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Philippe & al. Fossil wood and palaeobiogeography of Taxaceae
A palaeobiogeographical scenario for the Taxaceae based on a revised fossil wood
record and embolism resistance
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Abstract: Fossil Taxaceae are documented for the Cenozoic throughout most of the northern
hemisphere, but the pre-Cenozoic history of this group is still poorly known. The fossil wood
record is difficult but can shed light on this history. We critically evaluated the fossil woods
assigned to Taxaceae and then compared the fossil record of taxaceous woods to the fossil
record of taxaceous leaves and reproductive structures. We then considered the fossil record
in the context of family's molecular phylogeny. More than half of the fossil woods attributed
to Taxaceae lack diagnostic characters of the family (longitudinal tracheids with helical
thickenings and abietoid pitting on radial walls). Fossil wood that can be attributed to the
fossil genus Taxaceoxylon, as well as some specimens placed in the genus Protelicoxylon,
which differ only in having mixed type of intertracheary radial pitting, probably belong to
Taxaceae. The fossil wood record, as reappraised, is not informative about the history of
individual genera within the family, but fits that of leafy remains. Taxaceae wood shows
remarkable resistance to embolism and subsequent increased risks of conduit implosion that
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
- Key-words: *Taxaceoxylon; Protelicoxylon;* wood anatomy; palaeoecology; biogeography;
 Laurasia.
- 39
- 40 Highlights
- the fossil wood record of Taxaceae-like wood is reappraised
- 42 five biogeographically consistent groups are distinguished
- two of them biogeographically fit with the Taxaceae leafy remains record
- modern Taxaceae wood shows remarkable resistance to embolism
- 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 $(10 - 25^\circ)$ (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.

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

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 xylological terms here. The term "helical" is preferred here to the term "spiral", often also used, as a 113

114 115

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

spiral is normally a planar structure.

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).

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

Göppert (1850) also created two other genera *Spiropitys* and *Physematopitys* for fossil wood that he considered to be Taxaceae. *Spiropitys* has been little–used and is today completely forgotten. It is not wise to use this name because the type is not located and its protologue does not have a clear diagnosis. *Physematopitys* was originally supposed to be related to *Ginkgo*, which was then supposed to be related to the yews because of its fleshy 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 tracheidoxyls. Similarly, Herbstiloxylon Gnaedinger in Gnaedinger & Herbst is designed for 162 163 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.

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

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

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

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-Chelbodaeff 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**

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

Name	Authorship	Туре	Reappraisal	Note
Platyspiroxylon	Greguss,	Р.	Туре	A junior
	1961	heteroparenchymatosum	material	taxonomical
		Greguss	reviewed	synonym of

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

209 2.1.3 Genera with anaucarian 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 an aucarian TRP and tertiary thickenings,

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).

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

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

of this group belongs to the Palaeozoic, Mesozoic woods might have been misidentified.

Here mentioned fossil woods are referred to, as much as possible, under their basionym, without prejudging the merit of published (or to be published) taxonomical arguments in 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 $10^{\circ}-20^{\circ}$ 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 shrinkage during diagenesis (see Greguss, 1967 pl. 35 fig. 19b). They characteristically make 251 252 a low angle with the tracheid longitudinal axis, usually $30-40^\circ$, 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

have several times been confused with helical thickenings (see e.g. Kraus, 1887; Houlbert,

1910 and Philippe & Bamford, 2009; Fig. 4). These patterns are, however, made of closelyparallel but irregularly spaced lines.

265 Crystal cleavage plans can also be tricky, however they normally run across several266 tracheids.

Fungal hyphae can mimic grooves within a tracheid because hyphae often follow the S2 cell wall layer (see Greguss, 1967, pl. 32), however their disposition is rarely regular enough 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 araucarian radial TRP and helical thickenings were not considered (e.g. Taxopitys, 286 287 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).

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

been forgotten, we would be very grateful to get notice. We are confident that no significantdata 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 anaucarian 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
Protelicoxylon feriziense	Gnaedinger & Herbst, 2006
(Fahkr & Marguerier) Philippe	
Prototaxoxylon acevedoae	Gnaedinger & Herbst, 2006
Gnaedinger & Herbst	
Prototaxoxylon intertrappeum	Lutz et al., 1999
(Prakash & Srivastava)	
Prakash & Srivastava	
Prototaxoxylon intertrappeum	Gnaedinger & Herbst, 2006
(Prakash & Srivastava)	
Prakash & Srivastava	
Prototaxoxylon uniseriale	Gnaedinger & Herbst, 2006
Prasad	

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

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.

Taxon name, authority	Reference
Protocallitrixylon kanakense	Vozenin-Serra & Salard-
Vozenin-Serra & Salard-	Chelbodaeff, 1992
Chelbodaeff	

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

- 334
- 335
- 336
- 337

338 *Protelicoxylon* woods, as here revised, form another spatio-temporally coherent unit (Table

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

that indicates relatively wet settings (Philippe et al., 2017).

345

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
		1.80	Country
Protelicoxylon asiaticum	Serra, 1969	Early? Cretaceous	Cambodia
(Serra) Philippe			
Protelicoxylon feriziense	Fakhr &	Middle Jurassic	Iran
(Fakhr & Marguerier) Philippe	Marguerier, 1977		
Protelicoxylon lepennecii	Philippe, 1995	Toarcian	France
Philippe			
Protelicoxylon	Greguss, 1967	Toarcian	Hungary
parenchymatosum (Greguss)			
Philippe			

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

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

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

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 observed in the tangential section. These Indian woods can further be subdivided into two 368 369 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

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

improvements in stratigraphic ranges (Tripathi, 2008; Weishampel et al., 2004). The

attribution of these fossils to Taxaceae is questionable.

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

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

380 4 DISCUSSION

The wood fossil record includes many Mesozoic and Cenozoic specimens with some Taxaceae anatomical features. Only wood having helical thickenings and abietinean pitting (i.e. wood that is, or should be, assigned to *Taxaceoxylon*) is convincingly Taxaceae, although some other wood types (e.g. *Protocallitrixylon* and *Protelicoxylon*) may represent ancestral forms of the Taxaceae lineage. The record shows that five taxonomically and spatiotemporally well-circumscribed groups can be recognized among the Mesozoic or younger 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., Ferugliocladaceae or Buriadaceae). Thus a fossil fleshy aril would 423 probably not be unequivocal evidence of Taxaceae.

Although foliage of Taxaceae is more likely to be preserved than the arils, the gross
morphology of shoots and leaves of this family is little differentiated from that of several
other conifer clades. As a result, leaf and leafy twig fossils are largely uninformative when
cuticle is missing. The cuticle is distinctive for modern genera (Elpe et al., 2017), although
Taxaceae cuticle can resemble that of some completely unrelated taxa, e.g. within the
Monocots (Conran, 1997). Similarly, Jordan et al. (2013) observed Taxaceae-like cuticle in
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*, *Thomasiocladus* (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 spatio435 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.

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



Figure 6: Mean P_{50} values for the six conifer families. For the Taxaceae the mean values are provided by genera. Most extant conifers have a P_{50} ranging between -3 and -6 MPa. Values 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, the491 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

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





513 Figure 7: Dated molecular phylogeny used to discuss Taxaceae fossil wood record, based on514 Leslie et al. (2018).

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

abietinean TRP. It is probable that this change in the TRP had consequences on conduction.

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

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

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

less contemporaneous with the split of the two branches (*Torreya* + *Amentotaxus* and *Austrotaxus* + *Pseudotaxus* + *Taxus*). The Late Jurassic, during which this split might have
taken place (Fig. 7), is well known as a time of global drying of Northern Hemisphere
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 lepennecii 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 wall1028 alteration.
- 1029 Figure 2: confusing spiral-like patterns. A Podocarpoxylon 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.
- 1046



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).
- 1051



1053 Figure 7: Dated molecular phylogeny used to discuss Taxaceae fossil wood record, based on

- 1054 Leslie et al. (2018).