A new species of *Rhysocaryoxylon* (Juglandaceae) from the Lower Eocene Fur Formation of Mors island (northwest Jutland, Denmark)

JAKUB SAKALA & VLADIMÍR GRYC

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A new species of the morphogenus *Rhysocaryoxylon* Dupéron (*Rhysocaryoxylon madsenii* Sakala & Gryc sp. nov.) is described from the Lower Eocene of the Fur Formation, Mors island, Denmark. This permineralized fossil angiosperm wood is semi-ring-porous with distinct growth ring boundaries, vessels solitary or in radial multiples of 2–5, perforation plates exclusively simple, and tyloses abundant. Rays are 1–5-seriate and heterocellular with a body composed of procumbent cells and 1–4 rows of upright marginal cells. Axial parenchyma is reticulate with numerous prismatic crystals both in chambered cells and idioblasts, forming long chains up to 12 cells high. Its equivocal botanical affinities within the family Juglandaceae are discussed.

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Jakub Sakala [rade@natur.cuni.cz], Charles University in Prague, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, 128 43 Praha, Czech Republic. Vladimír Gryc [gryc@mendelu.cz], Mendel University in Brno, Faculty of Forestry and Wood Technology, Department of Wood Science, Zemědělská 3, 613 00 Brno, Czech Republic. Corresponding author: Jakub Sakala

The Fur Formation with interbedded argillaceous diatomites and ash layers has an extensive history in the Danish geological literature (see Pedersen & Surlyk 1983 for geological overview and historical background). Although its age has been a matter of controversy, it is today generally considered to be Early Eocene in age (Pedersen et al. 2004). The sediments are often fossiliferous. Manchester & Wheeler (2006) noted several taxa of fossil plants from quarries on the island of Mors, including the remains of fruits, leaves and wood. The present paper provides a detailed wood anatomical study of one part (2 \times 2 \times 3 cm) of a bigger fragment (11.5 \times 10 \times 5.5 cm) of a stem which was originally at least 30 cm in diameter (estimate by Manchester & Wheeler (2006) based on growth ring curvature). The specimen was found in 2005 by Henrik Madsen in the Ejerslev Moler open pit mine (see Pedersen et al. 2004, Fig. 1B) on the east coast of Mors (Fig. 1) and preliminary studies of this fossil were undertaken by Manchester & Wheeler (2006). They presented two hypotheses for the fossil wood: it either represents a relatively early occurrence

of *Juglans* or belongs to an extinct juglandaceous type. The aim of our study is to indicate which one of these two hypotheses is more likely.



Fig. 1. Map of Denmark showing the position of the island of Mors (dark grey) and the fossiliferous site of the Ejerslev Moler open pit mine (white star in inset).

Material and methods

Three thin sections currently housed in the palaeobotanical collections in the Florida Museum of Natural History, Gainesville, USA, were studied. They had been prepared following standard techniques and were observed under optical microscopes Olympus BX–51 and Leica DM2000 in normal transmitted light. The anatomical description is in accordance with the IAWA Hardwood List (IAWA Committee 1989).

Systematic Palaeobotany

Juglandaceae DC. ex Perleb, nom. cons. *Rhysocaryoxylon* Dupéron *Rhysocaryoxylon madsenii* Sakala & Gryc, sp. nov. (Figs 2, 3)

Diagnosis: Heteroxylous semi-ring-porous wood with distinct growth ring boundaries. Vessels are solitary or in radial multiples of 2–5, and can exceed 300 μ m in tangential diameter, perforation plates are exclusively simple, tyloses abundant. Rays are 1–5-seriate and heterocellular with body composed of procumbent cells and 1–4 marginal rows of upright cells. Axial parenchyma is reticulate with numerous prismatic crystals both in chambered cells and idioblasts, forming long (up to 12 cells high) vertical chains.

Holotype designated here: One piece of wood (No. UF 19079 – 49102) and three thin sections (49102tr, 49102tg, 49102rd), all housed in the palaeobotanical collections of the Florida Museum of Natural History, Gainesville, USA.

Locus typicus: Ejerslev Moler Pit, Mors island, northwest Jutland, Denmark.

Stratum typicum: Lower Eocene of the Fur Formation.

Etymology: Named for the finder Henrik Madsen. *Occurrence:* Known from the type locality only.

Macroscopic description: One silicified piece of fossil wood, dimensions of the analyzed sample $2 \times 2 \times 3$ cm, colour brown-black, interpreted as a fragment of a trunk.

Microscopic description: Growth rings: present. Wood: semi-ring-porous (Fig. 3A). Vessels: 4-6 per square mm, solitary (36%) or in radial multiples of 2–5 (generally 2–3, Fig. 2A); tangential diameter of early vessels 160–240–365 µm (minimum–mean–maximum), latewood vessels 80–140–280 μ m, vessels in the earlywood are distinctly larger than those in the latewood (gradual change), outline of solitary vessels round to radially elongated (oval) in transverse section; vessel element length 426–642 μ m (mean 522 μ m); vessels walls are thick (about 5 μ m); perforation plates are exclusively simple, end walls oblique; tyloses are abundant (Fig. 3F); intervessel pits alternate, polygonal in shape (Fig. 3C), medium in size $(7-10 \mu m)$. Rays: heterocellular up to 5 cells wide (18–98, mean 54 μ m), commonly 2–5 seriate (Figs 2B, 3G) and 128–573 μ m high (mean 281 μ m), uniseriate rays are rare, body of multiseriate rays is composed of procumbent and square cells with 1-4 rows of upright marginal cells (Fig. 3E); no crystalliferous elements observed; vesselray pits not observed. Axial parenchyma: reticulate with numerous prismatic crystals both in chambered cells and idioblasts forming long (up to 12 cells high) vertical chains (Fig. 3D), rarely paratracheal vasicentric (Fig. 3B). Fibres: undistinguishable pits, non-septate; walls medium-thick.

Discussion

The anatomy of this fossil wood was originally described by Manchester & Wheeler (2006) in Prague where they clearly showed its juglandaceous affinity and resemblance to the genus *Juglans*. The wood of Juglandaceae, both extant and extinct, has been reviewed several times (e.g., Kribs 1927; Heimsch

Fig. 2. **A**, frequency of solitary vessels and vessels in radial multiples of 2, 3, 4, and 5. **B**, ray seriation (ray width in cell numbers) in the holotype sample of *Rhysocaryoxylon madsenii*.



& Wetmore 1939; Stark 1953; Müller-Stoll & Mädel 1960; Manchester 1987; Dupéron 1988; Manchester & Wheeler 1993; Blokhina 2007; Cao 2008; InsideWood 2004–onwards) so the botanical affinities of our fossil wood can be ascertained with a good degree of certainty. As already stated by Manchester & Wheeler (2006), the lack of scalariform perforations distinguishes our fossil sample from wood of the subfamily Engelhardioideae Iljinskaya sensu Manos & Stone (2001), both modern (genera Engelhardia, Oreomunnea, Alfaroa and ?Alfaropsis) and fossil (morphogenus Engelhardioxylon defined by Manchester 1983). The lack of crystals in idioblasts in ray parenchyma sets our wood apart from the extant *Platycarya* and fossil *Clarnoxylon* defined by Manchester & Wheeler (1993); Platycarya also exhibits ring-porous wood with vasicentric tracheids and spiral thickening in vasicentric tracheids and small vessels (Heimsch & Wetmore 1939). The long mostly 1–3-seriate tangential lines of axial parenchyma with crystals differentiate our wood from Pterocarya and the sections Cardiocaryon, Trachycaryon and Juglans of the genus Juglans (Dupéron 1988 p. 274). Carya generally has very thick-walled smaller vessels, and if crystalliferous, crystals are solitary (or only a few) and placed in the significantly enlarged axial parenchyma cells (idioblasts). Our wood with long (up to 8–10 cells high) crystalliferous chains in axial parenchyma most closely resembles that of the section Rhysocaryon of Juglans, i.e., the so-called 'black walnuts'. Its features point to a particular position different from both wood anatomical groups in the section *Rhysocaryon*, i.e., north temperate black walnuts (semi-ring porous wood, enlarged axial parenchyma cells with crystals) and tropical black walnuts (absence of reticulate thickening, long crystalliferous chains in axial parenchyma with > 5 crystals), as distinguished by Miller (1976 p.



Fig. 3. Rhysocaryoxylon madsenii. A, semi-ring-porous wood with distinct growth ring boundaries (white arrows), TS. B, vessel surrounded by paratracheal vasicentric parenchyma (black arrows) and crystals in reticulate axial parenchyma (white arrow), TS. C, alternate intervessels pits, TLS. D, part of a 12 cell high crystalliferous chain in axial parenchyma with both chambered cells and idioblasts (at the bottom), RLS. E, heterocellular ray with four marginal rows of upright cells (black arrows), RLS. F, general view with abundant tyloses within vessels, RLS. G, general view with rays, TLS. Scale bars = $25 \,\mu m$ in C; 150 µm in B, D, E; 250 µm in F, G; 500 μ m in A. RLS = radial longitudinal section; TLS = tangential longitudinal section; TS = transverse section.

375) based on extant material. In fact, it seems that our wood belongs to an extinct type, not really attributable to a living group, mainly with respect to its unique crystalliferous axial parenchyma with long vertical chains of both chambered cells (shorter, slightly enlarged, rather typical of Juglans) and idioblasts (as long as normal axial parenchyma cells but significantly larger, rather typical of Carya). It must be stressed that a uniqueness of the crystalliferous parenchyma that we observed in our wood has already been recorded by Selmeier (1995) in Eucaryoxylon castellanii from the Eocene of France. However, Selmeier's (1995) climatically induced explanation, i.e. more frequent crystals occur in tropical species (see Miller 1976 p. 375) cannot be completely adopted for our wood which in contrast to Eucaryoxylon castellanii is semi-ring-porous with distinct growth ring boundaries.

Despite the presence of idioblasts, our wood is attributable to the morphogenus Rhysocaryoxylon which was defined by Dupéron (1988 p. 263) to accommodate fossil woods close to the section *Rhysocaryon* of *Juglans*. *Rhysocaryoxylon* was nomenclaturally superfluous when published and therefore illegitimate from the nomenclatural point of view, so either a proposal must be prepared for Taxon to conserve the name *Rhysocaryoxylon* against *Caryojuglandoxylon*, or new combinations must be published in the future. Nine species have so far been assigned to *Rhysocaryoxylon* (Gregory et al. 2009): type species R. schenkii (Felix) Dupéron, R. triebelli (Caspary) Dupéron, R. tertiarum (Prakash & Barghoorn) Dupéron, R. fryxellii (Prakash & Barghoorn) Dupéron, R. caucasicum (Gaivoronsky) Dupéron, R. pilinyense (Greguss) Dupéron, R. pravalense S. Iamandei & E. Iamandei, R. ocii S. Iamandei & E. Iamandei and R. transylvanicum S. Iamandei & E. Iamandei. The type species was originally described by Felix (1884) and later reinvestigated in more detail by Müller-Stoll & Mädel (1960). This wood is however very different from our new species in having only very narrow 1–2(3)-seriate rays. Similarly, R. triebelli also has very narrow rays and, moreover, presents smaller vessels (up to 200 μ m) and very long chains (up to 20 cells) of crystalliferous parenchyma (Müller-Stoll & Mädel 1960; Van der Burgh 1973). Wheeler & Dillhoff (2009) recently reviewed the type species of both *R. tertiarum* and *R. fryxellii*, which had originally been described by Prakash & Barghoorn (1961a, b) from the Middle Miocene Vantage Flora (Washington, USA). Although R. tertiarum is quite similar to our wood, both R. tertiarum and R. fryxellii have narrower homocellular rays which differentiate them from *R*. madsenii. Rhysocaryoxylon caucasicum is also very different in that its rays are only 1-2-seriate (Gaivoronsky 1962). Another species R. pilinyense was originally described by Greguss (1969). Thin sections of the type

species are deposited in the Botanical Department of the Hungarian Natural History Museum in Budapest under No. 2008.222.3., and they were recently studied by the first author. This species differs from ours by diffuse-porous wood with thinner rays and generally smaller vessels with thicker walls. Finally, there are three species of Rhysocaryoxylon described by Iamandei & Iamandei (2002, 2003) which can also be differentiated by their significantly smaller vessels with a tangential diameter up to 126 μ m, narrower 2–3-seriate rays and not very obvious tangential bands of axial parenchyma in R. ocii and R. transylvanicum. A unique combination of three anatomical features in our wood sample, namely, relatively big vessels (which can exceed 300 μ m), heterocellular rays 1–5 cells wide, and long chains (up to 12 cells) of crystalliferous parenchyma with chambered and significantly enlarged cells (idioblasts), allows its recognition as a new species within the morphogenus *Rhysocaryoxylon*: *R. madsenii* Sakala & Gryc, sp. nov.

Conclusions

Manchester & Wheeler (2006) preliminarily described this fossil wood and proposed that it might either represent a relatively early occurrence of Juglans or an extinct type related to juglandaceous fruit genera such as Juglandicarya or Cruciptera. Our detailed microscopical description clearly shows that the later hypothesis is the more plausible. The particularity of crystalliferous axial parenchyma does not allow us to conclude a direct similarity between our fossil wood and the genus Juglans as we know it today. It rather points to an extinct type, which is not in contradiction with its Early Eocene age. In support of this conclusion is the observation by S. R. Manchester that nuts of the section Rhysocaryon of Juglans (black walnuts), although morphologically distinctive and thick-walled (likely to be preserved), seem to be missing from the European fossil record (Manchester, personal communication 2011).

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