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## A paleobiogeographical scenario for the Taxaceae based on a revised fossil wood record and embolism resistance

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1 Philippe & al. **Fossil wood and palaeobiogeography of Taxaceae**

2

3 **A palaeobiogeographical scenario for the Taxaceae based on a revised fossil wood**  
4 **record and embolism resistance**

5

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20 Abstract: Fossil Taxaceae are documented for the Cenozoic throughout most of the northern  
21 hemisphere, but the pre-Cenozoic history of this group is still poorly known. The fossil wood  
22 record is difficult but can shed light on this history. We critically evaluated the fossil woods  
23 assigned to Taxaceae and then compared the fossil record of taxaceous woods to the fossil  
24 record of taxaceous leaves and reproductive structures. We then considered the fossil record  
25 in the context of family's molecular phylogeny. More than half of the fossil woods attributed  
26 to Taxaceae lack diagnostic characters of the family (longitudinal tracheids with helical  
27 thickenings and abietoid pitting on radial walls). Fossil wood that can be attributed to the  
28 fossil genus *Taxaceoxylon*, as well as some specimens placed in the genus *Protelicoxylon*,  
29 which differ only in having mixed type of intertracheary radial pitting, probably belong to  
30 Taxaceae. The fossil wood record, as reappraised, is not informative about the history of  
31 individual genera within the family, but fits that of leafy remains. Taxaceae wood shows  
32 remarkable resistance to embolism and subsequent increased risks of conduit implosion that  
33 might be prevented by the presence of tertiary helical thickenings. Our findings suggest a

34 palaeobiogeographical scenario for the Taxaceae, that involved a Western Europe Early  
35 Jurassic cradle and expansion to their Holarctic modern distribution.

36

37 **Key-words:** *Taxaceoxylon*; *Protelicoxylon*; wood anatomy; palaeoecology; biogeography;  
38 Laurasia.

39

40 Highlights

- 41 • the fossil wood record of Taxaceae-like wood is reappraised
- 42 • five biogeographically consistent groups are distinguished
- 43 • two of them biogeographically fit with the Taxaceae leafy remains record
- 44 • modern Taxaceae wood shows remarkable resistance to embolism
- 45 • a paleobiogeographical scenario is proposed for the Taxaceae.

46

## 47 1 INTRODUCTION

48

49 The Taxaceae (yew family) is a distinctive family of conifers. Although the family is  
50 small, with only six genera and 32 species (Farjon, 2010), it is ecologically important,  
51 extending widely across the northern hemisphere at mid latitudes (Farjon & Filer, 2013). The  
52 family is also of evolutionary and biogeographic interest due to its great age, intriguing  
53 distribution, peculiar dispersal strategy (endo-ornithochory) and wide habitat diversity. The  
54 family's stem age is likely to be Late Triassic to Early Jurassic and the crown age Mid  
55 Jurassic to earliest Cretaceous (Leslie et al. 2012, 2018; Lu et al. 2014; Renner 2009). The  
56 family occurs in diverse habitats from tropical rainforest to high latitude forest. Although a  
57 mainly northern hemisphere group, it includes the geographically disjunct genus, *Austrotaxus*,  
58 from New Caledonia in the South Pacific (Farjon & Filer, 2013).

59 Although Florin (1948, 1963) proposed a separate order, Taxales, for Taxaceae, molecular  
60 phylogenies clearly place the family within the Coniferales (Rai et al., 2008; Leslie et al.  
61 2012; Ryberg et al., 2012; Yang et al., 2012; Lu et al., 2014). These phylogenies also indicate  
62 that *Cephalotaxus* and *Amentotaxus* (once placed in a different family, Cephalotaxaceae) can  
63 be considered as part of Taxaceae (Lu et al., 2015; Ghimire et al., 2015). This enlarged  
64 Taxaceae is well established as being sister to Cupressaceae *sensu lato* (Rai et al., 2008;  
65 Leslie et al. 2012; Ryberg et al., 2012; Yang et al., 2012; Lu et al., 2014).

66 The fossil record of Taxaceae is sometimes considered poor and difficult to interpret

67 (Taylor et al., 2006; Xu et al., 2015). However, the family's fossil wood record has been little  
68 considered. Taxaceae show homogenous and distinctive wood anatomy across the family,  
69 except in *Austrotaxus* which has wood that is similar to that of Podocarpaceae (Ghimire et al.,  
70 2015). The key anatomical feature of modern Taxaceae wood is that the longitudinal tracheids  
71 usually have 1 to 3 thin and delicate helices running on the longitudinal walls (Göppert, 1841;  
72 IAWA, 2004). These are tertiary thickenings, usually making a variable but typically 45° –  
73 60° rarely up to 80° angle with the vertical (axial) direction. As they run along the tracheid,  
74 helical thickenings can be followed under light microscopy by adjusting the focus, drawing a  
75 low-angle zig-zag pattern. The helix tilt is normally much lower than that of the secondary  
76 wall microfibrils of “normal” tracheids (10 – 25°) (Fig. 1). As early as 1841, Göppert, on the  
77 sole basis of observing helical thickenings, assigned a fossil wood to “*Taxoxylon*” (fossil  
78 naming was largely based on supposed affinities at that time).

79 Helical thickenings occur in some other conifers, e.g., *Pseudotsuga* (Pinaceae). However,  
80 the tracheid wall thickenings in Pinaceae differ from those of Taxaceae in being thinner and  
81 more oblique. In addition, Taxaceae are the only extant conifers with the combination of  
82 helical thickenings, abietinean intertracheary pitting and smooth ray parenchyma cell walls  
83 (Phillips, 1948; for wood anatomy bases see IAWA committee, 2004; Bamford et al., 2016).

84 The Taxaceae fossil wood record deserves reconsideration. Yew-like fossil woods were  
85 reviewed by Kraus (1887), Kräusel (1920), Kräusel & Jain (1964) and more recently Süss &  
86 Velitzelos (1994). However, these reviews were incomplete, even the recent one, or are made  
87 problematic by some erroneous nomenclatural treatments. In particular, many wood fossils  
88 have been assigned to Taxaceae based on inadequate evidence. Moreover, several woods with  
89 possible affinities to the Taxaceae (e.g. Afonin & Philippe, 2014) have been recorded  
90 subsequent to those reviews.

91 We therefore review the fossil record for woods supposed to have affinities with Taxaceae.  
92 We then compare the fossil wood record with that of leaf and reproductive structures. As the  
93 wood of Taxaceae shows high resistance to embolism (Bouche et al., 2014) we discuss the  
94 link between this important physiological trait and the family's wood anatomy. These sources  
95 of evidence are then combined to propose a palaeobiogeographical scenario for the Taxaceae.

96

## 97 **2 MATERIALS & METHODS**

98 **2.1 Which genera to consider – a nomenclatural preamble** – fossil conifer wood, i.e.  
99 isolated pieces of homoxylous secondary xylem, or tracheidoxyls, are classified into a

100 parataxonomy (Philippe & Bamford, 2008). Thus, only in the exceedingly rare cases of an  
101 anatomical connection with leaf or reproductive organs can a fossil tracheidoxyl be assigned  
102 with high levels of confidence to a family, except possibly for woods younger than the  
103 Paleocene. The wood of extant Taxaceae (except *Austrotaxus*) has three key characteristics: 1)  
104 longitudinal tracheids with helical tertiary wall thickenings, 2) mostly abietinean pitting on  
105 the radial walls of longitudinal tracheids and 3) smooth ray parenchyma cell walls. After the  
106 mid-1960s, most fossil woods with these characteristics were assigned to *Taxaceoxylon* R.  
107 Kräusel & Jain, 1964, which is based on material from the Pleistocene of Japan (Kräusel &  
108 Jain, 1964). However, several other genera have been used for woods with helical thickenings  
109 and abietinean, or mixed or araucarian, intertracheary pitting on the radial wall of their  
110 tracheids (TRP thereafter, for “tracheid radial pitting”) and have been more or less explicitly  
111 claimed to be related to Taxaceae (Bamford et al., 2016). We reviewed all these genera.

112 The IAWA Softwood List (IAWA Committee, 2004) is our reference for all xylogenetic  
113 terms here. The term “helical” is preferred here to the term “spiral”, often also used, as a  
114 spiral is normally a planar structure.

115

### 116 **2.1.1 Fossil wood genera with abietinean radial pitting**

117 At least seven genera of fossil woods (Table 1) are thought to have affinities with the  
118 modern Taxaceae because of the occurrence of helical tertiary thickenings and of a mostly  
119 abietinean TRP. Although the names *Taxoxylon* Unger, 1842, and its junior homonym  
120 *Taxoxylon* Houlbert, 1910, have been widely used to describe yew-like fossil woods, it is  
121 unwise to use these names for yew-like fossil woods. Unger (1842) proposed *Taxoxylon* to  
122 name a Tertiary fossil wood from Slovakia, previously described by Göppert (1841) as  
123 *Taxites scalariformis*. However, the protologue diagnosis of *Taxoxylon* is somewhat  
124 ambiguous, the type specimens are poorly preserved, and most seriously, the helical  
125 thickenings are artefacts representing crystal chemical zoning patterns (Kraus, 1887, Pl. III  
126 fig. 3). In addition, many poorly preserved specimens of dubious affinities have been assigned  
127 to *Taxoxylon* (see e.g. Stopes, 1915: 204).

128 Also *Taxoxylon goeppertii* Unger, the original type species of *Taxoxylon*, is an illegitimate  
129 substitute name for *Taxites scalariformis* H.R. Goepfert. The name *Taxites* had, however,  
130 already been previously used by Brongniart (1828) for twigs with no preserved xylem (*T.*  
131 *tounalii*) from the Oligocene of Southern France. We do not consider it wise to use the same  
132 generic name for isolated leafy twigs or secondary xylem pieces when the name is a “form-  
133 taxon” (Bateman & Hilton 2009).

134 *Taxoxylon* Houlbert is a validly published junior homonym. However, the type species, *T.*  
135 *falunense* Houlbert, lacks helical thickenings and has been transferred to *Taxodioxylon*  
136 (Vaudois-Miéja, 1971). Moreover the syntype specimens for *T. falunense* are poorly  
137 preserved (Philippe & Bamford, 2009).

138 Göppert (1850) also created two other genera *Spiropitys* and *Physematopitys* for fossil  
139 wood that he considered to be Taxaceae. *Spiropitys* has been little-used and is today  
140 completely forgotten. It is not wise to use this name because the type is not located and its  
141 protologue does not have a clear diagnosis. *Physematopitys* was originally supposed to be  
142 related to *Ginkgo*, which was then supposed to be related to the yews because of its fleshy  
143 ovules.

144 Hartig (1848) published the name *Spiroxylon*. To the best of our knowledge this name has  
145 not been subsequently used. Although the genus is validly published, it is not possible to use  
146 it for yew-like fossil woods as the type has non-traumatic resin canals and normal resin canals  
147 are not a feature of the Taxaceae (Philippe, 1995). Almost a century later (1925), Walton,  
148 ignoring Hartig's contribution, used *Spiroxylon* for a South-African wood (*S. africanum*)  
149 from the Dwyka or Ecca stages (i.e. Late Carboniferous to Early Permian age). With its  
150 obvious araucarian TRP and its thick steep pitched helix, *S. africanum* is probably not closely  
151 related to Taxaceae.

152 In 1967 Greguss established *Torreyoxylon*, which he assigned to Taxaceae. But the  
153 araucarian anatomy of the type makes *Torreyoxylon* a junior taxonomical synonym of  
154 *Agathoxylon* (Philippe et al., 1999). Although etymologically suggestive, the genus  
155 *Protospiroxylon* von Lingelsheim, is for woods with anatomy consistent with *Picea*  
156 (Pinaceae), i.e. with thickened and pitted ray-cell walls and ray tracheids (Van der Burgh,  
157 1964). In 1995 Prakash et al. published the genus *Pseudotaxoxylon*, whose diagnosis and  
158 protologue illustration include araucarian TRP and araucarioid cross-field pits, hence this  
159 genus represents a wood with little affinities to modern yew woods. The diagnosis of the more  
160 recently described *Sommerxylon* (Pires & Guerra-Sommer, 2004) includes features of the  
161 primary structures (pith, primary xylem). Consequently, it cannot be used to name  
162 tracheidoxyls. Similarly, *Herbstiloxylon* Gnaedinger in Gnaedinger & Herbst is designed for  
163 *Protelicoxylon*-type of secondary xylem associated to primary structures (Gnaedinger &  
164 Herbst, 2006). Without explanations Zheng et al. (2008) assigned *Brachyoxylon* Hollick &  
165 Jeffrey to the Cephalotaxaceae, but the type of this genus wood lacks tertiary helical  
166 thickenings.

167

168 **Table 1**

169 Summary of nomenclatural and taxonomical features of the genera which were described (p.p.  
 170 erroneously) as having the diagnostic features of modern Taxaceae wood, i.e. abietinean  
 171 tracheid radial pitting (TRP); thin-walled, smooth ray parenchyma cell walls; and tertiary  
 172 helical thickenings in the axial tracheids.

Name	Authorship	Type	Reappraisal	Note
<i>Taxaceoxylon</i>	Kräusel & Jain, 1964	<i>T. torreyanum</i> (Shimakura) R.Kräusel & Jain	Type studied in Tohoku University, Japan	Can accommodate yew-like woods
<i>Physematopitys</i>	Göppert, 1850	<i>P. salisburioides</i> H.R.Goeppert	Type lost?	Possibly an earlier taxonomical synonym of <i>Ginkgoxylon</i> Saporta; type unlocated
<i>Pseudotaxoxylon</i>	Prakash, Du & Tripathi, 1995	<i>P. chinense</i> Prakash, Du & Tripathi	Not seen	Both the diagnosis and the illustration mention an araucarian TRP and araucarioid cross-fields; if not resulting from alteration bias the helical thickenings are of the broad <i>Prototaxoxylon</i> -type; possibly reworked Palaeozoic material; possibly a junior taxonomical synonym of <i>Prototaxoxylon</i>
<i>Spiropitys</i>	Göppert, 1850	<i>S. zobeliana</i> H.R.Goeppert	Type lost?	Genus described as having both horizontal and vertical resin canals, thus possibly an earlier synonym of <i>Piceoxylon</i>

				Gothan
<i>Spiroxylon</i>	Hartig, 1848	<i>S. ratzeburgii</i> Hartig	Type material reviewed by Kräusel, 1919	The type material, poorly preserved, has normal resin canals, hence a genus of dubious circumscription
<i>Taxites</i>	Göppert, 1850	<i>T. scalariformis</i> H.R.Goeppert	Not seen	An illegitimate synonym of <i>Taxites</i> Brongniart, 1828, which stands for leafy twigs
<i>Taxoxylon</i>	Unger, 1842	<i>T. scalariforme</i> (H.R.Goeppert) Seward	Type material reviewed by Kräusel (1919) and us	Elliptic diagnosis and poorly preserved type, probably with resin canals
<i>Taxoxylon</i>	Houlbert, 1910	<i>T. falunense</i> Houlbert	Type material reviewed by Philippe & Bamford, 2009	An illegitimate junior homonym
<i>Torreyoxylon</i>	Greguss, 1967	<i>T. boureauii</i> Greguss	Type material reviewed by Philippe et al., 1999	From the type material a junior taxonomical synonym of <i>Agathoxylon</i> Hartig

173

#### 174 2.1.2 Genera with mixed type of radial pitting

175 Three genera were used for woods described as having helical tertiary thickenings and  
176 mixed type of TRP (Table 2): *Platyspiroxylon* Greguss, 1961; *Protelicoxylon* Philippe, 1995;  
177 and *Prototaxoxylon* R. Kräusel & Dolianiti, 1958. Their anatomy is somewhat similar to that  
178 of *Protocallitrixylon* Yamazaki & Tsunada, 1982.



179 The type species of *Platyspiroxylon* (*P. heteroparenchymatosum* Greguss) is definitely  
 180 araucarian in its TRP, as is the second species included by Greguss in 1967 (Philippe et al.,  
 181 1999). The genus is thus a junior taxonomical synonym of *Prototaxoxylon* R.Kräusel &  
 182 Dolianiti. According to Greguss (1967) himself, who favored a link with *Callitris*  
 183 (*Cupressaceae*), *Platyspiroxylon* is not related to the *Taxaceae*. Later, however, Prasad (1986)  
 184 compared *Platyspiroxylon* and *Prototaxoxylon* and used the former name for woods with a  
 185 TRP said to be of the mixed type.

186 Although some woods with mixed type of TRP have been assigned to *Prototaxoxylon* (e.g.  
 187 Fakhr & Marguerier, 1977), it seems wiser to keep this genus for tracheidoxyls with  
 188 completely araucarian TRP as in the *Prototaxoxylon* type, *P. africanum* (Walton) R.Kräusel  
 189 & Dolianiti, and in accordance with the original diagnosis which states “*radial pits never*  
 190 *perfectly round or opposite*”.

191 *Protocallitrixylon* was described twice as a new genus, first by Yamazaki & Tsunada  
 192 (1982) and then by Vozenin-Serra & Salard-Chelboldaeff (1992). The first description is  
 193 validated by a *diagnosis generico-specifica* (ICBN, art. 38.5) based on *P. liassicum* Yamazaki  
 194 & Tsunada. These authors simultaneously described a “sp. A” and a “sp. B”, however since  
 195 the Sydney Code in 1981 a “monotypic genus” is understood as one for which a single  
 196 binomial is validly published even though the authors may indicate that other (unnamed)  
 197 species belong to the genus. Yamazaki & Tsunada described this genus as having araucarian  
 198 to mixed-type TRP. Independently, Vozenin-Serra & Salard-Chelboldaeff described  
 199 *Protocallitrixylon*, but with abietinean TRP and axial parenchyma. Both types (resp. *P.*  
 200 *liassicum* and *P. kanakense*) have helical thickenings, but these are predominantly of the  
 201 callitroid type, paired and transversal, not running on all tracheid faces. No *Protocallitrixylon*  
 202 species seem related to the *Taxaceae*.

203

204 **Table 2**

205 Summary of nomenclatural and taxonomical features of the genera which have been used for  
 206 yew-like fossil woods with mixed type tracheid radial pitting (TRP) and helical thickenings.

207

Name	Authorship	Type	Reappraisal	Note
<i>Platyspiroxylon</i>	Greguss, 1961	<i>P.</i> <i>heteroparenchymatosum</i> Greguss	Type material reviewed	A junior taxonomical synonym of

			by Philippe et al., 1999	<i>Prototaxoxylon</i> R.Kräusel & Dolianiti
<i>Protelicoxylon</i>	Philippe, 1995	<i>P. feriziense</i> (Fakhr & Marguerier) Philippe	Type not seen	
<i>Prototaxoxylon</i>	Kräusel & Dolianiti, 1958	<i>P. africanum</i> (Walton) R.Kräusel & Dolianiti	Type material reviewed by Kräusel & Dolianiti, 1958	Should not be used for woods with mixed type of TRP. Helical thickenings broad and at a 30-40° angle with the tracheid axis.

208

### 209 2.1.3 Genera with araucarian type of radial pitting

210 Numerous genera were occasionally said to be related to Taxaceae although they have  
211 been proposed for woods described as having araucarian TRP and tertiary thickenings,  
212 associated or not with primary structures: *Palaeospiroxylon* Prasad & Chandra, 1980;  
213 *Parapalaeospiroxylon* Pant & Singh, 1987; *Parataxopitys* Maniero, 1951; *Platyspiroxylon*  
214 Greguss; *Prototaxopitys* Agashe, 1977; *Prototaxoxylon* R.Kräusel & Dolianiti;  
215 *Sinopalaeospiroxylon* Zhang, Wang, Zheng, Yang, Li, Fu & Li, 2007; *Sommerxylon* Pires &  
216 Guerra-Sommer, 2004; *Spiroxylon* Walton; *Taxopitys* R.Kräusel in R.Kräusel & Range, 1928.  
217 These usually have bi-multiseriate radial bordered pits and their helical thickenings are  
218 usually thick, making an angle with the longitudinal direction usually not exceeding 40°  
219 (steep pitch). These woods are mostly reported from the Palaeozoic (late Carboniferous –  
220 Permian interval) and are typically Gondwanan (Mehta, 1952; Agashe & Shashi-Kumar,  
221 2002; Berthelin et al., 2003).

222 As both the Taxaceae and their sister-group the Cupressaceae have abietinean to weakly  
223 mixed TRP-type, fossil woods with typically araucarian TRP are probably not closely related  
224 to Taxaceae. Hence, we do not consider further *Palaeospiroxylon*, *Parapalaeospiroxylon*,  
225 *Parataxopitys*, *Platyspiroxylon*, *Prototaxoxylon*, *Sommerxylon*, *Spiroxylon* and *Taxopitys*,  
226 except for the few Mesozoic woods which were attributed to these genera. Indeed, as the core  
227 of this group belongs to the Palaeozoic, Mesozoic woods might have been misidentified.

228 Here mentioned fossil woods are referred to, as much as possible, under their basionym,  
229 without prejudging the merit of published (or to be published) taxonomical arguments in  
230 favor of a renaming.

231

## 232 **2.2 Causes for misinterpreting presence of helical thickenings**

233 There are multiple types of structures that are known to be easily confused with helical  
234 thickening (e.g. Kraus, 1887; Gothan, 1905; Shimakura, 1936). Despite this, numerous  
235 authors have been fooled, even recently. Tunneling bacteria, fungal attacks, differential  
236 mineral impregnations or shrinking cracks induced by wood diagenesis can all emphasize the  
237 microfibrils and create oblique structures that may be confused with helical thickenings (Fig.  
238 2). The microfibrillar patterns involved in these cases usually consist of several closely  
239 parallel strikes which usually do not curve towards the tracheid face rim. These strikes are at a  
240 variable angle with the longitudinal axis. This is well illustrated by Araujo et al. (2011, fig. 6  
241 F).

242 Compression wood longitudinal tracheids have checks in their walls that when observed  
243 with optical microscopy can be confused with helical thickenings (Boyd, 1973). The  
244 microfibril angle of compression wood tracheids is usually 30°–50° from the longitudinal  
245 axis, unlike “normal” tracheids with a predominant 10°–20° angle (Timell, 1986). Also, the  
246 tips of these cracks are usually pointed and straight, whereas it is not the case for the true  
247 helices. Such diagonal patterns, mentioned as checks or cracks, are well illustrated by Hickey  
248 et al. (2011). In some compression wood, borders around pits are usually small, while the pit  
249 aperture opens in tracheid lumen at the bottom of an oblique furrow. Such furrows have also  
250 been erroneously described as tertiary thickenings, especially when broadened by wood  
251 shrinkage during diagenesis (see Greguss, 1967 pl. 35 fig. 19b). They characteristically make  
252 a low angle with the tracheid longitudinal axis, usually 30–40°, are much broader than the  
253 true helical thickenings and have an aperture in their middle. In fossil woods with such  
254 patterns, the pale (supposedly “thin”) band is usually as broad as the dark (supposedly  
255 “thickened”) band under optical microscopy, while a pit set on the opposite tracheid wall can  
256 sometimes be seen behind the banded pattern (Fig. 3). This appearance is especially common  
257 in silicified araucaria-like woods. In a few cases, (e.g. Yamazaki et al. 1979, pl. IV) it is  
258 difficult to judge if some structures are yew-like helical thickenings or relatively thick bands  
259 sandwiched between two oblique furrows. The angle could then be diagnostic. Intensity of  
260 taphonomic processes seems to enhance diverse oblique structures (Evans, 1928).

261 Zoned patterns in some petrified fossil woods, caused by discontinuous crystal growth  
262 have several times been confused with helical thickenings (see e.g. Kraus, 1887; Houlbert,  
263 1910 and Philippe & Bamford, 2009; Fig. 4). These patterns are, however, made of closely  
264 parallel but irregularly spaced lines.

265 Crystal cleavage plans can also be tricky, however they normally run across several  
266 tracheids.

267 Fungal hyphae can mimic grooves within a tracheid because hyphae often follow the S2  
268 cell wall layer (see Greguss, 1967, pl. 32), however their disposition is rarely regular enough  
269 to convincingly suggest tertiary thickenings.

270 In extant *Taxus* and *Pseudotsuga* species helical cavities can occur within the tracheid  
271 wall, which curiously seem to be mutually exclusive with helical thickenings (Timell, 1978).

272 To sum up, it is easy to mistakenly interpret various oblique patterns in the tracheids as  
273 helical thickenings, as Kraus (1887) earlier warned. Later, in 1936, Shimakura wrote “As  
274 pointed out by Kraus, Lingelsheim, Seward, Stopes, Gothan and Kräusel, there are no true  
275 spiral thickenings in most species of *Taxoxylon* or *Taxites*”. Although numerous publications  
276 have warned that such helices can be mistakenly diagnosed, Shimakura’s statement is still  
277 today quite true. Scanning electron microscopy is a good means to determine whether or not  
278 helical wall thickenings are truly present (Philippe et al., 1999; Wan et al., 2016).

279

### 280 **2.3 Fossil woods with helical tertiary thickenings – a database**

281 We surveyed the palaeoxylogical literature for woods said to be related to Taxaceae. Based  
282 on previous information we focused on the genera whose anatomy conforms to modern  
283 Taxaceae, i.e. *Platyspiroxylon* Greguss, *Protelicoxylon* Philippe, *Prototaxoxylon* R.Kräusel &  
284 E.Dolianiti, *Sommerxylon* Pires & Guerra Sommer, *Taxoxylon* Houlbert, *Taxoxylon* Unger,  
285 *Taxaceoxylon* R.Kräusel & Jain and *Torreyoxylon* Greguss. Palaeozoic woods with strongly  
286 araucarian radial TRP and helical thickenings were not considered (e.g. *Taxopitys*,  
287 *Parataxopitys*). We also excluded *Oguraxylon* Nishida which has traumatic resin canals and  
288 axial parenchyma, features that are not reported for modern Taxaceae. We focused on the  
289 Mesozoic as this is a major phase in the radiation of conifers, with the establishment of basal  
290 genera (Leslie et al., 2012, 2018).

291 We located 61 records for 57 taxa. For each record we questioned the possibility that the  
292 described material was reworked, especially for fossils in alluvial sediments. As far as  
293 possible we examined the type material, to limit interpretation bias, and all protologues were  
294 accessed. Our database is complete to the best of our knowledge. Should some papers have

295 been forgotten, we would be very grateful to get notice. We are confident that no significant  
 296 data was overlooked.

297

### 298 **3 RESULTS**

299 From our reappraisal 12 of the 61 records were assigned to the *Prototaxoxylon* group  
 300 (araucarian TRP, thick helices with a steep pitch; Table 3), 6 to *Protocallitrixylon* (mixed type  
 301 of TRP, thin low pitch helices plus callitroid thickenings, Table 4), 8 to *Protelicoxylon* (mixed  
 302 type of TRP, thin low pitch helices; Table 5), and 11 to *Taxaceoxylon* (abietinean TRP, thin  
 303 low-pitch helices, no callitroid thickenings; Table 6). Only these three last genera will be  
 304 considered further. An extra group is recognized for 7 woods from India (Table 7). As the  
 305 analysis did not unequivocally support assignment to one of the five groups cited here above  
 306 43 records were discarded (Appendix),

307 Because of their araucarian radial tracheid pitting several Mesozoic woods belong to  
 308 *Prototaxoxylon*. It is striking that they are limited to the Gondwana, where they mostly occur  
 309 at high palaeolatitudes (Table 3 and Appendix).

310

#### 311 **Table 3**

312 Fossil woods described as having helical tertiary thickenings and araucarian type of pitting on  
 313 tracheid radial walls and which are consistent with the genus *Prototaxoxylon* Kräusel & Jain.

314

Taxon name, authority	Reference
<i>Protelicoxylon feriziense</i> (Fahkr & Marguerier) Philippe	Gnaedinger & Herbst, 2006
<i>Prototaxoxylon acevedoae</i> Gnaedinger & Herbst	Gnaedinger & Herbst, 2006
<i>Prototaxoxylon intertrappeum</i> (Prakash & Srivastava) Prakash & Srivastava	Lutz et al., 1999
<i>Prototaxoxylon intertrappeum</i> (Prakash & Srivastava) Prakash & Srivastava	Gnaedinger & Herbst, 2006
<i>Prototaxoxylon uniseriale</i> Prasad	Gnaedinger & Herbst, 2006

<i>Sommerxylon spiralosus</i> Pires & Guerra-Sommer	Pires & Guerra-Sommer, 2004
<i>Taxaceoxylon cupressoides</i> Sharma	Sharma, 1971
<i>Taxaceoxylon sahnii</i> Rajanikanth & Sukhdev	Rajanikanth & Sukhdev, 1989
<i>Taxaceoxylon</i> sp.	Mahabale, 1967
<i>Taxaceoxylon</i> sp.	Caminos et al., 1995
<i>Taxoxylon</i> sp.	Lakhanpal et al., 1976
Wood of type D	Yamazaki et al., 1979

315

316

317 Except for the New-Caledonian data (Vozenin-Serra & Salard-Chelbodaeff, 1992),  
318 *Protocallitrixylon* woods form a spatio-temporally coherent unit (Table 4). They are  
319 distributed exclusively in the Far-East Asia, from the Early Jurassic to the Early Cretaceous.  
320 First encountered at low to mid palaeolatitudes, their range subsequently shifted northward,  
321 within an area characterized by a cold-temperate flora (Oh et al., 2011). The occurrence of the  
322 genus in the Teremba terrane of New-Caledonia is questionable, as most palaeogeographic  
323 reconstructions have this area at the southern rim of a wide open oriental Tethys (Cluzel et al.,  
324 2012) during the Jurassic.

325

326 **Table 4**

327 Fossil woods with helical tertiary thickenings, mixed type pitting on tracheid radial walls and  
328 callitroid thickenings, here accepted as belonging to the genus *Protocallitrixylon* Yamazaki &  
329 Tsunada. The nov. comb. *Protocallitrixylon pulchrum* is based on the basionym *Taxoxylon*  
330 *pulchrum*, He Dechang, *The coal forming plants of Late Mesozoic in Dan Hinggan*  
331 *Mountains*, p. 13, pl. 8 figs. 3-3a, pl. 9, figs. 1-1f; 1995.

332

333

Taxon name, authority	Reference
<i>Protocallitrixylon kanakense</i> Vozenin-Serra & Salard- Chelbodaeff	Vozenin-Serra & Salard- Chelbodaeff, 1992

<i>Protocallitrixylon liassicum</i> Yamazaki & Tsunada	Yamazaki & Tsunada, 1982
<i>Protocallitrixylon pulchrum</i> (He Dechang) nov. comb.	He Dechang, 1995
<i>Protocallitrixylon</i> sp. A	Yamazaki & Tsunada, 1982
<i>Protocallitrixylon</i> sp. B	Yamazaki & Tsunada, 1982
<i>Protocallitrixylon</i> sp.	this work; Fig. 5

334

335

336

337

338 *Protelicoxylon* woods, as here revised, form another spatio-temporally coherent unit (Table  
339 5). They are distributed exclusively in Eurasia, from the Early Jurassic to the Mid-Jurassic –  
340 Early Cretaceous. First encountered in Western Europe, their range apparently shifted  
341 eastward. The exact age of the Cambodian data is unfortunately not well constrained (Philippe  
342 et al., 2004). *Protelicoxylon* is not reported to have co-existed with *Protocallitrixylon*. In Iran,  
343 it co-occurs with *Xenoxylon* Gothan (Nadjafi, 1982), a palaeoecologically significant genus  
344 that indicates relatively wet settings (Philippe et al., 2017).

345

346 **Table 5**

347 Fossil woods with helical tertiary thickenings and mixed type pitting on tracheid radial walls,  
348 here assigned to the genus *Protelicoxylon* Philippe.

349

Taxon name, authority	Reference	Age	Country
<i>Protelicoxylon asiaticum</i> (Serra) Philippe	Serra, 1969	Early? Cretaceous	Cambodia
<i>Protelicoxylon feriziense</i> (Fakhr & Marguerier) Philippe	Fakhr & Marguerier, 1977	Middle Jurassic	Iran
<i>Protelicoxylon lepenneccii</i> Philippe	Philippe, 1995	Toarcian	France
<i>Protelicoxylon</i> <i>parenchymatosum</i> (Greguss) Philippe	Greguss, 1967	Toarcian	Hungary

[ <i>Prototaxoxylon persicum</i> ]	Nadjafi, 1982	Early to Middle Jurassic	Iran
<i>Protelicoxylon</i> sp.	Barbacka & Philippe, 1997	Hettangian	Hungary
<i>Protelicoxylon</i> sp.	Philippe et al., 2006	Sinemurian	Romania
<i>Protelicoxylon</i> sp.	New data	Toarcian	France (Nancy)

350

351 First appearance date for the genus *Taxaceoxylon* is the Early Cretaceous. At that time it  
352 was exclusively distributed in North-Eastern Eurasia. By the Late Cretaceous it occurred in  
353 Northern America, and in the Tertiary it was distributed throughout the Palaeartic (Table 6).

354

355 **Table 6**

356 Fossil woods with helical tertiary thickenings and abietinean type pitting on tracheid radial  
357 walls, here considered assignable to the genus *Taxaceoxylon* Kräusel & Jain. The nov. comb.  
358 *Taxaceoxylon antiquum* is based on *Torreya antiqua* Boeshore & Gray, Amer. J. Bot. 28, p.  
359 525, textfigs. 1-14, 1936 (not validly published in Pirres and Guerra-Sommer, 2004).

360

Taxon name, authority	Reference	Age	Country
<i>Taxaceoxylon antiquum</i> (Boeshore & Gray) nov. comb.	Boeshore & Gray, 1936	Late Cretaceous	USA (Eastern)
<i>Taxaceoxylon biseriatum</i> Süss & Velitzelos	Süss & Velitzelos, 1994	Tertiary	Greece
<i>Taxaceoxylon jarmolenkoi</i> Shilkina	Shilkina, 1989	Early Cretaceous	Russia (Western)
<i>Taxaceoxylon liaoxiense</i> Duan	Duan, 2000	Early Cretaceous	China (Northern)
<i>Taxaceoxylon saghalienense</i> H. Nishida et Nishida	Nishida & Nishida, 1986	Late Cretaceous	Russia (Eastern)
<i>Taxaceoxylon</i> sp.	Afonin & Philippe, 2014	Early Cretaceous	Russia (Eastern)
<i>Taxaceoxylon torreyanum</i>	Shimakura, 1936	Pleistocene	Japan



(Shimakura) Kräusel & Jain			
<i>Taxoxylon</i> sp.	Dawson, 1875	Tertiary	Canada (Central)
<i>Taxoxylon</i> sp.	Mazen-Papier, 1965	Neogene	France
<i>Taxus</i> sp.	Stieber, 1955	Miocene	Hungary
<i>Taxus</i> sp.	Castañeda-Posadas et al., 2009	Miocene	Mexico

361  
362 A set of woods from India is questionable. Most of them have convincing illustration for  
363 helical thickenings but poorly preserved TRP (Table 7). In 1952 Bose described  
364 *Brachyphyllum spiroxylon* from the Rajmahal Hills, Jharkhand, India. The type material is a  
365 leafy twig with *Brachyphyllum*-like foliage, 4 mm in diameter, however it is described as  
366 having a wood of the *Taxaceoxylon*-type. Unfortunately, the cross-field pitting is not  
367 preserved, and TRP is observed only in juvenile wood. Also, helical thickenings were not  
368 observed in the tangential section. These Indian woods can further be subdivided into two  
369 subgroups, one from the earliest Jurassic of Central India (Eastern Maharashtra / northern  
370 Andra Pradesh), and another from the Early Cretaceous of Western India (Jharkhand). These  
371 two groups correspond to the two main Mesozoic wood provenances in India studied to date.

372  
373 **Table 7**  
374 The post-Palaeozoic Indian record for fossil woods with helical thickenings. Information on  
375 location and ages has been up-dated here to allow for geographic name changes and  
376 improvements in stratigraphic ranges (Tripathi, 2008; Weishampel et al., 2004). The  
377 attribution of these fossils to Taxaceae is questionable.

Specific names	Published	Provenance	Age given in the protologue	Actual age
<i>Spiroxylon intertrappeum</i>	Prakash & Srivastava, 1959	Dhar District, Madhya Pradesh, India	Early Tertiary	Berriasian – Aptian
<i>Taxaceoxylon cupressoides</i>	Sharma, 1971	Dhokuti, Santhal Pargana, Jharkhand	Middle Jurassic	–Berriasian - Aptian
<i>Taxaceoxylon</i>	Rajanikanth &	Kota Fm, Chandrapur,	Middle Jurassic	Hettangian-

<i>sahnii</i>	Sukhdev, 1989	Eastern Maharashtra		Pliensbachian
<i>Taxaceoxylon</i> sp.	Lakhanpal et al., 1976	Kota Fm, Chandrapur, Eastern Maharashtra	Early Jurassic	Hettangian- Pliensbachian
<i>Taxaceoxylon</i> sp.	Kräusel & Jain, 1964	Rajmahal Hills, Jharkhand	Early Cretaceous	Berriasian - Aptian
<i>Taxoxylon</i> <i>rajmahalense</i>	Bhardwaj, 1952b	Kulkipahar, Amrapara, Pakur district, Santhal Parganas, Jharkhand	Intertrappean beds (Rajmahal stage) Jurassic	Berriasian - Aptian
<i>Taxoxylon</i> sp.	Mahabale, 1967	Kota Fm., Pranhita/Godavari, Andhra Pradesh	Early Jurassic	Hettangian- Pliensbachian

379

#### 380 4 DISCUSSION

381 The wood fossil record includes many Mesozoic and Cenozoic specimens with some  
382 Taxaceae anatomical features. Only wood having helical thickenings and abietinean pitting  
383 (i.e. wood that is, or should be, assigned to *Taxaceoxylon*) is convincingly Taxaceae, although  
384 some other wood types (e.g. *Protocallitrixylon* and *Protelicoxylon*) may represent ancestral  
385 forms of the Taxaceae lineage. The record shows that five taxonomically and spatio-  
386 temporally well-circumscribed groups can be recognized among the Mesozoic or younger  
387 fossil tracheidoxyls with helical thickenings.

388 The first group has steep and wide thickenings and araucarian TRP. It occurs in  
389 Gondwana, mostly at high palaeolatitudes, and mostly in the Jurassic. It is anatomically close  
390 to the Palaeozoic *Prototaxoxylon* and will be referred to hereafter as “Mesozoic  
391 *Prototaxoxylon*”. It is possible that *Sommerxylon* is related to this group.

392 The two next groups have a mixed type of TRP. One (*Protocallitrixylon*) has both  
393 callitroid and helical thickenings; it is limited to the Mesozoic of far-east Asia and New-  
394 Caledonia. The fourth group (*Protelicoxylon*) is documented from Eurasia, only from the  
395 Mesozoic, and mostly from the Jurassic. Wood fossils similar to the wood of extant Taxaceae  
396 (*Taxaceoxylon*) are encountered throughout the Palearctic, from the Early Cretaceous to the  
397 Pleistocene. A fifth group, only encountered in the Mesozoic of India, has Taxaceae-like  
398 helical thickenings, and possibly mixed type of TRP (most of them have no preserved pitting).

399 This five group scheme is compared to the leaf and reproductive organ record for  
400 Taxaceae. This leads to the idea that only *Protelicoxylon* and *Taxoxylon* probably belong to  
401 Taxaceae. Furthermore, we propose that the helical thickenings of Taxaceae tracheids may

402 contribute to the family's very high resistance to hydraulic failure because – as observed in  
403 *Acer* species by Lens et al. (2011) – the more pronounced the thickenings on inner vessel  
404 walls, the more embolism resistance the species. However, the functional role of vessel wall  
405 thickening is still poorly understood and further research needs to be carried out to unravel its  
406 role in drought resistance. We here speculate that wall thickening does not play a direct role  
407 in preventing embolism formation but instead is involved in preventing xylem implosion. We  
408 then integrate the fossil record, estimated resistance to water stress and Meso-Cenozoic  
409 palaeoclimatology to create a biogeographic hypothesis.

410

#### 411 **4.1 Comparison of wood with the leaf and reproductive organ fossil record**

412 Taylor et al. (2006) concluded that it is difficult to trace the origin of Taxaceae from the  
413 fossil record of leaf, leafy twigs or reproductive organs only. The characteristic fleshy arils  
414 have little potential for fossilization, and none have been described from the Mesozoic or  
415 Palaeozoic (non-fleshy, or perhaps immature, arils have been described from putative Middle  
416 Jurassic Taxaceae like *Marskea* and *Proteridion*). Moreover, podocarp reproductive organs  
417 (epimatia) share a similar gross morphology with that of the Taxaceae, and it is difficult to tell  
418 apart an epimatium and an aril from fossil remains only. To compound the problem, the  
419 recent suggestion that Gnetales could be sister to the Pinaceae family (Bowe et al., 2000)  
420 suggests that a fleshy structure, whatever its ontogeny, can relatively easily be invented by the  
421 gymnosperms, and could have been present in some of the numerous little-known Mesozoic  
422 gymnosperm families (e.g., Ferugliocladales or Buriadaceae). Thus a fossil fleshy aril would  
423 probably not be unequivocal evidence of Taxaceae.

424 Although foliage of Taxaceae is more likely to be preserved than the arils, the gross  
425 morphology of shoots and leaves of this family is little differentiated from that of several  
426 other conifer clades. As a result, leaf and leafy twig fossils are largely uninformative when  
427 cuticle is missing. The cuticle is distinctive for modern genera (Elpe et al., 2017), although  
428 Taxaceae cuticle can resemble that of some completely unrelated taxa, e.g. within the  
429 Monocots (Conran, 1997). Similarly, Jordan et al. (2013) observed Taxaceae-like cuticle in  
430 fossil *Phyllocladus* (Podocarpaceae).

431 Several fossil genera based on foliar specimens and with relatively well-established  
432 affinities to the Taxaceae, e.g. *Marskea*, *Palaeotaxus*, *Poteridion*, *Thomasiocladius* (Taylor et  
433 al., 2006; Xu et al., 2015) have been described from the Jurassic. These genera are only  
434 reported from Eurasian mid-palaeolatitudes. In this respect, they fit well with known spatio-  
435 temporal distribution of *Protelicoxylon*, albeit they have not yet been recorded as far east as

436 the latter along Tethys northern rim. The record of above mentioned foliar fossil genera starts  
437 with *Palaeotaxus* from the Earliest Jurassic (Florin, 1958), which also fits with first  
438 *Protelicoxylon*, documented from the Hettangian.

439 A striking feature is that by the Early Cretaceous the record of Taxaceae fossil foliage  
440 record is centered on much higher palaeolatitudes. Although there are putative records from  
441 Belgium (Alvin, 1960), UK (Watson et al., 2001) and North Carolina (Berry, 1910), the  
442 strongholds are at higher palaeolatitudes than any presumed Jurassic records of the family:  
443 Greenland (Heer, 1883), Siberia (Krassilov, 1976; Samylina, 1988; Golovneva, 1994;  
444 Bugdaeva et al., 2006), Spitzbergen (Bose & Manum, 1990), north-eastern China (Xu et al.,  
445 2015). There is thus a similar northward shift for both leaf and reproductive organ record and  
446 wood record during the Jurassic – Cretaceous interval. This shift is concomitant with  
447 abietinean TRP becoming dominant in wood.

448 By the Cenozoic the Taxaceae were widespread over high latitude regions of the Northern  
449 Hemisphere, with fossil foliage records in North-America (e.g. Kvaček & Rember, 2007),  
450 Europe (e.g. Givulescu, 1973; Ferguson, 1978; Ferguson et al., 1978; Kvaček, 1986; Spjut,  
451 2007; Macovei, 2013) and Asia (Xu et al., 2015). This Cenozoic distribution fits again with  
452 that of fossil wood record.

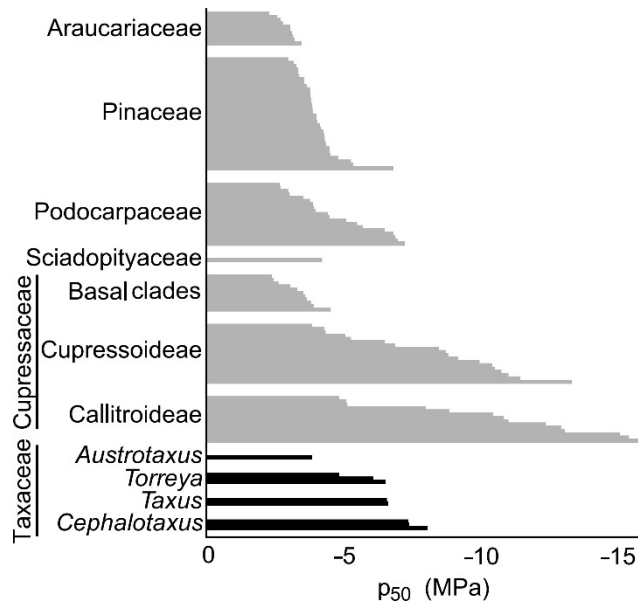
453 The enigmatic *Austrotaxus* has no fossil record of any kind. As its wood is similar to that  
454 of the Podocarpaceae (Bobrov et al., 2004), isolated secondary xylem of this genus would  
455 probably be referred to *Podocarpoxyton* Gothan, which is not considered here. Thus, the  
456 fossil wood record cannot be used to improve an understanding of the biogeographic history  
457 of this taxon.

458

#### 459 **4.2 Helical thickenings, and drought resistance**

460 Extant Taxaceae, especially *Cephalotaxus*, have a relatively high resistance to embolism  
461 (Delzon et al., 2010; Bouche et al., 2014; Figure 6). Thus, extant Taxaceae, with the notable  
462 exception of *Austrotaxus spicata*, have a lower  $P_{50}$  (i.e. greater resistance) than all  
463 Araucariaceae, all basal Cupressaceae and most species of Pinaceae and Podocarpaceae. Only  
464 a few genera of the Cupressoid and Callitroid clades of Cupressaceae have lower wood xylem  
465  $P_{50}$  than *Cephalotaxus*: the *Callitris* clade being by far the most embolism resistant group of  
466 trees in the world (Brodribb et al., 2015; Larter et al., 2015, 2017).

467



468  
 469 Figure 6: Mean  $P_{50}$  values for the six conifer families. For the Taxaceae the mean values are  
 470 provided by genera. Most extant conifers have a  $P_{50}$  ranging between -3 and -6 MPa. Values  
 471 taken from Bouche et al. (2014), except for *Austrotaxus*, which comes from Larter (2016).  
 472

473 Tracheids of embolism resistant species often experience low water potentials, increasing  
 474 the risk of conduit implosion (collapse), that could compromise the function of the xylem.  
 475 Collapse of xylem conduit walls during desiccation was reported in pine needles (Cochard et  
 476 al 2004). This concept extends to conifer wood because the pressure needed to cause conduit  
 477 implosion in lignified tracheids (estimated with the double cell-wall thickness) is related to  
 478 embolism resistance across conifers (Bouche et al., 2014). –Furthermore, collapse of xylem  
 479 conduit walls in response to desiccation has been observed in some Pinaceae wood with  
 480 severe reduction lignification in their secondary walls (Barnett, 1976; Donaldson, 2002) and  
 481 in pine needles (Cochard et al., 2004). Vulnerability to collapse is therefore highly related to  
 482 the tracheid anatomy. *Taxus*-like helices could be interpreted as a trade-off between  
 483 physiologically costly thick lignified walls, water transport and drought resistance. Tracheid  
 484 helical-thickenings would allow thinner cell walled tracheids to have similar mechanical  
 485 resistance to collapse (Roth-Nebelsick & Speck, 2000), while having a wider lumen, i.e. being  
 486 more efficient to transport sap. In fact, xylem wall collapse has been reported in several  
 487 species between the helicoidal thickening (Johnson, 1977; Turner & Somerville, 1997;  
 488 Cochard et al., 2004).

489 It is striking that both extant conifer taxa (Taxaceae and Callitroideae) with abundant  
 490 tertiary thickenings in their woods have high resistance to embolism (Fig. 6). Furthermore, the  
 491 only genus of Taxaceae without tertiary helical thickenings, *Austrotaxus*, is the most

492 vulnerable species to embolism in the family. This findings suggest that helical thickenings  
493 may play a role in preventing conduit implosion in high resistant species to embolism.

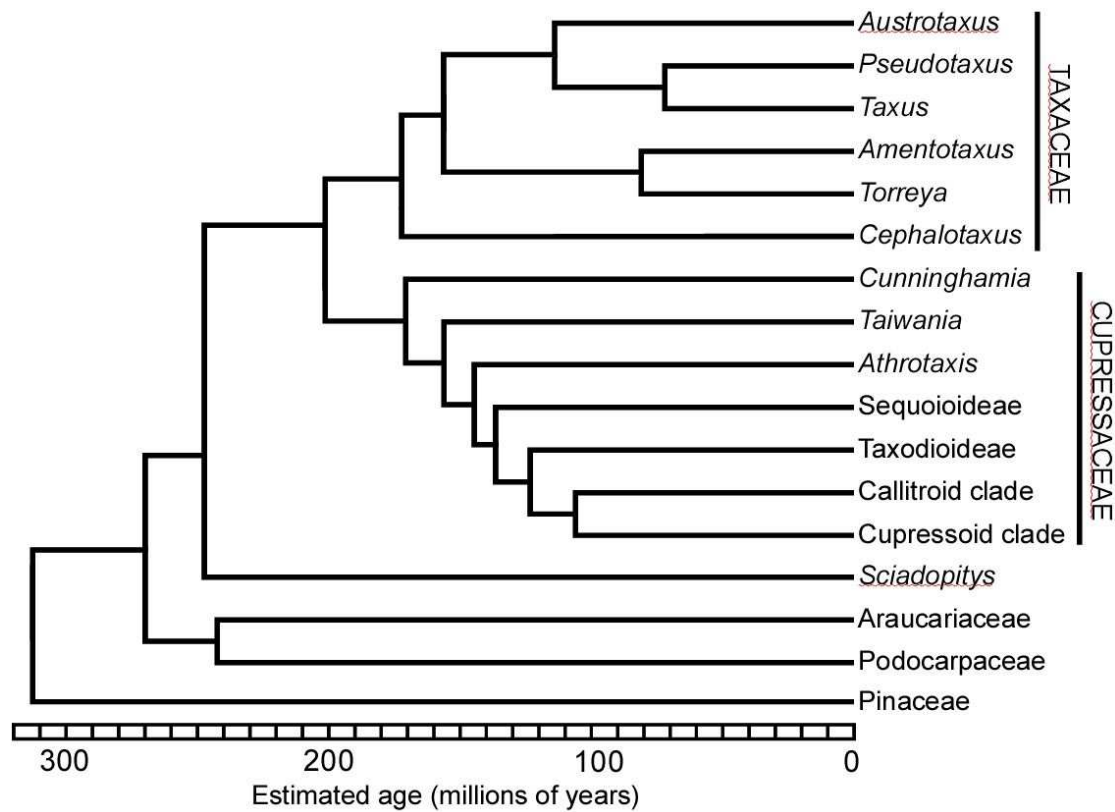
494 The high resistance to embolism is interesting because extant Taxaceae are rather  
495 mesophytic trees and shrubs, which may also be the case for most of their Cenozoic ancestors  
496 (Ferguson et al., 1978). However, this is in line with other physiological adaptations to  
497 drought observed in the Taxaceae (Hoffman et al., 1999; Feucht et al., 2012). Extant Taxaceae  
498 trees and shrubs are all shade tolerant. Their resistance to drought, together with their shade  
499 tolerance strategy, might have allowed Taxaceae to establish under angiosperm-dominated  
500 canopies.

501

### 502 **4.3 A palaeobiogeographical scenario for the Taxaceae**

503 Phylogeny of the Taxaceae genera and the supposedly monotypic family Cephalotaxaceae  
504 has been extraordinarily controversial (Cheng et al., 2000). Molecular phylogenies now  
505 converge to give a more consensual image (Fig. 7). Taxaceae are considered monophyletic,  
506 splitting from the sister-group, the Cupressaceae, during the Late Triassic or earliest Jurassic.  
507 *Cephalotaxus* branched during the Early to Middle Jurassic and the division between the two  
508 remaining clades of Taxaceae occurred during the Middle to Late Jurassic, one clade  
509 containing *Torreya* and *Amentotaxus*, the other *Austrotaxus*, *Pseudotaxus* and *Taxus* (Cheng  
510 et al., 2000; Renner, 2009; Leslie et al., 2018).

511



512  
 513 Figure 7: Dated molecular phylogeny used to discuss Taxaceae fossil wood record, based on  
 514 Leslie et al. (2018).

515  
 516 If the Mesozoic *Prototaxoxyla* are not considered safe evidence of Taxaceae, the fossil  
 517 wood record fits well with the image drawn by molecular phylogeny. With the Hettangian  
 518 (Earliest Jurassic, *ca.* 200 Ma) as its first appearance date, *Protelicoxylon* fits with a first  
 519 radiation of the Taxaceae within the Late Triassic / Early Jurassic. Accordingly, from the  
 520 fossil wood record it can be hypothesized that Taxaceae appeared in Western Europe at the  
 521 T/J boundary.

522 Evolutionary ecophysiology suggests that Triassic conifer stem groups had a limited  
 523 resistance to embolism (Pittermann et al., 2012; Larter et al., 2017). It further suggests that  
 524 resistance gradually increased for the Taxaceae during the Jurassic and likely had reached  
 525 modern values by the end of the Cretaceous at 65 Ma (Larter, 2016). This age fits well with  
 526 our taxonomical inferences, with intermediate and untypical woods classified here as  
 527 *Protelicoxylon* appearing during the Jurassic, and typical *Taxaceoxylon* appearing during the  
 528 Early Cretaceous, at higher and drier palaeolatitudes. During all the Mesozoic, at least,  
 529 Taxaceae family seems to have evolved under a strong constraint to become more drought  
 530 resistant. This evolution was parallel to a transition from a mixed type of TRP to an  
 531 abietinean TRP. It is probable that this change in the TRP had consequences on conduction.

532 This northward shift of the (*Protelicoxylon* + *Taxaceoxylon*) group during the Jurassic – Early  
533 Cretaceous interval fits well with a well-documented global poleward shift of the at least  
534 seasonally dry temperate climate zone (Hallam, 1985).

535 According to the phylogeny of Fig. 7 (based on Leslie et al., 2018) the stem group of the  
536 most embolism resistant genus of Taxaceae, *Cephalotaxus*, evolved at the end of the Early  
537 Jurassic and the crown group in the late Cenozoic. So the highly resistant wood may have  
538 evolved any time in this period. Thus, the Cretaceous record is entirely consistent with late  
539 evolution of resistance.

540 *Austrotaxus* radiated during the Early Cretaceous and remained highly isolated (Leslie et  
541 al., 2018). Thus, it is improbable that *Austrotaxus* is related to the Triassic *Protocallitrixylon*  
542 described from New-Caledonia by Vozenin-Serra & Salard-Chelbodaëff (1992). It might be  
543 derived from *Protocallitrixylon* which occurred during the Jurassic in South-Eastern Asia,  
544 however, the possibility of terrestrial species migration along the Eastern Tethys at that time  
545 is controversial (Vozenin-Serra, 1977). *Austrotaxus* is clearly divergent from the rest of the  
546 Taxaceae, in both wood anatomy and resistance to embolism, and also in the diffuse type of  
547 branching and plagiotropic branch growth (Chomicki et al., 2017). According to the  
548 phylogeny of Leslie et al. (2012) or Lu et al. (2014), both the Taxaceae-type wood anatomy  
549 and xylem resistance to embolism were either lost secondarily in *Austrotaxus* or evolved  
550 convergently in two clades (Fig. 7). It is noteworthy that it is endemic to New-Caledonia, a  
551 center of diversity for Araucariaceae (Farjon 2010), a family with a high vulnerability to  
552 embolism (Figure 6). In no fossil flora is *Taxaceoxylon* found associated with *Agathoxylon*,  
553 the wood fossil genus fitting with modern Araucariaceae, as if in the past these two groups  
554 always had different ecological requirements. The extant *Austrotaxus* case opens the  
555 possibility that some fossil woods assigned to *Podocarpoxyton* (e.g.), and possibly associated  
556 to *Agathoxylon*, might be cryptic Taxaceae woods lacking tertiary helical thickenings. The  
557 *Austrotaxus* thinner ray-cell walls, as compared to the other family members, might also be in  
558 line with a lower resistance to embolism.

559 If the *Cephalotaxus* Early Jurassic divergence from the rest of the Taxaceae is confirmed,  
560 it implies that abietinean TRP evolved at least twice within the Taxaceae: once in this genus  
561 and a second time in its sister group, the other Taxaceae. The Early Cretaceous age of the  
562 Cambodian *Protelicoxylon* (Table 5) is little substantiated, and might well be Middle to late  
563 Jurassic (Philippe et al., 2004). If so, the transition of the mixed type to the abietinean type of  
564 TRP in the *Cephalotaxus* sister-clade, as documented by the fossil record, would be more or



565 less contemporaneous with the split of the two branches (*Torreya* + *Amentotaxus* and  
566 *Austrotaxus* + *Pseudotaxus* + *Taxus*). The Late Jurassic, during which this split might have  
567 taken place (Fig. 7), is well known as a time of global drying of Northern Hemisphere  
568 climates.

569 Taxaceae have probably been through several ecological bottle-necks during the Jurassic,  
570 which selected embolism-resistant taxa. This resistance was maintained when they acquired  
571 their typical wood, i.e. *Taxaceoxylon* features. This genus first appeared during the Early  
572 Cretaceous, a time when it was to be found in eastern continental Eurasia only, at relatively  
573 high palaeolatitudes. This area is known to have been relatively dry at that time (Oh et al.,  
574 2011), with strongly influences of continental drought and the existence of an eastern coastal  
575 Cordillera. No Araucariaceae-like woods (i.e. genus *Agathoxylon*) are reported from this area  
576 at that time, while this type of wood was otherwise so common worldwide, possibly because  
577 of continental drought. Later, during the Late Cretaceous, at a time when North-America and  
578 Western Europe climates became more continental (Wolfe & Upchurch, 1987), *Taxaceoxylon*  
579 spread to these two areas. It persisted there through the Cenozoic, and until now, with modern  
580 Taxaceae spanning most of the temperate boreal area, except for the high-latitudes that were  
581 probably their Cretaceous cradle.

582

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1025 **Figure captions**

1026 Figure 1: *Protelicoxylon lepenneicii* Philippe, Early Jurassic of France; here can be seen both a  
 1027 low pitch right-handed helix and steep-pitched microfibrillar pattern due to secondary wall  
 1028 alteration.

1029 Figure 2: confusing spiral-like patterns. A - *Podocarpoxyylon woburnense* Stopes, sample  
 1030 58481 in British Museum of Natural History; steep angled microfibrillar pattern resulting  
 1031 from tracheid secondary wall differential attack. B - V13139 in British Museum of Natural  
 1032 History; low angled similar microfibrillar pattern, within a compression wood. C - V16556a  
 1033 in British Museum of Natural History; cleavage fractures running through tracheid walls in a  
 1034 mineralized wood. D - *Pityoxylon woodwardii*; oblique patterns interpreted as resulting of  
 1035 tunneling bacteria activity.

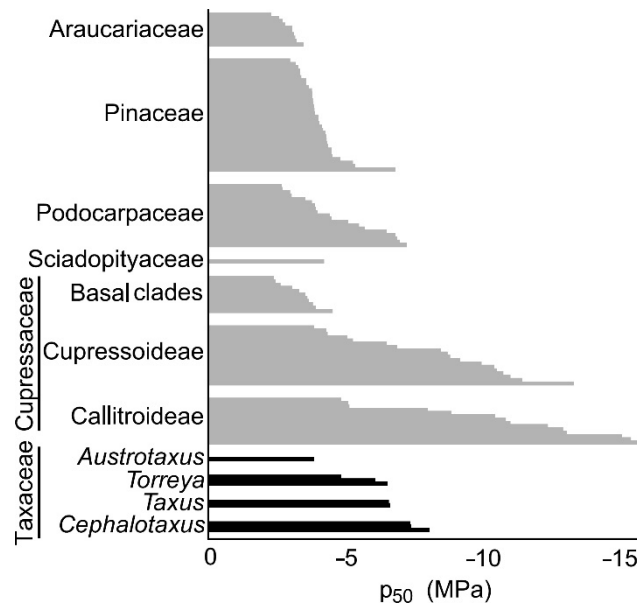
1036 Figure 3: formation of a large spiral-like ribbon from araucarioid radial pitting. A & B -  
 1037 *Xenoxylon wattarianum* Nishida holotype, Chuo University; two alteration stages in the same  
 1038 slide. C - *Xenoxylon phyllocladoides* sample n°686901. Symmetrical transitions, in two  
 1039 adjacent tracheids, from araucarian radial pitting to a broad spiral pattern.

1040 Figure 4: left, reproduction of Pl. III fig. 3 in Kraus (1887), warning about misinterpretation

1041 of crystal patterns; right, *Taxoxylon falunense* Houlbert, sample n°25 in the Musée du Grand-  
1042 Pressigny, Indre-et-Loire, France.

1043 Figure 5: Wood assigned to genus *Protocallitrixylon*, unpublished wood by collected by  
1044 Kazuo Terada, sample n°FPDM-P-1130 in Fukui Prefectural Dinosaur Museum, Japan; Early  
1045 Cretaceous, Kitadani Fm, Tetori Group, Japan.

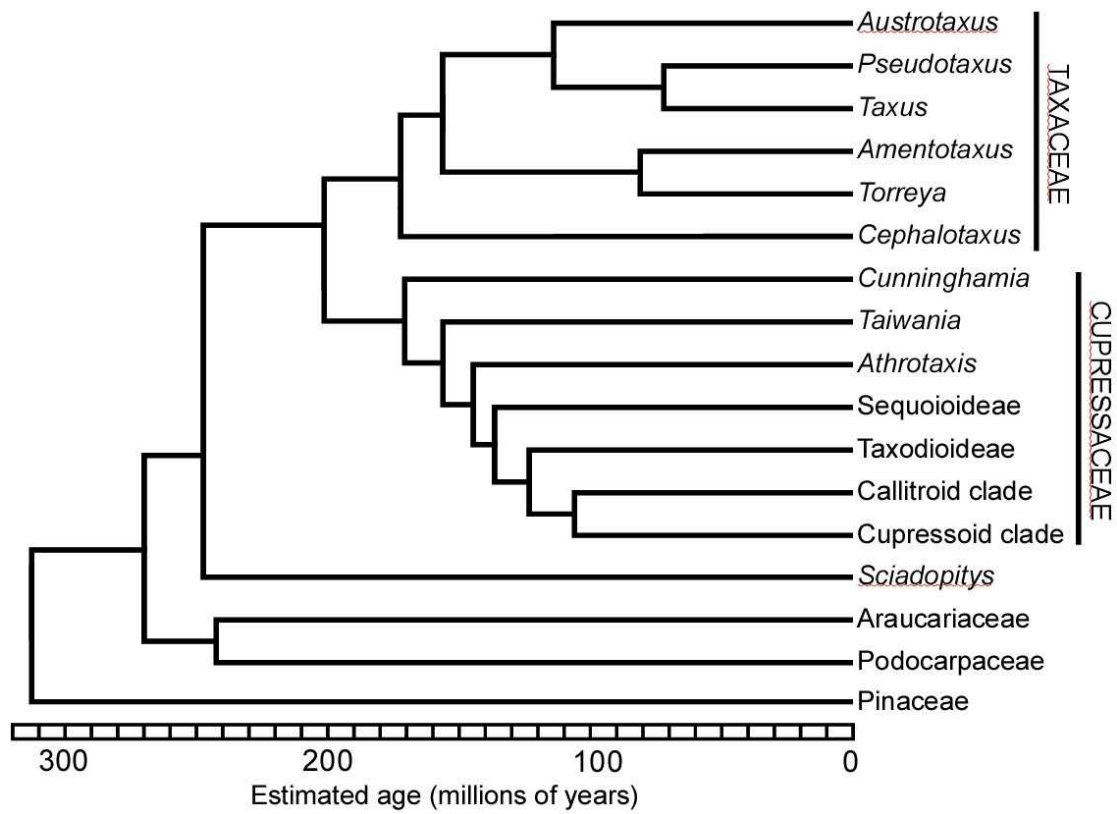
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1048 Figure 6: Mean  $P_{50}$  values for the six conifer families. For the Taxaceae the mean values are  
1049 provided by genera. Most extant conifers have a  $P_{50}$  ranging between -3 and -6 MPa. Values  
1050 taken from Bouche et al. (2014), except for *Austrotaxus*, which comes from Larter (2016).

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1053 Figure 7: Dated molecular phylogeny used to discuss Taxaceae fossil wood record, based on  
 1054 Leslie et al. (2018).

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1056