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ON SOME ASPECTS OF SYSTEMATICS AND EVOLUTION OF THE ENGELHARDIOIDEAE (JUGLANDACEAE) BY WOOD ANATOMY

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Abstract. Some aspects of systematics by wood anatomy as well as wood anatomy specialization of the subfamily Engelhardioideae (Juglandaceae) are discussed. The age variation of wood anatomy over the radius of stem has been examined in the Oligocene *Engelhardioxylon mameticum* from Kamchatka (Russian Far East); the formation of mature wood takes in this species 9-11(15) years. The ontogenetic variability of wood anatomy was examined in the subfamily Engelhardioideae for the first time. A comparative analysis of wood anatomy specialization within the fossil genus *Engelhardioxylon* has been done. The development of wood anatomy characters in *E. mameticum* is an example of heterobatmy in the genus. The data on wood anatomy specialization within the Juglandaceae members were summarized. The Engelhardioideae is, probably, the most primitive subfamily, while the Platycaryoideae is the most advanced one. Wood anatomical characters of *Engelhardioxylon mameticum* correlated with habitat conditions have been implicated for palaeoclimate reconstruction. During the Oligocene this species vegetated in Kamchatka under condition of well-pronounced seasonality with relatively mild warm temperate climate throughout the year, and a considerable humidity.

Keywords: Juglandaceae, Engelhardioideae, wood anatomy, systemstics, evolution.

INTRODUCTION

Firstly, the members of the family Juglandaceae A. Rich. ex Kunth: *Engelhardia* Lesch. ex Blume, *Oreomunnea* Oest. and *Alfaroa* Standl. combined in the tribe Engelhardieae Mann. were referred either to the subfamily Juglandoideae Leroy together with the tribes Juglandeae Nakai and Hicorieae Mann. (Manning, 1978; Takhtajan, 1987) or to the subfamily Platycaryoideae Mann. together with the tribe Platycaryeae Nakai (Manchester, 1987). However, the tribe Engelhardieae differs from the tribes Juglandeae and Hicorieae by the inflorescence, bract and pollen morphology and by wood anatomy (Iljinskaja, 1990). On the other hand the tribe Platycaryeae is peculiar in pollen morphology (Kupriyanova, 1956) and differs from other tribes of the Juglandaceae in certain other morphological features (Iljinskaja, 1990) as well as wood anatomy (Kribs, 1927; Heimsch & Wetmore, 1939). According to Iljinskaja (1990), the tribe Engelhardieae is a separate lineage of the family Juglandaceae and merits a rank of the subfamily Engelhardioideae (Mann.) Iljinskaja. This conception is taken in the present paper.

The modern genera *Engelhardia*, *Oreomunnea* and *Alfaroa* are closely related. For a long time the genus *Oreomunnea* had been assigned to *Engelhardia*, and the genus *Alfaroa* had been considered as an american section of *Engelhardia* (see Zhilin, 1980). According to Manning (1978), the genus *Engelhardia* comprises 5 species of two sections: Engelhardia Mann. and Psilocarpeae Nagel emend. Leroy. The section Psilocarpeae includes the single species *Engelhardia roxburghiana* Wall. (synonyms *E. wallichiana* Lindl. ex DC., *E. chrysolepis* Hance, *E. fenzelii* Merr. and *E. formosana* Hayata). In a view of Iljinskaja (1990), *E. roxburghiana* is characterized by a combination of features that can be found within the members of the section Engelhardia as well as the genus *Alfaroa* and partly *Oreomunnea*. Since, the *Alfaroa* characters are prevalent, Iljinskaja (1990) transferred *E. roxburghiana* to the genus *Alfaroa* – *A. roxburghiana* (Wall.) Iljinskaja (although, this species has been still attributed to the separate monotypic section Psilocarpeae), and later introduced a monotypic genus *Alfaropsis* Iljinskaja (Iskopaemye tsvetkovye, 1994). Thus, according to the modern conception, the subfamily Engelhardioideae includes 4 extant genera: *Engelhardia* (4 species), *Oreomunnea* (2 species), *Alfaroa* (7 species) and *Alfaropsis* (1 species).

The living Engelhardioideaes are evergreen or sometimes deciduous trees vegetated mainly in mountain forests under conditions of monsoon tropical or sometimes subtropical climate. Engelhardias reach up to 47 m high (occasionally up to 60 m high) with the trunk diameter up to 3 m, and usually they vegetate at the elevation up to 2200 m above sea level. The areal of extant *Engelhardia* ranges from north-western India to the east comprises also Nepal, Tibet, southern China, Indochina, Philippines, and Sumatra, Kalimantan, Java, New Guinea islands (Manning, 1978; Iljinskaja, 1990). *Oreomunnea* occurs in Mexico and Costa-Rica, and *Alfaroa* – in Mexico, the whole Central America, West-India and Columbia. Oreomunneas reach 48 m in height and 70 cm in trunk diameter, and Alfaroas comprises the highest trees of the tropics of West-India, both they vegetate at 900-1000 m above sea level. Growing in mountains Oreomunneas and Alfaroas prefer wet habitats

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(Manning, 1978; Iljinskaja, 1990; Zhilin, 1980). *Alfaropsis* grows in eastern Pakistan, southern China, Taiwan, Vietnam, Sumatra and Kalimantan islands (Manning, 1978; Iljinskaja, 1990). *Oreomunnea* and *Alfaroa*, in contrast to *Engelhardia* and *Alfaropsis*, are only evergreen trees vegetated only under tropical climate. At whole, Engelhardioideaes are spread more southern than the others of Juglandaceae except of two species of *Juglans* of the section Rhysocaryon Dode, which are distributed to approximately the latitude 30º growing in Bolivia and Argentina (Manning, 1978; Dupéron, 1988).

The present-day arials of Engelhardioideaes are restricted by approximately the 10º South and 40º North latitudes (Figure 1). Although, during the Tertiary they were widespread in Eurasia and North America mainly between 40º and 60º North latitudes (Manchester, 1987).

WOOD ANATOMICAL CHARACTERS OF THE ENGELHARDIOIDEAE

The main diagnostic feature of the Engelhardioideae is the presence of both simple and scalariform perforations, whereas the other members of the Juglandaceae have only simple perforation plates (*Table 1*). However, scalariform perforation plates occur only in narrow vessels. According to Manchester (1983), they are usually less frequent than simple perforation plates and not present in every vessel, therefore it sometimes necessary to investigate several radial sections (several growth rings) to determine these presence or absence with reasonable certainty.

In the meantime, the main diagnostic feature of the tribe Juglandeae is chambered pith, the Hicorieae - excessively thickened vessel walls, and the subfamily Platycaryoideae – the presence of vasicentric tracheids and helical thickenings (Manchester, 1983; Manchester& Wheeler, 1993).

The other anatomical characters of the Engelhardioideae are the presence of diffuse-porous to semi-ring-porous wood, thin-walled vessels, nonseptate pith, and the lack of helical thickenings and crystals (Manchester & Wheeler, 1993). Although, Kribs (1927), Heimsch & Wetmore (1939) and Müller-Stoll & Mädel (1960) reported rare crystals in axial and ray parenchyma.

Unfortunately, the extant genera of Engelhardioideae are almost indistinguishable each from other on the basis of wood anatomy despite the efforts of their separation. Thus, Kribs (1927) proposed to use as distinguishing features: the ratio between simple and scalariform perforations, the number of bars per scalariform perforation plate, the presence of crystals in the axial or ray parenchyma and the presence of gelatinous fibers; whereas Heimsch & Wetmore (1939) - the thickness of the vessel walls, angularity of the vessel lumens, proportion of solitary vessels and vessels arranged in radial rows as well as the type of vessel-ray and vessel-parenchyma pits.

For instance, *Alfaroa* contains crystals mainly in the ray parenchyma, in contrast to *Oreomunnea* that has crystals frequently in the axial parenchyma and rarely in ray parenchyma. Scalariform perforations are the most frequent in *Alfaroa*, less frequent in *Oreomunnea*, and substantially rare in *Engelhardia*. However, the data on the number of bars per scalariform perforation plate are rather different in the works. Kribs (1927) reported 1-9 (and more) bars in *Engelhardia* and 12 (and more) bars in *Alfaroa*, while Müller-Stoll & Mädel (1960) reported maximum 4 bars (often one bar) in *Engelhardia* and 3-5(9) bars in *Oreomunnea*. Gelatinous fibers are characteristic of *Oreomunnea*, whereas in *Alfaroa* they occur in only wood of branches. The vessel lumens of *Engelhardia* are more rounded (of some species are only rounded) than those of others Engelhardioideae. The thinnest walls of vessels are present in *Alfaroa.* Solitary vessels dominate in *Alfaroa*, whereas in *Engelhardia* the proportions of solitary vessels and vessels arranged in radial rows is approximately equal. According to Heimsch & Wetmore (1939), the vessel-ray and vessel-parenchyma pits of some species of *Engelhardia* are represented by only fine semi-bordered pits; those of other species of the genus are represented by fine semi-bordered pits and by simple scalariform pits, strongly elongated in horizontal direction, while those of *Alfaroa* are represented by only scalariform pits.

However, Manchester (1983) could not find foolproof criteria for recognizing of the extant genera of the subfamily Engelhardioideae by wood anatomy despite he investigated in total of 40 transparent thin sections made of 5 species of *Engelhardia* (including *E. roxburghiana*, to date is the genus *Alfaropsis*), 2 species of *Oreomunnea* and 4 species of *Alfaroa*. He suggested that all these features are highly variable within each genus to be considered diagnostic above the species level.

THE ENGELHARDIOIDEAE FOSSIL WOODS

The organ-genus *Engelhardioxylon* Manchester has been proposed by Manchester (1983) for the Juglandaceae fossil woods that demonstrated wood anatomical characters of all extant genera of the Engelhardioideae. Meanwhile, Wheeler & Landon (1992) also described the Juglandaceae fossil wood with both simple and scalariform perforations - *Manchesteroxylon* Wheeler & Landon. However, the Late Eocene wood *Manchesteroxylon* from Nebraska (USA) - *M. intermedium* Wheeler et Landon differs from the Engelhardioideae wood by the presence of vasicentric tracheids and a trend to the ring-porosity with diagonal arrangement of vessels. These features indicate that *Manchesteroxylon* is close to some extent to the Platycaryoideae wood, although, differs from the later in the lacking of helical thickenings in the vessels as well as crystals in the ray parenchyma. The fossil genus *Manchesteroxylon* has a combination of wood anatomical features that is not found in extant members of the family Juglandaceae, and it cannot be accommodated within its a single extant tribe or subfamily (Wheeler & Landon, 1992).

To date, only 4 species of the *Engelhardioxylon* are known (Figure 1): *E. nutbedensis* Manchester and *E. texana* Manchester both described from the Middle Eocene of correspondingly Oregon and Texas, the USA (Manchester, 1983); *E. macrocrystallosum* Gottwald – from the Late Eocene of Lower Saxony, Germany (Gottwald, 1992) and *E. mameticum* Blokh. et Snezhk. (Plate I, fig. 1-20) – from the Oligocene of Kamchatka, the Russian Far East (Blokhina et al., 2002). The Oligocene wood differs from the Eocene woods in the having of greater number of bars in scalariform perforation plates; wider and higher rays both uni- and multiseriate, longer uniseriate ends in multiseriate rays, and semi-ring-porous arrangement of vessels (*Table 2*). However, in the work by Wheeler & Manchester (2002) the Middle Eocene *E. nutbedensis* is characterized as a semi-ring-porous wood.

Ontogenetic variation of the Engelhardioxylon mameticum wood anatomy

The ontogenetic variation of the wood anatomy over the radius of the *E. mameticum* stem has been examined (Blokhina et al., 2002). The petrified wood specimen of *E. mameticum* had a well preserved pith and distinguishable by unaided eye 30 growth rings (from 0.3 to 2.3 mm wide), therefore we decided to try and trace an age variability of wood anatomy characters from the pith to the periphery (i.e. along the radius of stem) to reveal the individual age of the mature wood formation in this species. Namely, the characters of mature wood are used in identification and systematics. For microscopic investigation, 3 transverse, 8 radial and more than 20 tangential transparent thin sections have been made. The tangential sections were made through consecutive growth rings from the pith to the periphery.

Due to this investigation the age of appearance of the following mature wood anatomical characters has been determined:

in the growth ring 4, the square ray cells have appeared in the uniseriate rays in addition to the oval cells;

- in the growth ring 9, the rays of all types of seriation characteristic of the *E. mameticum* mature wood have appeared (*Table 2*), and the polygonal ray cells have begun to dominate over the oval cells in the multiseriate parts of rays;
- in the growth ring 10, the square ray cells have begun to dominate over the oval cells in the uniseriate ends of multiseriate rays;
- in the growth ring 11, the multiseriate rays with very short uniseriate ends have begun to dominate;
- in the growth ring 15, the multiseriate rays have begun to dominate over the uniseriate rays in the field of view.

As a result of the ontogenetic analysis one can suppose that the formation of mature wood takes in *E. mameticum* 9-11(15) years. Later, the wood anatomy does not change or change insignificantly depending on the growth parameters. The ontogenetic variability of wood anatomy over the radius of stem was examined in the subfamily Engelhardioideae for the first time.

Implication of the Engelhardioxylon mameticum wood anatomical characters for palaeoclimate reconstruction

Some wood anatomical attributes are correlated with habitat conditions, for example (Wheeler & Manchester, 2002):

- the syndrome of few vessels per sq. mm and wide vessel diameters is prevalent in modern tropical lowland rainforest trees;
- helical thickenings are common in modern woods of the temperate zone and rare in the tropics;
- semi-ring-porous woods are not common in the tropics today, even in seasonally dry or montane forests, but are relatively common in Northern Hemisphere woods;
- ring-porous and semi-ring-porous woods today are deciduous (in the past geological times the deciduousness could be correlated with seasonally in precipitation, temperature, or day length);
- a high proportion of woods with distinct growth rings often is used to infer a climate that is highly seasonal (trees that grow in tropical forests with dry seasonals of many months do not have growth rings as distinct as is characteristic of present-day trees of mid-latitudes, i.e. seasonality in precipitation alone is not associated with distinct growth rings as high as a cold season with temperatures below freezing is associated with distinct growth rings),
- the incidence of scalariform perforations occurs in modern lowland rainforest trees of savannas and monsoon forests, and within the range found in modern montane tropical forests and some subtropical to warm temperate woody floras.

On the basis of anatomical features that have featured prominently in discussions of ecological wood anatomy and are more highly correlated with habitats we decided to try and implicate specific wood anatomical characters of the Oligocene wood

E. mameticum for palaeoclimate reconstruction. For example, among the extant Engelhardioideaes distinct growth rings are present in the species that vegetate in warm moderate subtropical climate, whereas in tropical climate growth rings are absent. Although, a repetitively decreasing of cambium activity leads to the formation of thick-walled fiber tracheids and the wood seems to have growth rings. Thus, distinct growth rings bordered by a wide band (up to 4 layers) of radially flattened fibers as well as a trend to semi-ring-porous arrangement of vessels presented in the Oligocene wood *E. mameticum* are characteristic of well-pronounced seasonality. Then, gradual transition from the early to late wood (which is slightly more pronounced in narrow growth rings) is characteristic of relatively mild warm temperate climate throughout the year. And the presence of scalariform perforations believes a considerable humidity. Thus, upon the analysis of *E. mameticum* wood anatomical features it may be suggested that during the Oligocene this species vegetated in Kamchatka under condition of well-pronounced seasonality with relatively mild warm temperate climate throughout the year, and a considerable humidity (Blokhina et al., 2002).

THE ENGELHARDIOIDEAE WOOD ANATOMY SPECIALIZATION

Heimsch & Wetmore (1939) were the first who discovered the uniformity of wood anatomy among the modern genera of Engelhardioideae and tried to outline the ways of wood anatomy evolution within the family Juglandaceae. According to Manchester (1983, 1987), the occurrence of similar anatomy among the Paleogene species of *Engelhardioxylon* supports the view that xylem evolution has been relatively conservative in this subfamily, and wood anatomy of the Engelhardioideae has undergone relatively little specialization since Eocene, despite divergence in fruit and foliage morphology. The fact is, at least 3 fossil genera: *Paleocarya* Sap. (closing to *Oreomunnea* (Iljinskaja, 1990), *Paleooreomunnea* Dilcher, Potter et Crepet, and *Praengelhardia* Berry were established based on imprints of winged fruits (see Manchester, 1987; see Iljinskaja, 1990). Despite, wood anatomy of the *Engelhardioxylon* closely resembles that of the living *Engelhardia*, *Oreomunnea*, *Alfaroa* and *Alfaropsis* there is no assurance that species of this form-genus represent any of modern genera of the subfamily Engelhardioideae. During the Early Tertiary there was a complex of engelhardioid fruits combined features of more than one modern genus (Manchester, 1987).

According to the major trends of specialization in secondary xylem of dicotyledons (Yatsenko-Khmelevskyi, 1954; Heredeen et al., 1999) the following wood anatomical features are interpreted as more advanced characters: distinct growth rings, ring-porous arrangement of vessels, rounded lumens (outlines) of vessels in cross section, large diameter of vessels, short length of vessel elements, thick walls of vessels, alternate intervessel pitting, helical thickenings, simple perforation plates, a little number of bars per scalariform perforation plate, homocellular rays and wide multiseriate rays.

On the basis of major trends one can suppose that within the Engelhardioideae more advanced features will be the presence of distinct growth rings, semi-ring porous arrangement of vessels, rounded vessel outlines in cross section, short vessel elements, alternate intervessel pitting, simple perforation plates, few bars per scalariform perforation plate, and wide (five-seriate) rays.

A comparative analysis of wood anatomy specialization within the genus *Engelhardioxylon* has been done (Blokhina et al., 2002). The great number of bars in scalariform perforation plates, correlated with longer vessels, is evidence that wood anatomy of *E. mameticum* is more primitive than those of species from North America and Europe. On the other hand, the wider multiseriate rays (five-seriate) and semi-ring-porosity presented in the wood from Russian Far East are more advanced features than those of North American and European species. Thus, the development of wood anatomy characters in *E. mameticum* is an example of heterobatmy in the genus *Engelhardioxylon.* Heterobatmy is very characteristic within the family Juglandaceae.

Summarizing the data on wood anatomy specialization within the Juglandaceae members, one can hypothesized that the Engelhardioideae is the most primitive subfamily, in contrast to the both Juglandoideae and Platycaryoideae. The Engelhardioideae is characterized the most number of primitive features, namely, the presence of diffuse-porous arrangement of vessels, thin walls of vessels, long length of vessel elements, scalariform perforation plates and the absence of helical thickenings; whereas semi-ring-porosity and simple perforations may be interpreted as advanced characters. Thus, the Engelhardioideae shows the initial stage of the evolutionary sequence of wood anatomy specialization within the Juglandaceae.

In contrast to Engelhardioideae, the Platycaryoideae is the most advanced subfamily within the Juglandaceae. This subfamily has such the advanced characters as ring-porosity, short vessel elements, simple perforations and helical thickenings; although, thin-walled vessels are interpreted as primitive feature.

The tribe Hicorieae, characterized by the presence of ring-porous arrangement of vessels, thick walls of vessels, short vessel elements and simple perforation plates, is the more advanced tribe within the subfamily Juglandoideae; however, semi-ring-porosity and the absence of helical thickenings may be interpreted as more primitive characters.

Meanwhile, in contrast to Hicorieae, the tribe Juglandeae has some more number of primitive characters, namely, diffuse-porous arrangement of vessels, thin walls of vessels and the lack of helical thickenings.

Similar conclusions were obtained by Manning (1978) on the basis of flower, fruit and inflorescence morphology. However, on the basis of pollen morphology Platycaryoideae is the most primitive subfamily within the Juglandaceae (Bolotnikova, 1975, 1978).

CONCLUSIONS

Some aspects of systematics of the Engelhardioideae (Juglandaceae) by wood anatomy as well as wood anatomy specialization of this subfamily are discussed. The main diagnostic feature of the Engelhardioideae is the presence of both simple and scalariform perforations. The other anatomical characters of the subfamily are the presence of diffuse-porous to semi-ring-porous wood, thin-walled vessels, nonseptate pith, and the lack of helical thickenings and crystals, although, some authors reported rare crystals in axial and ray parenchyma.

The extant genera of Engelhardioideae are almost indistinguishable each from other on the basis of wood anatomy despite the efforts of their separation. Therefore, the organ-genus *Engelhardioxylon* includes the Juglandaceae fossil woods that demonstrate wood anatomical characters of all extant genera of the Engelhardioideae.

To date, the following species of the *Engelhardioxylon* are known: *E. nutbedensis* and *E. texana* from the Middle Eocene of the USA, *E. macrocrystallosum* – from the Late Eocene of Germany and *E. mameticum* – from the Oligocene of the Russian Far East. The Oligocene wood differs from the Eocene woods in the having of greater number of bars in scalariform perforation plates; wider and higher rays both uni- and multiseriate, longer uniseriate ends in multiseriate rays, and semi-ring-porous arrangement of vessels.

The age variation of the *E. mameticum* wood anatomy over the radius of the stem has been examined. As a result of the ontogenetic analysis one can supposed that the formation of mature wood takes in the Oligocene *E. mameticum* 9-11(15) years. Later, the wood anatomy does not change or change insignificantly depending on the growth parameters. The ontogenetic variability of wood anatomy over the radius of stem was examined in the subfamily Engelhardioideae for the first time.

According to major trends of specialization in secondary xylem of dicotyledons the following wood anatomical features can be interpreted as more advanced characters within the Engelhardioideae: the presence of distinct growth rings, semi-ring porous arrangement of vessels, rounded vessel outlines in cross section, short vessel elements, alternate intervessel pitting, simple perforation plates, few bars per scalariform perforation plate and wide (five-seriate) rays.

Summarizing the data on wood anatomy specialization within the Juglandaceae members, one can hypothesized that the Engelhardioideae is the most primitive subfamily, in contrast to the both Juglandoideae and Platycaryoideae, because the former is characterized the most number of primitive features. The tribe Hicorieae is the more advanced tribe within the subfamily Juglandoideae, while the tribe Juglandeae has some more number of primitive characters. Platycaryoideae is the most advanced subfamily within the Juglandaceae on the basis of wood anatomy. Heterobatmy is very characteristic within the family Juglandaceae.

A comparative analysis of wood anatomy specialization within the fossil genus *Engelhardioxylon* has been done, and heterobatmy has been observed in the development of wood anatomy characters in the Oligocene *E. mameticum.*

Wood anatomical characters of *E. mameticum* correlated with habitat conditions were implicated for palaeoclimate reconstruction. Distinct growth rings bordered by a wide band (up to 4 layers) of radially flattened fibers as well as a trend to semi-ring-porous arrangement of vessels presented in *E. mameticum* are characteristic of well-pronounced seasonality. Gradual transition from the early to late wood (which is slightly more pronounced in narrow growth rings) is characteristic of relatively mild warm temperate climate throughout the year. And the presence of scalariform perforations believes a considerable humidity. Thus, upon the analysis of *E. mameticum* wood anatomical features it may be suggested that during the Oligocene this species vegetated in Kamchatka under condition of well-pronounced seasonality with relatively mild warm temperate climate throughout the year, and a considerable humidity.

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REFERENCES

Blokhina, N.I., Popov, A.M. & Snezhkova, S.A. 2002, Fossil Wood of *Engelhardioxylon mameticum* sp. nov. (Juglandaceae) from the Paleogene of Kamchatka. *Paleontological Journal*, 36/4, p. 429-437, pl. 10, Moscow.

Bolotnikova, M.D. 1975, The Evolution of the Juglandaceae on the Basis of Palinological Data. In: *Biologicheskie issledovaniya na Dal'nem Vostoke* (Biological Investigations in the Far East), Kryvolutskaya, G.O., Ed., p. 62-65, Izdatel'stvo Dal'nevostochnogo Nauchnogo Tsentra Akademii Nauk SSSR, Vladivostok.

Bolotnikova, M.D. 1978, Morphology and Evolution of the Juglandaceae Kunth Pollen. In: *Palynologicheskie issledovania na Dal'nem Vostoke* (Palynological Investigations in the Far East), Grichuk, M.P. & Korotkiy, A.M., Ed., p. 44-49, Izdatel'stvo Dal'nevostochnogo Otdelenia Akademii Nauk SSSR, Vladivostok.

Dupéron, J. 1988, Les bois fossils de Juglandaceae: inventaire et revision. *Review of Palaeobotany and Palynology*, 53, p. 251-282, Amsterdam.

Gottwald, H. 1992, Hölzer aus Marinen Sanden des Oberen Eozän von Helmstedt (Niedersachsen). *Palaeontographica*, Abt. B, 225/1-3, S. 27-103, 20 tf., Stuttgart.

Heimsch, C. & Wetmore, R.H. 1939, The Significance of Wood Anatomy in the Taxonomy of the Juglandaceae. *American Journal of Botany*, 26/8, p.650-660, Burlington.

Heredeen, P.S., Wheeler, E.A. & Baas, P. 1999, Angiosperm Wood Evolution and the Potential Contribution of Paleontological Data. *The Botanical Review*, 65/3, p. 278-300, New York.

Iljinskaja, I.A. 1990, On the Systematics and Phylogeny of the family Juglandaceae. *Botanicheskyi Zhurnal*, 75/6, p. 702-803, St.-Petersburg.

Iskopaemye tsvetkovye rasteniya Rossii i sopredel'nykh gosudarstv, III: Leitneriaceae - Juglandaceae (Fossil Angiosperms of Russia and Adjacent Countries, III: Leitneriaceae - Juglandaceae), 1994, 118 p., 85 pl., Budantsev, L.Yu., Ed., Izdatel'stvo Botanicheskogo Instituta Rossiyiskoi Akademii Nauk, St.-Petersburg.

Kribs, D.A. 1927, Comparative Anatomy of the Woods of the Juglandaceae. *Tropical Woods*, 12, p. 16-21, Connecticut.

Kupriyanova, L.A. 1956, Palinologiya serezhkotsvetnykh (Amentiferae) (Palynology of the Amentiferae), 215 p., Izdatel'stvo “Nauka”, Moscow- Leningrad.

Manchester, S.R. 1983, Fossil Wood of the Engelhardieae (Juglandaceae) from the Eocene of North America: *Engelhardioxylon* gen. nov. *Botanical Gazette*, 144/1, p. 157-163, Chicago.

Manchester, S.R. 1987, The Fossil History of the Juglandaceae. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 21, 137 p., Kansas.

Manchester, S.R. & Wheeler, E.A. 1993, Extinct Juglandaceous Wood from the Eocene of Oregon and its Implications for Xylem Evolution in the Juglandaceae. *IAWA Journal*, 14/1, p. 101-111, Leiden.

Manning, W.E. 1978, The Classification within the Juglandaceae. *Annals of the Missouri Botanical Garden*, 65/4, p. 1058-1087, Kansas.

Müller-Stoll, W.R. & Mädel, E. 1960, Juglandaceen-Hölzer aus dem Tertiär des pannonischen Beckens. *Senckenbergiana lethaea*, 41/1-6, S. 255-295, 7 tf., Frankfurt am Main.

Takhtajan, A.L. 1987, Sistema magnoliofitov (The System of the Magnoliophyta), 611 p., Izdatel'stvo "Nauka", Leningrad.

Wheeler, E.A. & Landon, J. 1992, Late Eocene (Chadronian) Dicotyledonous Woods from Nebraska: Evolutionary and Ecological Significance. *Review of Palaeobotany and Palynology*, 74/3-4, p. 267-282, Amsterdam.

Wheeler, E.A. & Manchester, S.R. 2002, Woods of the Eocene Nut Beds Flora, Clarno Formation, Oregon, USA. *IAWA Journal*, Supplement 3, 188 p, Leiden.

Zhilin, S.G. 1980, The Order Juglandales. In: Zhizn' rasteniy (Live of Plants), 5/1, p. 329-342, Takhtadzhan, A.L., Ed., Izdatel'stvo “Prosveschenie”, Moscow.

Yatsenko-Khmelevskyi, A.A. 1954, Osnovy i metody anatomicheskogo issledovaniya drevesiny (Principals and Methods of Anatomical Investigation of Wood), 337 p., Izdatel'stvo Akademii Nauk SSSR, Moscow-Leningrad.

PLATE I.

Figures 1-20. – Engelhardioxylon mameticum Blokh. et Snezhk., holotype.

Fig. 1, 2, transverse section: diffuse-porous (1) and semi-ring-porous (2) arrangement of vessels, x26. Fig. 3, transverse section: the pith and the first growth ring, x35. Fig. 4, radial section, heterocellular rays, x206. Fig. 5, tangential section, uniseriate ray of growth ring 1, x206. Fig. 6, tangential section, long uniseriate end of biseriate ray of growth ring 9, x206. Fig. 7, tangential section, biseriate ray of growth ring 3, x206. Fig. 8, tangential section, biseriate ray of growth ring 9, x103. Fig. 9, tangential section, densely spaced rays of growth ring 11, x206. Fig. 10, radial section, vessel-ray pitting, x826. Fig. 11, tangential section, outlines of ray cells of uniseriate ray of growth ring 19, x206. Fig. 12, tangential section, axial parenchyma, x206. Fig. 13, radial section, intervessel pitting, x826. Fig. 14, radial section, scalariform perforation plate, x826.Fig. 15, radial section, a vessel element with simple perforation and long tail, x206. Fig. 16, tangential section, pith fleckt, x35. Fig. 17, tangential section, wide part of a ray with five-seriate layers, growth ring 11, x206. Fig. 18, tangential section, triseriate ray of growth ring 9, x155. Fig. 19, tangential section, four-seriate ray containing layers of five-seriate cells, growth ring 9, x103. Fig. 20, tangential section, outlines of ray cells of biseriate ray of growth ring 19, x206.

Table 1. The main diagnostic wood anatomical features of the subfamilies within the family Juglandaceae A. Rich. Ex Kunth

Subfamilies	Pith		Perforation plates		Porosity			Vessel walls		Vasicentric tracheids	Helical thicke-nings	Crystal inclusions	
	solid	Cham-bered	Scalari-form	simple	diffuse-porous	semi-ring-porous	ring-porous	thin	thick			in axial parenchyma	in ray paren-chyma
Platycaryoideae Mann.	+	-	-	+	-	-	+	+	-	+	+	-	+
Engelhardioideae (Mann.) Iljinskaja	+	-	+	+	+	+ -	-	+	-	-	-	-	-
Juglandoideae Leroy													
Juglandeae Nakai	-	+	-	+	+	+ -	-	+	-	-	-	+	-
Hicorieae Mann.	+	-	-	+	-	+	+	-	+	-	-	+	+ -

Table 2. Comparative anatomy of wood structures in members of the genus *Engelhadioxylon* Manchester

Anatomical characters	Age			
	Middle Eocene		Late Eocene	Oligocene
	Locality			
	USA: Oregon	USA: Texas	Germany: Lower Saxony	Russia: Kamchatka
	Species			
	E. nutbedensis Manchester (Manchester, 1983; Wheeler & Manchester, 2002)	E. texana Manchester, 1983	E. macro-crystallosum Gottwald, 1992	E. mameticum Blokh. et Snezhk. (Blokhina et al.,2002)
Growth rings	+	?	-	+
Vessel arrangement:				
- diffuse-porous	+	+	+	+
- semi-ring-porous	+ -	-	-	+ -
Vessel groupings:				
- solitary	+	+	+	+
- number of vessels in radial multiples	2-4	2-4	2-6	2-5
Number of bars per scalariform perforation plate	1-3	1-10	2-4	4-20
Intervessel pitting:				
- alternate	+	+	+	+
- pit diameter, μm	7	5-6	6	3.6-4.8(6)
Axial parenchyma:				
- terminal	?	?	?	+
- metatracheal	+	+	+	+
- width (in cell numbers) of tangential bands in transverse section	1-2	1-3	1-2(3)	1(2)
- number of cells in parenchyma strand	8	?	?	6-8
Rays:				
- uni-biseriate	+	+	+	+
- triseriate	+	+	+ -	+
- four seriate	+	+	-	+
- five seriate	-	-	-	+ -
Ray height in cell numbers:				
- uniseriate	?	?	2-8	2-42
- multiseriate	?	?	?	7-103
Uniseriate ends in multiseriate rays	1-7	1-6	?	2-23

Note: (+) – present, (-) – absent, (+ -) – rare, (?) – no data

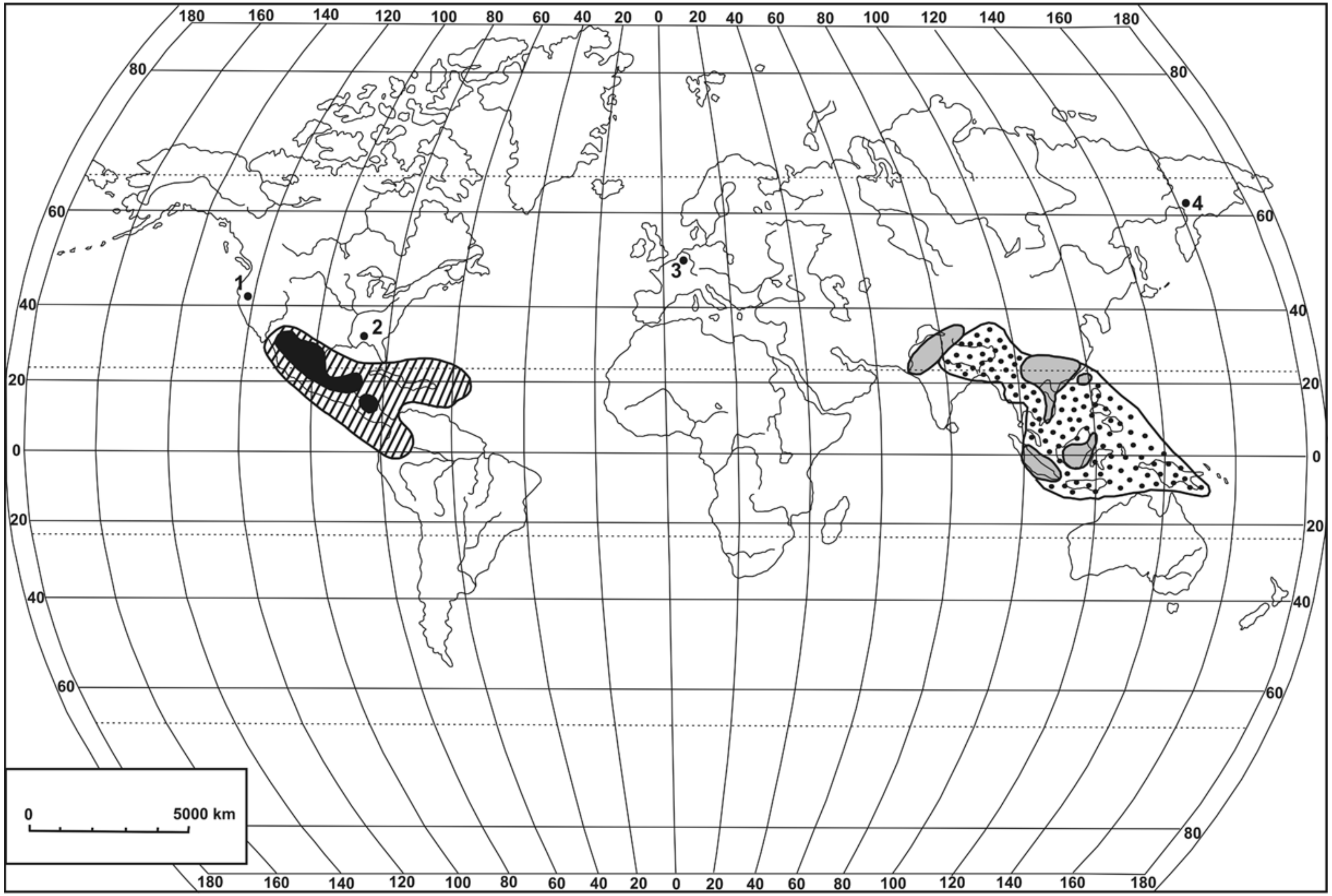
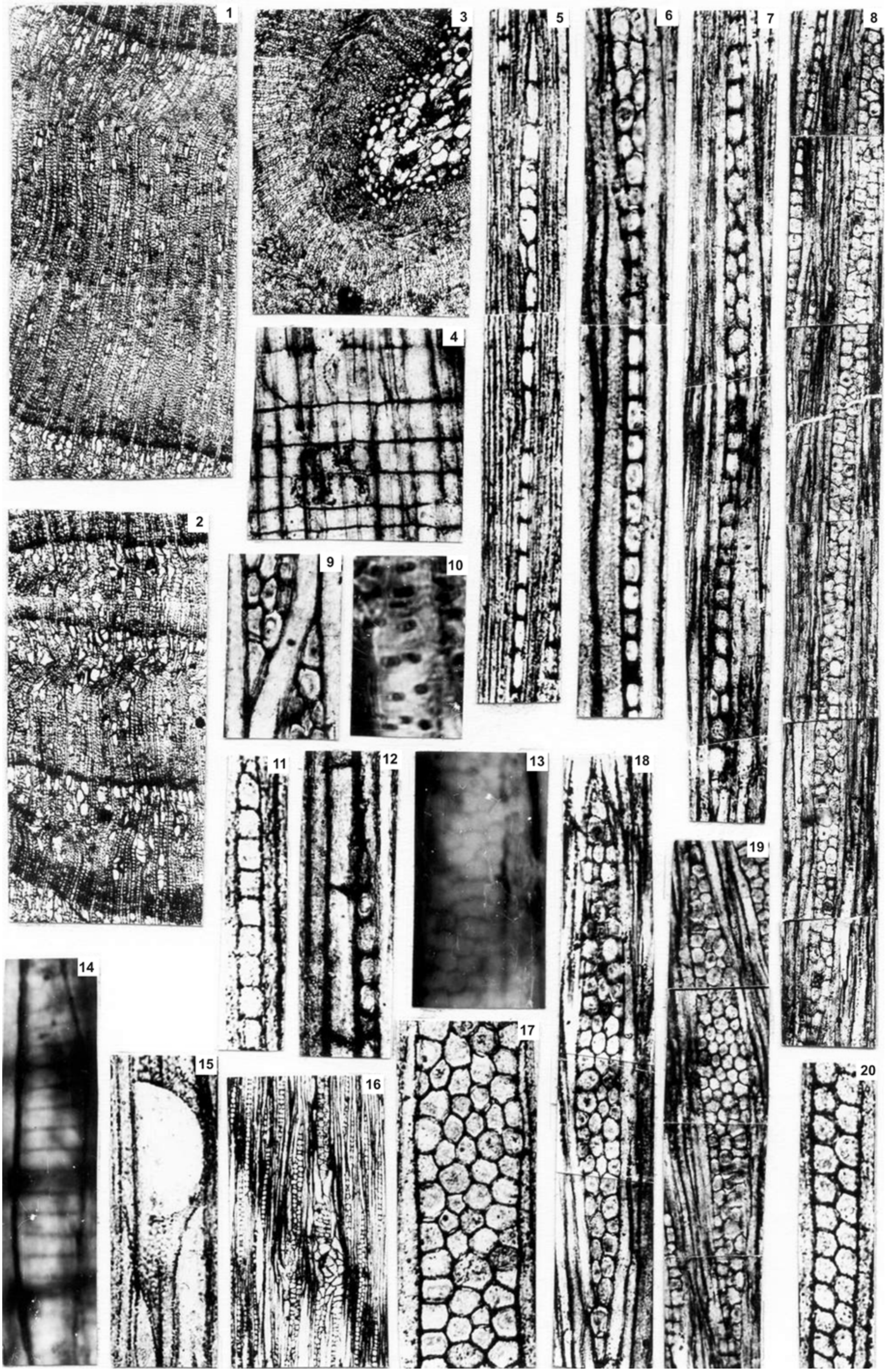


Figure !. Present-day distribution of Alfaroa, Oreomunnea, Engelhardia and Alfaropsis and localities of Engelhardioideae fossil woods.

- Oreomunnea
- Alfaroa
- Alfaropsis
- Engelhardia

1. Engelhardioxylon nutbedensid
2. E. texana
3. E. macrocrystallosum
4. E. mameticum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