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Running title: Cenomanian Vesselless Angiosperm

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An early record of a vesselless angiosperm from the middle Cenomanian of the Envigne valley (Vienne,  
Western France)

A. Boura<sup>1\*</sup>, G. Saulnier<sup>1</sup>, D. De Franceschi<sup>1</sup>, B. Gomez<sup>2</sup>, V. Daviero-Gomez<sup>2</sup>, D. Pons<sup>1</sup>,  
G. Garcia<sup>3</sup>, N. Robin<sup>1</sup>, J-M. Boiteau<sup>4</sup> and X. Valentin<sup>3,5</sup>

<sup>1</sup> CR2P, UMR7207, MNHN, Sorbonne Université, CNRS, 57 rue Cuvier, CP 48, F-75005, Paris, France

<sup>2</sup> LGL, UMR 5276, Université Lyon 1, Villeurbanne 69622, France

<sup>3</sup> PALEVOPRIM, UMR7262 CNRS INEE, Université de Poitiers, 6, rue Michel-Brunet, 86073 Poitiers cedex,  
France.

<sup>4</sup> 81 Avenue Jean Mermoz, 86100, Châtellerault, France

<sup>5</sup> Palaios, Research Association, 86300 Valdivienne, France

\*corresponding author: [anais.boura@sorbonne-universite.fr](mailto:anais.boura@sorbonne-universite.fr)

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Running title: Cenomanian Vesselless Angiosperm

21 **Abstract**

22

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

32

33 **Keyword:** Fossil wood, Winteraceae, Cretaceous, *Sherwinoxylon* gen. nov.

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## 37 **Introduction**

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

45 Conifers are the most abundant and diversified fossil wood in this assemblage, representing around 90%  
46 and at least five different taxa. They consist of large logs transported into an estuarine or a near-shore  
47 environment. Although angiosperms are less abundant (only 9.8 %) and have smaller diameters,  
48 they have a higher diversity with at least nine different taxa (Saulnier *et al.* 2018). Angiosperm  
49 pollen grains and leaves have been frequently reported from the Cenomanian of western France  
50 (Crié 1884; Juignet & Médus 1971; Azéma *et al.* 1972; Laing 1975; Pons *et al.* 1980; Gomez *et al.*  
51 2004, 2008; Néraudeau *et al.* 2005, 2008, 2013, 2017; Peyrot *et al.* 2005; Valentin *et al.* 2014;  
52 Fleury *et al.* 2017), but they were not yet related to fossil wood. So far described contemporary  
53 wood consisted only of lignitized conifer genera (Néraudeau *et al.* 2003, 2008, 2013, 2017;  
54 Fleury *et al.* 2017). These two fossil plant assemblages are thus of great interest in the  
55 understanding of the spread and rise to dominance of woody angiosperms in Europe and  
56 worldwide during the Cretaceous. In this context, vesselless angiosperms are also of particular  
57 interest, and here we describe a new form genus in this category of homoxylous woods.

58 A vesselless angiosperm wood is a "wood without vessel elements, composed only of imperforate  
59 tracheary elements and parenchyma [...] Amborellaceae, Tetracentraceae, Trochodendraceae,  
60 Winteraceae" (IAWA committee 1989). Nevertheless, the presence of perforated vessel elements was  
61 recently highlighted in Trochodendraceae (Ren *et al.* 2007; Li *et al.* 2011) or in *Sarcandra* Gardner  
62 (Chloranthaceae) (Carlquist 1987). In other genera such as *Amborella* Baill., *Bubbia* Tiegh or *Drimys*  
63 J.R.Forst. ex G.Forst., tracheary cells show a tendency toward differentiation of end wall pitting  
64 (Feild *et al.* 2000; Carlquist & Schneider 2002). According to the last angiosperm phylogeny  
65 (Angiosperm Phylogeny Group IV 2016) and data on wood structure (Carlquist 1975, 2001; Insidewood

66 2004; Wheeler 2011), vesselless wood is found in the basal angiosperms (ANA grade with  
67 Amborellaceae), Magnoliids (Winteraceae), Chloranthales (Chloranthaceae) and in one of the early  
68 branching eudicot clades, Trochodendrales (Trochodendraceae (including former Tetracentraceae)) (Fig.  
69 1).

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

83 The fossil record of most vesselless angiosperm families is quite ancient : Early Cretaceous for Winteraceae  
84 with the pollen type *Walkeripollis gabonensis* Doyle, Hotton & J. V. Ward (Doyle *et al.* 1990) and for  
85 Chloranthaceae (Barremian–Aptian) with the pollen type *Asteropollis* Hedlund & Norris related to  
86 the extant genus *Hedyosmum* Sw. (Friis *et al.* 1994, Tanaka 2008), Late Cretaceous (early Coniacian)  
87 for Trochodendraceae with the flower *Archaestella verticillatus* Takahashi, Herendeen & Xiao (Takahashi  
88 *et al.* 2017).

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

91 The family Winteraceae includes 6 valid and 3 unresolved or synonymous genera according to The Plant  
92 List (2013) of shrubs, trees and lianas in the montane tropics and temperate rainforests, mostly in the  
93 Southern Hemisphere occurring from southern North America to South America (Mexico, Ecuador,  
94 Venezuela, Brazil, Chile, Juan Fernandez Islands), Madagascar, the Philippines, Borneo, Sulawesi, New

95 Guinea, the Solomon Islands, New Caledonia, eastern Australia, Tasmania and New Zealand (Christenhusz  
96 *et al.* 2017).

97 Although extant Winteraceae are only distributed in the Southern Hemisphere, fossils attributed to this  
98 family (leaves, wood and pollen) have been reported from both Northern and Southern Hemispheres (for  
99 a review see Doyle 2000, Friis *et al.* 2011 and Grímsson *et al.* 2018). Winteraceae have a unique type of  
100 pollen/tetrad easily recognizable (Walker & Walker 1984; Grímsson *et al.* 2017). During the  
101 Cretaceous winteraceous pollen have been reported from the late Barremian-early Aptian of  
102 Gabon (Doyle *et al.* 1990), Albian of Israel (Walker *et al.* 1983; Schrank 2013), middle Campanian  
103 (Dettmann & Jarzen 1990), and Maastrichtian of Australia (Stover and Partridge, 1973), and the  
104 latest Cretaceous of New Zealand (Mildenhall & Crosbie 1979). In the Southern Hemisphere,  
105 Poole and Francis (2000) also described *Winteroxylon jamesrossi* Poole & Francis, a fossil wood from the  
106 Santonian–Campanian of Antarctica. A few fossils attributed to Winteraceae have been described  
107 outside the range of extant members as for example the type species of *Winteroxylon* Gottwald,  
108 *W. mundlosi* Gottwald from the Eocene of Europe (Gottwald 1992). Doyle (2000) suggested that the  
109 geographical range of the family could have been larger than previously thought and may have included  
110 Laurasia or that they were a wrong attribution. The recent report of Winteraceae pollen tetrads from the  
111 early Paleocene of western Greenland (Grímsson *et al.* 2018) has brought new elements for the  
112 understanding of the past distribution of this family and have challenged recent theories that  
113 interpret the Winteraceae as a Southern Hemisphere clade with a possible origin in Northern  
114 Gondwana (Doyle & Endress 2000; Thomas *et al.* 2014). There are two occurrences of fossil  
115 leaves attributed to the Winteraceae in the Northern Hemisphere: the first from the mid-  
116 Cretaceous of Nebraska (Upchurch & Dilcher 1990) and the second from the Eocene of Oregon  
117 (Chaney & Sanborn 1933). Nevertheless, winteraceous leaves are not very distinctive (Doyle  
118 2000), and ancient records should be re-examined, in particular with regards to cuticle  
119 characters.

120 Extant Chloranthaceae are distributed in Southeast Asia, Madagascar, Central and South  
121 America, and Caribbean Islands. Unequivocal fossils include diverse inflorescences, flowers and  
122 fruits, that were common worldwide (for reviews see Eklund *et al.* 2004 and Doyle & Endress  
123 2014). A single fossil wood species has been described in Chloranthaceae, *Mulleroxylon*

124 *eupomatioides* Page from the Late Cretaceous of North America (Page 1968), but its structure is  
125 heteroxylous as in several extant Chloranthaceae genera.

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

132 The aim of this article is to describe the wood of a vesselless angiosperm collected from the middle  
133 Cenomanian of the Envigne valley in western France. Systematic affinities with extant and fossil vesselless  
134 angiosperms are discussed. In later publications we will describe the remaining conifer and  
135 angiosperm wood types and provide more detailed analyses of the fossils and their  
136 palaeoenvironment.

137

## 138 **Material and methods**

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

142 Around a thousand samples were examined with a stereomicroscope. Fifteen of the latter were identified  
143 to the new taxon described herein. Transverse, radial and tangential sections of the fossil wood were  
144 prepared from five samples at the Muséum national d'Histoire naturelle (MNHN) of Paris, France following  
145 standard techniques (Jones and Rowe, 1999). They were described following the IAWA Hardwood List  
146 (IAWA committee 1989). Botanical affinities were determined using the Insidewood database (Insidewood  
147 2004; Wheeler 2013) and literature on fossil and extant vesselless angiosperms (e.g., Metcalfe and Chalk  
148 1950, 1987; Suzuki *et al.* 1991; Carlquist 1975, 2001; Gregory *et al.* 2009 and references therein; for a  
149 complete list of references see Table 1).

150 All microscopic slides, including one transverse, one radial longitudinal and one tangential longitudinal  
151 section per specimen and remains of the original specimens are housed in the palaeontological collections

152 of Université de Poitiers (Centre de Valorisation des collections scientifiques de l'Université de Poitiers),  
153 France under the numbers UP.SCF.17.003 to UP.SCF.17.007. Photographs of the fossil wood sections were  
154 taken with a Nikon D300 digital camera attached to a Nikon Eclipse 80i microscope.

155

## 156 **Results**

### 157 **'Family unknown'**

#### 158 ***Sherwinoxylon* Boura & Saulnier , gen. nov.**

159 **Type:** *Sherwinoxylon winteroides* Boura & Saulnier, sp. nov. (UP/SCF.17.004 (field number: VI83)  
160 (6.747x1.886 cm))

161 **Repository:** Université de Poitiers

162 **Type locality:** Fouilloux, Scorbé-Clairvaux

163 **Stratigraphic horizon:** green sandstones of La Pallu, middle Cenomanian

164 **Etymology:** In honor of the great work by Professor Sherwin Carlquist on wood anatomy in general and  
165 more particularly on vesselless angiosperms.

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

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

171 **Holotype:** UP/SCF.17.004 (field number: VI83) (6.7x1.9 cm)

172 **Additional specimens:** UP/SCF.17.003 (field number: VI16) (2.7 cm diam.), UP/SCF.17.005 (field number:  
173 VI87) (5.668x1.606 cm), UP/SCF.17.006 (field number: VI147) (6.967x2.691 cm), UP/SCF.17.007 (field  
174 number: VI183) (3.637x2x4.27 cm) (all three thin transverse, tangential and radial sections).

175 **Repository:** Université de Poitiers

176 **Type locality:** Fouilloux, Scorbé-Clairvaux

177 **Stratigraphic horizon:** green sandstones of La Pallu, middle Cenomanian

178 **Etymology:** To highlight the resemblance between the species and modern Winteraceae

179 **Diagnosis:** Vesselless wood with indistinct growth rings. Tracheids medium to thick-walled with  
180 exclusively circular to elliptical uniseriate bordered pits, more abundant in the radial than tangential



181 walls. Rays multiseriate, up to 9 cells wide, high, composed of square cells with up to four upright  
182 marginal cells. Ray cells thick-walled with abundant simple to weakly bordered pits. Axial  
183 parenchyma diffuse and diffuse-in-aggregates.

184 **Description:** Homoxylous and pycnoxylic fossil wood (Figs. 7 & 8). Faint growth ring boundaries marked by  
185 1 to 3 rows of flattened latewood tracheids with thicker walls (Fig. 9). Tracheids relatively thick-walled; 2–  
186 13  $\mu\text{m}$  (average  $6.7 \pm 1.7 \mu\text{m}$ ) thick; about 2 mm long; tangential diameter 15–48  $\mu\text{m}$  (average  $29.9 \pm 4.9$   
187  $\mu\text{m}$ ) (Fig. 9 & 10). Tracheid-tracheid pits bordered, more abundant in radial walls (Figs. 15 & 16) but also  
188 frequent in the tangential walls (Figs. 13 & 14); uniseriate, circular to elliptic all along the tracheid body and  
189 in overlapping ends; pit apertures elliptic and oblique with different orientations from one tracheid to its  
190 neighbor, which gives a fairly characteristic cross-shaped appearance to the apertures in radial sections.  
191 Axial parenchyma abundant, irregularly distributed; diffuse to diffuse-in-aggregate (Figs. 8 & 11); in strands  
192 of up to 16 cells. Uniseriate rays absent. Rays 3- to 9-seriate (Figs. 12 & 13), mostly 4- to 5-seriate,  
193 composed of square cells, with 1 to 8 rows of upright marginal cells (Fig. 17); a few procumbent cells are  
194 sometimes visible among square cells; larger rays 1.03–10.53 mm high (average  $4.24 \pm 1.65 \text{ mm}$ ) and 10–  
195 170  $\mu\text{m}$  wide (average  $80 \pm 14 \mu\text{m}$ ) (Figs. 12 & 13). Ray cell walls thick (Fig. 18), with numerous small,  
196 simple to weakly bordered pits, without particular arrangement (Figs. 18 & 19). Rays 3–4 per tangential  
197 mm. Tracheid pits to rays not observed. Oil cells and storied structure absent. Crystals not observed. Pith  
198 elliptic (partly crushed) composed of thin-walled parenchymatous cells (Fig. 6).

199

200

### Affinities

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

205 Lack of vessels is one of the characteristic features of Coniferophyta. It also characterizes several other  
206 extant and fossil clades of both free-sporing or seed plants like Progymnosperms, Ginkgophyta,  
207 Pteridospermatophyta, Cycadales, Bennettitales and a few genera of angiosperms. Conifers, Ginkgophyta  
208 and Progymnosperms have almost exclusively short and uniseriate rays usually composed of radially rather

209 than vertically elongated parenchyma cells (Bailey 1944; Greguss 1955). The Scorbé-Clairvaux's specimens  
210 described here with rays composed of up to 9 cells wide differ from these three latter taxa. Cycadales and  
211 Bennettiales also show either one or a combination of several anatomical features that differ significantly  
212 from our specimens, like a large and well-developed pith with vascular bundles in the pith (Cycadales)  
213 associated with mucilage canals (Cycadales and Bennettiales); a narrow woody cylinder; a broad cortex;  
214 scalariform wall pitting of the secondary xylem sometimes with leaf traces; polyxyly (Cycadales) (Stevenson  
215 1990; Jud *et al.* 2010).

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

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

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

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

256 **E/F** = Extant or Fossil, E = Extant, F = Fossil; **GRB** = Growth ring boundaries, + = present, +/- = indistinct or absent, - =  
 257 absent, v = variable among species; **TTP** = tracheid-tracheid pits, r = pits confined largely to radial walls, t = presence  
 258 of pits commonly in tangential walls, s = scalariform, (s) = rarely scalariform, c = circular, (c) = rarely circular, ew =  
 259 earlywood, lw = latewood, v = variable among species; **TOEP** = tracheid overlapping ends pits, s = scalariform, c =  
 260 circular, (s) = rarely scalariform, v = variable among species; **PAR** = Axial parenchyma, + = present, - = rare or absent, s  
 261 = scanty, d = diffuse, d&a = diffuse-in-aggregate, m = marginal bands, b = thin bands, top = tangentially oriented pairs;  
 262 **STDL** = Strand length, 8+ = over eight cells; **UR** = Uniseriate rays, + = present, - = absent, (1-2) = uniseriate or  
 263 sometimes biseriate, He = Heterocellular, Ho = homocellular, p = all ray cells procumbent, us = all ray cells upright  
 264 and/or square, m = rays with procumbent, square and upright cells mixed throughout the ray; **RW** = Larger ray width;  
 265 **RT** = Larger ray type, He = Heterocellular, Ho = Homocellular, p = all ray cells procumbent, us = all ray cells upright  
 266 and/or square, (p) = few files of procumbent cells present in wider rays, m = rays with procumbent, square and  
 267 upright cells mixed throughout the ray, (2-4us)p = body ray cells procumbent with mostly 2-4 rows of upright and/or  
 268 square marginal cells, (4+us)p = body ray cells procumbent with over 4 rows of upright and/or square marginal cells;  
 269 **SC** = sheath cell, + = present, - = absent, v = variable; **OC** = Oil or mucilage cells, + = present, - = absent.

270  
 271 References : Mathiesen 1932 (1); Bailey & Swamy 1948 (2); Swamy & Bailey 1950 (3); Hergert & Phinney  
 272 1954 (4); Bailey 1957(5); Greguss 1963 (6); Page 1968 (7); Patel 1974 (8); Meylan & Butterfield 1978 (9);

273 Carlquist 1981 (10); Carlquist 1982 (11); Keating & Bolza 1982 (12); Scott & Wheeler 1982 (13); Carlquist  
274 1983a (14); Carlquist 1983b (15); Carlquist 1987 (16); Carlquist 1988(17); Carlquist 1989 (18); Crane *et al.*  
275 1991 (19); Suzuki *et al.* 1991 (20); Carlquist 1992 (21); Gottwald 1992 (22); Nardi & Edlmann 1992 (23);  
276 Carlquist 2000 (24); Richter & Dallwitz 2000 (25); Poole & Francis 2000 (26); Carlquist & Schneider 2001  
277 (27); Gasson *et al.* 2011 (28); Sakala *et al.* 2018 (29); this study (30).  
278

E/F	Species	Locality (F)	Horizon (F)	Ref.	GRB	TTP	TOEP	PAR	STD L	UR	RW	RT	SC	OC
E	<i>Amborella trichopoda</i>			2, 5, 27	+/-	r s(ew) c(lw)	s	+ d	5-8	+(1-2) Ho, us	(2)3-5	Ho us, (p)	v	-
E	<i>Sarcandra glabra</i> (Thunb.) Nakai			2, 16, 21	+	r s(ew) c(lw)	c	+ v (d, s) top	?	+ Ho, us	2-5(10)	Ho Us	v	-
E	<i>Trochodendron aralioides</i> Siebold & Zucc.			12, 25	+	r, t s	?	+ d&a top	3-6 5-8	+ Ho, us	2-8(10)	He (2-4us)p	-	-
E	<i>Tetracentron sinense</i> Oliv.			20, 28	+	r s(ew) c(lw)	?	+ d, d&a rare top	2-8	+ Ho, p	4-10	Ho p	v	-
F	<i>Tetracentron japonoxylum</i> Suzuki, Joshi & Noshiro	Japan	Mio.	20	+	r s(ew) c(lw)	?	+ d	?	+ Ho, us	2-4	He (1-4us)p	-	-
F	<i>Tetracentronites hartzii</i> Mathiesen	Greenland	Tert.	1	+	r s(ew) c(lw)	?	+ d	?	+ Ho, us	2-8	He (4+us)p	-	-
F	<i>Tetracentronites hungaricus</i> Greguss	Hungary	Mio.	6, 29	+/-	r c	?	-	?	+ He, m	2(3)	He M	-	-
F	<i>Tetracentronites panochetii</i> Page	California USA	Up. Cret.	7	+	r s, c	?	+ s	?	+ Ho, us	2-8	Ho Us	+	-
F	<i>Trochodendron beckii</i> (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	<i>Nordenskiöldia borealis</i> (Heer) Crane, Manchester & Dilcher	Spitsberg	Pal.	19	?	c	?	+ d&a	?	+ Ho, us	-	-	-	-
E	<i>Takhtajania perrieri</i> (Capuron) M. Baranova & J.-F. Leroy			24	-	r c, s	c, s	+ s, d	5-6	+ Ho, us	2-5	Ho us, (p)	-	-
E	<i>Tasmania</i> 14 species			18	v (-, +/-)	r c, (s)	c, (s)	v (-, +, d, s)	?	+ Ho, us	2-5(10)	Ho, us, (p)	-	-

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

Several fossil genera have been erected for the fossil woods of homoxyloous 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 *Homoxyylon* Hartig, *Sahnioxylon* Bose & Sah and *Pataloxylon* Sahni were also sometimes used for homoxyloous angiosperms but they most probably represent conifers, bennettites or even heteroxyloous 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 Francis & Poole (2000) for vesselless 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. jamerossi* 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 these those clades has been dated around 91 Ma (Thomas *et al.* 2014), which is consistent with the age of the locality.

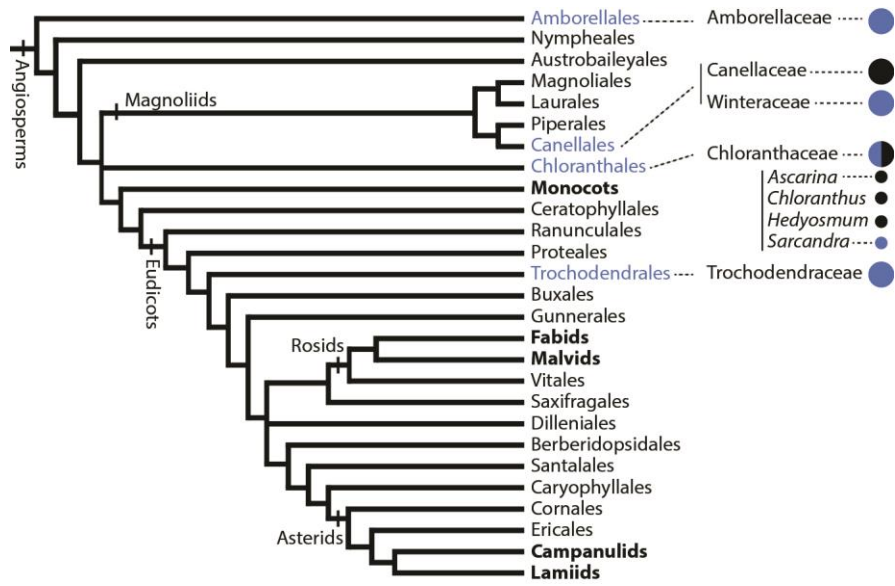
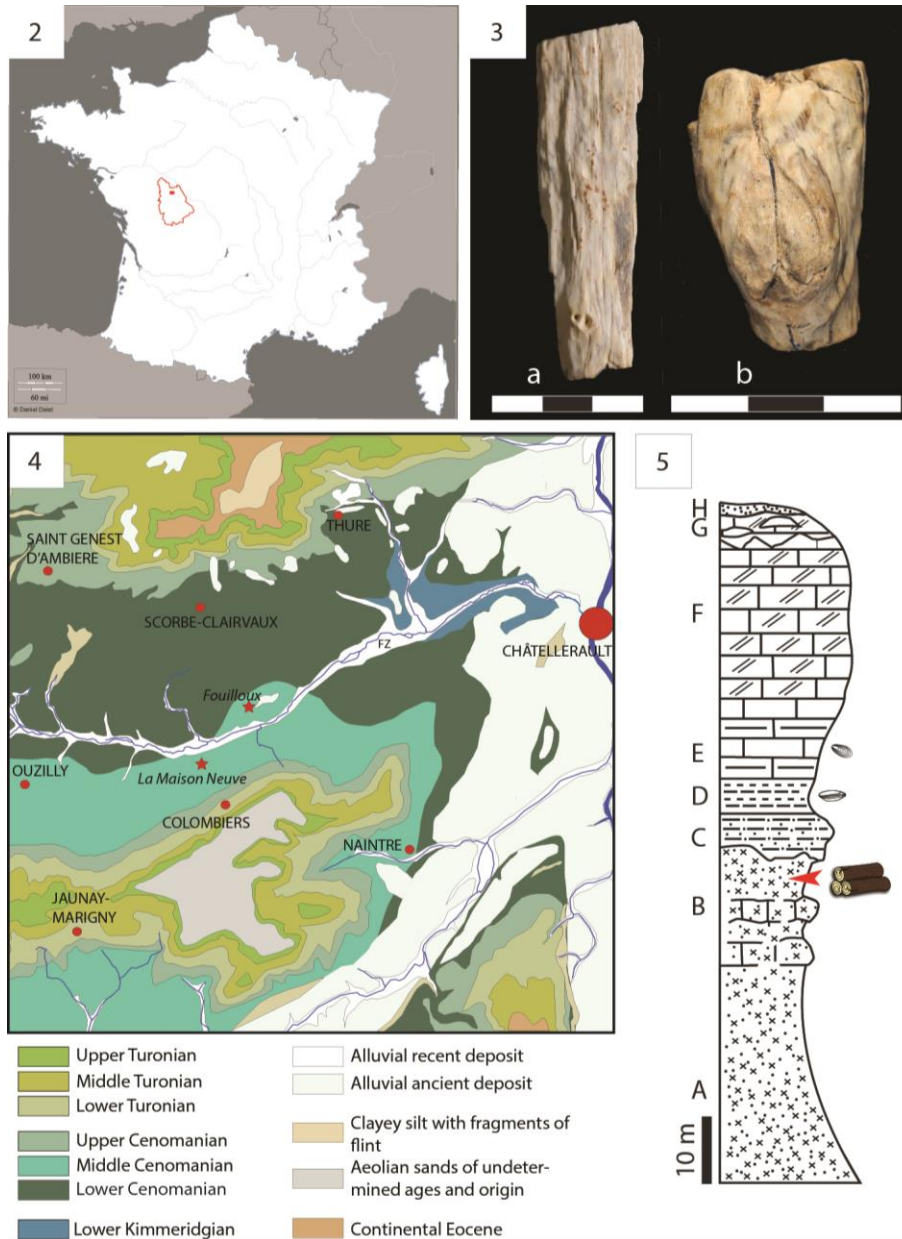
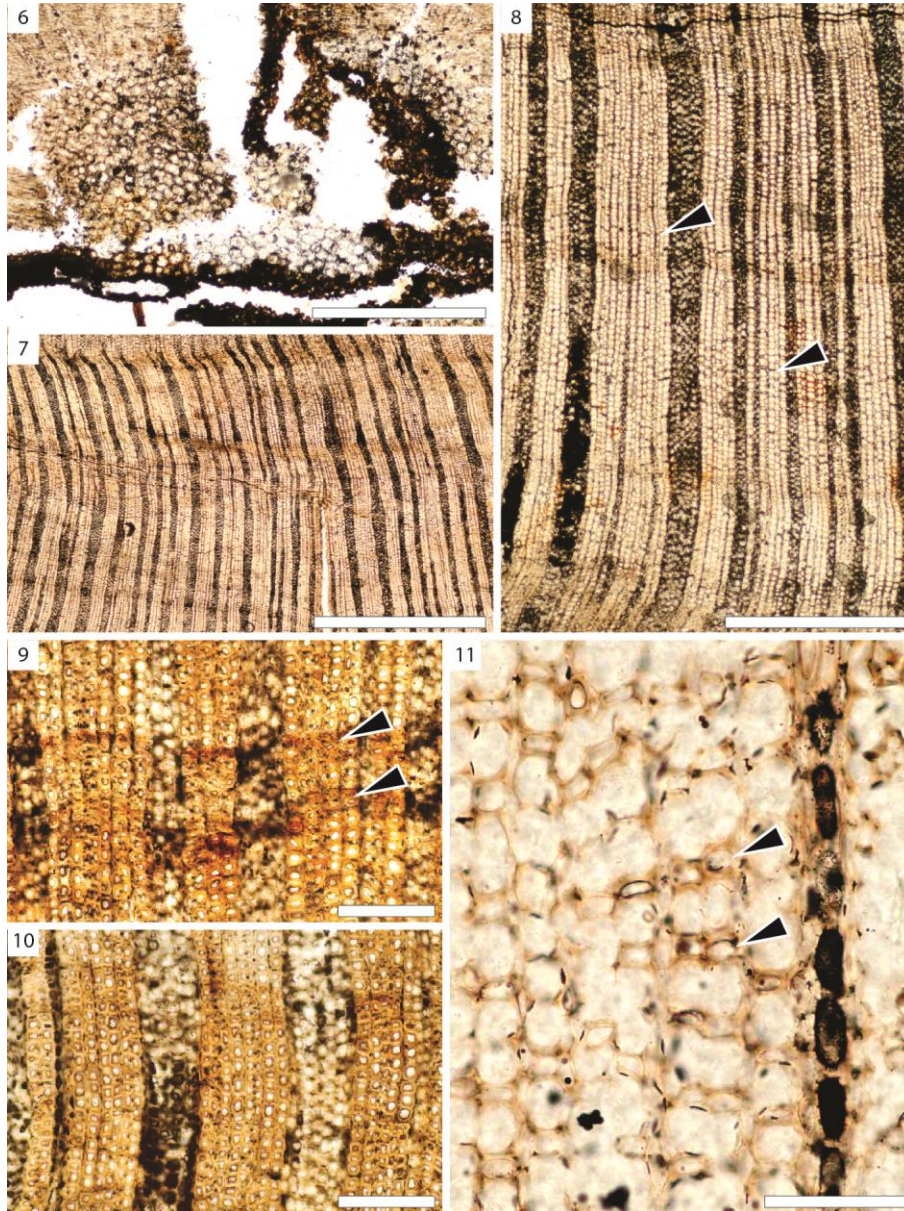


Fig. 1– Occurrence of vesselless wood in angiosperms. Blue circle, homoxyloous or vesselless, Black circle heteroxyloous or vessel-bearing. Modified from Angiosperm Phylogeny Group (2016).

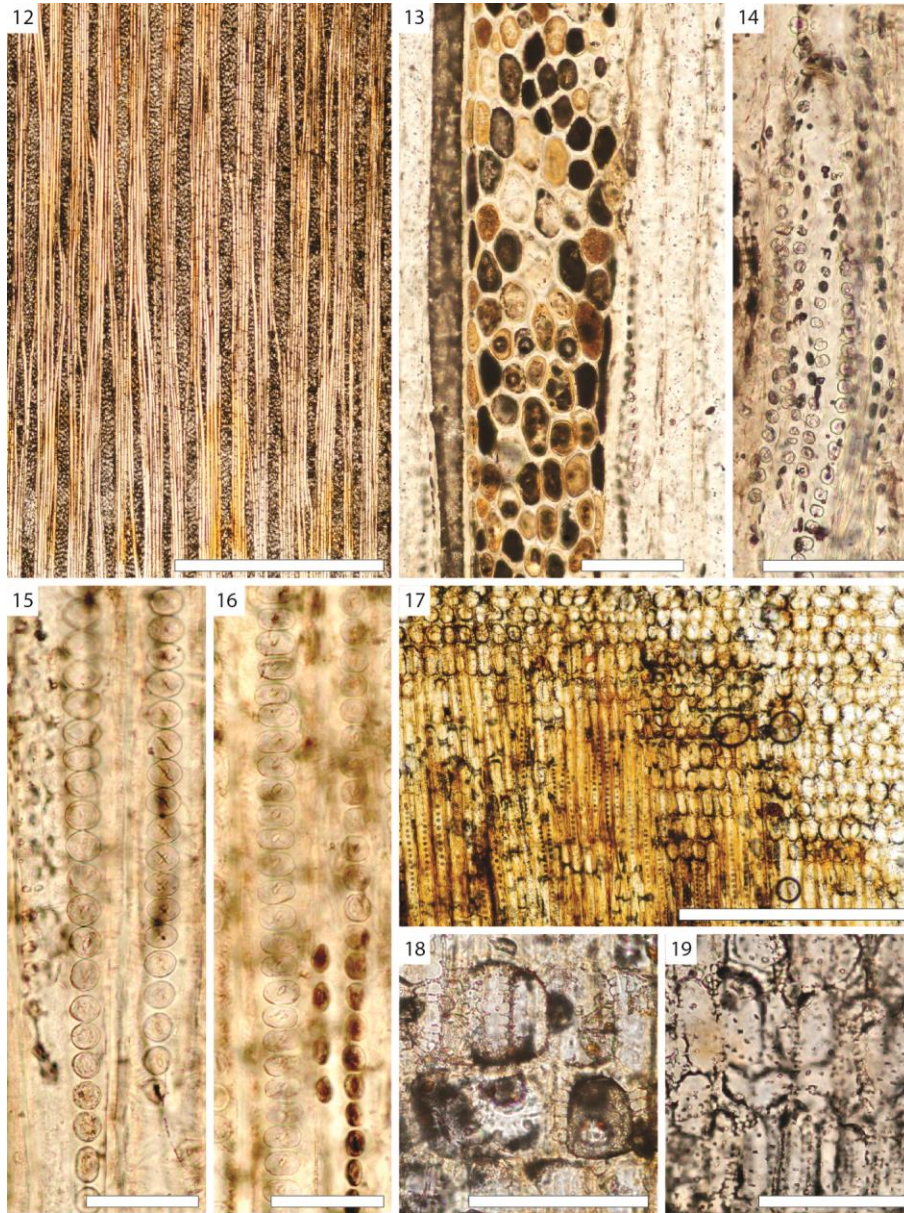




Figs. 2–5. –2 Map of France showing the Vienne department (outline in red), the type locality, Scorbé-clairvaux, is included in the red rectangle. The area represented by this rectangle is magnified in 4; – 3: Two fossil wood samples a = UP.SCF.17.004 and b = UP.SCF.17.007. Scale bars 3 cm. Multiseriate 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' (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 Bourguéil *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.* 2018) (upper Turonian). Studied wood remains were collected from the green sandstones and claystones of La Pallu (indicated in B).



Figs. 6–11. Transverse sections of *Sherwinoxylon winteroides* Boura & Saulnier, sp. nov. – 6: Parenchymatous pith, UP/SCF.17.007. – 7–8: Homoxyloous wood with broad rays, axial parenchyma diffuse-in-aggregates (arrow heads), UP/SCF.17.005. – 9–10 Thick-walled tracheids; note the indistinct growth rings (arrow heads) marked by 1–3 rows of flattened tracheids with thickened walls, UP/SCF.17.004. – 11: Axial parenchyma diffuse-in-aggregates (arrow heads), UP/SCF.17.003. – Scale bar 6 = 1 mm, 7 = 2 mm, 8 = 500  $\mu$ m, 9–10 = 250  $\mu$ m, 11 = 100  $\mu$ m.



Figs. 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  $\mu$ m, 13 = 250  $\mu$ m, 14, 18 & 19 = 100  $\mu$ m, 15–16 = 50  $\mu$ m.

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