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ABSTRACT

Thousands of silicified wood fragments were recently collected from the middle Cenomanian of Vienne in western France at less than 10 km away from a historical locality where in 1870 the French geologist Alphonse Le Touzé de Longuemar reported silicified wood. The plant assemblage is very diverse, and includes several species of ferns, conifers, and angiosperms. We describe and discuss the systematic affinities of a new vesselless angiosperm. Many of its characters are shared by extant and fossil Winteraceae. Nevertheless, the absence of uniseriate rays makes the anatomy of these specimens unique. Its combination of characters justifies the establishment of a new genus of vesselless fossil angiosperm wood of uncertain affinity, *Sherwinoxylon* gen. nov.

Keywords: Fossil wood, Winteraceae, Cretaceous, *Sherwinoxylon* gen. nov.

INTRODUCTION

In recent years, thousands of silicified wood fragments have been collected from the middle Cenomanian of two localities in the Envigne valley (Vienne department, western France) (Robin *et al*. 2018). Only trunks and branches of various lengths and diameters have been preserved. Both fossil assemblages are exceptional in their high plant diversity and the exquisite tissue preservation, as well as in their association with animal fossils. For instance, some of the petrified woods have allowed for the preservation of the oldest shipworms described with soft parts (Robin *et al*. 2018). Shipworms, bivalve molluscs of the family Teredinidae, are notorious for boring into wood that is immersed in sea water.

Conifers are the most abundant and diversified fossil wood in this assemblage, representing around 90 % and at least five different taxa. They consist of large logs transported into an estuarine or a near-shore environment. Although angiosperms are less

abundant (only 9.8%) and have smaller diameters, they have a higher diversity with at least nine different taxa (Saulnier *et al.* 2018). Angiosperm pollen grains and leaves have been frequently reported from the Cenomanian of western France (Crié 1884; Juignet & Médus 1971; Azéma *et al.* 1972; Laing 1975; Pons *et al.* 1980; Gomez *et al.* 2004, 2008; Peyrot *et al.* 2005; Néraudeau *et al.* 2005, 2008, 2013, 2017; Valentin *et al.* 2014; Fleury *et al.* 2017), but they were not yet related to fossil wood. So far described contemporary wood consisted only of lignitized conifer genera (Néraudeau *et al.* 2003, 2008, 2013, 2017; Fleury *et al.* 2017). These two fossil plant assemblages are thus of great interest in the understanding of the spread and rise to dominance of woody angiosperms in Europe and worldwide during the Cretaceous. In this context, vesselless angiosperms are also of particular interest, and here we describe a new form genus in this category of homoxylous woods.

A vesselless angiosperm wood is a "wood without vessel elements, composed only of imperforate tracheary elements and parenchyma [...], Amborellaceae, Tetracentraceae, Trochodendraceae, Winteraceae." (IAWA Committee 1989). Nevertheless, the presence of perforated vessel elements was recently highlighted in Trochodendraceae (Ren *et al.* 2007; Li *et al.* 2011) or in *Sarcandra* Gardner (Chloranthaceae) (Carlquist 1987). In other genera such as *Amborella* Baill., *Bubbia* Tiegh. or *Drimys* J.R. Forst. *ex* G. Forst., tracheary cells show a tendency toward differentiation of end wall pitting (Feild *et al.* 2000; Carlquist & Schneider 2002). According to the last angiosperm phylogeny (Angiosperm Phylogeny Group 2016) and data on wood structure (Carlquist 1975, 2001; InsideWood 2004-onwards; Wheeler 2011), vesselless wood is found in the basal angiosperms (ANA grade with Amborellaceae), Magnoliids (Winteraceae), Chloranthales (Chloranthaceae) and in one of the early branching eudicot clades, Trochodendrales (Trochodendraceae, including former Tetracentraceae) (Fig. 1).

The wood structure in these different vesselless angiosperms clearly shows similarity with that of homoxylous wood clades in gymnosperms (*e.g.* conifers). This character has long been considered to be a plesiomorphic state of the water conducting elements in the secondary xylem as the families showing it were found in the basal groups of angiosperms in former phylogenies (*e.g.*, Young 1981; Hufford & Crane 1989; Chase *et al.* 1993). In the APG IV (Angiosperm Phylogeny Group 2016), *Amborella trichopoda* Baill. represented a sister group to all other angiosperms. Baas and Wheeler (1996) argued in favour of vessellessness being basal in angiosperms, with unparsimoneous parallel origins of vessels. On the other hand, homoxylous wood in angiosperms might also result from convergent environmental pressures. Interestingly numerous plants showing this character grow in temperate to subtropical moist environments with a high annual temperature amplitude. Vesselless wood might be seen as an adaptation to frost-prone environments as Feild *et al.* (2002) suggested for Winteraceae. Therefore, vesselless wood might be either an ancestral or a derived character depending on the family considered, and thus its phylogenetic significance within angiosperms still remains controversial.

The fossil record of most vesselless angiosperm families is quite ancient: early Cretaceous for Winteraceae with the pollen type *Walkeripollis gabonensis* Doyle, Hotton &
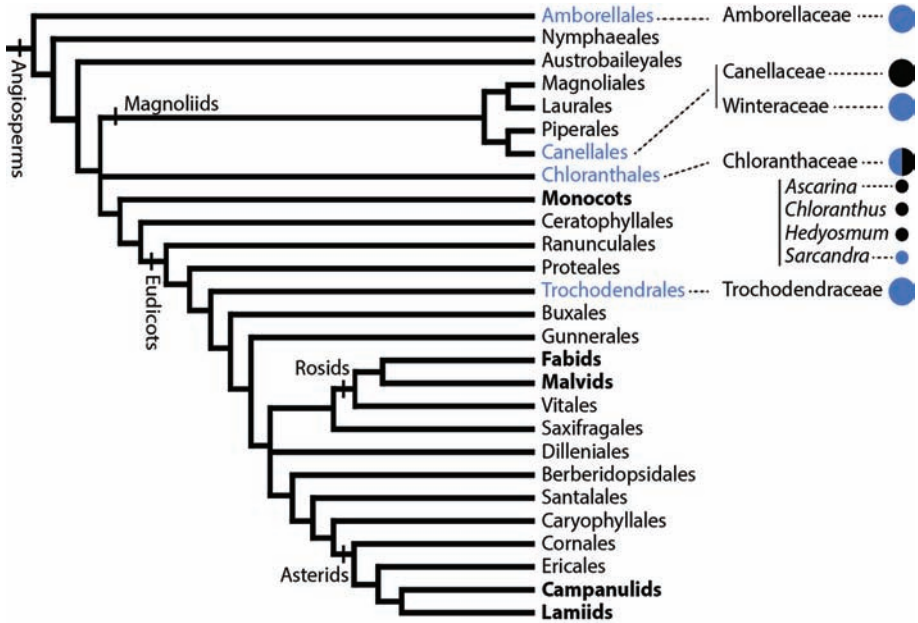
Figure 1. Occurrence of vesselless wood in angiosperms. Blue circle = homoxylous or vessel-less, black circle = heteroxylous or vessel-bearing. Modified from Angiosperm Phylogeny Group (2016).

J.V.Ward (Doyle *et al*. 1990) and for Chloranthaceae (Barremian–Aptian) with the pollen type *Asteropollis* Hedlund & Norris related to the extant genus *Hedyosmum* Sw. (Friis *et al*. 1994; Tanaka 2008); late Cretaceous (early Coniacian) for Trocho-dendraceae with the flower *Archaestella verticillatus* Takahashi, Herendeen & Xiao (Takahashi *et al*. 2017).

The family Amborellaceae includes a single genus and species, *Amborella tricho-poda*, which grows as understory shrubs that are endemic in New Caledonia. No fossil record for this family is known so far.

The family Winteraceae includes 6 valid and 3 unresolved or synonymous genera according to The Plant List (2013) of shrubs, trees and lianas in the montane tropics and temperate rainforests, mostly in the Southern Hemisphere occurring from southern North America to South America (Mexico, Ecuador, Venezuela, Brazil, Chile, Juan Fernandez Islands), Madagascar, the Philippines, Borneo, Sulawesi, New Guinea, the Solomon Islands, New Caledonia, eastern Australia, Tasmania, and New Zealand (Christenhusz *et al*. 2017).

Although extant Winteraceae are only distributed in the Southern Hemisphere, fossils attributed to this family (leaves, wood, and pollen) have been reported from both Northern and Southern Hemispheres (for a review see Doyle 2000, Friis *et al*. 2011, and Grímsson *et al*. 2018). Winteraceae have a unique type of pollen/tetrad easily recognizable (Walker & Walker 1984; Grímsson *et al*. 2017). During the Creta-ceous winteraceous pollen have been reported from the late Barremian–early Aptian

of Gabon (Doyle *et al.* 1990), Albian of Israel (Walker *et al.* 1983; Schrank 2013), middle Campanian (Dettmann & Jarzen 1990), and Maastrichtian of Australia (Stover & Partridge 1973), and the latest Cretaceous of New Zealand (Mildenhall & Crosbie 1979). In the Southern Hemisphere, Poole and Francis (2000) described *Winteroxylon jamesrossi* Poole & Francis, a fossil wood from the Santonian–Campanian of Antarctica. A few fossils attributed to Winteraceae have been described outside the range of extant members as, for example, the type species of *Winteroxylon* Gottwald, *W. mundlosi* Gottwald from the Eocene of Europe (Gottwald 1992). Doyle (2000) suggested that the geographical range of the family could have been larger than previously thought and may have included Laurasia or that the European fossils were a wrong attribution. The recent report of Winteraceae pollen tetrads from the early Paleocene of western Greenland (Grímsson *et al.* 2018) has brought new elements to the understanding of the past distribution of this family and has challenged recent theories that interpret the Winteraceae as a Southern Hemisphere clade with a possible origin in Northern Gondwana (Doyle & Endress 2000; Thomas *et al.* 2014). There are two occurrences of fossil leaves attributed to Winteraceae in the Northern Hemisphere: the first from the mid-Cretaceous of Nebraska (Upchurch & Dilcher 1990) and the second from the Eocene of Oregon (Chaney & Sanborn 1933). Nevertheless, winteraceous leaves are not very distinctive (Doyle 2000), and ancient records should be re-examined, in particular with regard to cuticle characters.

Extant Chloranthaceae are distributed in Southeast Asia, Madagascar, Central and South America, and the Caribbean Islands. Unequivocal fossils include diverse inflorescences, flowers and fruits, that were common worldwide (for reviews see Eklund *et al.* 2004 and Doyle & Endress 2014). A single fossil wood species has been described in Chloranthaceae, *Mulleroxylon eupomatioides* Page from the Late Cretaceous of North America (Page 1968), but its structure is heteroxylous as in several extant Chloranthaceae genera.

Extant Trochodendraceae are distributed in eastern Asia, from northeastern India to Japan, and only comprise two monospecific genera, *Trochodendron* Siebold & Zucc. and *Tetracentron* Oliv. (Endress 1986). The geographical range of this family was much larger in the past. Unequivocal fossils of flowers, infructescences and wood have been reported from North America, Greenland, Iceland, and Asia (for reviews see Suzuki *et al.* 1991 and Takahashi *et al.* 2017). The oldest vesselless wood attributed to Trochodendraceae is *Tetracentronites* Page from the Maastrichtian of North America (Page 1970).

The aim of this article is to describe the wood of a vesselless angiosperm collected from the middle Cenomanian of the Envigne valley in western France. Systematic affinities with extant and fossil vesselless angiosperms are discussed.

In later publications we describe the remaining conifer and angiosperm wood types and provide more detailed analyses of the fossils and their paleoenvironment.

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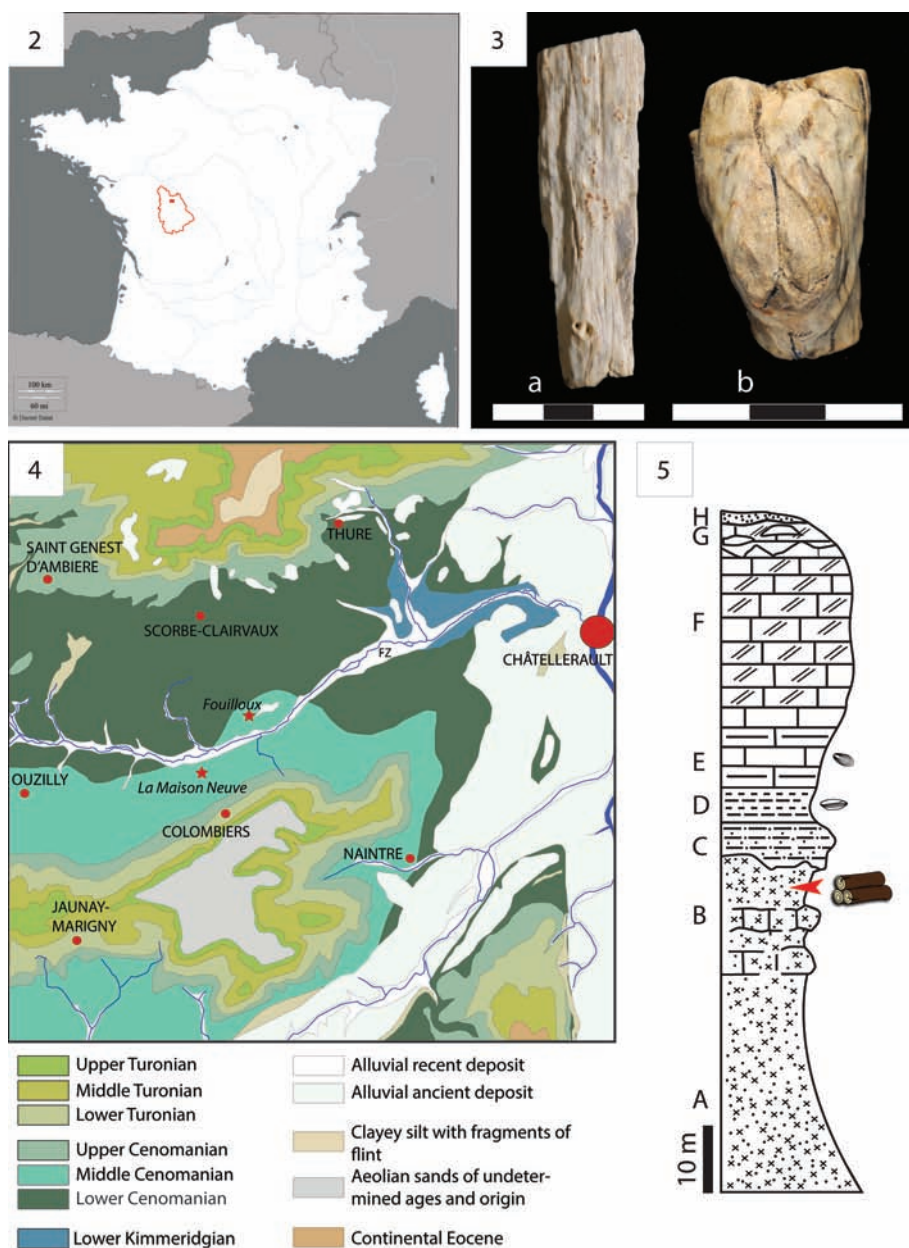
Figure 2–5. – 2: Map of France showing the Vienne department (outline in red), the type locality, Scorbé Clairvaux, is included in the red rectangle. The area represented by this rectangle is magnified in 4. – 3: Two fossil wood samples, a = UP.SCF.17.004, b = UP.SCF.17.007. Scale bars = 3 cm. Multiseriate rays are visible to the naked eye. – 4: Simplified geologic map showing the two new localities: Fouilloux (type locality, Scorbé-Clairvaux) and 'La Maison Neuve'

MATERIAL AND METHODS

Several thousand fossil woods were collected during fieldwork campaigns in 2015 and 2016 from the green sandstones and claystones of La Pallu, Envigne valley, Vienne department, France (Fig. 2, 4 & 5). They are all silicified (Fig. 3a & 3b). For a detailed geological setting see Robin *et al.* (2018).

Around a thousand samples were examined with a stereomicroscope. Fifteen of the latter were identified to the new taxon described here. Transverse, radial and tangential sections of the fossil wood were prepared from five samples at the Muséum national d'Histoire naturelle (MNHN) of Paris, France following standard techniques (Jones & Rowe 1999). They were described following the IAWA Hardwood List (IAWA Committee 1989). Botanical affinities were determined using the InsideWood database (InsideWood 2004-onwards; Wheeler 2011) and literature on fossil and extant vesselless angiosperms (*e.g.*, Metcalfe & Chalk 1950, 1987; Carlquist 1975, 2001; Suzuki *et al.* 1991; Gregory *et al.* 2009 and references therein; for a complete list of references see Table 1).

All microscopic slides, including one transverse, one radial longitudinal and one tangential longitudinal section per specimen and remains of the original specimens are housed in the paleontological collections of the Université de Poitiers (Centre de Valorisation des collections scientifiques de l'Université de Poitiers), France under the numbers UP.SCF.17.003 to UP.SCF.17.007. Photographs of the fossil wood sections were taken with a Nikon D300 digital camera attached to a Nikon Eclipse 80i microscope.

RESULTS

'Family unknown'
Sherwinoxylon Boura & Saulnier, *gen. nov.*

Type: Sherwinoxylon winteroides Boura & Saulnier, *sp. nov.* (UP/SCF.17.004 (field number: VI83) (6.747 × 1.886 cm)).

Repository: Université de Poitiers.

Type locality: Fouilloux, Scorbé-Clairvaux.

Stratigraphic horizon: green sandstones of La Pallu, middle Cenomanian.

←

(Colombiers) are illustrated by red stars. Jaunay-Marigny represents the historical locality where in 1870 the French geologist A. Le Touzé de Longuemar has reported for the first time silicified wood. Modified from Médioni *et al.* (1974) and Bourgueil *et al.* (1976). – 5: Stratigraphic column modified after Gabilly & Cariou (1997): A, claystones and white sandstones of Vierzon (lower Cenomanian); B, green sandstones and C, sandy-claystones of La Pallu (middle Cenomanian); D, plastic claystones and white marlstones with oysters (upper Cenomanian); E, clayey limestones and chalkstones with *Inoceramus labiatus* (lower Turonian); F, white tufa (micaceous glauconitic chalk, middle Turonian); G–H, altered yellow tufa and clayey sandstones with silicified nodules with plants (Gomez *et al.* 2019) (upper Turonian). Studied wood remains were collected from the green sandstones and claystones of La Pallu (indicated in B).

Etymology: In honour of Professor Sherwin Carlquist for his great works on wood anatomy in general and on vesselless angiosperms in particular.

Diagnosis: Vesselless wood. Tracheids with circular to elliptical, closely spaced uniseriate bordered pits, present in both radial and tangential walls. Rays multiseriate. Ray cells with numerous simple to weakly bordered pits. Uniseriate rays absent. Axial parenchyma abundant, diffuse to diffuse-in-aggregates.

Sherwinoxylon winteroides Boura & Saulnier, *sp. nov.*

Holotype: UP/SCF.17.004 (field number: VI83) (6.7 × 1.9 cm).

Additional specimens: UP/SCF.17.003 (field number: VI16) (2.7 cm diam.), UP/ SCF.17.005 (field number: VI87) (5.668 × 1.606 cm), UP/SCF.17.006 (field number: VI147) (6.967 × 2.691 cm), UP/SCF.17.007 (field number: VI183) (3.637 × 2 × 4.27 cm) (all three thin transverse, tangential and radial sections).

Repository: Université de Poitiers.

Type locality: Fouilloux, Scorbé-Clairvaux.

Stratigraphic horizon: green sandstones of La Pallu, middle Cenomanian.

Etymology: To highlight the resemblance between the species and modern Winteraceae.

Diagnosis: Vesselless wood with indistinct growth rings. Tracheids medium- to thick-walled with exclusively circular to elliptical uniseriate bordered pits, more abundant in the radial than tangential walls. Rays multiseriate, up to 9 cells wide, high, composed of square cells with up to four upright marginal cells. Ray cells thick-walled with abundant simple to weakly bordered pits. Axial parenchyma diffuse and diffuse-in-aggregates.

Description

Homoxylous and pycnoxylic fossil wood (Fig. 7 & 8). Faint growth-ring boundaries marked by 1 to 3 rows of flattened latewood tracheids with thicker walls (Fig. 9). Tracheids relatively thick-walled; walls 2–13 μm (average 6.7 ± 1.7 μm) thick; about 2 mm long; tangential diameter 15–48 μm (average 29.9 ± 4.9 μm) (Fig. 9 & 10). Tracheid-tracheid pits bordered, more abundant in radial walls (Fig. 15 & 16) but also common in the tangential walls (Fig. 13 & 14); uniseriate, circular to elliptic all along the tracheid body and in overlapping ends; pit apertures elliptic and oblique with different orientations from one tracheid to its neighbour, which gives a fairly characteristic cross-shaped appearance to the apertures in radial sections. Axial parenchyma abundant, irregularly distributed; diffuse to diffuse-in-aggregates (Fig. 8 & 11); in strands of up to 16 cells. Uniseriate rays absent. Rays 3- to 9-seriate (Fig. 12 & 13), mostly 4- to 5-seriate, composed of square cells, with 1 to 8 rows of upright marginal cells (Fig. 17); a few procumbent cells are sometimes visible among square cells; larger rays 1.03–10.53 mm high (average 4.24 ± 1.65 mm) and 10–170 μm wide (average 80 ± 14 μm) (Fig. 12 & 13). Ray cell walls thick (Fig. 18), with numerous small, simple to weakly bordered pits, without particular arrangement (Fig. 18 & 19). Rays 3–4 per tangential mm. Tracheid pits to rays not observed. Oil cells and storied structure absent. Crystals not observed. Pith elliptic (partly crushed), composed of thin-walled parenchymatous cells (Fig. 6).
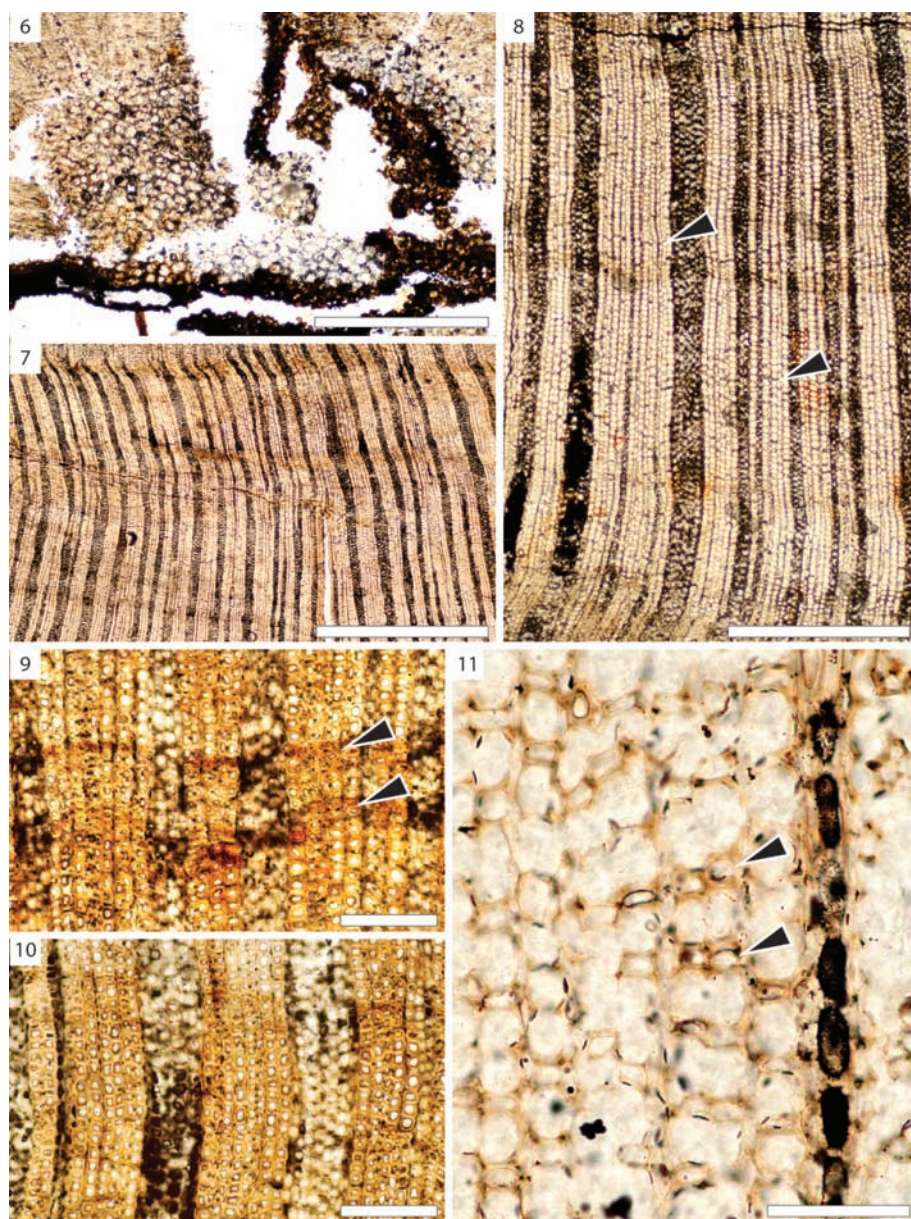
Figure 6–11. Transverse sections of *Sherwinoxylon winteroides* Boura & Saulnier, *sp. nov.* – 6: Parenchymatous pith, UP/SCF.17.007. – 7, 8: Homoxylous wood with broad rays, axial parenchyma diffuse-in-aggregates (arrowheads), UP/SCF.17.005. – 9, 10: Thick-walled tracheids; note the indistinct growth rings (arrowheads) marked by 1–3 rows of flattened tracheids with thickened walls, UP/SCF.17.004. – 11: Axial parenchyma diffuse-in-aggregates (arrowheads), UP/SCF.17.003. – Scale bar 6 = 1 mm, 7 = 2 mm, 8 = 500 µm, 9 & 10 = 250 µm, 11 = 100 µm.
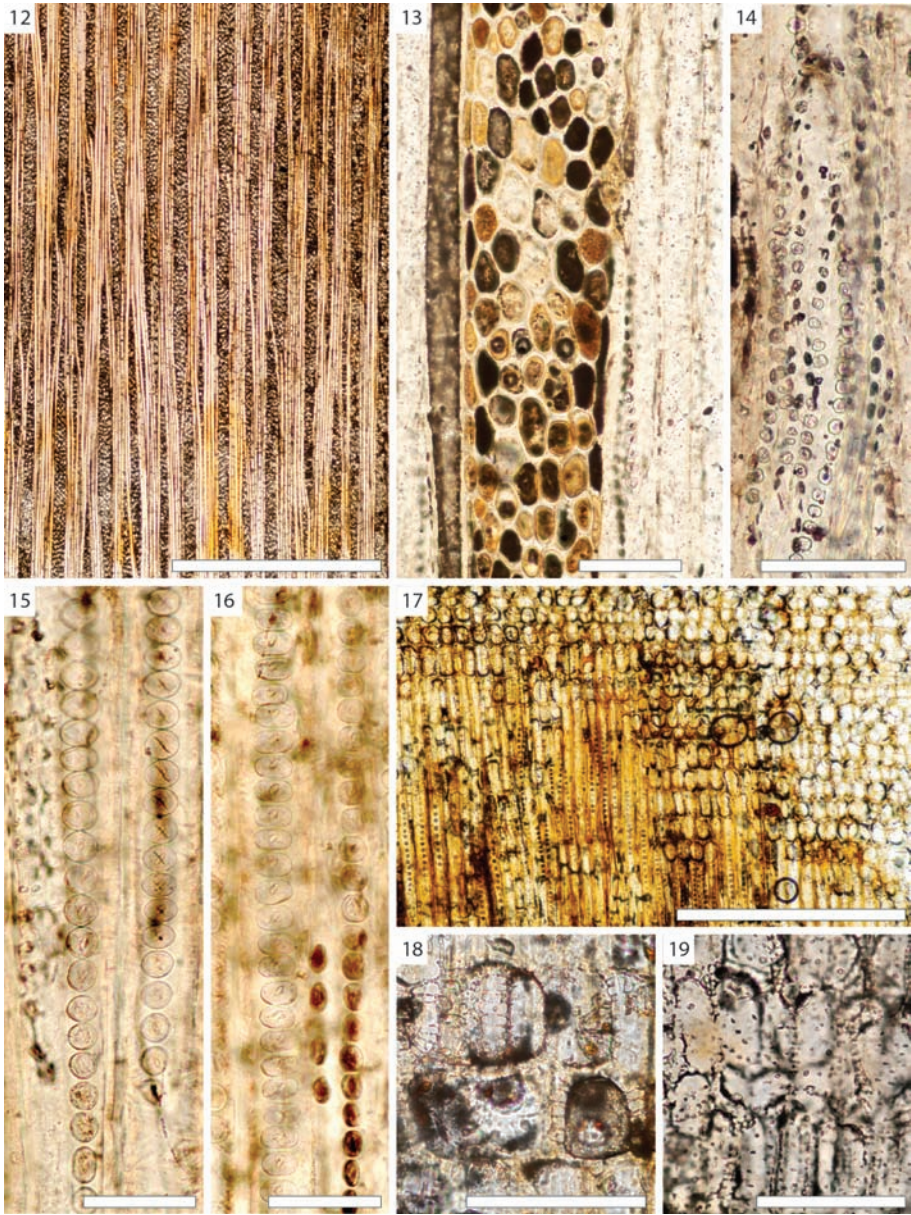
Figure 12–19. Longitudinal sections of *Sherwinoxylon winteroides* Boura & Saulnier, *sp. nov.* – 12 & 13: TLS, exclusively multiseriate rays, UP/SCF.17.004 (12) & UP/SCF.17.003 (13). – 14: TLS, bordered pits in tangential walls of tracheids, UP/SCF.17.003. – 15 & 16: RLS, circular to elliptical often contiguous bordered pits, UP/SCF.17.004. – 17: RLS, rays composed of square cells, with several rows of upright marginal cells, UP/SCF.17.006. – 18: RLS, thick-walled ray cells with simple to weakly bordered pits (funnel-shaped in section), UP/SCF.17.005. – 19: RLS, ray cell pitting, UP/SCF.17.006. – Scale bar 12 = 2 mm, 17 = 500 μm, 13 = 250 μm, 14, 18, 19 = 100 μm, 15, 16 = 50 μm.

Affinities

The specimens described above are characterized by the rare combination of 1) homoxylous pycnoxylic wood with faint growth rings, 2) very broad (up to 9 cells wide) and high rays. Additionally they also show 3) exclusively circular to oval, often contiguous, bordered pits with oblique apertures, and 4) axial parenchyma diffuse to diffuse-in-aggregates and in short uniseriate bands.

Lack of vessels is one of the characteristic features of Coniferophyta. It also characterizes several other extant and fossil clades of both free-sporing or seed plants like Progymnosperms, Ginkgophyta, Pteridospermatophyta, Cycadophyta, Bennettitales and a few genera of angiosperms. Conifers, Ginkgophyta and Progymnosperms have almost exclusively short and uniseriate rays usually composed of radially rather than vertically elongated parenchyma cells (Bailey 1944; Greguss 1955). The Scorbé-Clairvaux specimens described here with rays composed of up to 9 cells wide differ from these three latter taxa. Cycadales and Bennettitales also show either one or a combination of several anatomical features that differ significantly from our specimens, like a large and well-developed pith with vascular bundles in the pith (Cycadales) associated with mucilage canals (Cycadales and Bennettitales); a narrow woody cylinder; a broad cortex; scalariform wall pitting of the secondary xylem sometimes with leaf traces; polyxyly (Cycadales) (Stevenson 1990; Jud *et al.* 2010).

A few Paleozoic fossil genera show a structure similar to that of the specimens described herein. The presence of a homoxylous wood with broad rays can be observed for instance in the species of the genus *Pitys* Witham. Philippe *et al.* (2010) and Sakala *et al.* (2018) pointed out that such a type of wood can be collected from more recent rocks due to the reworking during the burying process as this probably happened for the specimen attributed to *Tetracentronites hungaricus* Greguss. This explanation does not apply to the Scorbé-Clairvaux specimens. The fossil deposit is located on the southwestern edge of the Paris basin, and in this area the oldest rocks are posterior to Kimmeridgian. The green sandstones bearing the fossil wood specimens and the white sandstones of Vierzon, just below, lie on the lower Kimmeridgian yellow limestones. In addition, the specimens described here were collected with many other fossil wood specimens. They all have a homogeneous appearance. A preliminary analysis (Saulnier *et al.* 2018) proved that the plant assemblage was typically Cretaceous in age consisting of several specimens of *Tempskya* Corda, several conifer species (including one which belongs to Pinaceae) and several species of heteroxylous angiosperms. Furthermore, all *Pitys* species have multiseriate radial tracheid pits (between 3- and 5-seriate) (J. Galtier, pers. comm.), which is not the case in our specimens.

The combination of homoxylous wood and broad rays most probably indicates that the specimens described here belong to a vesselless angiosperm. The absence of vessels occurs in several genera and species of several families: *Amborella* Baill. in the Amborellaceae, all genera in the Winteraceae (*Drimys* J. R. Forst. & G. Forst., *Pseudowintera* Dandy, *Takhtajania* M. Baranova & J.-F. Leroy, *Zygogynum* Baill., *Bubbia* Tiegh., *Exospermum* Tiegh., *Tasmannia* R. Br. *ex* DC., *Belliolum* Tiegh.), *Sarcandra* in the Chloranthaceae, *Trochodendron* and *Tetracentron* in the Trochodendraceae (see Table 1 for a comparison of the anatomy of extant and fossil vessel-

Table 1. Overview of extant and fossil vesselless angiosperm woods.

E/F = Extant or Fossil, E = extant, F = fossil – **GRB** = Growth-ring boundaries, + = present, +/− = indistinct or absent, − = absent, v = variable among species – **TTP** = Tracheid-tracheid pits, r = pits confined largely to radial walls, t = presence of pits commonly in tangential walls, s = scalariform, (s) = rarely scalariform, c = circular, (c) = rarely circular, ew = earlywood, lw = latewood, v = variable among species – **TOEP** = Tracheid overlapping end pits, s = scalariform, c = circular, (s) = rarely scalariform, v = variable among species – **PAR** = Axial parenchyma, + = present, − = rare or absent, s = scanty, d = diffuse, d & a = diffuse-in-aggregates, m = marginal bands, b = thin bands, top = tangentially oriented pairs – **STD L** = Strand length, 8+ = over eight cells – **UR** = uniseriate rays, + = present, − = absent, (1-2) = uniseriate or sometimes biseriate, He = heterocellular, Ho = homocellular, p = all ray cells procumbent, us = all ray cells upright and/or square, m = rays with procumbent, square and upright cells mixed throughout the ray – **RW** = larger ray width – **RT** = larger ray type, He = heterocellular, Ho = homocelular, p = all ray cells procumbent, us = all ray cells upright and/or square, (p) = few files of procumbent cells present in wider rays, m = rays with procumbent, square and upright cells mixed throughout the ray, (2-4 us) p = body ray cells procumbent with mostly 2-4 rows of upright and/or square marginal cells, (4+us) p = body ray cells procumbent with over 4 rows of upright and/or square marginal cells – **SC** = Sheath cell, + = present, − = absent, v = variable – **OC** = Oil or mucilage cells, + = present, − = absent.

References: Mathiesen 1932 (1); Bailey & Swamy 1948 (2); Swamy & Bailey 1950 (3); Hergert & Phinney 1954 (4); Bailey 1957 (5); Greguss 1963 (6); Page 1968 (7); Patel 1974 (8); Meylan & Butterfield 1978 (9); Carlquist 1981 (10); Carlquist 1982 (11); Keating & Bolza 1982 (12); Scott & Wheeler 1982 (13); Carlquist 1983a (14); Carlquist 1983b (15); Carlquist 1987 (16); Carlquist 1988 (17); Carlquist 1989 (18); Crane *et al*. 1991 (19); Suzuki *et al*. 1991 (20); Carlquist 1992 (21); Gottwald 1992 (22); Nardi & Edlmann 1992 (23); Carlquist 2000 (24); Richter & Dallwitz 2000 (25); Poole & Francis 2000 (26); Carlquist & Schneider 2001 (27); Gasson *et al*. 2011 (28); Sakala *et al*. 2018 (29); this study (30).

E/F	Species	Locality (F)	Horizon (F)	*Ref.*	GRB	TTP	TOEP	PAR	STD L	UR	RW	RT	SC	OC
E	*Amborella trichopoda* Baill.			2, 5, 27	+/−	r s (ew) c (lw)	s	+ d	5-8	+ (1-2) Ho, us	(2) 3-5	Ho, us (p)	v	−
E	*Sarcandra glabra* (Thunb.) Nakai			2, 16, 21	+	r s (ew) c (lw)	c	+ v (d, s) top	?	+ Ho, us	2-5 (10)	Ho, us	v	−
E	*Trochodendron aralioides* Siebold & Zucc.			12, 25	+	r t s	?	+ d & a top	3-6 5-8	+ Ho, us	2-8 (10)	He (2-4 us) p	−	−
E	*Tetracentron sinense* Oliv.			20, 28	+	r s (ew) c (lw)	?	+ d, d & a rare top	2-8	+ Ho, p	4-10	Ho p	v	−

(continued)

(Table 1 continued)

E/F	Species	Locality (F)	Horizon (F)	*Ref.*	GRB	TTP	TOEP	PAR	STD L	UR	RW	RT	SC	OC
F	*Tetracentron japon-oxylon* Suzuki, Joshi & Noshiro.	Japan	Mio.	20	+	r s (ew) c (lw)	?	+ d	?	+ Ho, us	2-4	He (1-4 us) p	–	–
F	*Tetracentronites hartzi* Mathiesen	Greenland	Tert.	1	+	r s (ew) c (lw)	?	+ d	?	+ Ho, us	2-8	He (4 + us) p	–	–
F	*Tetracentronites hungaricus* Greguss	Hungary	Mio.	6, 29	+/–	r c	?	–	?	+ He, m	2 (3)	He m	–	–
F	*Tetracentronites panochetri* Page	California, USA	Up. Cret.	7	+	r s c	?	+ s	?	+ Ho, us	2-8	Ho us	+	–
F	*Trochodendron beckii* (Hergert & Phinney) Scott & Wheeler	Oregon, USA	Eoc Oli.	4, 13	+	r s (ew) c (lw)	?	+ d, d & a	?	+ Ho, us	2-10	He (4 + us) p	–	–
F	*Nordenskioldia borealis* (Heer) Crane, Manchester & Dilcher	Spitsberg	Pal.	19	?	c	?	+ d & a	?	+ Ho, us	–	–	–	–
E	*Takhtajania perrieri* (Capuron) M.Baranova & J.-F. Leroy			24	–	r c, s	c, s	+ s, d	5-6	+ Ho, us	2-5	Ho, us (p)	–	–
E	*Tasmannia* R. Br. *ex* DC., 14 species			18	v (–,+/–)	r c, (s)	c, (s)	v (–,+,d,s)	?	+ Ho, us	2-5 (10)	Ho, us (p)	–	–
E	*Zygogynum* Baill. 6 species			10	+/–	v (c, s)	v (c, s)	v (+, s, d, d & a, b)	5-8 +	+ He, m	4-10	He (4+us) p	+	+

(Table 1 continued)

E/F	Species	Locality (F)	Horizon (F)	*Ref.*	GRB	TTP	TOEP	PAR	STD L	UR	RW	RT	SC	OC
E	*Drimys* J.R.Forst. *ex* G.Forst. 7 species			14, 17, 23	v (+/–, +, –)	r, c, (s) (ew)	c c (lw)	+ d, d&a	?	+ Ho, us	2-10	He (4+us) p	–	–
E	*Pseudowintera* Dandy, 3 species			8, 9	v (+/–, +)	r c	?	d, d&a, m	2-12	+ Ho, us	7-29	He (4+us) p	v	–
E	*Bubbia* Tiegh. ?			10, 15	v (-, +/-)	v (c,s)	v (c,s)	v (+,d,b)	2-8	+ Ho, us	4-10	He (1-4us) p	v	+
E	*Exospermum stipitatum* (Baill.) Tiegh. (unresolved according to plant list			11	–	c	c	+ d, b	5-8 +	+ Ho, us	4-10	He (4+us) p	v	+
F	*Winteroxylon mundlosi* Gottwald	Europe	Eoc.	22	+/-	c, s	?	+ b	?	+	3-7	He (1-4us) p	–	+
F	*Winteroxylon jamesrossi* Poole & Francis	Antarctica	Up. Cret.	26	+/-	r c, s	s	+ d, d&a	?	+ Ho, us	4-13	He m	+	–
F	***Sherwinoxylon winteroides*** **gen. nov., sp. nov.**	**Europe**	**Cen.**	**30**	**+/-**	**r c**	**c**	**+ d, d&a**	**8+**	**–**	**4-9**	**Ho us**	**–**	**–**

less angiosperms). *Amborella trichopoda* has predominantly uniseriate rays and scalariform end walls in earlywood tracheids. Both *Tetracentron* and *Trochodendron* in the Trochodendraceae and *Sarcandra* in the Chloranthaceae are characterized by well-marked growth-ring boundaries and scalarifom tracheid-tracheid pits at least in earlywood, tangentially oriented pairs of axial parenchyma strands deriving from a single fusiform cambial initial (rare in *Tetracentron*) (Bailey 1944; Swamy & Bailey 1950; Carlquist 1983b; Table 1). Numerous characteristics of the specimens described here are present in the genera of Winteraceae (Table 1) like 1) indistinct growth rings (*Tasmannia*, *Zygogynum*, *Pseudowintera*, *Bubbia*); 2) bordered pits circular or slightly elongated (*Pseudowintera*, *Exospermum*); 3) axial parenchyma diffuse in aggregates (*Zygogynum*, *Drimys*, *Pseudowintera*, *Bubbia*), 4) long parenchyma strands often of up to 8 cells (*Zygogynum*, *Pseudowintera*, *Exospermum*) and 5) Presence of numerous and small pits in the ray cell walls (*Bubbia*, *Drimys*, *Zygogynum*, *Pseudowintera*). Nevertheless, all these genera differ from the Scorbé-Clairvaux specimens because 1) they show both uniseriate and multiseriate rays, 2) tracheid pits are largely confined to radial walls. Yet we consider it likely that the specimens studied here belong to the Winteraceae, despite the differences mentioned above. It is difficult to attribute those specimens to any of the extant genera. The specimens share several characters of the Winteraceae (in the crown group [*Zygogynum* – *Bubbia* – *Pseudowintera* – *Drimys*] or in its sister group, the genus *Tasmannia*) (for phylogeny and distribution of vessveless wood, see Doust and Drinnan (2004), Feild *et al*. (2002), and Thomas *et al*. (2014).

Several fossil genera have been erected for the fossil woods of homoxylous angiosperms: *Nordenskioldia* Heer for twigs associated with fruits and leaves of this same genus (Trochodendraceae), *Tetracentronites* Mathiesen (Trochodendraceae), *Winteroxylon* Gottwald (Winteraceae). Also several fossil woods were attributed to extant *Tetracentron* and *Trochodendron,* like *Tetracentron japonoxylum* Suzuki, Joshi & Noshiro and *Trochodendron beckii* (Hergert & Phinney) Scott & Wheeler (syn. *Trochodendroxylon beckii* Hergert & Phinney), when the fossil specimens closely resembled and were only comparable to a single living genus. As observed in living species of Trochodendraceae, the fossil specimens attributed to *Trochodendroxylon* and *Tetracentronites* must have, based on their diagnoses, distinct growth-ring boundaries, scalariform pits at least at the end of the tracheids and two distinct types of rays, uniseriate and multiseriate. The genera *Homoxylon* Hartig, *Sahnioxylon* Bose & Sah and *Pataloxylon* Sahni were also sometimes used for homoxylous angiosperms but they most probably represent conifers, bennettites or even heteroxylous angiosperms (for a review see Suzuki *et al*. 1991). Several specimens were transferred to *Sahnioxylon* Bose & Sah and *Phoroxylon* Sze, which are now considered to be Bennettitales or Cycadales (Suzuki *et al*. 1991; Gregory *et al*. 2009). *Winteroxylon* was erected by Gottwald (1992) and later emended by Poole and Francis (2000) for vessveless angiosperms with indistinct growth rings, circular pits, apotracheal parenchyma diffuse or in short uniseriate bands and presence of both uniseriate and multiseriate rays (among other features). Two species of *Winteroxylon* were already described: the first, *W. mundlosi* Gottwald from the upper Eocene of Europe, the second from the Upper Cretaceous of Antarctica, *W. jamesrossi* Poole & Francis. The absence of uniseriate rays makes *Sherwinoxylon*

quite unique among vesselless angiosperms in general and Winteraceae in particular. The fossils show some similarities with extant Winteraceae and *Winteroxylon*, but due to the absence of uniseriate rays, we consider it prudent and justified to erect a new genus of vesselless fossil angiosperm wood. As stated by Doyle (2000), when discussing the affinities of *Winteroxylon mundlosi*, other vesselless angiosperm lineages that resemble Winteraceae, but are unrelated, may have existed in the past. In view of its singularities, our specimens may belong to such an extinct group, either unrelated to Winteraceae or placed at the base of the main clade of the Winteraceae. The splitting between those clades has been dated around 91 Ma (Thomas *et al*. 2014), which is consistent with the age of the locality.

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