inclination of the terminal wall of vessel segment	–	+	+–	–
	Scalariform perforation plates	–	+	–	–
	Intervessel pits are scalariform	–	–	–	–
	Growth rings are not developed	–	–	–	–
	Solitary vessels	+	+	+	+
	Solitary vessels prevail	–	+–	–	–
	Diffuse-porous wood	–	+	+	–
	Vascular tracheids are present	+	–	–	–
	Fibre-tracheids	+	+	+	+
	Fibre tracheids are thin-walled	+	+	+	+
	Bordered pits on walls of vascular tracheids are large	–	+	+–	–
	Helical thickenings are present	+	–	–	–
	Rays are heterocellular	–	+	–	–
	Multiseriate rays are narrow	–	+	–	–
	Mean diameter of vessel segments	+	–	+	–
	Mean length of vessel segments	–	–	+	–
	Thickened walls of vessel segments	+	–	+	–
	Moderate inclination of the terminal wall of vessel segment	+	–	+	+
	Intervessel pits are opposite	–	–	–	–
	Growth rings are weakly developed	–	+	–	–
	Semi-ring-porous wood	–	+–	+–	+
	Fibre-tracheids are thickened	+	+	+–	+
	Bordered pits on walls of vascular tracheids are moderate in size	+	–	+	–
	Rays are weakly heterocellular	+	–	+–	+–
	Multiseriate rays are moderately wide	–	–	+	+
Evolutionary advanced	Large diameter of vessel segments	–	–	–	+
	Short vessel segments	+	–	–	+
	Circular solitary vessel outlines	++	+	+	++
	Thick walls of vessel segments	–	–	+–	+
	Right or narrow right inclination of terminal wall of vessel segment	+–	–	–	+
	Simple perforation plates	+	–	+	+
	Intervessel pits are alternate	+	+	+	+
	Distinct growth rings	+	+	+	+
	Grouped vessels	+	+	+	+
	Vessels are arranged in patterns	++	–	+–	+
	Ring-porous wood	+	–	–	+
	Vascular tracheids are lacking	–	+	+	+
	Fibre-tracheids are thick-walled	+	–	+	–
	Bordered pits on wall of vascular tracheids are small	–	+	–	+
	Libriform fibres				
	Helical thickenings are lacking	–	+	+	+
	Rays are homocellular	–	–	++	+
	Multiseriate rays are wide	+	–	–	–

Note: (+) character is present, (–) character is absent, (++) character prevails, (+–) character is occasionally present, (+––) character occurs very rarely.

believed that the presence in wood of variously specialized characters testifies to physiological necessity rather than to the evolutionary level of the taxon, since complicated structural mechanisms are aimed to stabilize biological processes and enhance coordination relations between water-conductive, storage, and mechanical elements.

Analyzing wood structural diversity, the environmental influence should be taken into account. In particular, specialization of wood in many members of the Juglandaceae was related to inhabiting areas of temperate climate. Some such characters appeared already in tropical members of the family and served as a prerequisite for their development of the temperate zone, where these characters are adaptive. For example, vascular tracheids in many plants, including *Platycarya*, function as an additional conductive system and are adapted to the growth under conditions of periodical water deficit. The presence of vascular tracheids in tropical plants may be considered as a preadaptation to their spreading in temperate areas.

Helical thickenings (on walls of narrow vessels and vascular tracheids in *Platycarya*) possibly increase hydration of walls of vessels and vascular tracheids, improve water conduction, impart a rotatory movement to the water current, or strengthen the walls of these elements. It is believed that they occur more often in plants growing under temperate and arid conditions than in the tropics. It is conceivable that the presence of helical thickenings is one more preadaptation to the conditions of temperate areas. Apparently, analogous conclusions can be drawn about the presence of reticulate thickenings on walls of narrow vessels in latewood of some species of *Rhrysocaryon* (*Juglans*).

If vascular tracheids are lacking, contacts between vessels become more important. Such contacts are maintained by grouping of vessels and increased number of vessels in multiples and groups, providing additional routes of water transport in case of gas embolism in some vessels if the plants grow under conditions of drought or water deficit (Carlquist, 1984). Therefore, I can suppose that semi-ring-porous wood only occurs in deciduous trees of *Engelhardia*, growing under conditions of a monsoon climate, with a hot summer with abundant precipitation and a relatively dry cooler winter, and that it is restricted only to narrow growth rings. Unfortunately, studies of ecological wood anatomy of modern Engelhardioideae are virtually lacking. Ring-porous wood characterizes arborescent species of only temperate areas.

The adding of simple perforation plates to scalariform perforation plates promoted a more active settling of dryer substrates and high-mountain, temperate, and cold areas (Chavchavadze and Sizonenko, 2002). Simple perforations increase the effectiveness of water conduction, and scalariform perforations secure the hydraulic system, protecting the vessels from embolism. Scalariform perforation plates with numerous bars are usually correlated with longer vessel segments: *Alfaroa* has 12 bars (vessel segment length is 901 μm), and *Engelhardia* has four bars (vessel segment length is 806 μm).

The most ancient reliable remains of the Juglandaceae belong to the Early Paleocene and represent fruits *Amurcarya* with characters of the Engelhardioideae and Platycaryoideae (Kodrul and Krassilov, 2006). Fossil fruits of *Casholdia*, resembling fruits of the Engelhardioideae and, in some characters, the Platycaryoideae, and pollen of *Platycaryopollenites* Nagy emend. Frederiksen et Christopher (Platycaryoideae) are dated to the Late Paleocene (Manchester, 1987). In the Paleocene, fruits of *Cyclocarya*, leaf remains resembling leaves of *Juglans*, *Pterocarya* (Juglandeae), and *Carya*, pollen of *Caryapollenites* Raatz (Hicorieae) and *Monipites* Woodehouse (it possibly belongs to *Cyclocarya*), and fruits of some ancient members of the Juglandaceae described as *Polyptera* and *Juglandicarya* are found (Manchester, 1987).

According to Manchester (1987), the principal divergence of the Juglandaceae into modern tribes took place in the Paleogene. The Eocene is characterized by the maximal generic diversity, which was mostly restricted to middle latitudes of the Northern Hemisphere (Iljinskaja, 1990). Early Eocene remains of the Juglandaceae are fruits of the genera *Pterocaryopsis* and *Paleoplatycarya* (Platycaryoideae), Middle Eocene remains are fruits of *Hooleya* (Platycaryoideae), *Paraengelhardtia*, *Paleooreomunnea*, and *Paleocarya* (Engelhardioideae), and *Pterocarya* and *Juglans* (Juglandeae), and Late Eocene fruits belong to *Carya* (Hicorieae) (Manchester, 1987; Iljinskaja, 1990).

So far, no Paleocene juglandaceous wood has been found. The geological distribution of wood remains of the Juglandaceae (Table 2) shows that Eocene members of the family had wood of *Clarnoxylon* and *Manchesteroxylon* types, combining anatomical characters unknown in modern genera, and *Engelhardioxylon* (Engelhardioideae) and *Pterocaryoxylon* (Juglandeae); as early as the Oligocene, there were members of the Juglandaceae with wood of the *Rhysocaryoxylon*-type (*Juglans*); in the end of the Oligocene, wood of the *Eucaryoxylon*-type (*Carya*) appeared. Fossil wood of Platycaryoideae has not yet been found, although some characters of *Platycarya* are observed in the Eocene *Clarnoxylon* and *Manchesteroxylon*. On the other hand, Upper Eocene wood *Manchesteroxylon*, described from Nebraska, United States, also shows some structural characters of the wood of the Engelhardioideae (Wheeler and Landon, 1992). The combination of characters of the Engelhardioideae and Platycaryoideae was also discovered in the Early Paleocene fruits of *Amurcarya* from the Amur Region (Kodrul and Krassilov, 2006). Some extinct members of the Juglandaceae with fruits of *Amurcarya*-type and wood of *Manchesteroxylon*-type possibly existed in the Paleocene–Eocene. They appeared in the Early Paleocene in eastern Asia and spread to North America, where they existed until the end of the Eocene.

CONCLUSIONS

The summary of data on fossil wood of the Juglandaceae and their anatomical features and comparison with the wood anatomy of modern Juglandaceae resulted in an identification key for modern and fossil members of the family based on their wood anatomy.

Comparative-anatomical lines (morphoclines) are constructed taking into consideration the main evolutionary trends in secondary xylem of dicots and primitive/advanced states of structural characters of wood. Modern genera of the Juglandaceae are ranged in the direction of the change of a given character. Data on the evolution of structural characters of wood within the Juglandaceae show that the Engelhardioideae is the most primitive subfamily and the genus *Alfaroa* is probably situated at the beginning of the evolutionary line. The tribe Juglandeae is situated farther (*Juglans* is a more advanced genus in comparison with *Pterocarya*). By several characters, the subfamily Platycaryoideae occupies a more advanced position. The Hicorieae is the most evolutionarily advanced tribe based on anatomical characters of the wood. The conclusions obtained differ slightly from the data of Heimsch and Wetmore (1939), who believed that the Platycaryoideae is the most specialized subfamily within the Juglandaceae. This discrepancy is mostly explained by different evaluations of the evolutionary primitiveness of vascular tracheids with helical thickenings, the presence of those in *Platycarya* was considered by Heimsch and Wetmore (1939) as a highly specialized feature; they probably supposed that vascular tracheids might have secondarily originated from vessel segments.

The comparative analysis of the morphoclines shows that rates of specialization in structural elements of the secondary xylem of the Juglandaceae were uneven. Therefore, the mature xylem of some members shows both primitive and advanced characters. This is most distinct in *Platycarya*, in which such very primitive characters as vascular tracheids and helical thickenings are present, but in general the wood is relatively highly specialized. The Platycaryoideae is the most advanced subfamily in floral morphology (Manning, 1978), but the most primitive subfamily in the morphology of pollen grains (Bolotnikova, 1975), thus being a striking example of heterobathmy in the Juglandaceae.

The varying degree of evolutionary primitiveness of characters (heterochrony of characters) both increases the ecological flexibility of plants, allowing them to occupy various ecological niches, and can indicate the evolutionary fate of a given taxon. In many members of the Juglandaceae, wood specialization was related to inhabiting areas of temperate climate. However, some characters had already appeared in tropical members of the family and served as a prerequisite for their development in the temperate zone. These characters are vascular tracheids and helical thickenings on walls of narrow vessels and vascular tracheids in *Platycarya* and, apparently, reticulate thickenings on walls of narrow vessels in latewood of some species of *Rhrysocaryon* (*Juglans*). The appearance of simple perforation plates in addition to scalariform perforation plates probably facilitated the growth of Engelhardioideae in high-mountain areas.

The analysis of geological distribution of fossil juglandaceous wood shows that in the Eocene members of the Juglandaceae had the wood of *Clarnoxylon* and *Manchesteroxylon* types with a combination of characters lacking in modern members of the family, as well as *Engelhardioxylon* (Engelhardioideae) and *Pterocaryoxylon* (Juglandeae); in the Oligocene, members of the Juglandaceae had the wood of *Rhysocaryoxylon* (*Juglans*) type; and in the end of the Oligocene, they were characterized by wood of the *Eucaryoxylon* (*Carya*) type. Although fossil wood with anatomical characters of the subfamily Platycaryoideae has not yet been found, some characters of *Platycarya* are observed in the Eocene *Clarnoxylon* and *Manchesteroxylon*. Some structural characters of the Engelhardioideae are also present in the Upper Eocene wood of *Manchesteroxylon*. A combination of characters of the Engelhardioideae and Platycaryoideae has been discovered in the Early Paleocene fruit remains of the genus *Amurcarya* (Kodrul and Krassilov, 2006). A hypothesis was proposed that fruits of *Amurcarya* and wood of *Manchesteroxylon* belonged to some extinct members of the Juglandaceae, which appeared in the Early Paleocene in eastern Asia and spread to North America, where they existed until the end of the Eocene.

ACKNOWLEDGMENTS

We are grateful to Prof. Valentin Krassilov (Paleontological Institute, Russian Academy of Sciences) for the valuable discussion of the results. The study was supported by the Russian Foundation for Basic Research, project no. 05-04-49907, Presidium of the Russian Academy of Sciences and Presidium of the Far East Division, Russian Academy of Sciences, grants no. 06-I-P11-022 (Program *Scientific Grounds of Biodiversity Conservation in Russia*) and no. 06-I-P18-081 (Program *Origin and Evolution of the Biosphere*), and to the Presidium of the Far East Division, Russian Academy of Sciences, grant no. 06-III-A-06-139.

REFERENCES

1. *Atlas of Wood and Wood Fibers for Paper*, Ed. by E. S. Chavchavadze (Klyuch, Moscow, 1992) [in Russian].
2. P. Baas and E. A. Wheeler, "Parallelism and Reversibility in Xylem Evolution—A Review," IAWA J. **17**, 351–364 (1996).
3. I. W. Bailey, "The Cambium and Its Derivative Tissues: II. Size Variations of Cambium Initials in Gymnosperms and Angiosperms," Am. J. Bot. **7** (9), 355–367 (1920).

4. I. W. Bailey, "Evolution of the Tracheary Tissue of Land Plants," Am. J. Bot. **40** (1), 4–8 (1953).
5. I. W. Bailey, "The Potentialities and Limitations of Wood Anatomy in the Study of Phylogeny and Classification of Angiosperms," J. Arnold Arbor. **38** (3), 243–254 (1957).
6. N. I. Blokhina and S. A. Snezhkova, "Distinctive Features of the Anatomical Structure of Wood in Extant and Fossil Engelhardioids (Engelhardioideae, Juglandaceae)," in *Plants in Monsoonal Climate: Proc. 3rd Int. Conf.* (BSI Dal'nevost. Otdel. Ross. Akad. Nauk, Vladivostok, 2003), pp. 209–214 [in Russian].
7. N. I. Blokhina, A. M. Popov, and S. A. Snezhkova, "Fossil Wood of *Engelhardioxylon mameticum* sp. nov. (Juglandaceae) from the Paleogene of Kamchatka," Paleontol. Zh., No. 4, 104–111 (2002) [Paleontol. J. **36** (4), 429–437 (2002)].
8. M. D. Bolotnikova, "Evolution of Juglandaceae Based on Data from Palynology," in *Biological Investigations in the Russian Far East* (Dal'nevost. Nauchn. Tsentr Akad. Nauk SSSR, Vladivostok, 1975), pp. 62–65 [in Russian].
9. S. Carlquist, "Vessel Grouping in Dicotyledon Wood: Significance and Relationship to Imperforate Tracheary Elements," Aliso **10** (4), 505–525 (1984).
10. S. Carlquist, *Comparative Wood Anatomy: Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood* (Springer-Verlag, Berlin, Heidelberg, New York, London, Paris, Tokyo, 1988).
11. E. S. Chavchavadze and O. Yu. Sizonenko, *Structural Features of Wood in Shrubs and Subshrubs of the Arctic Flora of Russia* (Rostok, St. Petersburg, 2002) [in Russian].
12. J. Dupéron, "Les bois fossiles de Juglandaceae: inventaire et révision," Rev. Palaeobot. Palynol. **53**, 251–282 (1988).
13. *Fossil Flowering Plants of Russia and Adjacent Countries*, Vol. 3: *Leitneriaceae–Juglandaceae*, Ed. by L. Yu. Budantseva (Bot. Inst. Ross. Akad. Nauk, St. Petersburg, 1994) [in Russian].
14. F. H. Frost, "Specialization in Secondary Xylem of Dicotyledons. I. Origin of Vessels," Bot. Gaz. **89** (1), 67–94 (1930a).
15. F. H. Frost, "Specialization in Secondary Xylem of Dicotyledons: II. Evolution of End Wall of Vessel Segment," Bot. Gaz. **90** (1), 198–212 (1930b).
16. A. F. Gammerman, A. A. Nikitin, and G. I. Nikolaeva, *Guide to Wood Identification Based on Characteristic Microscopical Features* (Akad. Nauk SSSR, Moscow, 1946) [in Russian].
17. H. Gottwald, "Hölzer aus marinen Sanden des Oberen Eozän von Helmstedt (Niedersachsen)," Palaeontographica Abt. B **225** (1–3), 27–103 (1992).
18. P. Greguss, *Tertiary Angiosperm Wood in Hungary* (Acad. Kiadó, Budapest, 1969).
19. C. Heimsch and R. H. Wetmore, "The Significance of Wood Anatomy in the Taxonomy of the Juglandaceae," Am. J. Bot. **26** (8), 651–660 (1939).
20. P. S. Herendeen, "Angiosperm Phylogenetic Systematics: Is There a Role for Wood Anatomical Studies in Cladistic Analyses?," IAWA J. **17**, 250–251 (1996).
21. P. S. Herendeen, E. A. Wheeler, P. Baas, "Angiosperm Wood Evolution and the Potential Contribution of Paleontological Data," Bot. Rev. **65** (3), 278–300 (1999).
22. S. Iamandei and Eu. Iamandei, "New Juglandaceous Fossil Wood in the Middle Miocene Lignoflora of Prăvăleni-Ociu (South Apuseni)," in *Acta Palaeontologica Romaniae* (Vasiliana, Iaşi, 2002), Vol. 3, pp. 185–198.
23. S. Iamandei and Eu. Iamandei, "A New Juglandaceous Fossil Wood from the Badenian of Prăvăleni-Ociu (South Apuseni)," Studii şi Cercetări de Geol. **48**, 91–98 (2003).
24. I. A. Iljinskaja, "A Contribution to the Systematics and Phylogeny of the Family Juglandaceae," Bot. Zh. **75** (6), 702–803 (1990).
25. G. B. Kedrov, "Interrelationship between Some Characters of Dicotyledonous Wood and Its Evolutionary Significance," in *Morphology of Flowering Plants* (Nauka, Moscow, 1967), pp. 179–198 [in Russian].
26. G. B. Kedrov, "On the Structure and Some Functions of the Living System of Wood," in *Morphology of Flowering Plants* (Nauka, Moscow, 1971), pp. 121–136 [in Russian].
27. T. M. Kodrul and V. A. Krassilov, "New Juglandaceous Fruit Morphotype from the Paleocene of Amur Province, Russian Far East," Acta Palaeobot. **45** (2), 139–144 (2006).
28. G. Kraus, "Beiträge zur Kenntnis der fossilen Hölzer. I. Hölzer aus den Schwefelgruben Siciliens," Abh. Naturf. Ges. Halle **16**, 79–109 (1882).
29. D. A. Kribs, "Comparative Anatomy of the Wood of the Juglandaceae," Tropical Wood, No. 12, 16–21 (1927).
30. D. A. Kribs, "Salient Lines of Structural Specialization in the Wood Rays of Dicotyledons," Bot. Gaz. **96** (3), 547–557 (1935).
31. D. A. Kribs, "Salient Lines of Structural Specialization in the Wood Parenchyma of Dicotyledons," Bull. Torrey Bot. Club **64** (2), 177–186 (1937).
32. S. R. Manchester, "Fossil Wood of the Engelhardieae (Juglandaceae) from the Eocene of North America: *Engelhardioxylon gen. nov.,"* Bot. Gaz. **144** (1), 157–163 (1983).
33. S. R. Manchester, *The Fossil History of the Juglandaceae: Monographs in Systematic Botany from the Missouri Botanical Garden, Vol. 21* (Missouri Bot. Gard., Kansas, 1987).
34. S. R. Manchester, "*Cruciptera, a New Juglandaceous Winged Fruit from the Eocene and Oligocene of Western North America,*" Systematic Bot. **16**, 715–725 (1991).
35. S. R. Manchester and E. A. Wheeler, "Extinct Juglandaceous Wood from the Eocene of Oregon and Its Implication for the Xylem Evolution in the Juglandaceae," IAWA J. **14** (1), 103–111 (1993).
36. W. E. Manning, "The Classification within the Juglandaceae," Ann. Missouri Bot. Gard. **65** (4), 1058–1087 (1978).
37. C. R. Metcalfe and R. Chalk, *Anatomy of the Dicotyledons* (Clarendon Press, Oxford, 1950), Vols. 1–2.
38. R. B. Miller, "Reticulate Thickenings in Some Species of *Juglans,*" Am. J. Bot. **63** (6), 898–901 (1976a).
39. R. B. Miller, "Wood Anatomy and Identification of Species of *Juglans*," Bot. Gaz. **137** (4), 368–377 (1976b).

40. W. R. Müller-Stoll and E. Mädel, “Juglandaceen-Hölzer aus dem Tertiär des pannonischen Beckens,” Senckenberg. Leth. **41** (1/6), 255–295 (1960).
41. W. R. Müller-Stoll and E. Mädel-Angeliewa, “Fossile Hölzer mit schmalen apotrachealen Parenchymbändern. I. Arten aus der Gattung *Eucaryoxylon Müller-Stoll et Mädel*,” Feddes Repert. **94** (9–10), 655–667 (1983).
42. V. D. Nashchokin, “Fossil Wood of Broad-Leaved Trees from the Tertiary Deposits of the Krasnoyarsk Krai,” Dokl. Akad. Nauk SSSR **131** (5), 1149–1151 (1960).
43. C. Privé, “*Pterocaryoxylon subpannonicum* n. sp., bois fossile de Juglandaceae provenant du Cantal,” Rev. Gén. Bot. **81**, 243–257 (1974).
44. D. E. Stone, “Juglandaceae,” in *The Families and Genera of Vascular Plants,* Ed. by K. Kubitzki, J. C. Rohwer, and V. Bittrich, (Springer-Verlag, Berlin, 1993), Vol. 2, pp. 348–359.
45. O. Tippo, “The Role of Wood Anatomy in Phylogeny,” Am. Midland Naturalist **36** (2), 362–372 (1946).
46. F. Unger, *Synopsis plantarum fossilium* (Leopoldum Voss Bibliopolam, Leipzig, 1845).
47. V. E. Vikhrov, *Diagnostic Characters of the Wood of Major Forest-Forming and Commercial Timber Species of the USSR* (Akad. Nauk SSSR, Moscow, 1959) [in Russian].
48. G. I. Voroshilova and S. A. Snezhkova, *Wood of Dominant and Subdominant Species of the Russian Far East* (Dal’nevost. Gos. Univ., Vladivostok, 1984) [in Russian].
49. E. A. Wheeler and P. Baas, “A Survey of the Fossil Record for Dicotyledonous Wood and Its Significance for Evolutionary and Ecological Wood Anatomy,” IAWA Bull., N.S. **12**, 275–332 (1991).
50. E. A. Wheeler and J. Landon, “Late Eocene (Chadronian) Dicotyledonous Woods from Nebraska: Evolutionary and Ecological Significance,” Rev. Palaeobot. Palynol. **74** (3/4), 267–282 (1992).
51. E. A. Wheeler and S. R. Manchester, “Woods of the Eocene Nut Beds Flora, Clarno Formation, Oregon, USA,” IAWA J. (Suppl. 3), 1–188 (2002).
52. E. A. Wheeler, R. A. Scott, and E. S. Barghoorn, “Fossil Dicotyledonous Woods from Yellowstone National Park, II,” J. Arnold Arbor. **59** (1), 1–26 (1978).
53. A. A. Yatsenko-Khmelevskii, *Fundamentals and Methods of Anatomical Examination of Wood* (Akad. Nauk SSSR, Moscow-Leningrad, 1954) [in Russian].
54. A. A. Yatsenko-Khmelevskii and M. S. Gzyryan, “Wood Anatomy and Ecological Evolution of Dicotyledons,” in *Problems of Botany* (Akad. Nauk SSSR, Moscow-Leningrad, 1954), pp. 827–839 [in Russian].