Silicified Angiosperm wood from the Dangu locality (Ypresian of the Gisors region, Eure, France): the problem of root wood

Bois silicifiés d'Angiospermes du gisement de Dangu (Yprésien de la région de Gisors, Eure, France) : le problème du bois de racine

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Abstract — The problem of root wood is discussed. Based on several specimens of silicified wood from the Dangu locality (Lower Eocene of the Paris Basin), the authors have attempted to explain variations in the wood structure by the origin of the studied woods within the tree. A new species with two new forms is also established. (© Académie des sciences / Elsevier, Paris.)

Paris Basin / France / Ypresian / silicified Angiosperm wood / root wood / new species

Résumé — Le problème du bois de racine est discuté à partir de plusieurs spécimens de bois silicifiés du gisement de Dangu (Éocène inférieur du bassin de Paris) ; les auteurs tentent d'expliquer les variations de structure ligneuse par la localisation supposée des échantillons au sein de l'arbre. Une nouvelle espèce est aussi définie, sous deux formes. (© Académie des sciences / Elsevier, Paris.)

bassin de Paris / France / Yprésien / bois silicifié d'Angiospermes / bois de racine / nouvelle espèce

Version abrégée (voir p. 556)

1. Introduction

The Dangu locality is situated in the Paris Basin, 65 km northwest of the capital, in the 'Vexin normand' (Eure), 7 km WSW of Gisors and 1.5 km NNW of the village of Dangu, on the hill on the right bank of the Epte river. Kœniguer (1981), in his study of the fossil peat, mentioned a great quantity of mineralized (essentially silicified) wood, attributed to Gymnosperms and Angiosperms. The present paper reviews the main results of the Master's thesis of Jakub Sakala (1998) focusing on the problem of root wood. The work consisted of a study of some samples of fossil Angiosperm woods from the Dangu locality. The problem of root wood is not often discussed: except for the

manuals where the question is treated generally (Schweingruber, 1978; Metcalfe and Chalk, 1983; Cutler et al., 1987), there are only two recent papers (Machado et al., 1997; ter Steege et al., 1997) devoted to this subject. It is applied to the study of fossil wood.

2. Geological setting

The fossils, associated with lignitic peat remains, occur in sands to conglomerates with flint pebbles known as 'galets avellanaires'. It is a residual formation which comes from an altered terminal level of the Lower Ypresian (top of the *sparnaciens* facies) which sedimented in a

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C. R. Acad. Sci. Paris, Sciences de la terre et des planètes / *Earth & Planetary Sciences*
1999. 328, 553–557

553

fluvio-marine regime (Kuntz et al., 1976). Generally, many pebbles together with fossil woods are distributed more or less in the north–south direction, following a channel of the detrital supply which seems to have come from the anticlinal of Bray, in the north (Kuntz et al., 1976).

3. Systematic part

Five different entities of Dicotyledons were recognized in the Dangu locality on the basis of seven wood samples. They belong probably to the families Combretaceae, Caesalpiniaceae or Mimosaceae, Rubiaceae and Hamamelidaceae.

Three types of fossil Angiosperm wood reveal interesting questions about the origin of variations in the wood structure, and are dealt with in the following text.

?Rubiaceae

Grangeonixylon Privé-Gill

Grangeonixylon danguense sp. n. – stem form (*figures 1a* and *1b*)

Anatomical study. *Growth rings:* vaguely distinct to the naked eye (emphasized by secondary mineralization), no more visible under the microscope. *Vessels:* diffuse porous, solitary, circular to elliptical; 20–60 pores per mm^2; walls 3–10 µm thick; tangential diameter of solitary pores 18–80 µm, mean 47 µm for the sample W2, 53 µm for the sample 203A, 48 µm for the sample W13; radial diameter of solitary pores 26–109 µm; vessel elements 80–656 µm

long; simple perforation plates; intervascular pits bordered, circular to elliptical (2–4 µm long axis, 2–3 µm short axis), alternate, not vestured. *Fibres:* pentagonal to hexagonal in cross-section, walls 3–6 µm thick; 1–15 radial rows between the rays; tangential diameter 8–20 µm; radial diameter 8–23 µm; lumen diameter 2–6 µm; nonseptate. *Vertical parenchyma cells:* quite abundant, apotracheal diffuse, irregularly distributed and in short aggregates or locally paratracheal vasicentric; cell dimensions (tangential diameter × radial diameter × height) 7–29 µm × 7–36 µm × 47–118 µm. *Rays:* heterogeneous, uni-, biseriate, rarely locally triseriate (Kribs's type I); 17–20 per mm horizontal tangential; uniseriate rays max. 26 µm wide and 1–11 cells (58–323 µm) high; multiseriate rays 22–37 µm wide and 3–31 cells (139–1 201 µm) high; upright cells form the extremities of the multiseriate rays and the uniseriate rays; procumbent and square cells or only procumbent cells form the bodies of the multiseriate rays; tangential cell dimensions (height × width) 11–106 × 11–29 µm; examples of the radial cell dimensions (height × length): upright cells 62 × 33, 44 × 18... µm, square cells 29 × 27, 40 × 44... µm, procumbent cells 20 × 51, 18 × 76... µm.

Grangeonixylon danguense sp. n. – root form (*figures 1c* and *d*)

Anatomical study. *Growth rings:* slightly distinct to the naked eye (emphasized by secondary mineralization), under the microscope no more visible. *Vessels:* diffuse porous, solitary, circular to elliptical; 14–43 pores per mm^2; walls 3–5 µm thick; dark plug always present; tangential
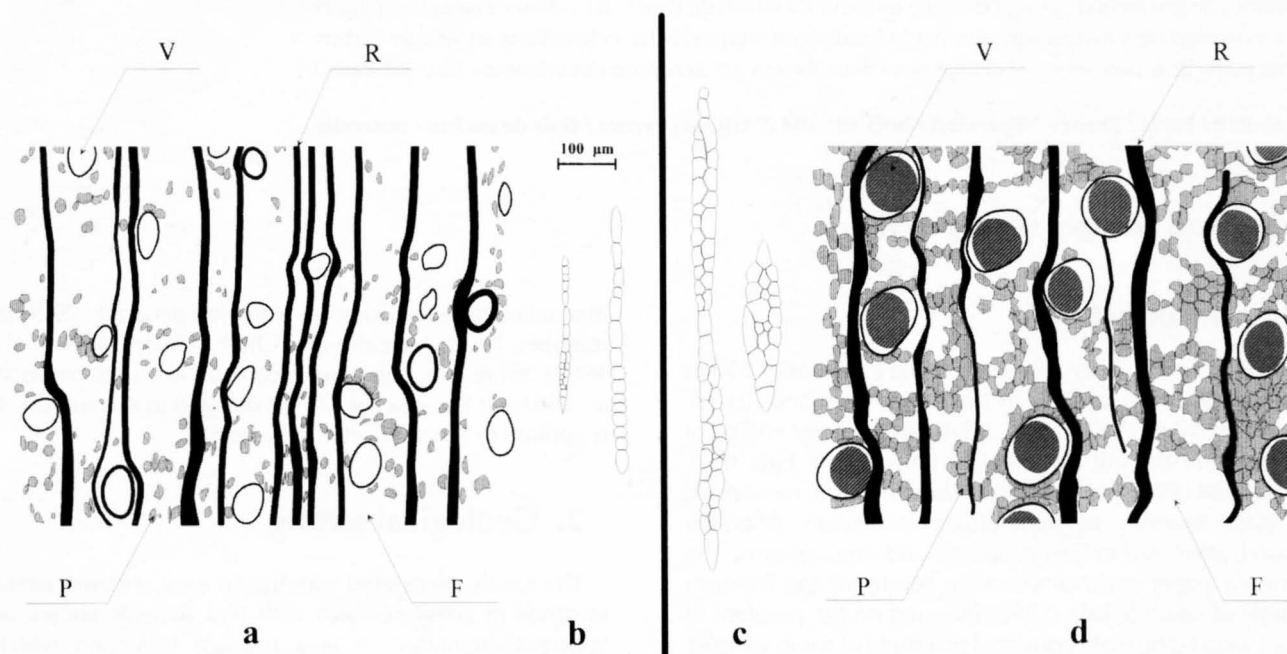

Figure 1. *Grangeonixylon danguense* sp. n. (a, b: stem form; c, d: root form, same scale). a, d: cross-sections with vessels (V), vertical parenchyma (P), rays (R) and fibres (F). b, c: rays in tangential section; in b the uniseriate ray is abnormally well-developed.

Grangeonixylon danguense sp. n. (a, b : bois de tronc ; c, d : bois de racine, même échelle). a, d : coupes transversales montrant la disposition des vaisseaux (V), du parenchyme vertical (P), des rayons (R) et des fibres (F). b, c : rayons en section tangentielle ; en b, le rayon unisérié est anormalement bien developpé.

554

C. R. Acad. Sci. Paris, Sciences de la terre et des planètes / *Earth & Planetary Sciences*
1999. 328, 553–557

diameter of solitary pores 36–142 µm, mean 82 µm; radial diameter 44–142 µm; vessel elements 165–750 µm long; simple perforation plates; intervascular pits bordered, alternate, round, 3–4 µm areola diameter, 1–2 µm aperture diameter. *Fibres:* tangential diameter 7–29 µm; radial diameter 9–36 µm; walls 5–14 µm thick; lumen diameter 3–18 µm; tangential pits (diameter 3–4 µm) distinctly bordered, disposed in longitudinal lines; circular apertures; septa not present. *Vertical parenchyma cells:* very abundant, apotracheal diffuse, irregularly distributed and in short uniseriate tangential aggregates (5–7 by 500 radial µm) or slightly paratracheal vasicentric; cell dimensions (tangential diameter × radial diameter × height) 11–33 µm × 11–36 µm × 70–108 µm. *Rays:* multiseriate (particularly biseriate), 2–4 cells (33–80 µm) wide; 5–33 cells (120–936 µm) high; 8–11 per mm horizontal tangential; heterogeneous (Kribs's type II); upright and square cells in the extremities; procumbent (sometimes procumbent and square) cells in the bodies; tangential cell dimensions (height × width) 9–52 × 23–56 µm; examples of the radial cell dimensions (height × length): upright cells 38 × 26, 80 × 29, 47 × 36... µm, square cells 29 × 29, 33 × 36; 33 × 33... µm, procumbent cells 23 × 35, 18 × 98, 43 × 62... µm.

Discussion

The characters shared by the two woods described above are: solitary vessels, apotracheal parenchyma and rather narrow heterogeneous rays. They lead to place our woods to the proximity of three families: Myrtaceae, Rubiaceae and Santalaceae. The family Rubiaceae seems to be most closely related to our woods, but an exact taxinomic ranking is not evident.

In spite of the differences between our two woods (vessel diameter, abundance of parenchyma, ray characters), their ligneous structures are very similar and very rare among the fossils so far described. Because of that and of the fact that the number of woody Angiosperms types of Dangu is restricted, we have attempted to find a natural explanation for the variations due to the localisation of the studied woods within the tree. The main differences which can be found between both structures are: the higher abundance of the parenchyma in the second form together with the larger diameter and the lower frequency of the pores, while in the first form, the rays are thinner and more frequent. The same differences can be noticed in the root wood, in comparison with the normally developed trunk wood (Felix, 1884; Schweingruber, 1978; Metcalfe and Chalk, 1983; Cutler et al., 1987; Machado et al., 1997). Therefore, we suggest the following interpretation: both woods belong to the same species — the first one can represent a trunk or branch wood, the second one shows characters of a root wood.

The generic name *Grangeonixylon* is retained, its diagnosis fits the Dangu woods well. *Grangeonixylon* was originally established by Privé-Gill (1983) for the species *G. apocynorubioides* of uncertain (Apocynaceae, Rubiaceae) affinities (Oligocene transported wood from Allier,

France); this species differs from the Dangu woods by the ray morphology. We propose a new species *G. danguense*. The specific name points to the locality of the wood samples near the Dangu village.

Diagnosis

Grangeonixylon danguense sp. n. Growth rings present, but hardly visible. Vessels very small (47–52 µm for the trunk form) to small (82 µm for the root form), numerous, exclusively solitary; vessel elements long, simple perforation plates, intervascular pits bordered, small. Vertical parenchyma cells fairly abundant (in the trunk form) to very abundant (in the root form), diffuse, irregularly distributed or in short aggregates, locally paratracheal vasicentric. Rays short, of small width, 1- to 4-seriate (1- to 3-seriate in trunk form and 2- to 4-seriate in root form), heterogeneous I to II. Fibre tracheids not septate of medium width.

Holotype: specimen n° W2 (trunk form), R. Wyns collection.

Paratypes: specimens n° W13 and 203A (trunk form) and specimen n° W1 (root form), R. Wyns collection.

Type locality: Dangu near Gisors (Eure, France).

Type level: Lower Eocene (Lower Ypresian, top of the *sparnaciens* facies).

Hamamelidaceae

Liquidambaroxylon Felix
cf. *Liquidambaroxylon* sp.
(*figure 2*)

Anatomical study. *Growth rings:* not present. *Vessels:* diffuse porous, angular, solitary and in radial multiples of 2–4; density 70 vessels (100 pores) per 1 mm², tangential diameter of solitary pores 36–76 µm, mean 56 µm; radial diameter 55–109 µm; vessel elements about 1 000 µm long; lateral pits scalariform, pit dimensions 11–37 × 6–8 µm; scalariform perforation plates, about 20 bars, observation difficult. *Fibres:* few; generally pentagonal to hexagonal in cross-section, thick-walled (6–9 µm); tangential diameter 12–40 µm (enlarged by cracking); radial diameter 23–39 µm; lumen diameter 15–25 µm. *Vertical parenchyma cells:* diffuse, very abundant; in the cross-section parenchyma cells, very often as big as the vessels, constitute with the vessels the ground of the structure, at the expense of the fibres; cell dimensions (tangential diameter × radial diameter × height) 40–80 µm × 40–80 µm × 40–400 µm (most common value: 170 µm). *Rays:* heterogeneous, 2–3 seriate (Kribs's type II), very high; 7–15 per mm horizontal tangential; multiseriate bodies (37–80 µm wide; 4–30 cells, max. 1 240 µm high) formed by procumbent and square cells, upright cells form long uniseriate extremities (max. 27 cells, 400 µm high); sometimes several rays join together (up to 3 540 µm high).

Discussion

Despite the bad preservation and compression of the structure, this wood shows a certain number of valuable characters: angular pores (*figure 2a*), scalariform perfora-

C. R. Acad. Sci. Paris, Sciences de la terre et des planètes / *Earth & Planetary Sciences*
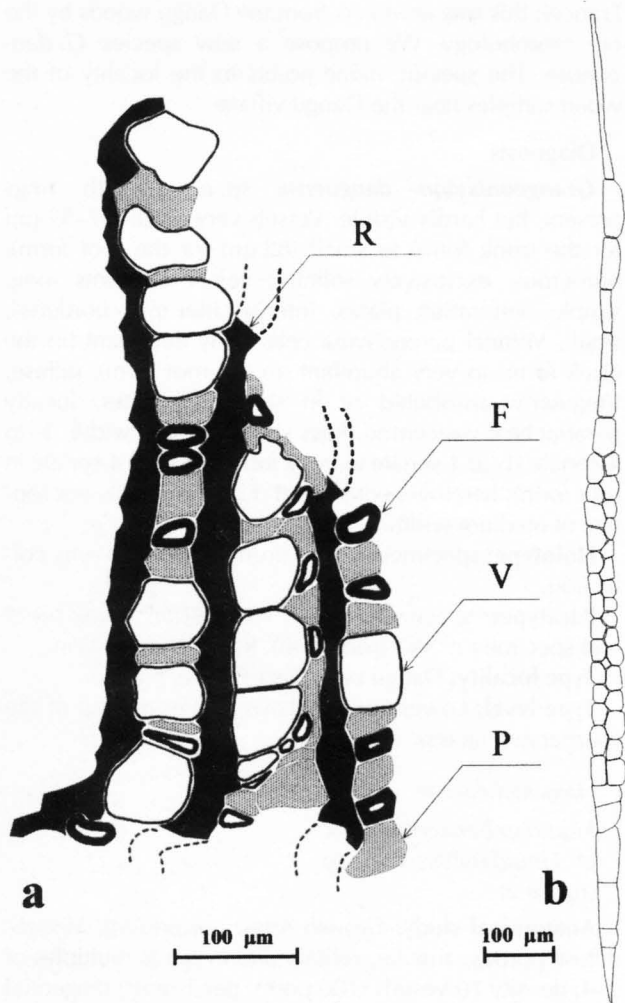1999. 328, 553–557

555

Figure 2. cf. *Liquidambaroxylon* sp. a: cross-section with vessels (V), vertical parenchyma (P), rays (R) and fibres (F). b: one ray in the tangential section.

cf. *Liquidambaroxylon* sp. a : section transversale avec vaisseaux (V), parenchyme vertical (P), rayons (R) et fibres (F). b : un rayon en section tangentielle.

tions and pitting, multiseriate heterogeneous rays with very long uniseriate extremities formed by upright cells (*figure 2b*), abundant axial parenchyma and not numerous thick-walled fibres (*figure 2a*).

These characters, according to Kœniguer (1981), allow to place this wood to the proximity of the Hamamelidaceae family. Kœniguer (1981) assigned it close to the

recent genera *Altingia*, *Bucklandia*, *Rhodoleia* and *Liquidambar*, perhaps *Sycopsis*. We found similarities with the fossil hamamelidaceous woods of *Liquidambaroxylon* Felix (1884) or *Hamamelidoxylon* Lignier (1907). A resemblance to a fossil wood of the Nyssaceae family (Mädel, 1959) must be also mentioned.

However, all the compared fossil woods (*Liquidambaroxylon*, *Hamamelidoxylon*, and especially *Nyssoxylon* Mädel, 1959) show a parenchyma not abundant, rather rare and exceptionally not present. In our wood the parenchyma cells are very abundant, nearly as large as the pores and constitute with the vessels the ground wood tissue (see *figure 2a*).

We propose two possible explanations.

Applying the same way of reasoning as in the previous discussion, our wood is a piece of a root wood – the abundance of the parenchyma at the expense of the fibres is linked to the nature of the root where the stocking (number increasing of the parenchyma cells) and conduction are privileged to the support (number decreasing of the fibres) taken over rather by the trunk. This proposition matches well the fact that the Dangu wood was found included in a fossil peat which is, itself, composed of numerous roots (Kœniguer, 1981).

Otherwise, our specimen could represent an extinct type, close to the two families mentioned above, a type not yet known by its wood. The genus which we have to consider first is *Steinhauera*, established by Presl (see Mai, 1968) on the basis of reproductive structures. *Steinhauera*, on one hand, shows affinities to the recent genera *Altingia* and *Liquidambar*, on the other hand it is considered as a 'notorious' element in the palaeotropical Eocene European floras with a vast distribution from England to Russia (Mai, 1968). Therefore, *Steinhauera* should explain our problem, but because of the extraordinary abundance of parenchyma in the fossil, we prefer the first hypothesis.

4. Conclusions

Variations in fossil wood structure have been considered here as due to the localisation of the specimens in the trees: trunk, branch, root. This way of reasoning, based on the knowledge of recent structures, is in opposition to the artificial splitting of fossil taxa in palaeoxylology, which would result from a taxonomic interpretation of these variations. It therefore proposes a more natural palaeobotanical view taking into account the intra-specific and individual variability.

Version abrégée

Introduction

Le gisement de Dangu, situé dans le bassin de Paris, près de Gisors, livre dans une tourbe ligniteuse une grande quantité de bois silicifiés appartenant aux Gymnospermes et aux Angiospermes (Kœniguer, 1981). Cet article résume les principaux

résultats du mémoire de DEA présenté en 1998 par l'un des auteurs (J.S.) et tente d'appliquer à l'étude des bois fossiles ce que l'on sait de la variabilité entre le bois de tronc et celui de racine.

556

C. R. Acad. Sci. Paris, Sciences de la terre et des planètes / *Earth & Planetary Sciences*
1999. 328, 553–557

Cadre géologique

Les fossiles, associés à des vestiges de tourbe ligniteuse, se rencontrent dans des sables passant à des poudingues à galets avellanaires. Il s'agit vraisemblablement d'une formation résiduelle provenant d'un niveau terminal démantelé de l'Yprésien inférieur, que l'on peut considérer comme étant le sommet des faciès « sparnaciens » (Kuntz et al., 1976).

Partie systématique

Cinq essences différentes de Dicotylédones, appartenant probablement aux familles des Combretaceae, des Caesalpiniaceae ou Mimosaceae, des Rubiaceae et des Hamamelidaceae ont été reconnues.

Trois types de bois posent des questions intéressantes du point de vue de leur localisation dans les arbres.

Deux formes de bois sont décrites et présentent les caractères suivants : vaisseaux petits, solitaires, perforations simples, parenchyme apotrachéal diffus ou en courts agrégats tangentiels, localement vasicentrique, rayons hétérocellulaires 1-4 sériés et fibres non septées. Elles ont des affinités probables avec les Rubiaceae. On peut distinguer deux formes : le bois de tronc et le bois de racine, car les variations observées entre certains des spécimens (abondance du parenchyme, taille et fréquence des vaisseaux, largeur des rayons) sont du même ordre que celles reconnues entre les bois de tronc et de racine de nombreuses espèces actuelles (Felix, 1884 ; Schweingruber, 1978 ; Metcalfe and Chalk, 1983 ; Cutler et al., 1987 ; Machado et al., 1997). Les spécimens ont été attribués au genre fossile *Grangeonixylon* (Privé-Gill, 1983) et dénommés *G. danguense* sp. n. (*figure 1*), d'après le nom de la localité où ont été découverts les fossiles, près du village de Dangu.

Le dernier bois (*figure 2*) présente de petits vaisseaux solitaires, diffus, anguleux, à perforations et ponctuations scalariformes, du parenchyme diffus très abondant et des rayons nettement hétérocellulaires, 2–3 sériés. Ces caractères le rapprochent des Hamamelidaceae et notamment d'*Altingia*, *Bucklandia*, *Rhodoleia*, *Liquidambar* (Kœniguer, 1981) et *Sycopsis*. Une comparaison avec *Liquidambaroxylon*, *Hamamelidoxylon* et *Nyssoxylon* montre, cependant, que le spécimen de Dangu se distingue par l'abondance extrême du parenchyme. Il est dénommé cf. *Liquidambaroxylon* sp. Une première hypothèse consiste à considérer ce bois comme un fragment de racine. L'abondance du parenchyme aux dépens des fibres est liée à la nature et à la fonction de la racine où la mise en réserve (parenchyme) et la conduction sont privilégiées par rapport au soutien (fibres) assuré par le bois de tronc. Une seconde possibilité est de considérer le bois de Dangu comme un type éteint, *Steinhauera* Presl (voir Mai, 1968), voisin des Hamamelidaceae, non encore connu par le bois, mais seulement par ses structures reproductrices. *Steinhauera*, connu de l'Angleterre à la Russie, est un élément des flores paléotropicales éocènes.

Nous préférons la première hypothèse, du fait que le parenchyme est très développé et que le bois de Dangu se trouvait inclus dans la tourbe fossile, elle-même comportant de nombreuses racines (Kœniguer, 1981).

Conclusions

Des variations de structures ligneuses fossiles ont été considérées comme étant en relation avec la localisation des bois dans l'arbre : tronc, branche, racine. Cette démarche, qui s'appuie sur l'observation des structures actuelles, devrait limiter la multiplication artificielle des taxons fossiles en paléoxylologie, résultant d'une interprétation taxinomique de ces variations. Elle propose en cela une vision plus naturelle de la paléobotanique, prenant en compte la variabilité intraspécifique et individuelle.

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C. R. Acad. Sci. Paris, Sciences de la terre et des planètes / *Earth & Planetary Sciences*
1999. 328, 553–557

557