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Eucaryoxylon castellanii n. sp., (Juglandaceae), a silicified wood from the Eocene of Castellane, France

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With 18 Text-figures

Abstract

Tertiary sediments from Castellane, France, yielded in the past several pieces of fossil wood assigned to Hamamelidaceae, Icacinaceae, Rosaceae, Sapindaceae and Sapotaceae (GRAMBAST-FESSARD 1966, 1968, 1969). The new fossil, *Eucaryoxylon castellanii*, family Juglandaceae, has an excellent preserved wood structure. Its anatomical features are similar to extant *Carya* species. A conspicuous feature of the fossil are crystalliferous chains in axial parenchyma and enlarged barrel-shaped cells (idioblasts). The crystals of the fossil are formed in what may be called a „mirror-image" fashion (CARLQUIST 1988: 221).

Kurzfassung

Ein Kieselholz aus Castellane, Frankreich, zeigt die anatomischen Merkmale der rezenten Gattung *Carya*, Familie Juglandaceae (Walnußgewächse). Das Holz aus dem Eozän ist in seiner mikroskopischen Struktur hervorragend erhalten geblieben. Es wird als *Eucaryoxylon castellanii* n. sp. beschrieben. Ein auffallendes Merkmal des dunklen Holzes ist das Vorkommen zahlreicher Einzelkristalle in axialen Parenchymzellen sowie in Idioblasten.

Contents

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1. The *Carya* wood from Castellane

The fossil wood, deposited in the Bavarian State Collection of Palaeontology and historic Geology, Munich (Collection R. BAUMGARTNER), was found in Eocene sediments of Castellane, Basses-Alpes, SE France. Several fossil woods from tertiary sediments of Castellane have been described in the past (GRAMBAST-FESSARD 1966, 1968, 1969). The anatomical structure of the new silicified wood is partly excellent preserved, especially the rays, the crystalliferous chambered parenchyma strands and the idioblasts.

Tertiary sediments from Castellane have yielded up to date the following silicified wood specimens (GRAMBAST-FESSARD 1966, 1968, 1969):

Sapindoxylon elattostachyoides	(1966) – Sapindaceae
Maloidoxylon castellanii	(1966) – Rosaceae
Manilkaroxylon crystallophora	(1968) – Sapotaceae
Palaeosideroxylon flammula	(1968) – Sapotaceae
Apodytoxylon hamamelidoides	(1969) – Icacinaceae
Hamamelidoxylon castellanii	(1969) – Hamamelidaceae

1.1 Anatomical description

Juglandaceae

Eucaryoxylon MÜLLER-STOLL & MÄDEL (1960)

Generotype: *E. crystallophorum* MÜLLER-STOLL & MÄDEL (1960: 275)

Eucaryoxylon castellanii n. sp.

Material: One silicified specimen, 11,5 cm long, maximal diameter 5,5 cm, color dark, 4 thin-section slides; Inv.-No. BSP 1990 IV, Bayerische Staatssammlung für Paläontologie und historische Geologie, München (Collection R. BAUMGARTNER).

Locality: Castellane, Basses-Alpes, SE France. No further information about the finding site is available. The surrounding of Castellane has yielded in the past several silicified dicotyledonous woods (GRAMBAST-FESSARD 1966, 1968, 1969).

Age: After the label "Eozän", Eocene.

Derivation of the name "castellanii": Locality Castellane.

Diagnosis

Growth rings absent or inconspicuous.

Wood diffuse-porous, vessels solitary (21 %) and radial multiples up to 6 pores, tangential diameter 55-105 µm, thick-walled, ca. 10 µm, perforation plates exclusively simple, vessel elements 315-610 (middle 476) µm, intervessel pits ca. 5 µm, vessel-ray pits similar, not enlarged or gash-like; jellowish brown to dark deposits, thin-walled tyloses (?).

Axial parenchyma apotracheal, scattered wavy parenchyma bands 1-2 cells wide, only few individual parenchyma cells associated with vessels, abundant conspicuous chambered parenchyma cells (strands) with prismatic crystals and large idioblasts.

Fibres thick-walled, polygonal in cross section, mostly in radial rows.

Rays 1-2seriate, decidedly heterocellular with procumbant and upright cells, more than 4 rows of upright cells common, bi-seriate portions of rays partly not wider than uniseriate portions, large rays up to 880 µm high, exceptionally 1,4 mm; crystals in ray cells absent.

Microscopic features
(Fig. 1–16)

Silicified secondary dicotyledonous wood without pith or bark.

Transverse thin-section slides: isolated patches with wood structure are interrupted by dark compression zones (partly with prismatic crystals).

Growth rings

Absent, without any zones; locally by microscopic enlargment inconspicuous 4-7 radial flattened fibres. No significant variation in the vessel diameter is noticed.

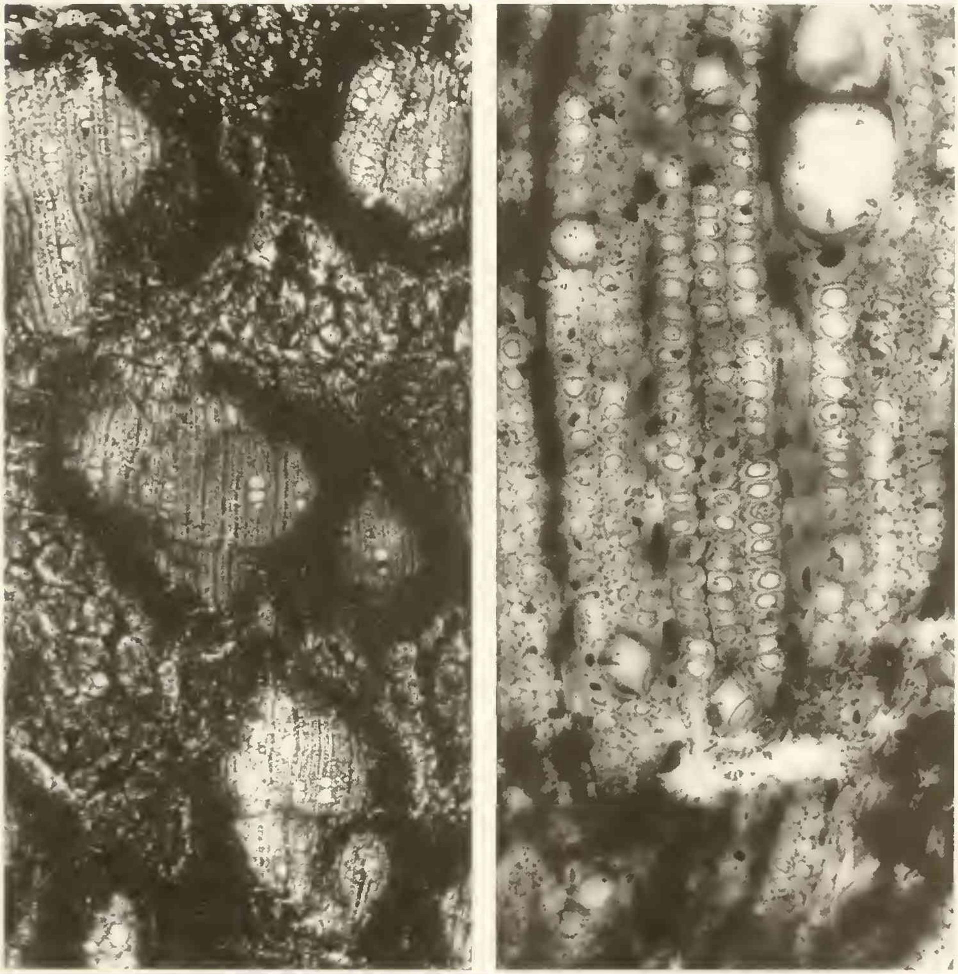

Fig. 1. Cross section. Left: Dark compression zones and isolated patches with wood structure. × 25. Right: Thick-walled fibres in radial rows, four parenchyma cells with rhomboid crystals. × 185.

Vessels

Diffus-porous. Solitary 21%, radial multiples of two 38%, three 25%, four 7%, five 3%, six 6% and a faint tendency to tangential, nest-like clusters; shape of vessel outline circular to oval, 22-33 vessels/mm² (counting method: IAWA List 1989; WHEELER 1986).

Tangential diameter of solitary vessels 55-85 μm, multiples of two (radial : tangential) 135:70 μm, multiples of three 170:70 μm, 175:100 μm, 205:105 μm, multiples of four 250:96 μm, multiples of five to six vessels 230:50 μm, 325:90 μm, 450:80 μm; clusters with 7 vessels, 260:135 μm; vessels thick-walled, ca. 10 μm (transverse section); yellowish brown to dark deposits (Fig. 8, left), thin-walled tyloses (?).

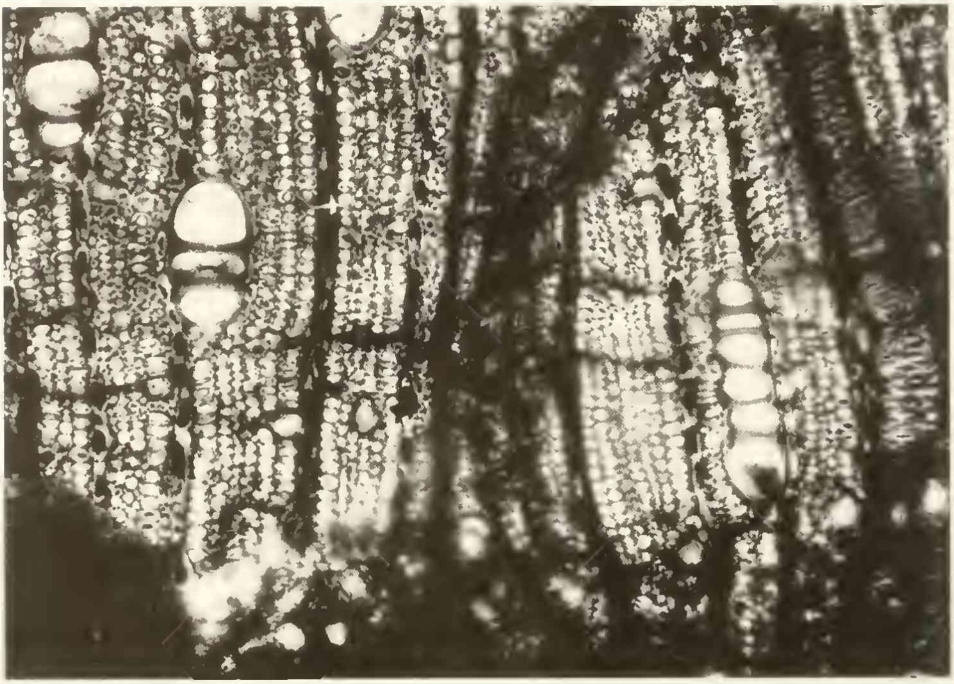

Fig. 2. Cross section. Vessels in radial multiples of 3–6, tangential parenchyma bands and crystalliferous parenchyma cells. × 115.

Large vessel members 315–610 (middle 476) μm long, small vessel members 65–142 μm long, perforation plates exclusively simple, end walls of short elements mostly with right angles, large elements often showing caudate ends, attenate-tailed on both sides (Fig. 6, right), intervessel pits 4–5 μm (Fig.7), alternate, arranged in diagonal rows, the outline of crowded pits is polygonal in surface view.

Vessel-ray and parenchyma-ray pitting in size and shape similar to intervessel pits, not enlarged or gash-like; vessel-ray pits in crossfields crowded, polygonal, e.g. crossfield 8×32 μm with about 34 vessel-ray pits.

Ground tissue

Fibres libriform, main part of the ground tissue, mostly in radial rows, 2–8 rows between two rays, diameter 15–20 μm, moderatly thick-walled, ca. 5 μm (Fig. 5).

Axial parenchyma

Predominatly apotracheal, scattered interrupted bands, 1–2 cells wide with dark deposits, locally a net-like structure with the rays, distance of two bands in radial direction e.g. 60 µm.

Parenchyma cells very scarse in contact with vessels, parenchyma cells e.g. axial 50–80 µm, radial 25–30 µm.

Hundreds of diffuse distributed parenchyma cells with prismatic crystals, conspicuous already in transverse section (Fig. 1–3, 6 left), partly also within the dark compression zones. Longitudinal slides: chambered strands with crystals abundant, 2–5 strands/mm in radial section, 1–3 strands/mm in tangential section (Fig. 8, 15). Number of vertical chambered cells (e.g.): 7 cells (185 µm), 8 (430-575 µm), 9 (470 µm), 12 (410 µm), 14 (580 µm), 16 (550–600 µm), 19 (750 µm), 22 (835 µm); locally 2 axial parenchyma strands in contact, radial 75–110 µm wide.

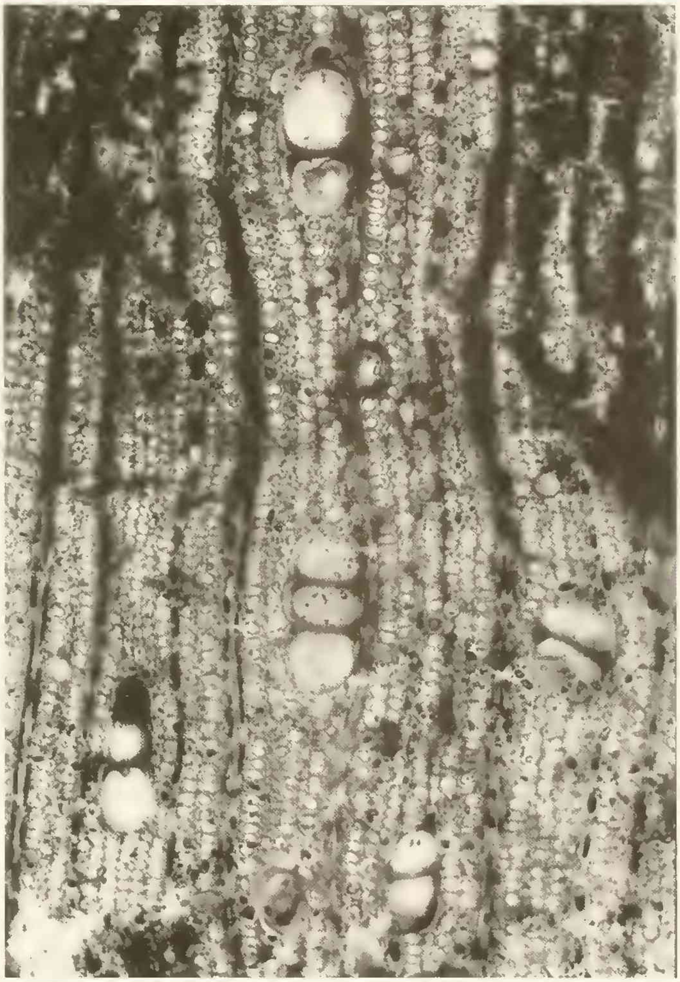

Fig. 3. Cross section. Vessels in multiples of 2–3, fibres in radial rows, rays and parenchyma cells with crystals (above). x 115.

Pocket-like idioblasts measuring 50–95 µm in axial and 25–60 µm in radial section containing single rhomboid crystals, maximal diameter of large prismatic crystals 40–60–(72) µm (Fig.13–14, 16).

Rays

1–2seriate, 11–14 rays/mm; uniseriate rays e.g. 2–13 cells high, (105-335 µm), mostly 4–12–(18) cells; 1–2seriate rays 20–40 cells in height, mostly 340–882 µm, exceptionally up to 1,4; rays decidedly heterocellular, part of uniseriate sections often not larger than sections with procumbant cells, procumbant cells 15–35 µm, axial elongated cells 65–80 µm, ray cells mostly filled by dark plugs (Fig. 9–12).

Anatomical features of the *Carya* wood from Castellane, Inv.-No. BSP 1990 IV, according IAWA List of microscopic features for hardwood identification (ed. by WHEELER, BAAS & GASSON, 1989).

Feature No.	List of features
2	Growth ring boundaries indistinct or absent
5	Wood diffuse-porous
10	Vessels in radial multiples of 4 or more common
13	Simple perforation plates
22	Intervessel pits alternate
23	Shape of altenerate pits polygonal
25	Intervessel pit size small, 4 - 7 µm
30	Vessel-ray pits similar to intervessel pits
41	Mean tangential diameter of vessel lumina, 50-100 µm
48	Vessels per square millimetre, 20-40
53	Mean vessel element length, 350-800 µm
56	Tyloses common (?)
58	Brown deposits in vessels
69	Fibres thin- to thick-walled
86	Axial parenchyma in narrow bands or lines up to three cells wide
97	Ray width 1 to 3 cells
108	Body ray cells procumbent with over 4 rows of upright and/or square marginal cells
115	Rays per millimeter 4–12/mm
136	Prismatic crystals present
142	Prismatic crystals in chambered axial parenchyma cells
156	Crystals in enlarged cells

1.2 Comparison with extant woods

The anatomical structure of the fossil was compared with microscopic descriptions: BOUREAU (1957); BRAZIER & FRANKLIN (1961); CHATTAWAY (1955, 1956); DETZNER (1910); DUPÉRON (1988); GASSON & CUTLER (1990); GREGUSS (1959); IAWA List (1989); ILIC (1991); KRIBS (1927, 1928); LECOMTE (1921, 1925); MANCHESTER (1983); METCALFE & CHALK (1950); MILLER (1976); MULLER-STOLL & MADEL (1960); PANSHIN & ZEEUW (1964); RECORD (1934); SCURFIELD & MICHELL (1973); WHEELER (1986, 1991a, 1991b).

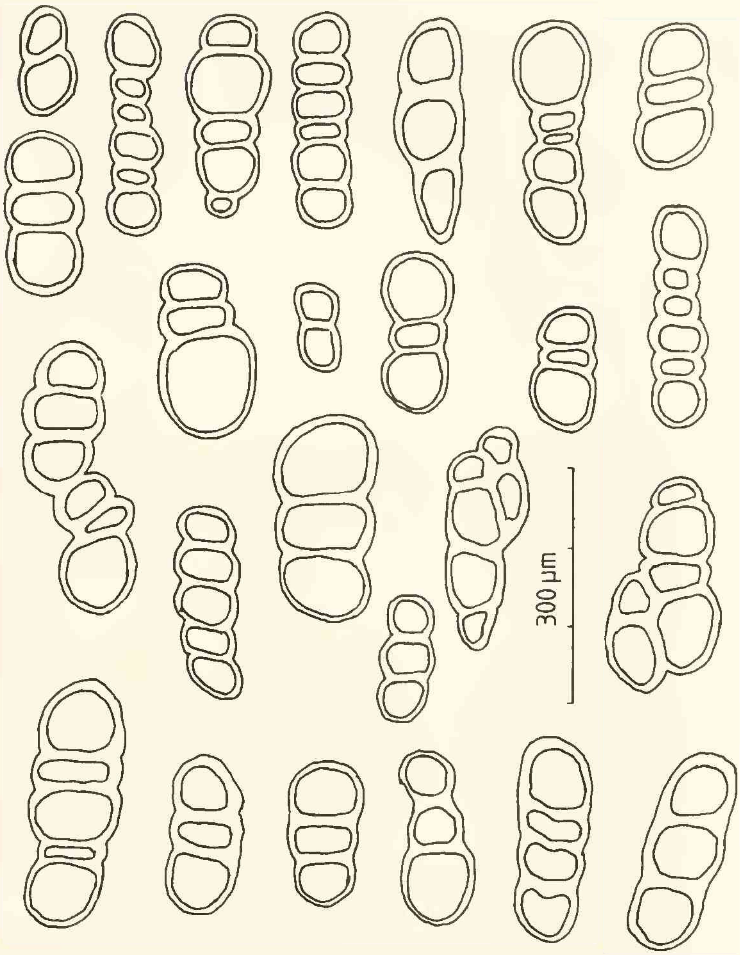

Fig. 4. Cross section. Vessel groupings, vessels thick-walled.

Thick-walled vessels, comparatively few pores, vessel perforations exclusively simple, fine apotracheal wavy tangential parenchyma bands, inconspicuous rays, crystal-bearing axial parenchyma strands, barrel-shaped cells with large rhomboid crystals (idioblasts) are characteristic features from the present silicified wood. The fossil resembles the wood of the genus *Carya*, family Juglandaceae.

The Juglandaceae comprise 4 tribes with 8 extant genera: Juglandeae (*Juglans, Pterocarya, Cyclocarya*), Engelhardieae (*Engelhardia, Oreomunnea, Alfaroa*), Hicorieae (*Carya*) and Pterocaryeae (*Platycarya*). Anatomical features important in distinguishing the 4 extant tribes are presented by MANCHESTER & WHEELER (1993: 107, Tab. 1). The most fundamental differences involve pith and vessel element perforations.

The wood anatomy of extant genera of the Juglandaceae has been investigated mainly by KRIBS (1927, 1928), HEIMSCH & WETMORE (1939), STARK (1953), MULLER-STOLL & MADEL (1960), MILLER (1976) and MANCHESTER (1981). Further references, see GREGORY (1994: 71-72).

KRIBS (1927), based on the limited material available to him, has published a first key for identification and separation, emended by MÜLLER-STOLL & MADEL (1960: 261, Tab. 1), MANCHESTER (1983: 163) and DUPÉRON (1988: 274). The anatomical keys to fossil and extant juglandaceous woods from MANCHESTER (1983) and DUPÉRON (1988) are a valuable aid for identification of the present fossil: MANCHESTER - "Vessel perforations plates exclusively simple - vessels very thick-walled - crystals, when present, in large solitary idioblasts of the axial parenchyma - *Eucaryoxylon, Carya*." DUPÉRON - II, B, 2, a. "Cristeaux dans les grosses cellules en forme de tonneau, isolées ou en files de 2–3 - *Eucaryoxylon* spp."

Barrel-shaped idioblasts (Fig. 12–16), thick-walled vessels (Fig. 2-5) and exclusively simple perforation (Fig. 6-7) are definitely three conspicuous features of the present fossil. MULLER-STOLL & MADEL-ANGELIEWA (1983: 662):

Idioblasts are within the Juglandaceae a typical feature for the genus *Carya* („Sobald jedoch Kristallidioblasten vorhanden sind, können sie sicher auf *Carya* bezogen werden"). The taxonomic value of idioblasts in axial parenchyma (not in rays; exeption *Carya myristicaeformis*) is a consistent feature of *Carya* (MANCHESTER & WHEELER 1993: 108).

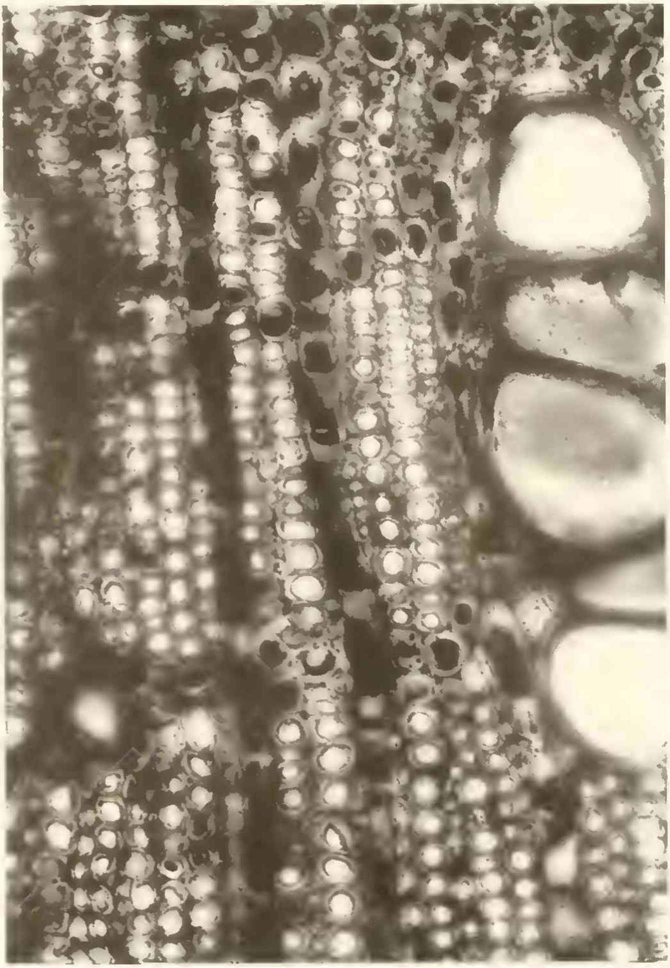

Fig. 5. Cross section. Thick-walled vessels, thick-walled fibres and dark parenchyma cells, 2 crystals. × 185.

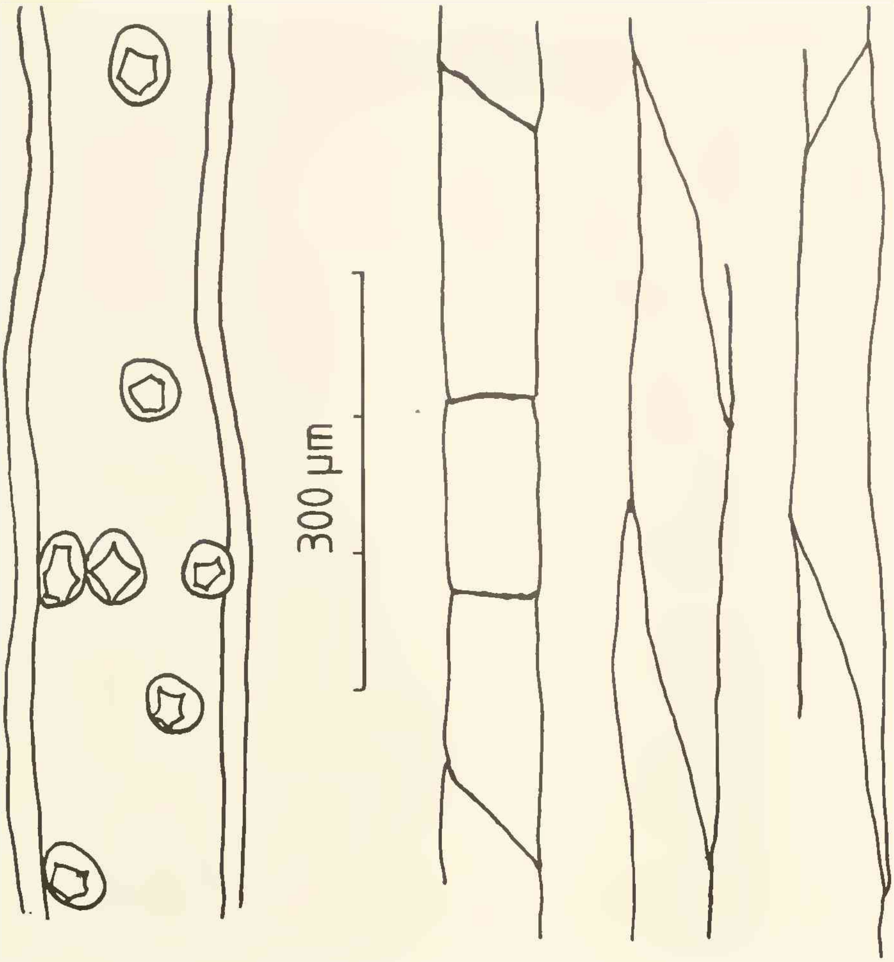

Fig. 6. Cross section (left): Crystalliferous parenchyma cells between two rays. Tangential section (right): Vessel elements with single perforation.

The structural features of this fossil, particularly idioblasts in combination with a suite of other features diagnostic of the Juglandaceae, clearly indicate its affinities with the genus *Carya*.

P r i s m a t i c c r y s t a l s

The most distinctive feature of the fossil from Castellane is the abundant occurence of crystals (Fig. 12-16):

a) crystalliferous chains with septate cells in axial parenchyma, is a typical feature of *Juglans* (Muller-Stoll & Madel 1960: 259, Abb.5; Fig. 18, this paper)
b) idioblasts with large rhomboidal crystals (if present), is a typical feature of *Carya* (Muller-Stoll & Madel 1960: 259, Abb.6; Fig. 18, this paper).

The fossil wood does not possess crystals (idioblasts) in the rays – see extinct Juglandaceae *Clarnoxylon* Manchester & Wheeler (1993), with „rhomboidal crystals common in rays" or

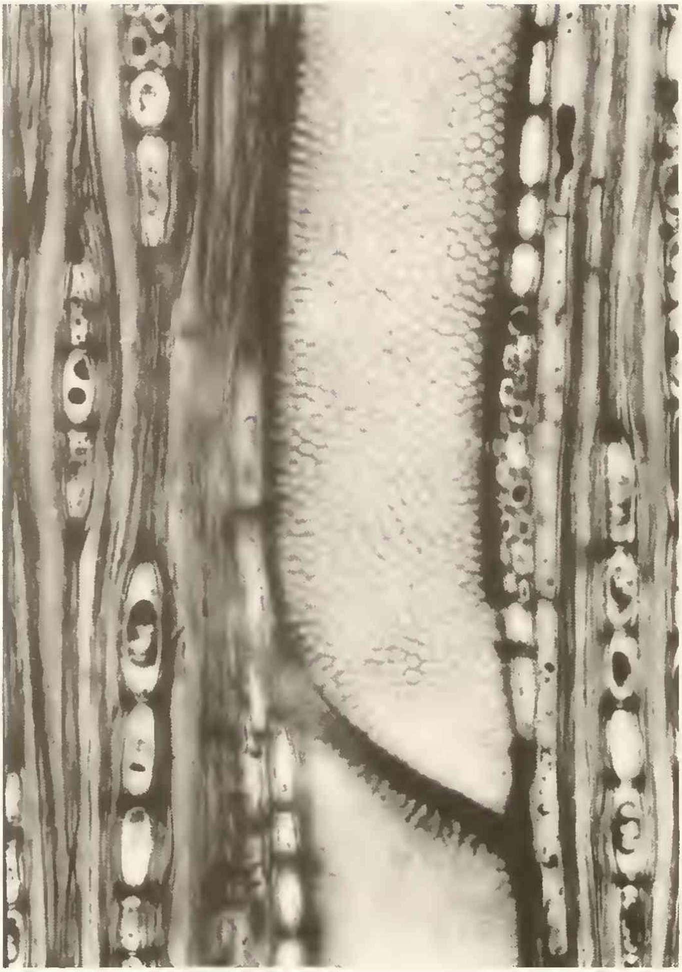

Fig. 7. Tangential section. Vessels with simple perforation, intervessel pits alternate, heterocellular rays. × 290.

Juglandaceae *Engelhardioxylon macrocrystallosum* GOTTWALD (1992), with enlarged crystals in the procumbent ray parenchyma.

All available thin-sections (Xylothec Dr. GROSSER; – STERN 1988, Index Xylariorum, p. 229 –230) and published descriptions of extant *Carya* were compared. There was not an single species with similar occurrence and distribution of crystals like the fossil (abundant cristalliferous parenchyma strands + idioblasts). After MULLER-STOLL & MADEL (1960) and MANCHESTER & WHEELER (1993: 108) crystalliferous chains of axial parenchyma are a consistent feature in *Juglans*, idioblasts in axial parenchyma a typical feature of *Carya*.

Crystalliferous cells are obviously not allways a consistent feature within all taxa or samples of extant and fossil Juglandaceae (e.g. *Carya*). However, the presence of large barrel-shaped cells (idioblasts) is of great diagnostic value to separate definitely *Carya* and *Juglans* (DUPÉRON 1988, pl. I, 2 - *Carya tonkinensis*; pl. I, 4 - *Juglans neotropica*). The long chain of 23 crystalliferous parenchyma cells from *Juglans neotropica* (DUPÉRON 1988: 255) is similar with the numerous axial parenchyma chains of the fossil wood from Castellane.

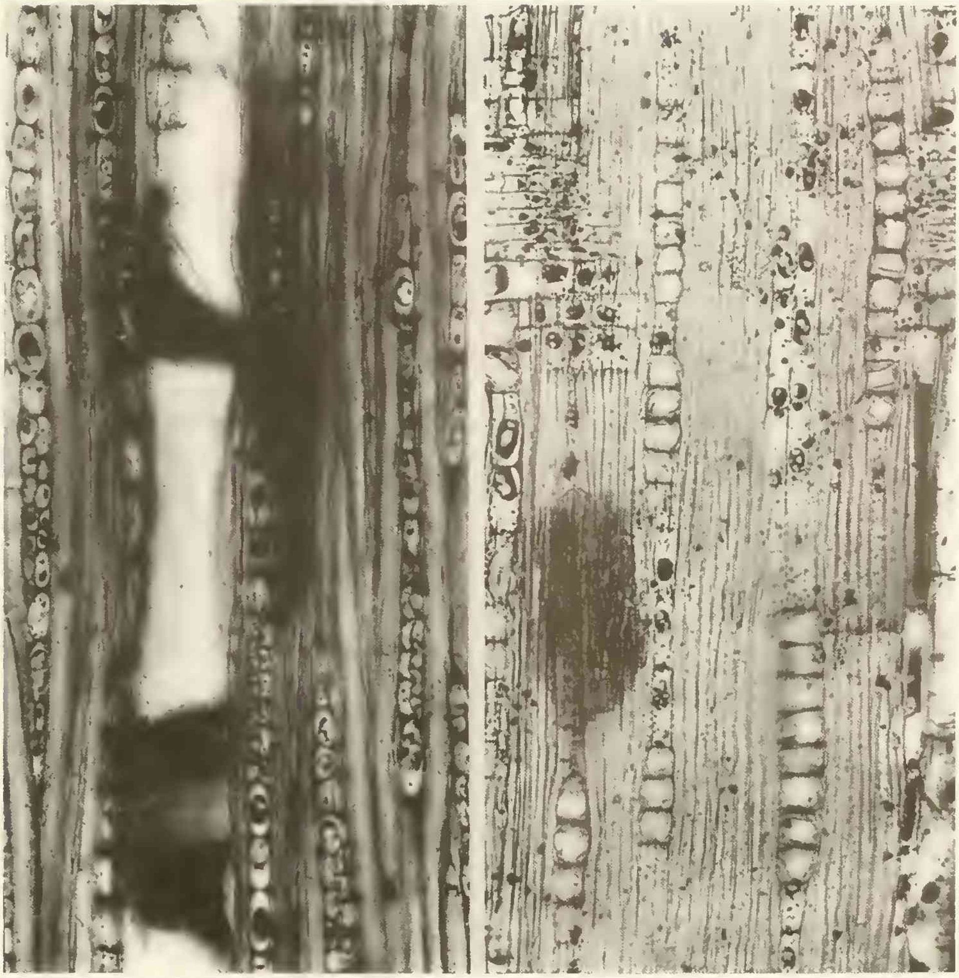

Fig. 8. Tangential section (left): Brown deposits in vessels. × 185. Radial section (right): crystalliferous chambered parenchyma strands. × 115.

The fossil wood resembles in transverse section, but only with regard to the abundant occurrence of crystals, *Carya tonkinensis* LECOMTE (HEIMSCH & WETMORE 1939: 657, Fig. 21; see Fig. 17, this paper). Especially in longitudinal sections, the crystals of the fossil are formed in what may be called a "mirror-image" fashion (CARLQUIST 1988: 221; Fig. 7.2.1-4). Mention should be made of these various manifestations, which are according CARLQUIST (1988) of systematic value.

MÜLLER-STOLL & MADEL (1960) emphasises that they have found either crystalliferous parenchyma strands (*Juglans*-species, asiatic *Carya*-species) or idioblasts (american *Carya*-species). In the fossil wood from Castellane both crystalliferous cell types are present (Fig. 14-16).

The literature on crystals in wood does not indicate that climate or latitude influences crystal arrangement (MILLER 1976: 375). After the experience of R. B. MILLER (1976) crystals occur more abundant in tropical species than in temperate species. Species in tropical zones seem to accumulate crystals more frequently (BAAS 1973; MILLER 1976).

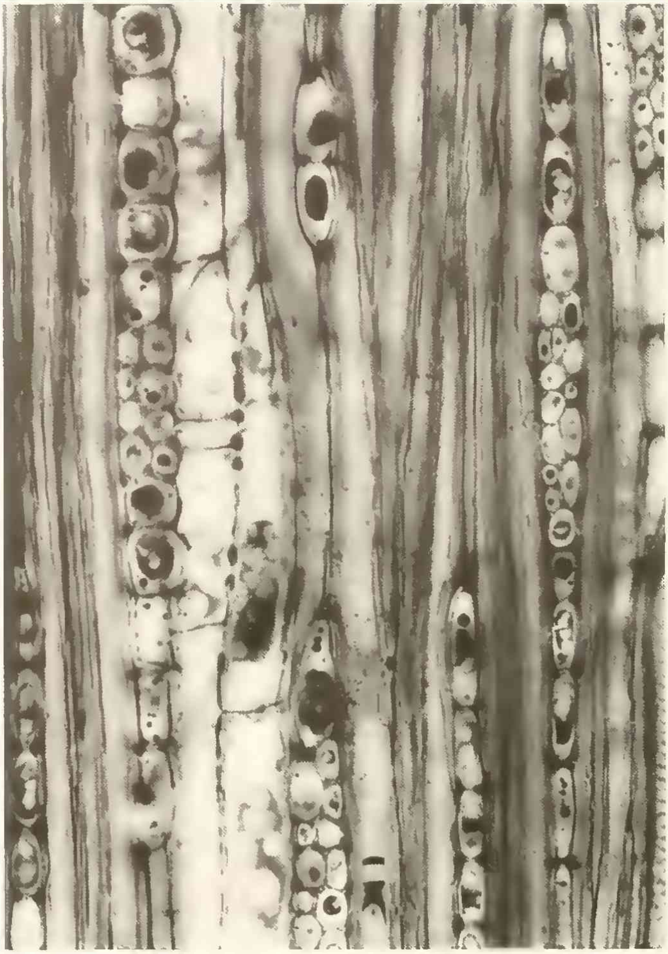

Fig. 9. Tangential section. Rays heterocellular, axial parenchyma cells and nonseptate fibres. × 290.

Vessels

The majority of the extant *Carya* species (25; MANCHESTER & WHEELER 1993: 108)) is distinctive ring-porous (taxa of North Amerika). However, there are some taxa with semi-porous or diffuse porous structure (DUPÉRON 1988: 253, "certains *Carya*, comme beaucoup des *Juglans*, ont des bois semi-poreux a diffus"; PRIVE (1974: 250, "chez les especes asiatique de *Carya*, les pores sont diffus ou disposes en zones semi-poreuses; MANCHESTER & WHEELER (1993, Tab. 1; Hicorieae - ring-porous & semi).

The fossil wood has indistinct (absent) growth rings with locally some radially flattened fibres. The vessels are diffuse-porous, perhaps with a tendency to semi-ring-porous. Vessels and fibres are thick-walled (Fig. 2–5).

Finally, it should be stressed that the vessel grouping of the fossil (radial multiples of 4–6) is untypical in most of the extant *Carya* species (available thin sections and published

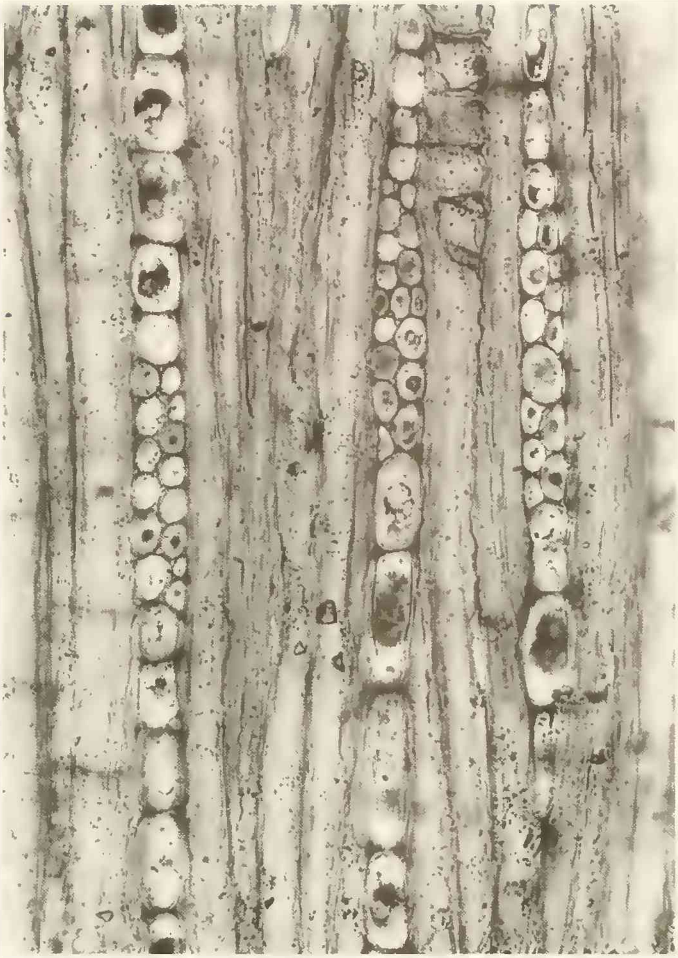

Fig. 10. Tangential section. Decidedly heterocellular rays with procumbent and upright cells, 1–2seriate. × 290.

descriptions of stem wood). Only *C. tonkinensis* LECOMTE, an asiatic ring-porous species, has radial multiples of 2–4 with occasional short chains and clusters. But the pores are "chiefly solitary", however only 21 % of the pores in the present fossil wood. Although variability in the anatomical characters of *Carya* trunck wood has been studied by various authors, published comparable work on *Carya* root or branch wood was not available. Root wood is more difficult to obtain, and its economic importance is slight (CUTLER 1976: 143).

Rays

The rays of the fossil are distinctly heterocellular, but only 1–2seriate (Fig. 9–12). In the collection of trunck wood slides or in published descriptions no similar extant *Carya* sample with this ray type was available. The rays of *C. tonkinensis* are heterocellular. As KRIBS (1928) states, the rays of *C. tonkinensis* are more heterogeneous as those of the american species.

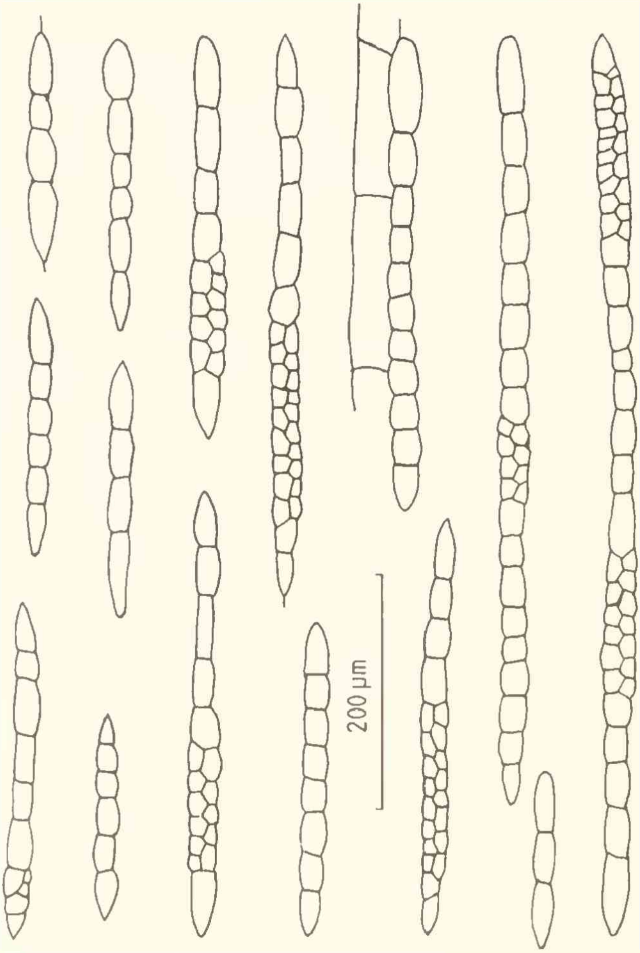

Fig. 11. Tangential section. Heterocellular rays, 1-2seriate, body ray cells procumbent with over 4 rows of upright and/or square marginal cells; feature No. 108 of the IAWA List of microscopic features for hardwood identification (1989).

R e s u l t

Characteristics which serve to distinguish the fossil wood from the american and asiatic extant *Carya* species are predominantly the following features: a) vessels diffuse-porous, solitary only 21 %, multiples 2–6, b) crystals in long axial parenchyma strands (*Juglans* type) + idioblasts (*Carya* type) c) decidedly heterocellular rays, 1–2seriate.

On closer consideration the fossil *Carya* wood from Castellane is perhaps a small silicified piece of a root (twig, branch) with unknown topographical position in the eocene tree individuum. In this case, the fossil wood is not a material suitable for comparative studies with trunc anatomy (CUTLER, RUDALL, GASSON & GALE 1987; GASSON & CUTLER 1990).

R e m a r k s

At the begin of identification certain species of Apocynaceae (*Alstonia, Aspidosperma, Lacmellia*, etc.) have been compared with the fossil. In a personel communication (24. 05. 1994)

Dr. P. DETIENNE, CIRAD, Nogent sur Marne, remarks: „Il me semble plutôt qu'il s'agit d'une Juglandacee, ayant l'aspect de Juglans americain, ou d'un autre genre.“

1.3 Comparison with fossil woods

Fossil woods assigned to the familiy Juglandaceae are known from a wide range of localities in the Northern Hemisphere.

MULLER-STOLL & MADEL (1960) established the 3 genera *Caryojuglandoxylon*, *Eucaryoxylon* and *Pterocaryoxylon* for junglandaceous fossil woods. Additional fossil generea: *Engelhardioxylon* MANCHESTER (1983), *Eucaryoxylon* MULLER & STOLL-MADEL, emend. DUPÉRON (1988: 236), *Rhysocaryoxylon* DUPÉRON (1988) and *Clarnoxylon* MANCHESTER & WHEELER (1993).

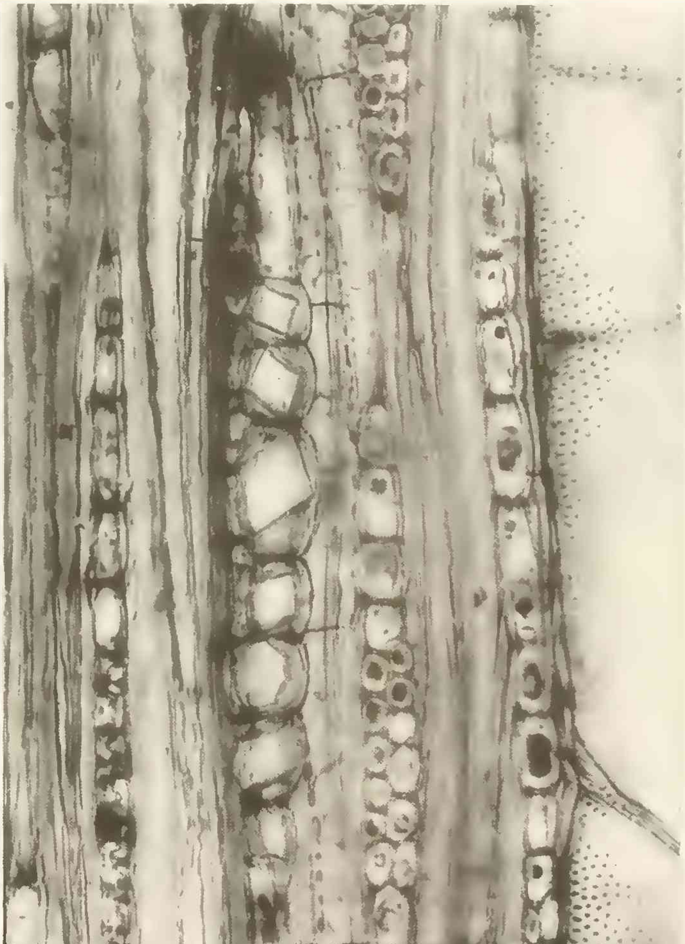

Fig. 12. Tangential section. Prismatic single crystals in axial parenchyma cells, heterocellular rays and vessels with alternate pits. × 290.

One of the distinctive features of the genus *Eucaryoxylon* is the occurrence of barrel-shaped parenchyma cells (idioblasts) with large rhomboidal crystals. MULLER-STOLL & MADEL-ANGELIEWA (1983, p. 662): „Sobald jedoch Kristallidioblasten vorhanden sind, können sie sicher auf *Carya* bezogen werden und gehören dann zu *Eucaryoxylon*". DUPERON (1988, p. 263): "Si les cristeaux sont dans les grosses cellules gonflées le plus souvent isolées, il s'agit d'un *Carya*".

The fossil wood from Castellane has numerous large barrel-shaped idioblasts outside of the rays. A conspicuous feature of the fossil is further the abundant presence of long crystalliferous parenchyma strands.

DUPERON (1988) has given an inventar of all fossil woods ascribed to the family Juglandaceae, including G. F. BECKS collection from the western United States. To date, about 10 fossil woods of the genus *Eucaryoxylon* MULLER-STOLL & MADEL (1960) have been described.

Finding site	Identification	References
Washington, Oregon; USA	*Carya* sp., (BECK 1942)	DUPERON (1988: 258)
Hungary	*E. crystalliphorum*	MULLER-STOLL & MADEL (1960)
Hungary	*E. budense*	GREGUSS (1969)
Canada	*E. canadensis* (Betulaceae ?)	ROY & STEWART (1971); (MANCHESTER 1981)
France	*E. boureaui*	DUPERON (1975, 1977)
Washington, USA	*Carya* sp. MANCHESTER (1981)	DUPÉRON (1988: 258)
Willershausen, Germany	*E.* sp.	GOTTWALD (1981)
Wagenhofen, Germany	*E. guembelii* (FELIX)	MULLER-STOLL & MADEL-ANGELIEWA (1983)
Neu-Isenburg, Germany	*E. moenanum*	MULLER-STOLL & MADEL & ANGELIEWA(1983)
Attenfeld, Germany	*E. crystallophorum*	SELMEIER (1986)
Bergheim, Germany	*E.* sp.	SELMEIER (1986)
Hoyerswerda, Germany	*E. crystallophorum*	SELMEIER (1990)
Castellane, France	*E. castellanii*	(1995)

Anatomical criteria for recognising fossil woods of the above listed *Eucaryoxylon*-Taxa have been reviewed and compared with the present fossil from Castellane.

The fossil wood must be assigned to the genus *Eucaryoxylon* MULLER-STOLL & MADEL (1960). But the range of structural variation in the secondary xylem of the fossil is not exact to determine.

The fossil under consideration differs markedly from all the above listed *Eucaryoxylon*-Taxa, also from *Carya tertiaria* PRAKASH & BARGHORN (1961). *Rhysocaryoxylon* DUPÉRON (1988: 263) has 1-3-(5)seriate homocellular rays and is without idioblasts.

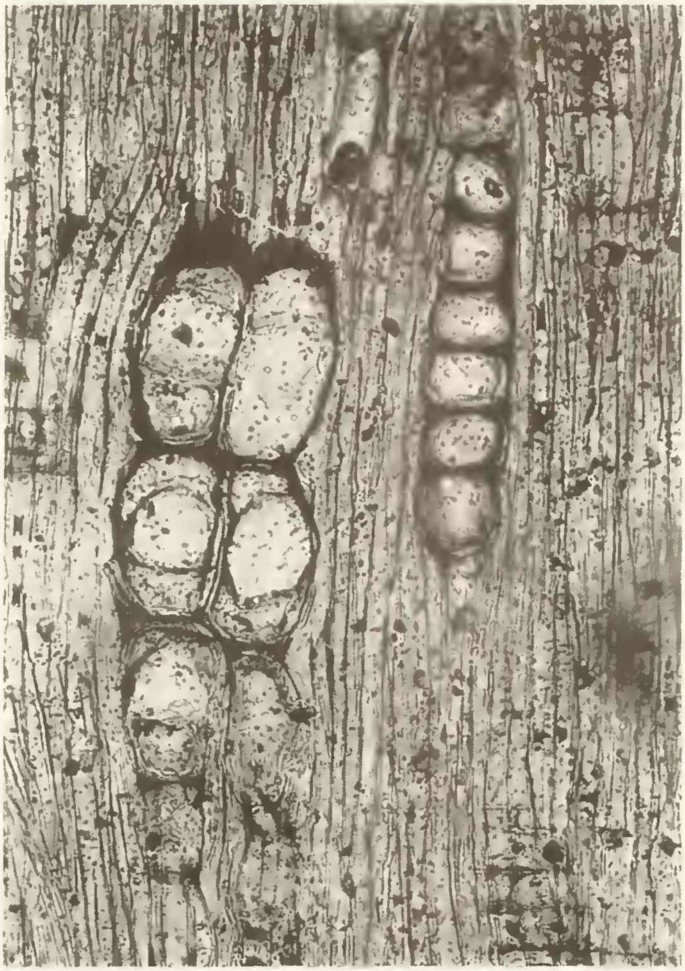

Fig. 13. Radial section. Crystalliferous axial parenchyma cells and separated by some fibres 4 (5) idioblasts with prismatic single crystals. × 290.

Important anatomical differences of the present fossil are mainly: a) vessel grouping and arrangement, b) decidedly heterocellular ray structure, exclusively 1-2seriate rays, c) crystalliferous cells as long axial parenchyma strands + idioblasts.

The fossil wood sample from the Eocene of Castellane clearly represents a new species: *Eucaryoxylon castellanii.*

2. Fossil record of the Juglandaceae

The Juglandaceae have an excellent fossil record in the Tertiary of the Northern Hemisphere. The fossil record includes both extant and extinct genera (MANCHESTER 1983, 1987, 1989; STONE 1989). The major radiation of the family occured during the early Tertiary, recorded in the diversification of pollen, in fruit types and in types of juglandaceous foliage (MANCHESTER 1989; MANCHESTER, COLLINSON & GOTH 1994; THIELE-PFEIFFER 1988; WILDE 1989). Among the

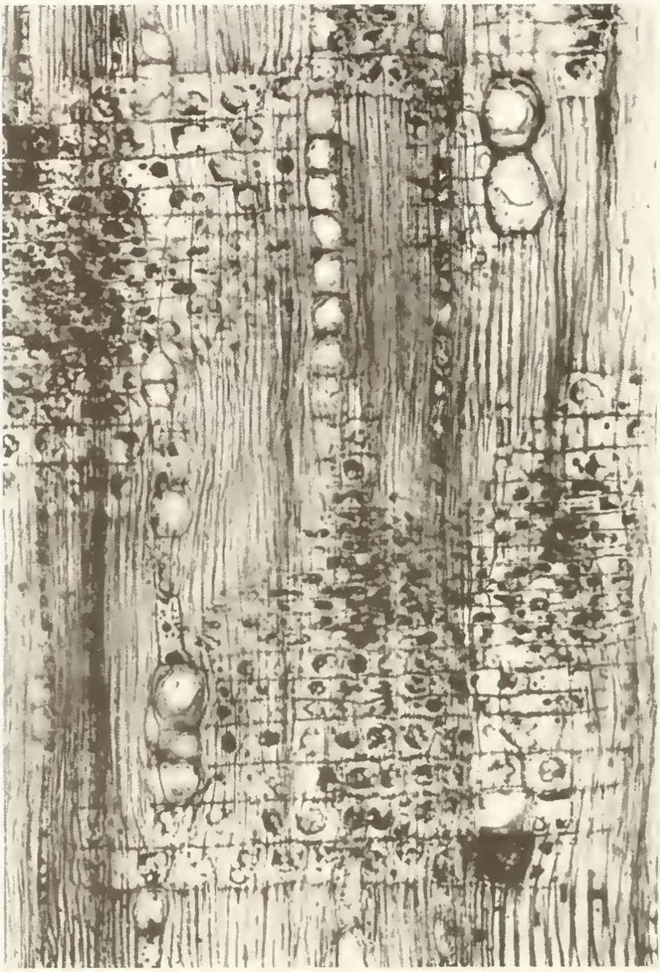

Fig. 14. Radial section. Crystalliferous axial parenchyma strands, idioblasts and cellular composition of the rays. × 115.

juglandaceous pollen taxa recognized at Messel by THIELE-PFEIFFER (1988), Hicorieae is represented by 2 species of *Caryapollenites*. The middle Eocene Messel flora (Germany), well known for their excellent preserved animal and plant fossils, provided many of the most useful characters for generic distinction among extant and extinct Juglandaceae. Three genera of fruits belonging to the Juglandaceae among the collections from Messel: *Palaeocarya*, *Hooleya* and *Cruciptera*.

Detailed information about fruits, leaves and pollen, assigned to fossil and extant juglandaceous taxa, see MANCHESTER, COLLINSON & GOTH (1994). Comparative plant material from the Tertiary of western North America and from the Tertiary of Europe: It is more similar to each other than to the Asian species (MANCHESTER 1987).

The tertiary flora from the northalpine molasse basin and adjacent regions has provided as well numerous remains of Juglandaceae (leaves, fruits, pollen and wood): e.g., JUNG (1963, *Carya serraefolia*; 1970); GREGOR (1978, 1982); KIRCHNER (1984) and THIELE-PFEIFFER (1980);

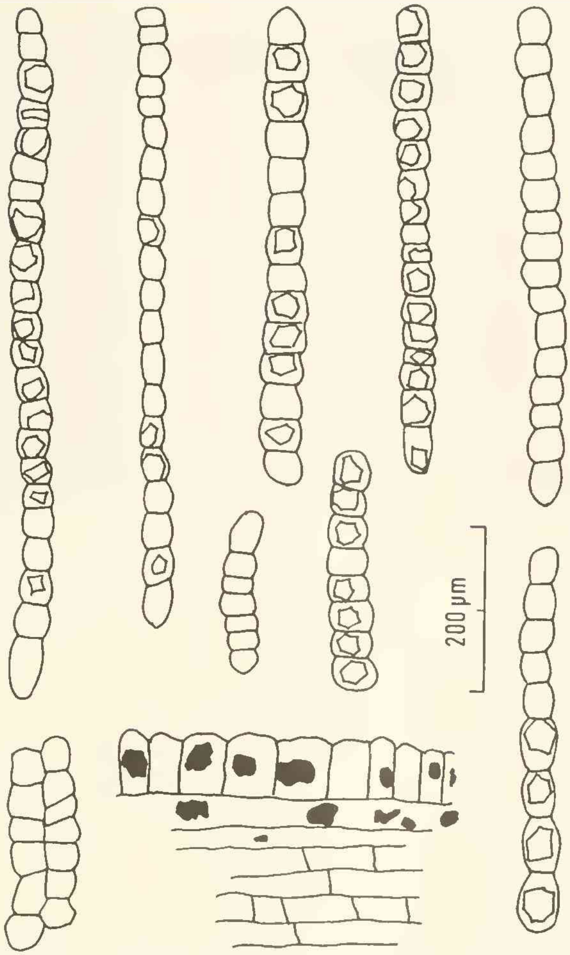

Fig. 15. Radial section. Crystalliferous axial parenchyma strands and cellular composition of a ray.

SELMEIER (1985, 1986, 1995). Further information about tertiary leaves and fructifications of Juglandaceae in central Europe, see MANCHESTER, COLLINSON & GOTH (1994) and SELMEIER (1986: 76). The genus *Carya*, on the whole, possesses (probably) the most specializised conditions of the inflorescence in the family (MANCHESTER 1987; MANNING 1978; STOJAN 1972).

Fossil wood has the potential to record several aspects of the palaeoenvironment it which it grew (CHAPMAN (1994). But many anatomical features vary within a tree depending on position of the wood. As mentioned above (1.2), the growing position of the eocene fossil fragment from Castellane is not identified.

The fossil record for dicotyledonous wood supports the BAILEYAN model for xylem evolution (WHEELER & BAAS 1991). The incidence of 'primitive' features (e.g., scalariform perforation plates) is much higher in the Cretaceous than in the Tertiary, while the incidence of 'advanced' features (e.g., simple perforation plates) is lower.

Percent incidence 'Perforation all simple' during the Eocene 69–95% (WHEELER & BAAS 1991, Tab. 1), 'Intervessel pits alternate' during the Eocene 68–93% (Tab. 3).

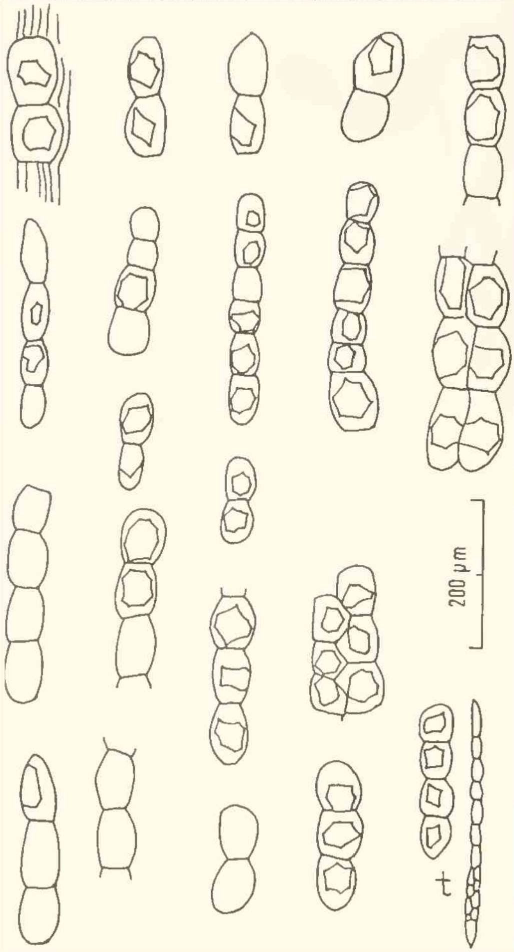

Fig. 16. Barrel-shaped enlarged cells in radial and in tangential (t) section. Diagnostic crystal feature No. 156 of the IAWA List of microscopic features for hardwood identification (1989).

'Ray structure heterocellular' during the Eocene 70% (Tab. 10), 'More than 4 rows of upright/square marginal cells in heterocellular rays' during the Eocene 12–17% (Tab. 11).

The four above mentioned features are well preserved in the eocene wood from Castellane.

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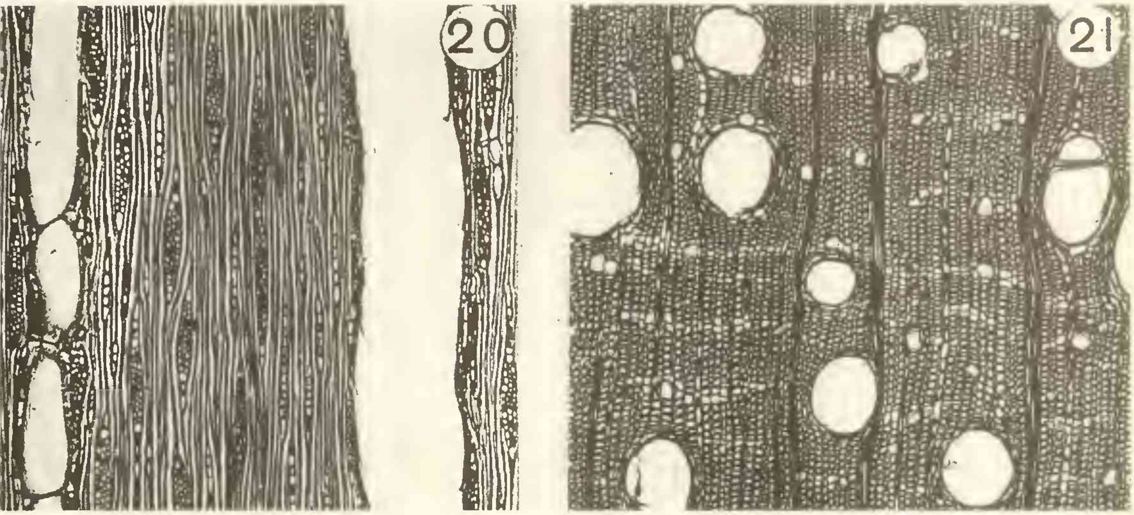

Fig. 17. *Carya tonkinensis* LECOMTE. Tangential section (left) showing heterocellular rays and cross section (right) with solitary vessels, banded parenchyma and prismatic crystals (HEIMSCH & WETMORE 1939: 657). *C. tonkinensis* differs markedly from the fossil in the wood structure, but similar is the abundant occurrence of crystals.

Information about Castellane and/or fossil wood remains from this locality: CATHÉRINE PRIVÉ-GILL, (Lab. Paléobotanique, Paris), NICOLE GRAMBAST-FESSARD (Montpellier, France), GERO MOOSLEITNER (Salzburg-Morzg, Austria).

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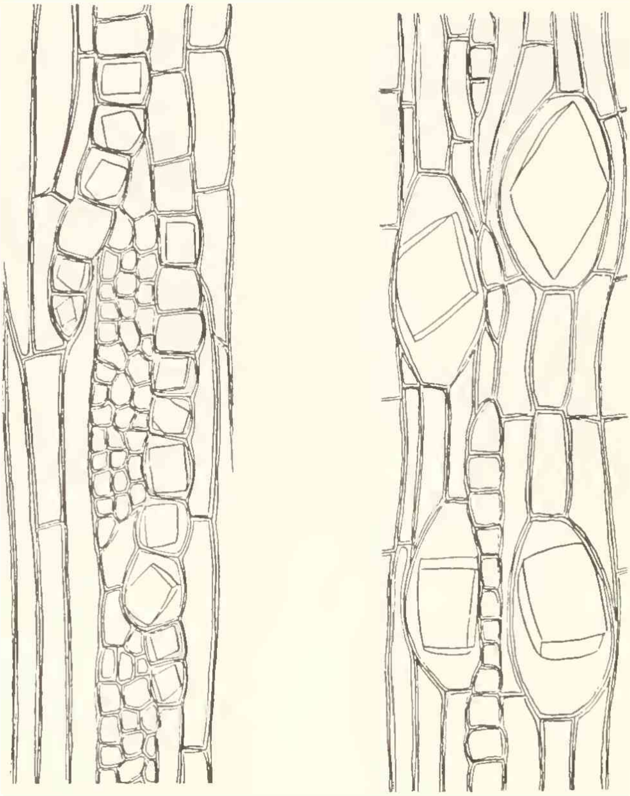

Fig. 18. *Juglans nigra* (left). Cristalliferous axial parenchyma cells. × 190. *Carya alba* (right). Four idioblasts with prismatic crystals. × 190. MUELLER-STOLL & MÄDEL (1960: 259).

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