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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^{1*}, G. Saulnier¹, D. De Franceschi¹, B. Gomez², V. Daviero-Gomez², D. Pons¹,
G. Garcia³, N. Robin¹, J-M. Boiteau⁴ and X. Valentin^{3,5}

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

² LGL, UMR 5276, Université Lyon 1, Villeurbanne 69622, France

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

⁴ 81 Avenue Jean Mermoz, 86100, Châtellerault, France

⁵ Palaios, Research Association, 86300 Valdivienne, France

*corresponding author: 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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36

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 μm (average $6.7 \pm 1.7 \mu\text{m}$) thick; about 2 mm long; tangential diameter 15–48 μm (average 29.9 ± 4.9
187 μm) (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 μm 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.

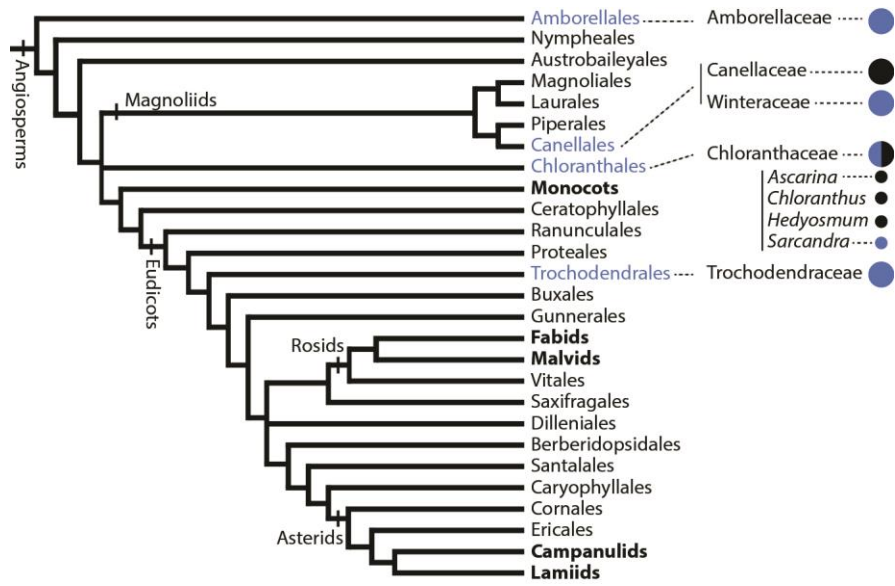
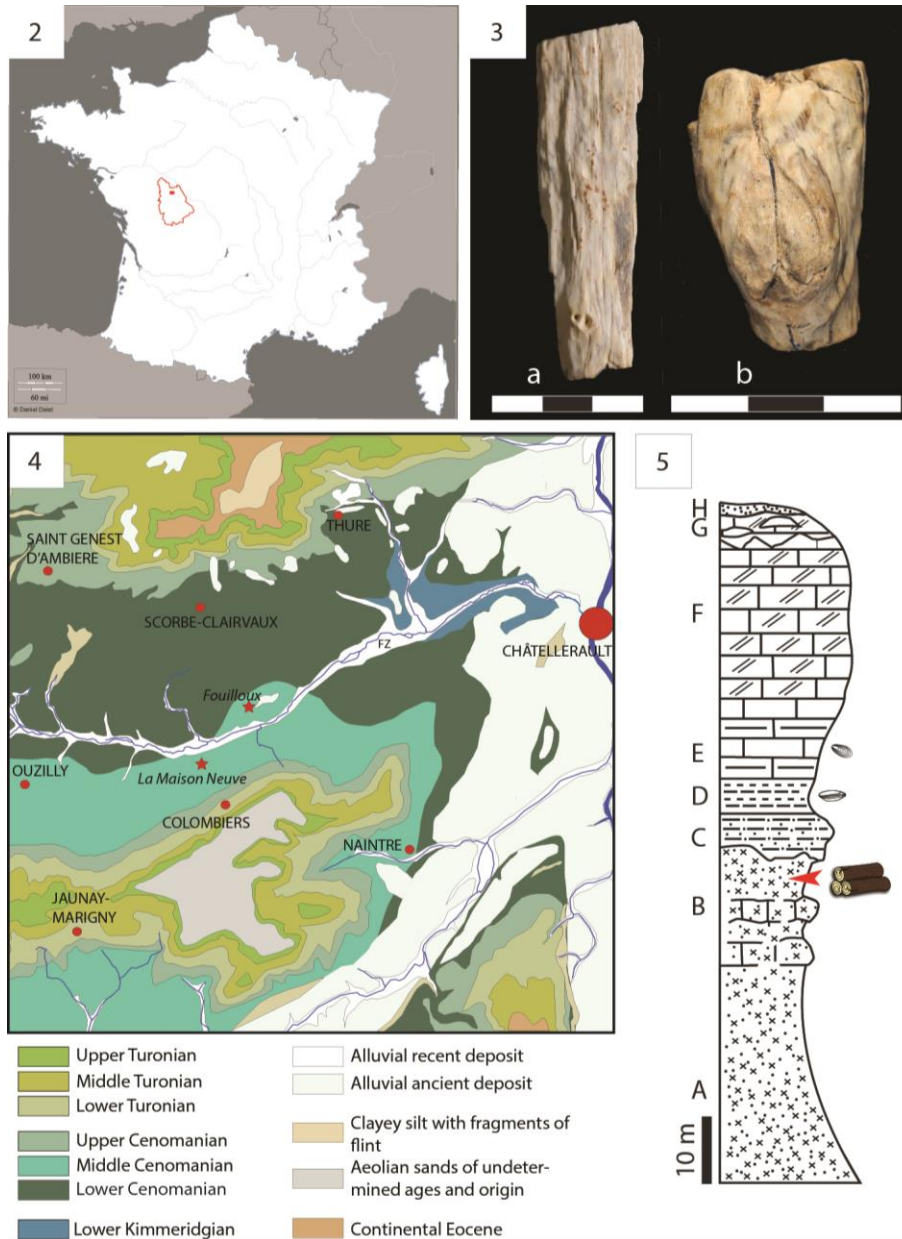
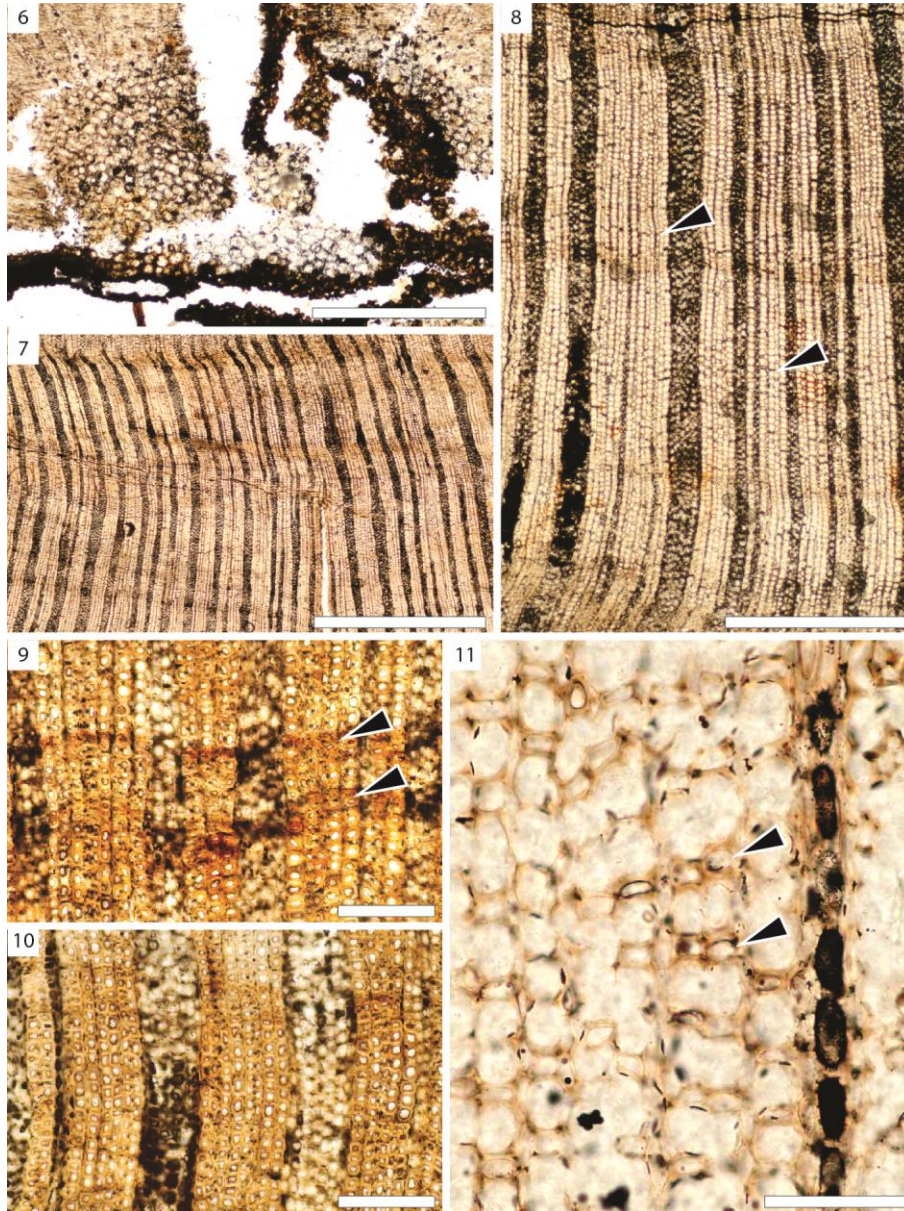


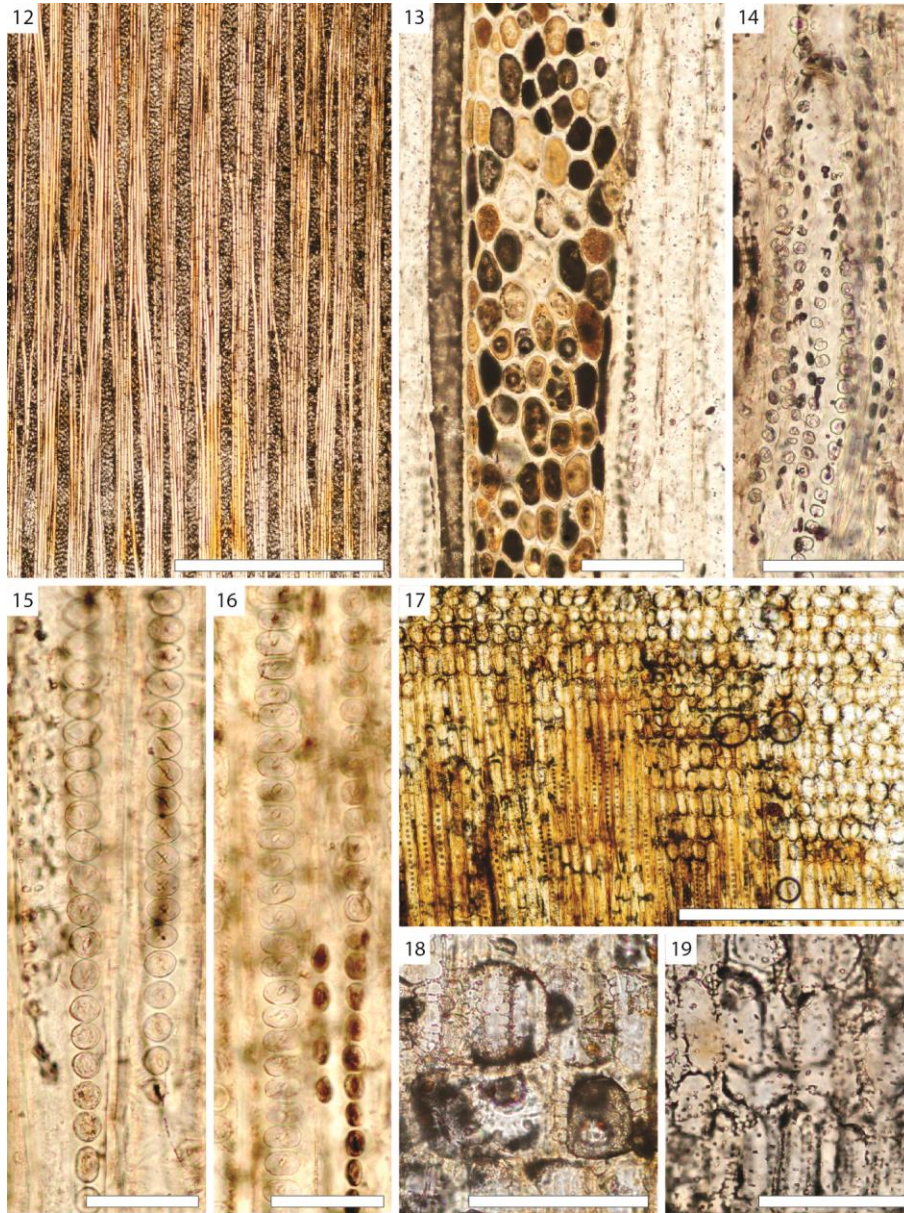
Fig. 1– Occurrence of vesselless wood in angiosperms. Blue circle, homoxylous or vesselless, Black circle heteroxylous or vessel-bearing. Modified from Angiosperm Phylogeny Group (2016).



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: Homoxylous 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 μ m, 9–10 = 250 μ m, 11 = 100 μ 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 μ m, 13 = 250 μ m, 14, 18 & 19 = 100 μ m, 15–16 = 50 μ m.

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