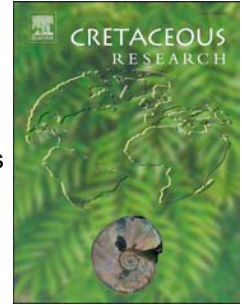


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A new cupressaceous wood from the Lower Cretaceous of Central Patagonia reveals possible clonal growth habit

Cristina I. Nunes, Josefina Bodnar, Ignacio H. Escapa, María A. Gandolfo, N. Rubén Cúneo



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21 presence of ray tracheids are two traits of particular interest in the context of systematic
22 affinities. The fragments were collected from two stumps found in life position attached to each
23 other by a main root, consequently, the disposition of the stumps suggests a case of clonal
24 growth by root suckering. This is the second report of such mechanisms in the fossil records
25 worldwide and the first one for South America.

26 **Keywords:** *Cupressaceae, Early Cretaceous, Fossil woods, Root suckering, Clonal growth*

27

28 **1. Introduction**

29 Cupressaceae *s.l.* is a cosmopolitan family that comprises approximately 30 genera and
30 more than 100 species, distributed among the warm and temperate regions of both
31 Hemispheres (Brunsfeld et al., 1994; Farjon, 2005, 2010; Little, 2006; Page, 1990; Schulz and
32 Stützel, 2007). Cupressaceous species are evergreen, sometimes deciduous, trees or shrubs
33 (monoecious or dioecious), with spirally arranged, ternate, or decussate (rarely quadrate)
34 leaves (young linear and adult scale-like) and a highly diverse reproductive morphology (Covas,
35 1995; Farjon, 2005; Gadek et al., 2000; Page, 1990; Schulz and Stützel, 2007). The family
36 comprises the monophyletic group Cupressaceae *s.s.* and the traditional Taxodiaceae as a basal
37 paraphyletic grade in the family phylogeny (Atkinson et al., 2014; Gadek et al., 2000; Mao et al.,
38 2012; Schulz and Stützel, 2007; Yang et al., 2012). Based on molecular and combined analyses,
39 seven subfamilies are usually recognized: Cunninghamioideae, Taiwanoideae, Athrotaxoideae,
40 Sequoioideae, Taxodioideae, Callitroideae, and Cupressoideae (e.g., Atkinson et al., 2014;
41 Farjon, 2010; Gadek et al., 2000; Little, 2006).

42 Interestingly, extant Cupressaceae wood anatomy is highly homogeneous and all
43 members are characterized by the presence of the following characters: axial tracheids without
44 helical thickenings, cupressoid or taxodioid cross-field pits, abietinean tracheid radial pitting,
45 resinous content in ray parenchyma cells, and presence of axial parenchyma in one or different
46 combinations (Gadek et al., 2000; Greguss, 1955; Román-Jordán et al., 2017). Although,
47 absence of ray tracheids has also been mentioned as a common feature for many

48 cupressaceous species (e.g., Greguss, 1955; Román-Jordán et al., 2017), the presence of this
49 type of cells has been reported for some genera (e.g., Bonetti, 1966; Boureau, 1956; Boutelje,
50 1955; Gadek et al., 2000; Peirce, 1937).

51 The oldest whole plant concept of Cupressaceae is represented by *Austrohamia minuta*
52 from the Lower Jurassic of Patagonia, Argentina (Bodnar and Escapa, 2016; Escapa et al., 2008).
53 *A. minuta* has been reconstructed from impressions and compressions of leafy twigs attached
54 to ovulate and pollen cones, and associated silicified wood. *Austrohamia* branches and cones
55 remains have also been reported for the Upper Jurassic in China (Dong et al., 2018; Zhang et al.,
56 2012). However, other reports of isolated organs suggesting affinities to the family, such as
57 ovulate cones, leaves, wood remains, and leafy twigs, are known from the Upper Triassic of
58 France (Lemoigne, 1967), and the Middle and Upper Triassic of Argentina (Bodnar et al., 2015;
59 Bonetti, 1966).

60 Several Cupressaceae fossil woods have been reported from southern South America
61 (Bodnar and Artabe, 2007; Brea et al., 2016); among them the Triassic *Protojuniperoxylon*
62 (Bodnar and Artabe, 2007; Bonetti, 1966) and *Cupressinoxylon* (Bodnar et al., 2015); the
63 Jurassic genera *Protelicoxylon*, *Herbstiloxylon* (Gnaedinger, 2007), *Protojuniperoxylon*
64 (Gnaedinger et al., 2013), and *Protaxodioxylon* (Bodnar and Escapa, 2016); and finally
65 *Cupressinoxylon* (e.g. Brea et al., 2016; Egerton, 2011; Egerton et al., 2016; Kräusel, 1949;
66 Martínez, 2010; Pujana et al., 2015; Ruiz et al., 2017) and *Taxodioxylon* (Egerton et al., 2016)
67 from the Cretaceous to the Cenozoic. Nevertheless, many of the species assigned to these
68 genera are dubiously related to the family based due to incomplete descriptions, poor

69 preservation, and the presence of characters of ambiguous affinity (e.g., Gnaedinger, 2007;
70 Kräusel, 1949; Vaudois and Privé, 1971).

71 Sprouting (i.e., the ability to produce secondary trunks, generally induced by injury or
72 dramatic environmental changes) is a rare mechanism in conifers, although it has been
73 reported for a few unrelated genera such as *Pinus* (Pinaceae) *Podocarpus* (Podocarpaceae) and
74 *Sequoia* (Cupressaceae) (Bond and Midgley, 2001; Del Tredici, 2001). *Sequoia sempervirens* is
75 referred to be exceptional at its ability to resprout and grow clonally after disturbances
76 (Douhovnikoff and Dodd, 2007; Douhovnikoff et al., 2004; Rogers, 2000; Rydelius and Libby,
77 1993). Also, *Athrotaxis cupressoides* can propagate by root suckering, while other taxodiaceous
78 species frequently develop root collars (Bond and Midgley, 2001; Cullen and Kirkpatrick, 1988;
79 Worth et al., 2016). This attribute is ecologically significant because it represents a mechanism
80 for surviving in stressful environmental conditions, regenerate after massive disturbances, and
81 propagate vegetatively in the cases of sprouting by root suckering.

82 Like sprouting, the development of root suckers is unusual in conifers (Bond and
83 Midgley, 2001; Del Tredici, 2001). The only detailed anatomical description of this mechanism is
84 based on sprouts in damaged roots of *Araucaria cunninghamii* (Araucariaceae; Burrows, 1990).
85 Root suckers have been also documented for *Araucaria araucana* (Araucariaceae; Grosfeld et
86 al., 1999) and *Aghatis robusta* (Araucariaceae; Haley, 1957), *Phyllocladus alpinus*
87 (Podocarpaceae; Barker, 1995), and *Athrotaxis cupressoides* and *Fitzroya cupressoides*
88 (Cupressaceae; Bond and Midgley, 2003; Lara et al., 1999; Veblen and Ashton, 1982; Worth et
89 al., 2016). Despite the fact that this mechanism is ecologically relevant in species that can

90 propagate and regenerate after environmental disturbances through root suckers (e.g.,
91 *Athrotaxis cupressoides*, *F. cupressoides*; Veblen and Ashton, 1982; Worth et al., 2016), the
92 evolution of this feature is sparsely known and poorly documented in the fossil record. It has
93 been reported only for *Notophytum* (Voltziales; Bomfleur et al., 2013; Decombeix et al., 2011)
94 and there are not previous reports of this type of vegetative propagation in the fossil
95 Cupressaceae.

96 A megaflora associated to the titanosaur species *Patagotitan mayorum* was discovered
97 in Lower Cretaceous deposits of the Chubut Group, in central Patagonia (Carballido et al.,
98 2017). The fossil carrying sediments were assigned to the upper Albian Cerro Castaño Member
99 of the Cerro Barcino Formation (Carballido et al., 2017). Plant remains were collected at the
100 same stratigraphic level from two close localities (200 m) to the sauropod excavation. The flora
101 consists of impressions and compressions of fern pinnules, conifer leaves and cones,
102 angiosperm leaves and flowers, and silicified woods. The angiosperms are preserved as
103 impressions and compressions, whereas the conifers dominate the fossil wood assemblage.
104 Remarkably, only one specimen of angiosperm wood was found and assigned to the genus
105 *Carlquistoxylon* (Nunes et al., 2018).

106 In this contribution, a new genus and species with affinities to the family Cupressaceae
107 is described on the base of two well preserved specimens. The specimens are stumps found in
108 life position and connected through a main root, revealing a possible case of clonal growth by
109 root suckering.

110

111 2. Geological Setting

112 The samples were collected at the “La Flecha” ranch, in a site referred as “La Flecha Pb
113 1” (FLPb1), Chubut Province, central Patagonia, Argentina (Fig. 1). The specimens were found in
114 life position, in deposits of the Cerro Castaño Member of the Cerro Barcino Formation, Chubut
115 Group (Figari et al., 2015), 200 meters distant from a quarry containing titanosaur remains
116 (Carballido et al., 2017).

117 The Cerro Barcino Formation of the Chubut Group is composed of fluvial volcanoclastic
118 sediments and comprises four members, from bottom to top: Puesto La Paloma, Cerro Castaño,
119 Las Plumas and Puesto Manuel Arce (Figari et al., 2015; Rauhut et al., 2003; Umazano et al.,
120 2017). The Cerro Castaño Member comprises sheet-to ribbon-channel sandstone bodies
121 intercalated within tuffaceous and fine-grained sediments (Umazano et al., 2017). U-Pb dating
122 of tuffs collected from an ash layer at the titanosaur excavation, a few meters below the plant
123 horizon, indicates an age of ca. 101.6 ± 0.11 Ma (late Albian, Early Cretaceous) for the Cerro
124 Castaño Member (Carballido et al., 2017).

125 The plant bearing deposits comprise siltstones and fine to medium-grained sandstones
126 that represent sandy floodplains and meandering channels (Carmona et al., 2017; Umazano et
127 al., 2017). The stumps herein described were found in connection to each other, in life position
128 at FLPb 1 site, in an exhumated sequence of clay and sandstone layers. Samples were collected
129 from both stumps and the main root that connected them. Other permineralized conifer wood
130 remains and a single angiosperm wood fragment were collected from a conglomerate layer that
131 lies on top of the clay and sandstone layers. Impressions and compressions of leaves and

132 reproductive structures of angiosperms and conifers were found associated to the stumps, at
133 both sides of the main root. Additional impression samples were collected from another site
134 referred as “La Flecha Pb 2” (FLPb 2), with similar sedimentology and stratigraphically
135 equivalent to FLPb 1 (Nunes et al., 2015; Nunes et al., 2018).

136

137 **3. Materials and methods**

138 The specimens were permineralized with silica. Only secondary xylem is preserved (Fig
139 2–7). Transverse, tangential longitudinal, and radial longitudinal thin sections were prepared
140 following standard methodology (Archangelsky, 1962; Jones and Rowe, 1999). Also, slides of
141 disaggregated wood were prepared when possible. Slides were observed using transmitted
142 light and epifluorescence microscopy. All images were taken with a Nikon DS-Fi1 camera
143 connected to a Nikon Eclipse 80i microscope. General views of the transverse sections were
144 taken using a Canon 7D camera with a Canon macro lens of 60 mm, in a light box with
145 fluorescent tubes. Additionally, small fragments were observed with scanning electron
146 microscope (JEOL JSM-6460), without gold/palladium coat, at 15Kv, 28Pa, at ALUAR lab (Puerto
147 Madryn). Radial longitudinal wood sections of extant species *Fitzroya cupressoides* and
148 *Pilgerodendron uviferum* were also observed under transmitted light microscope; the sections
149 are housed at the xylotheque of the Cátedra de Xilología (Museo de La Plata). We used an
150 image-stacking technique for obtaining greater depth of focus for high magnification images
151 (Bercovici et al., 2009). Helicon Focus software
152 (<http://www.heliconsoft.com/heliconfocus.html>) was used, with the “Method B” (Depth Map)

153 parameter, and the resulting image was carefully checked for the presence of artifacts. Several
154 smaller, partially overlapping images were merged to create high-quality images of critical
155 features. This technique was applied both manually and using the Adobe Photoshop CS5
156 Photomerge macro. For the description, a minimum of 30 measurements or observations of
157 each character were obtained. Measurements are expressed as the mean followed by the range
158 between brackets. For the wood anatomy description, the terminologies suggested by the
159 IAWA Committee (2004), Philippe (1995) and Phillippe and Bamford (2008) were followed. In
160 order to estimate the tree height of the fossil stumps, the formula of Niklas (1994a, b, c), revised
161 by Niklas and Spatz (2004), was used, in which the estimated height is calculated as follows:
162 $Hest = 27.8 \times D^{0.430}$, where D is the tree diameter.

163 The macro-specimens and specimen thin sections are housed at the Paleobotanical
164 Collection of the Museo Egidio Feruglio, under accession numbers MPEF-Pb 7000–7002, MPEF-
165 Pb 7007, and MPEF-Pb 7008.

166

167 **4. Systematic Paleontology**

168

169 Order Pinales (=Coniferales)

170 Family Cupressaceae *s.l.*

171

172 Genus ***Austrocupressinoxylon*** Nunes, Bodnar, et Escapa, *gen. nov.*173 Type species *Austrocupressinoxylon barcinense* Nunes, Bodnar, et Escapa, *gen. et sp. nov.*

174

175 *Generic diagnosis.* Picroxylic and homoxylic secondary xylem. Growth ring boundaries
176 distinct; transition from earlywood to latewood gradual. Axial parenchyma diffuse.

177 Tracheid pitting in radial walls predominantly abietinean. Cross-fields pits cupressoid,
178 arranged in both cupressoid and araucarioid patterns. Rays uniseriate heterocellular. End
179 and horizontal walls of ray parenchyma cells smooth or slightly nodular. Ray tracheids with
180 smooth walls.

181

182 ***Austrocupressinoxylon barcinense*** Nunes, Bodnar, et Escapa, *sp. nov.*

183 Figs. 2–7

184

185 *Holotype*. MPEF-Pb 7001.

186 *Paratype*. MPEF-Pb 7008.

187 *Studied material*. MPEF-Pb 7000–7002, MPEF-Pb 7007, and MPEF-PB 7008

188 *Locality and stratigraphic horizon*. “La Flecha” quarry, Chubut Province, Argentina; Cerro
189 Castaño Member (upper Albian, Lower Cretaceous), Cerro Barcino Formation, Chubut Group.

190 *Derivation of name*. *Austrocupressinoxylon* refers to the anatomical similarity with the fossil
191 wood genus *Cupressinoxylon* and with the woods of extant austral (southern) Cupressaceae;
192 *barcinense* refers to the geological unit Cerro Barcino Formation where the fossil wood was
193 found.

194 *Specific diagnosis*. *Picnoxylic and homoxylic secondary xylem. Growth ring boundaries*
195 *distinct; transition from earlywood to latewood gradual. Axial parenchyma diffuse. Tracheid*
196 *pitting in radial walls uniseriate, very occasionally biseriate, predominantly spaced,*
197 *occasionally contiguous and slightly compressed. Tracheid pitting in tangential walls present.*
198 *Pits circular with a distinct torus. Cross-fields with cupressoid oculipores arranged in*
199 *cupressoid and araucarioid patterns; cupressoid cross-fields up to 4 cells arranged in 1–2*
200 *rows; araucarioid cross-fields of 5 or more cells arranged in 1–3 rows. Rays uniseriate,*
201 *heterocellular, very low. Intercellular spaces within the ray body present. Ray parenchyma*
202 *cells with dark contents, and horizontal and end walls smooth or slightly nodular. Indentures*
203 *present. Ray tracheids with smooth walls.*

204

205 **Description.** The two studied specimens are stems similar in diameter (ca. 25 cm). They
206 are orthotropic and bear horizontal roots, and are connected by a main horizontal root of
207 approximately 15 cm of diameter. They are ca. 1 m apart from each other (Fig. 2a–b), and
208 bearing several branch traces. The horizontal roots also show several spiral patterns and
209 branch traces (Fig. 3a–c).

210 The specimens are permineralized by silicates, and preserved homoxylic picnoxylic
211 secondary xylem although they are decorticated and the pith is not preserved.

212 Growth ring boundaries are distinct, the transition from earlywood to latewood is
213 gradual (Fig. 4a–b). False rings are present (Fig. 4c).

214 Transverse section of the tracheids is circular to polygonal in outline (Fig. 4b–d).
215 Tangential tracheid diameter is 25.5 (12–43) μm ; the radial diameter is 20 (9–28) μm in the
216 earlywood and 10 (6–16.5) μm in the latewood. Double-wall thickness in the earlywood is 3.4
217 (2–5) μm . Latewood tracheids are thin-walled, wall thickness is 4 (2–6.5) μm .

218 Axial parenchyma is diffuse (Fig. 4b), hardly distinguishable in longitudinal section but it
219 is recognizable at transversal section from the presence of dark contents. The transverse end
220 walls of the axial parenchyma cells are smooth. (Fig. 4e).

221 Pitting in the radial walls of the tracheids is of abietinean type (Fig. 4f–g) *sensu* Philippe
222 and Bamford (2008). Pits are circular, bordered, uniseriate, very occasionally biseriate, spaced
223 and sometimes with small contiguous groups at the end of the tracheid (Fig. 4f–g; Fig. 5a–b; Fig.
224 6a); slightly compressed pits are occasionally observed (Fig. 5b). Pits are 14 (11–17.5) μm in

225 radial diameter and 13 (9.5–17) μm in vertical diameter. Pit apertures are circular to oval with a
226 well-defined torus (Fig. 5a–b; Fig. 6a–b).

227 Pitting is also observed on the tangential walls of the tracheids (Fig. 6c). Tangential pits
228 are circular, bordered, uniseriate, and spaced (Fig. 6d); and they are 9 (4–13) μm in tangential
229 diameter and 8.5 (5–12) μm in vertical diameter. Helical fissures, possibly due to compression
230 wood, are also observed (Fig. 6e).

231 Cross-field pits consist of cupressoid oculipores *sensu* Philippe (1995). These pits are
232 bordered, with circular to oval aperture, when oval horizontal to oblique, and they are 4.5 (1.5–
233 7) μm in radial diameter. Oculipores (=bordered pits; Torrey, 1923) are arranged in both
234 cupressoid and araucarioid patterns *sensu* Philippe (1995) and Philippe and Bamford (2008)
235 (Fig. 5c–d; Fig. 6f–g). Cupressoid cross-fields have one to four pits, spaced or contiguous,
236 arranged in one or two rows (Fig. 6f), while araucarioid cross-fields consist of five or more (10)
237 pits, crowded, often polygonal in outline, and arranged in two or three alternate rows (Fig. 5d;
238 Fig. 6g).

239 Rays are exclusively uniseriate, of very low average height, that is 3 (1–11) cells, or 76.5
240 (19–207) μm high (Fig. 6c). Rays are heterocellular, composed of procumbent parenchyma cells
241 and ray tracheids (Fig. 5e; Fig. 7a, d–f). Ray parenchyma cells have smooth or distinctly pitted
242 horizontal walls, and smooth or slightly nodular end walls (Fig. 7b). Indented parenchyma cells
243 are present as well (Fig. 7c); intercellular spaces present within the ray body (Fig. 7a, e). Some
244 radial parenchyma cells are filled with dark contents (Fig. 7b).

245 In the roots, the secondary xylem is very similar to the stem wood, except for the
246 seriation of pits in the tracheids tangential walls, which are both uniseriate and biseriate in the
247 roots (Fig. 3e); and the type of cross-field, which are exclusively cupressoid, with one or two
248 pits per cross-field in the roots (Fig. 3f).

249

250 **5. Discussion**

251 *5.1. Systematic affinities and comparisons with extant taxa*

252 The stumps found in life position at the “La Flecha” ranch site were assigned to the
253 family Cupressaceae because they share the apomorphic features of the family, which include
254 axial tracheids with abietinean radial pitting and without helical thickenings, rays with
255 cupressoid cross field pits, ray parenchyma with dark contents, and presence of axial
256 parenchyma. Nonetheless, these fossils show a novel combination of features that includes the
257 growth ring boundaries distinct, the transition from earlywood to latewood gradual, axial
258 parenchyma diffuse, the radial tracheid pitting predominantly abietinean, cross-field pits of
259 cupressoid type with both cupressoid and araucarioid arrangements, rays uniseriate and
260 heterocellular, end and horizontal walls of ray parenchyma cells smooth or slightly nodular, and
261 ray tracheids with smooth walls. This combination of characters is unique to the Patagonian
262 fossils and is not recorded in other fossil wood taxa (see Table 2); therefore, the establishment
263 of a new genus for placing these fossils was necessary and warranted.

264 Araucarioid cross-fields would link *Austrocupressinoxylon* to Araucariaceae or
265 Cheirolepidiaceae (e.g., Alvin et al., 1981; IAWA, 2004; Philippe, 1995). However, Araucariaceae

266 are characterized by multiseriate and alternate tracheid pits, axial parenchyma generally absent
267 and ray cell walls smooth (Greggus, 1955; IAWA, 2004; Phillips, 1948). On the other hand,
268 Cheirolepidiaceae woods differ from *Austrocupressinoxylon* in the mixed type tracheid pitting
269 and ray cells with smooth walls (Alvin et al., 1981; Bodnar et al., 2013).

270 The axial tracheid wall morphology (abietinean pitting and without helical thickenings),
271 together with the cupressoid cross-field pits, resinous content in ray parenchyma cells, and
272 presence of axial parenchyma, relate the anatomy of *Austrocupressinoxylon* with the
273 Cupressaceae *s.l.* (Greguss, 1955; IAWA, 2004, Román-Jordán et al., 2017). Cross-fields similar
274 to araucarioid type and ray tracheids are very occasionally present in some taxa of the family
275 (Gadek et al., 2000; Greguss, 1955; IAWA, 2004; Peirce, 1937; Philippe and Bamford, 2008).

276 Within the family Cupressaceae *s.l.* the greatest similarities are found with the extant
277 genera *Fitzroya* and *Pilgerodendron* which belong to the clade Cupressaceae *s.s.* The three
278 genera share the presence of occasional ray tracheids or at least ray parenchyma cells
279 interpreted by some authors as tracheids (e.g. Boutelje, 1955). Additionally, *Fitzroya* and
280 *Austrocupressinoxylon* have ray parenchyma cells with nodular and pitted walls and
281 *Austrocupressinoxylon* also has indented ray parenchyma cells like *Pilgerodendron* (see Table 1;
282 Fig. 7a–f; Fig. 8a–d).

283 5.2. Comparisons with fossil woods

284 *Austrocupressinoxylon* clearly shares characters with Cupressaceae fossil wood and
285 with several conifer families (see Table 2). In this regard, radial tracheid pitting and cross-field
286 pit arrangement are generally considered as diagnostic features in order to classify fossil wood

287 genera (IAWA, 2004; Philippe and Bamford, 2008). The abietinean tracheid pitting and
288 cupressoid/araucarioid cross-fields of *Austrocupressinoxylon* (Fig. 4f–g; Fig. 5a–d; Fig. 6a–b, f–g)
289 can also be seen in cupressaceous wood taxa like *Callitrixylon*, *Chamaecyparixylon*,
290 *Cupressinoxylon*, *Juniperoxylon*, *Libocedroxylon*, *Tetraclinoxylon*, and *Widdringtonioxylon*
291 (Bodnar and Artabe, 2007; Philippe and Bamford, 2008), as well as in *Podocarpoxyton*
292 (Podocarpaceae; see Pujana and Ruiz, 2017) and *Taxaceoxyton* (Taxaceae; e.g., Brea et al.,
293 2009; Roy, 1971). However, araucarioid cross-fields are not observed in those taxa with
294 exclusively abietinean tracheid pitting. Araucarioid cross-fields characterize *Agathoxyton*,
295 *Brachyoxylon* and *Baieroxylon*, taxa that exhibit araucarian or mixed tracheid radial pitting (see
296 Philippe and Bamford, 2008). *Austrocupressinoxylon* has some contiguous to compressed
297 tracheid pits; nevertheless, this is not a sufficient condition to classify them as mixed pitting.

298 The presence of axial parenchyma and smooth or slightly nodular ray parenchyma
299 walls together with the abietinean pitting and cupressoid cross fields, make
300 *Austrocupressinoxylon* most similar to *Chamaecyparixylon* from the Cenozoic of Occidental
301 Europe and ex URSS, the widespread genus *Cupressinoxylon* present in Mesozoic and Cenozoic
302 sediments, and *Tetraclinoxylon* and *Widdringtonioxylon* from the “Tertiary” of Europe (Bodnar
303 and Artabe, 2007; Phillippe and Bamford, 2008). However, the latter genera do not have
304 araucarioid cross-fields and ray tracheids.

305

306 *5.3. Character discussion*

307 Based on the previous discussion, the disposition of the pits in the cross-fields and the
308 presence of ray tracheids are undoubtedly the two traits most relevant of
309 *Austrocupressinoxylon*.

310 The studied woods exhibit oculipores of cupressoid type in their cross-fields (Fig. 6f–g).
311 In this regard, cupressoid pits have the aperture included and definitely they are narrower than
312 the border; while the long axis of the aperture varies in position from vertical to horizontal even
313 within a single specimen (Greggus, 1955; IAWA, 2004; Phillips, 1941). In extant and extinct taxa,
314 the cupressoid pits are usually disposed in two different cross-field patterns: cupressoid pattern
315 with one to four (rarely five or six) spaced pits per field, and araucarioid pattern with more than
316 4 pits per field, arranged in alternate rows with a tendency for crowding (Philippe, 1995;
317 Philippe and Bamford, 2008). In living plants, the cupressoid pattern is characteristic of most
318 Cupressaceae *s.l.* (Greggus, 1955; Román-Jordán et al., 2017) whereas the araucarioid pattern is
319 restricted to Araucariaceae (IAWA, 2004). Nonetheless, several Cupressaceae can occasionally
320 show cross-fields resembling the araucarioid type, in particular when they have more than six
321 pits per field (Esteban et al., 2002; Greggus, 1955; Philippe and Bamford, 2008). In
322 *Austrocupressinoxylon*, cross-fields compatible with both araucarioid and cupressoid patterns
323 were found in the same section (Fig. 5c–d; Fig. 6f–g).

324 Ray tracheids are imperforate wood cells with bordered pits forming part of a ray
325 (IAWA, 1964). They commonly occur along the margins of the rays, one or more cells in depth,

326 but may be interspersed among the layers of parenchyma cells (Evert, 2006). To verify the
327 presence of ray tracheids, bordered pits must be searched very carefully, especially in common
328 end walls of two adjoining marginal and/or sub-marginal ray cells. Unfortunately, in
329 archaeological and paleontological material, the pit borders can be distorted or obscured by
330 physical degradation and decay of cell walls (IAWA, 2004).

331 The Cupressaceae are regarded as lacking ray tracheids, except in *Xanthocyparis*
332 *nootkatensis*, in which some rays may consist entirely of tracheids, and others only of
333 parenchyma cells (Evert, 2006; IAWA, 2004). Ray tracheids have also occasionally been
334 described in other species of the family, e.g. *Cupressus arizonica*, *C. bakeri*, *C. duclouxiana*, *C.*
335 *lusitanica*, *C. macrocarpa*, *Sequoia sempervirens*, and *Thujopsis dolobrata* (Bannan, 1934;
336 Belyea, 1919; De Magistris, 1997; Gordon, 1912; Holden, 1913; Román-Jordán et al., 2016;
337 Thompson 1910).

338 In southern Cupressaceae taxa, *Fitzroya cupressoides* and *Pilgerodendron. uviferum*,
339 have elongated cells with pitted walls in the wood rays (Plate 8, Fig. a-b); these cells were
340 described as ray tracheids by Boutelje (1955) or ray parenchyma by other authors (e.g., Roig,
341 1992). In the type material of *Austrocupressinoxylon*, wood rays are composed mainly of
342 procumbent rectangular parenchyma cells, however in some rays there are fusiform cells
343 interspersed with rectangular cells. These fusiform cells have tapering ends and thin walls, and
344 are longer than rectangular cells (Fig. 7d–f). Although the bordered pit on the walls of these cells
345 were not well preserved, their morphology corresponds to tracheids, and thus we consider that
346 *Austrocupressinoxylon* has heterocellular rays.

347

348

5.4. Sprouting, root suckering and clonal growth

349 In normal conditions, most tree species would develop a single, erect woody trunk (Ng,
350 1999); yet, secondary trunks can be produced in response to external environmental factors
351 such as injuries in the primary trunk or root system, displacement of the primary stem from the
352 normal vertical orientation, or pronounced environmental disturbances (Hallé, 1999; Hallé et
353 al., 1978; Putz and Sharits, 1991; Sakai et al., 1995). This ability to produce secondary trunks,
354 generally induced by injury or dramatic environmental changes, is recognized as sprouting (Del
355 Tredici, 2001).

356 Sprouting can constitute a form of clonal growth when the secondary trunks are
357 produced a measurable distance away from the base of the primary trunk, having the potential
358 to become autonomous at some point in the future (Del Tredici, 2001). Many more species are
359 sprouters than are clonal, though all clonal woody species sprout (Bond and Midgley, 2003).

360 There are four basic sprouting types: collar sprouts from the base of the trunk, sprouts
361 from specialized underground stems (lignotubers and rhizomes), opportunistic sprouts from
362 layered branches, and sprout from roots (root suckering) (Del Tredici, 2001). In the last case,
363 root suckers can be produced after environmental stresses or to be part of the normal
364 development in clonal species. In this sense, plants can propagate vegetatively through root
365 suckering, spreading from the original site of establishment (Bond and Midgley, 2003,
366 Decombeix et al., 2011).

367 Sprouting through root suckering is rare in conifers (Bond and Midgley, 2003; Del
368 Tredici, 2001). This mechanism has been reported for the Araucariaceae species *Araucaria*
369 *cunninghamii* (Burrows, 1990), *A. araucana* (Grosfeld et al., 1999) and *Agathis robusta* (Haley,
370 1957), *Phyllocladus alpinus* within the Podocarpaceae (Barker, 1995), and *Athrotaxis*
371 *cupressoides* and *Fitzroya cupressoides* within the Cupressaceae (Bond and Midgley, 2003; Silla
372 et al., 2001; Veblen and Ashton, 1982; Worth et al., 2016). However, it has been anatomically
373 described only in buds developed on injured roots of *Araucaria cunninghamii* (Burrows, 1990).

374 The evolutionary aspects related to root suckering and sprouting in conifers are still
375 scarcely explored, and the presence of these mechanisms is hardly evidenced in the fossil
376 record (Bond and Midgley, 2003). Very few examples of fossil root suckering conifers have been
377 described. The only two previous reports correspond to the Voltziales from the Triassic of
378 Antarctica with excellent anatomical preservation (Bomfleur et al., 2013; Decombeix et al.,
379 2011).

380 The general morphology of the Patagonian samples and the architecture of the stumps
381 indicate that the underlying process was actually sprouting directly from roots (Fig. 2a–b; Fig.
382 3a–c). The considerable distance (90 cm approximately) between the two specimens and their
383 diameters, suggest that this plant produced root suckers as mechanism of clonal growth. The
384 size of the two stumps is similar, and the roots emerging from the stumps seem to continue
385 under the buried sediments (Fig. 2a–b). Thus, we can not determine which is the parental plant
386 and if there are more clones undiscovered. According to the formulas of Niklas (1994a,b,c,
387 based on tree diameter) and Niklas and Spatz (2004), these trees would have reached an

388 estimated height of 15.3 m. The wood samples present several branch traces, which strongly
389 indicate that the trees were regularly branched.

390

391 6. Conclusions

392 The specimens described here are assigned to a new fossil-genus:
393 *Austrocupressinoxylon* based on a novel and unique combination of characters that resembles
394 the fossil-taxon *Cupressinoxylon* and some southern extant Cupressaceae (i.e. *Fitzroya* and
395 *Pilgerodendron*).

396 The combination of identified features is more compatible with Cupressaceae wood
397 anatomy than with any other conifer group, and based on the presence of cross-fields with
398 araucarioid pattern with Araucariaceae and Cheirolepidiaceae.

399 Among extant Cupressaceae, the greatest affinities are found with members of the
400 Cupressaceae s.s., especially with the southern taxa *Fitzroya* and *Pilgerodendron*. These genera
401 and *Austrocupressinoxylon* share very similar ray morphology.

402 The general morphology and architecture of the specimens found in life position
403 suggest that this plant produced root suckers as a mechanism for clonal propagation, indicating
404 that, at least for the Cupressaceae, this attribute was already developed in the late Early
405 Cretaceous. In addition, this record is one of the very few examples of root suckering in fossil
406 conifers, and the first one for a family that has extant representatives. This example, together

407 with the Antarctic Voltziales, provides a basis for identifying evolutionary patterns of this
408 mechanism in the fossil records.

409 The fossil wood assemblage found at the “La Flecha” locality is definitely dominated by
410 conifers, including the cupressaceous clonal species described here, suggesting that the
411 conifers were the major component of this Albian forest although impressions and
412 compressions of six angiosperm leaf morphotypes and several pentamerous flowers, and an
413 angiospermous wood fragment assigned to the species *Carlquistoxylon australe*, also occur in
414 the same sediments (Nunes et al., 2018). This evidence adds additional information to previous
415 southern South America reports that indicate angiosperms were increasing their participation
416 in forests dominated by gymnosperms and ferns during the transition from Early to Late
417 Cretaceous (see Archangelsky et al., 2009; Passalia et al. 2015), including arboreal forms as
418 suggested by the estimated original diameter of *Carlquistoxylon australe* (Nunes et al., 2018).

419

420

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427

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TABLE CAPTIONS

- 672 **Table 1.** Comparison of *Austrocupressinoxylon gen nov.* with extant genera of Cupressaceae
673 *sensu lato*. Abbreviations: GD= geographic distribution; GR= growth rings; ATS= axial tracheid
674 cross section; ATRP= axial tracheid radila pitting; CT= callitroid thickenings; ATTP= axial tracheid
675 tangential pitting; AP= axial parenchyma; APW=axial parenchyma walls; APA= axial parenchyma
676 arrangement; RW= ray width; RH= ray height; RPEW= ray parenchyma end walls; RPHW= ray
677 parenchyma horizontal walls; IN= indentures; RPR= ray parenchyma resinous; CFPT= cross field

678 pit type, CFPN= cross field pit number; RT= Ray tracheids. Between () characters which appear
 679 occasionally. Information taken from Esteban et al. (2002, 2004), Román-Jordán et al. (2017).
 680 *According to Boutelje (1955); **According to Gadek et al. (2000), ***According to Gordon
 681 (1912); ****According to Sugawa and Fujii (1992).

682 **Table 2.** Comparison of *Austrocupressinoxylon gen nov.* with similar fossil-genera. Bold letters
 683 indicate characters shared with *Austrocupressinoxylon*. Abbreviations: TTS= tracheid transversal
 684 section; RTP= radial tracheid pitting; TTP= tangential tracheid pitting; AP= axial parenchyma;
 685 CF= cross-fields; RPHW= ray parenchyma horizontal walls; RPEW = ray parenchyma end walls;
 686 RT= ray tracheids; RC= resin canals; DC= distinct characters. Information taken from: Vaudois
 687 and Privé (1971), Bodnar and Artabe (2007), Phillippe and Bamford (2008), Brea et al. (2009),
 688 Pujana and Ruiz (2017).

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FIGURE CAPTIONS

692 **Figure 1.** Location map of the “La Flecha” ranch (star), Chubut Province, Argentina.

693 **Figure 2.** Specimens of *Austrocupressinoxylon barcinense gen. et sp. nov.* found in life position
 694 at the site FLPb 1. -- a. The specimens are connected by a main root; the architecture is
 695 compatible with root suckering. -- b. General view of the site excavation and the studied
 696 specimens. -- Scale bar for a = 22 cm, for b = 19 cm.

697 **Figure 3.** *Austrocupressinoxylon barcinense gen. et sp. nov.* MPEF-Pb 7000-7001, MPEF-Pb
 698 7007-7008. -- a. General view of tangential section of root showing spiral pattern. – b, c.
 699 General view of tangential section of root showing secondary root trace. – d. Transverse section
 700 (TS) of root. – e. Tangential longitudinal section (TLS) of root showing pit seriation, biseriate pits
 701 present (black arrow). – f. Radial longitudinal section (RLS) of root showing abietinean pitting
 702 and cupressoid cross-field. – Scale bar for a = 1 cm; for b and c = 2 mm; for d and e = 150 μm ;
 703 for f = 20 μm

704 **Figure 4.** *Austrocupressinoxylon barcinense gen. et sp. nov.* MPEF-Pb 7000-7001, MPEF-Pb
 705 7007-7008. -- a. General view of growth ring boundaries distinct, (TS). -- b. Tracheids circular to
 706 polygonal in outline, growth ring boundary narrow, transition from latewood to earlywood
 707 gradual (white arrow), axial parenchyma diffuse (black arrows), (TS). -- c. False rings (white
 708 arrow), (TS). -- d. Detail of tracheids, occasional compressed small tracheids (black arrows), (TS).
 709 – e. Detail of axial parenchyma (TLS). –f. General view of radial longitudinal section. Tracheids
 710 with uniseriate radial pits. – Biseriate radial pits in tracheids, (RLS). -- Scale bar for a = 0.5 cm;
 711 for b, c and f = 150 μm ; for d and g = 50 μm ; for e = 30 μm .

712 **Figure 5.** *Austrocupressinoxylon barcinense gen. et sp. nov.* MPEF-Pb 7000-7002, MPEF-Pb
 713 7007-7008. -- a. Detail of uniseriate radial pits in tracheids, (RLS). – b. Torus in different
 714 positions, in tracheid pits, (dissaggregated wood slide). – c. General view of tangential
 715 longitudinal section showing uniseriate rays and tracheid tangential walls with uniseriate pits
 716 (white arrow). -- d. Detail of tracheids and tangential tracheid pits, (TLS). – e. Helical fissures in
 717 tracheid walls, (TLS). – f. Detail of cupressoid cross-fields, (RLS). – g. Detail of araucarioid cross-

718 fields (RLS). Scale bar for a and d = 50 μm ; for b and e = 30 μm ; for c = 100 μm ; for f and g = 20
719 μm .

720 **Figure 6.** *Austrocupressinoxylon barcinense* gen. et sp. nov. Scanning electron microscope
721 images. -- a. Tracheids with abietinean radial pitting. – b. Detail of tracheid radial pits,
722 contiguous and slightly compressed. – c. Detail of ray with araucarioid cross-fields. – d. Detail of
723 araucarioid cross-fields. – e. General view of tracheids and heterocellular ray. -- Scale bar for a,
724 c and e= 100 μm ; for b and d = 20 μm .

725 **Figure 7.** *Austrocupressinoxylon barcinense* gen. et sp. nov. MPEF-Pb 7000-7002, MPEF-Pb
726 7007-7008. -- a. Heterocellular ray with procumbent and fusiform cells, spaces within the ray
727 body present, (dissagregated wood slide). – b. Pitted horizontal walls of ray parenchyma cell
728 (black arrows) and nodular end walls of ray pranchyma cells (white arrows), (RLS). – c.
729 Indentures in ray parenchyma cells (black arrow), (RLS). -- d. Tapering end of a ray tracheid
730 (white arrow), (RLS). – e. Spaces within ray body and cell with tapering end, (dissagregated
731 wood slide). – f. Detail of ray tracheid. -- Scale bar for a, b, d, e and f = 30 μm ; for c= 50 μm .

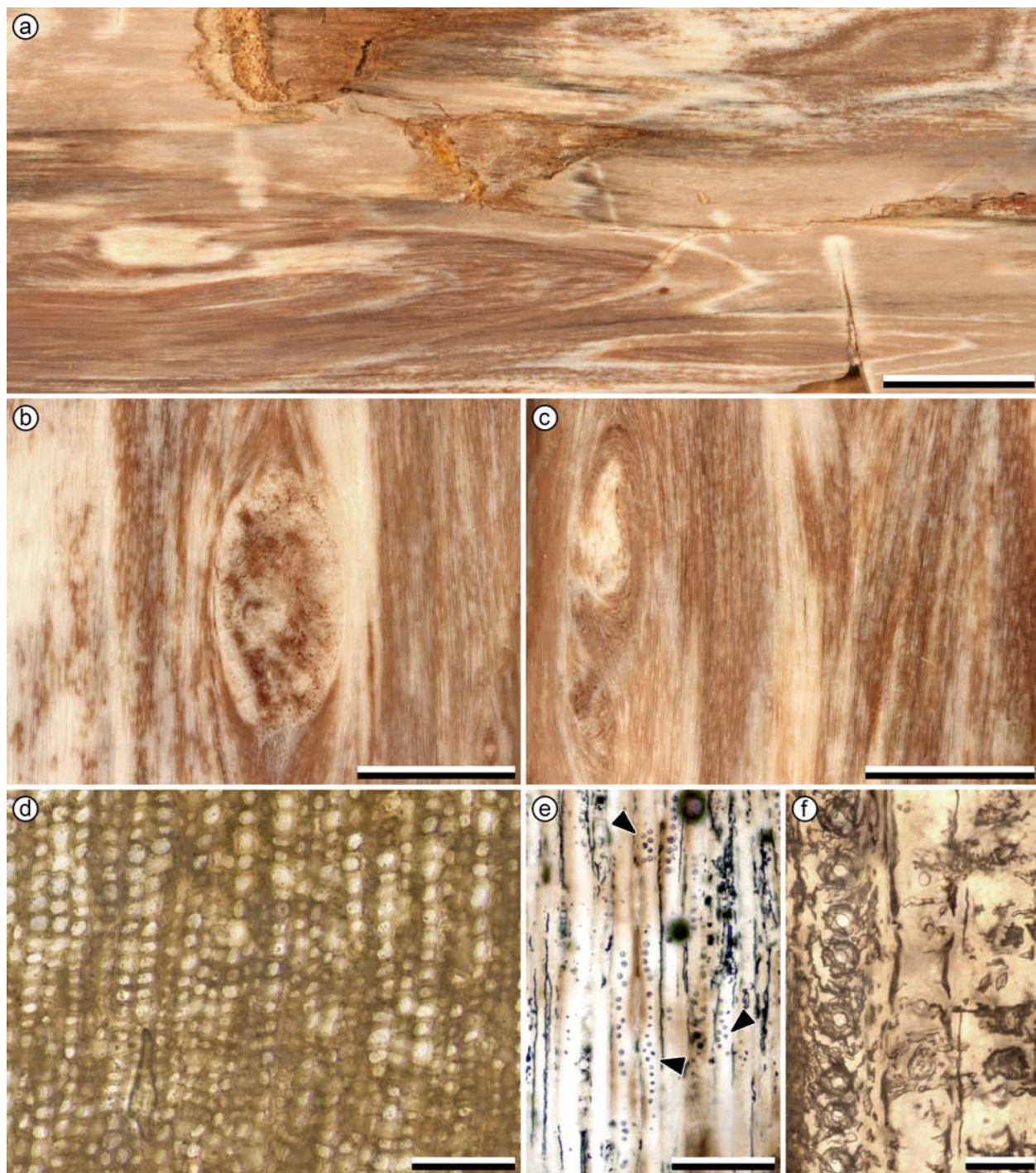
732 **Figure 8.** Extant Cupressaceae heterocellular rays. -- a; b. Rays of *Pilgerodendron uviferum*.
733 Space within the ray body (white arrow), ray cells with tapering ends (black arrow) -- c; d. Rays
734 of *Fitzroya cupressoides*. Spaces within the ray body (white arrow); Cells with tapering ends and
735 slightly pitted walls (black arrow). -- Scale bar for a = 30 μm ; for b and d = 60 μm ; for c = 75 μm .

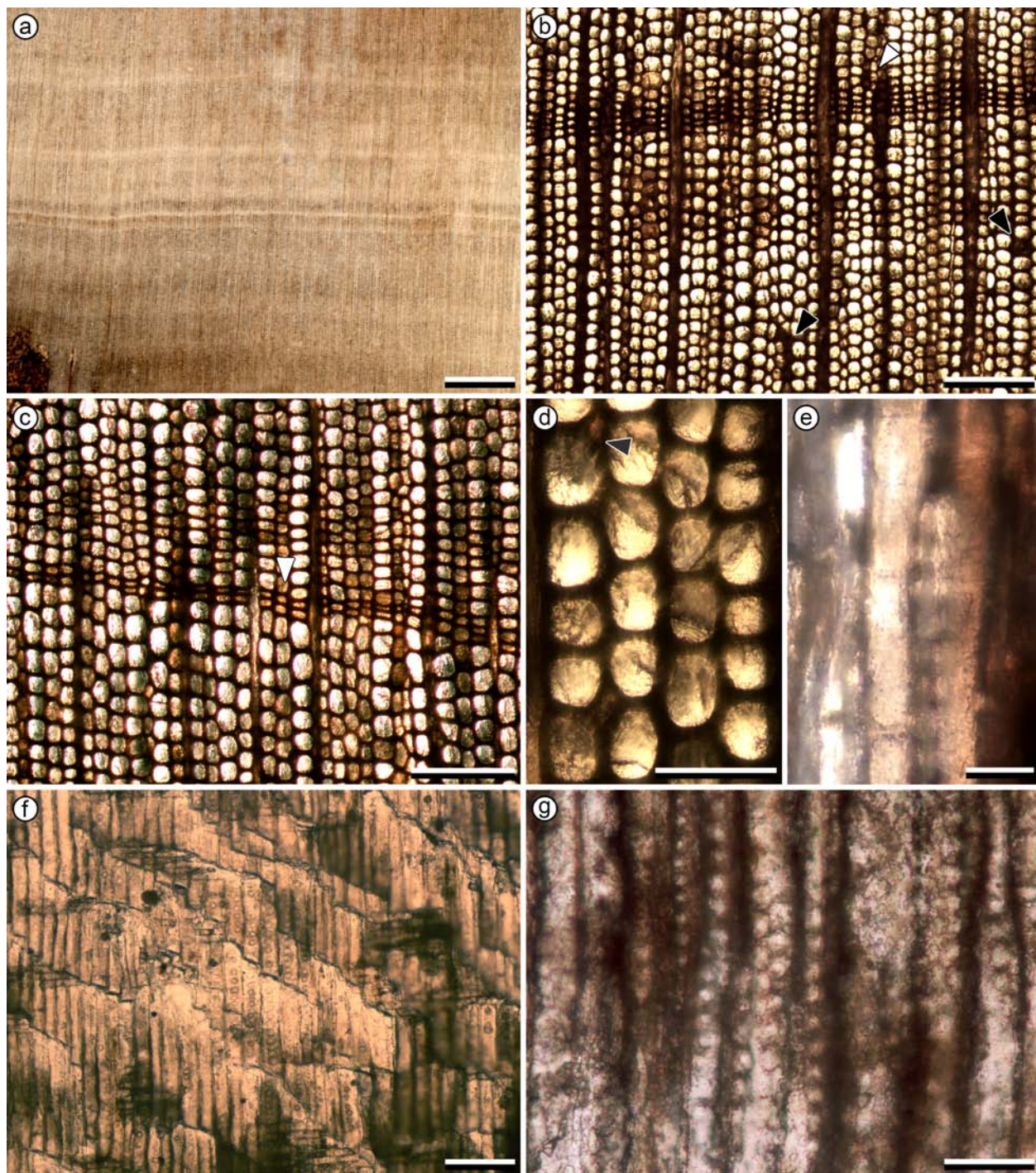
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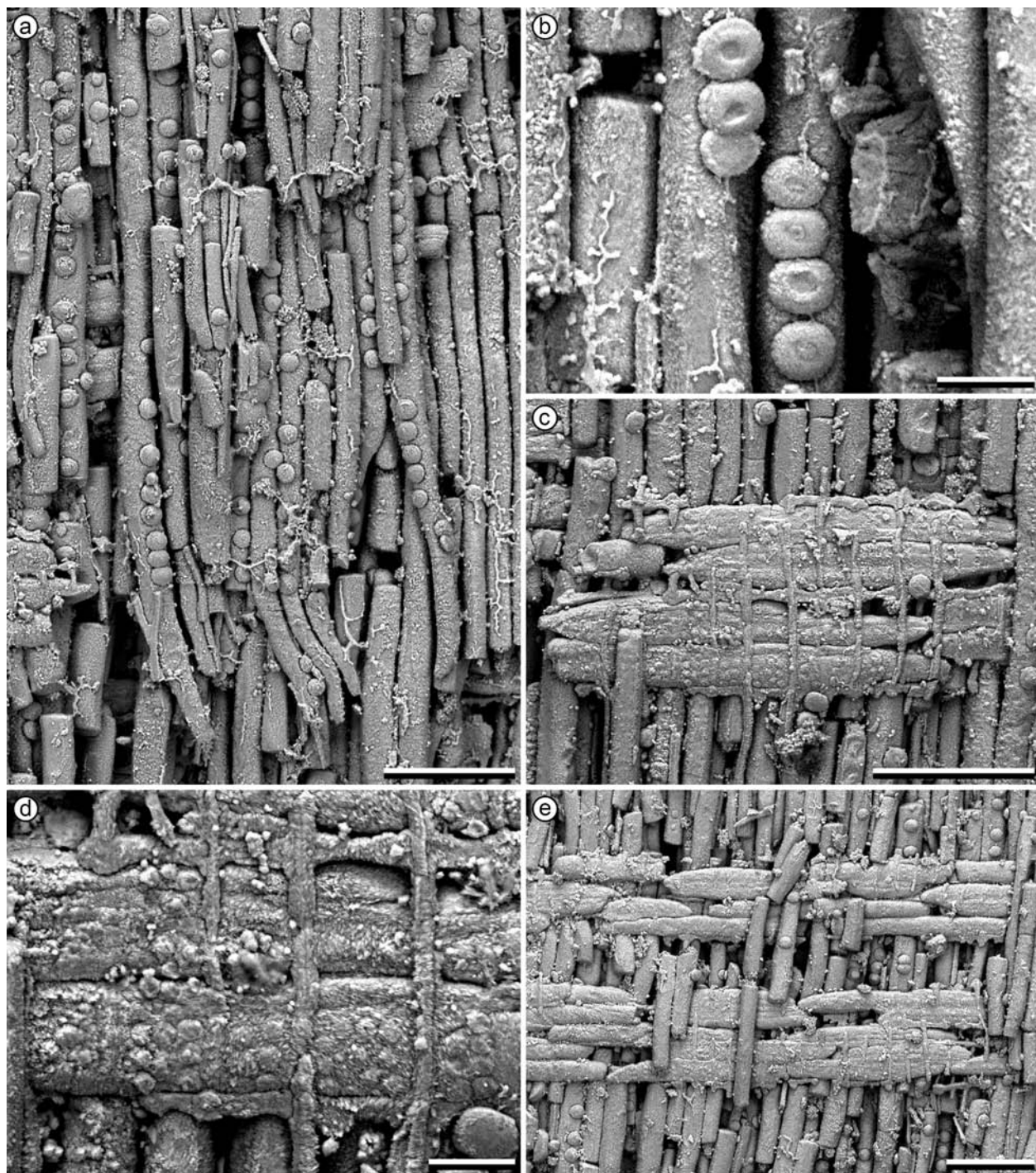
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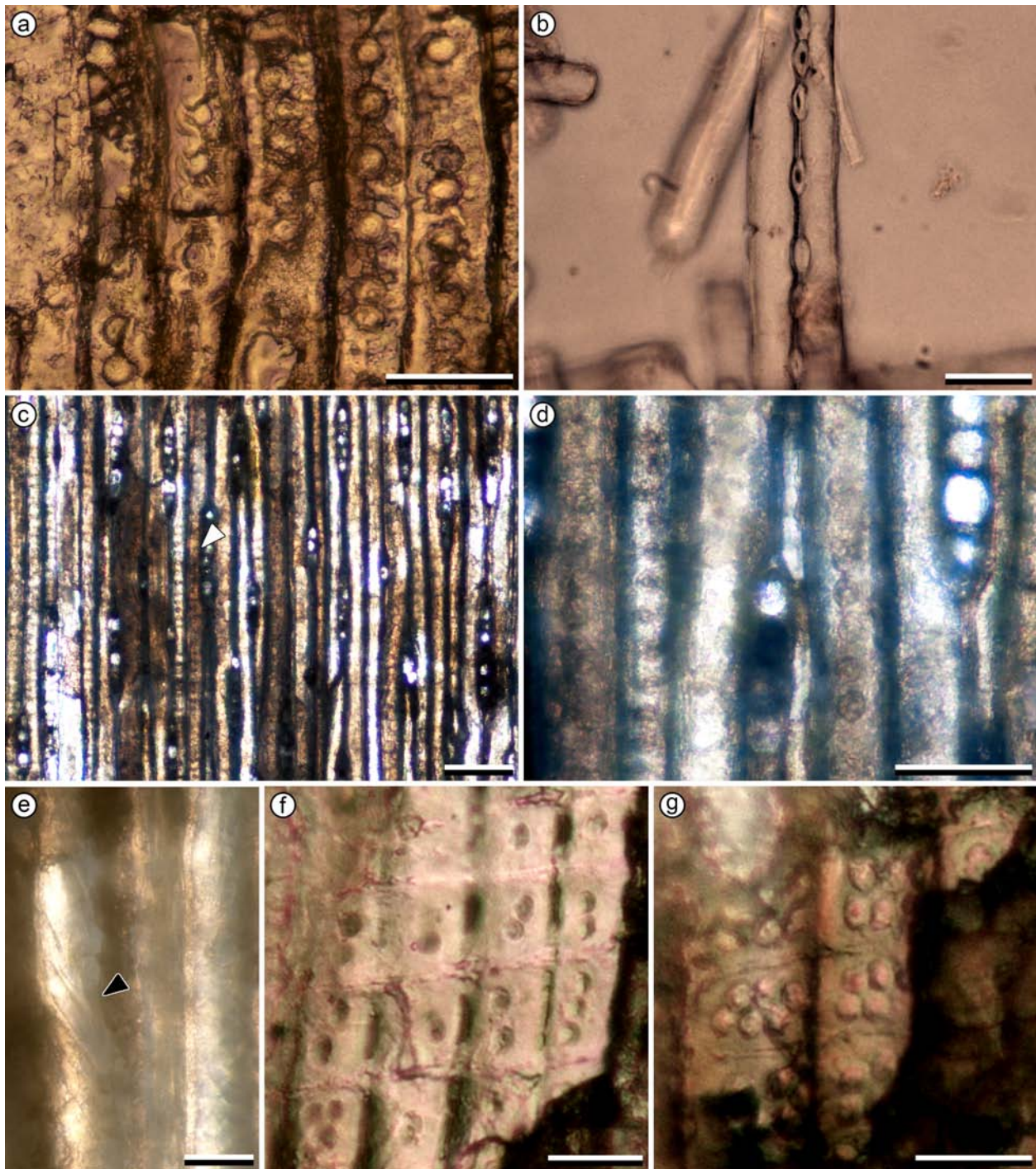
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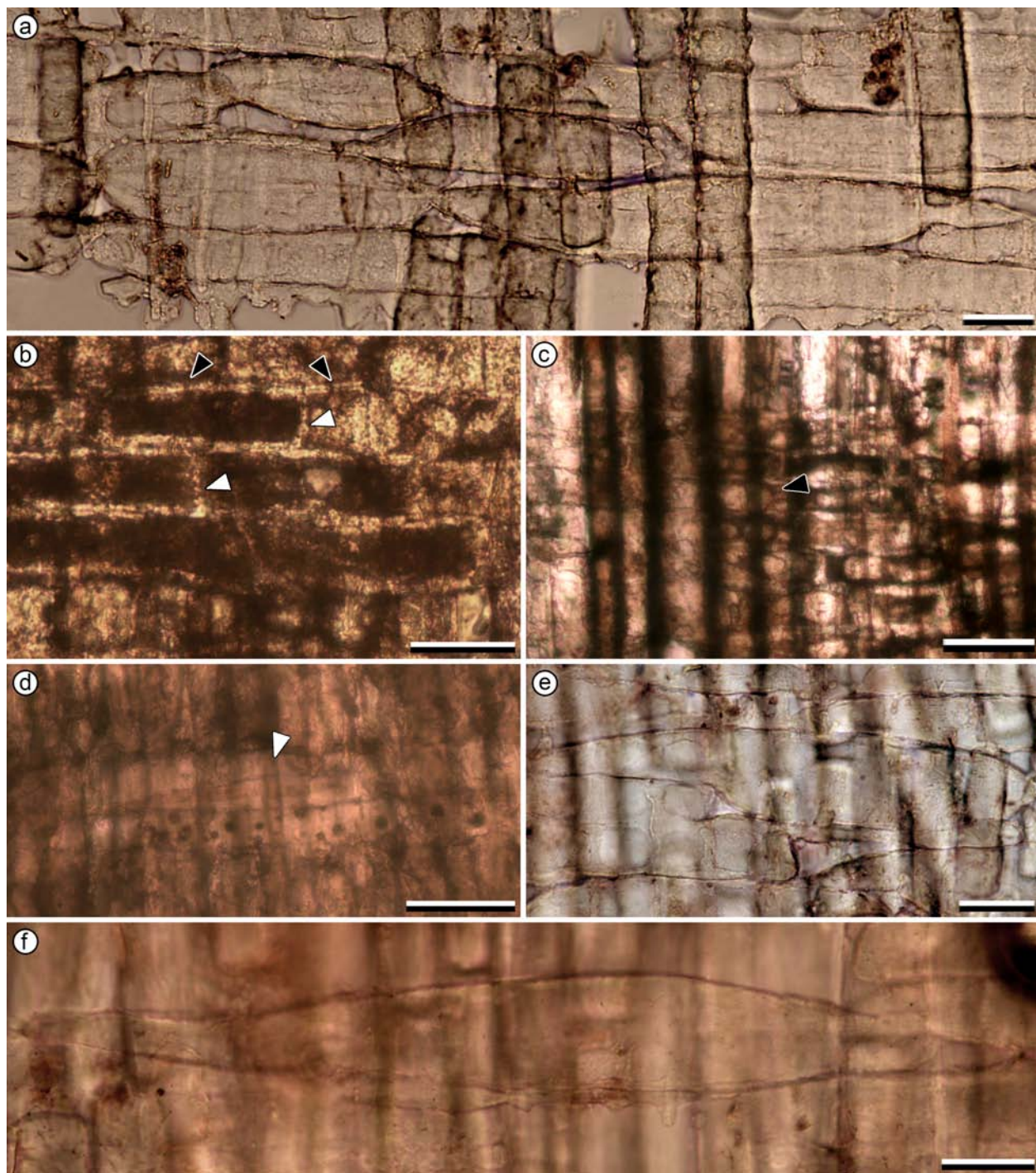


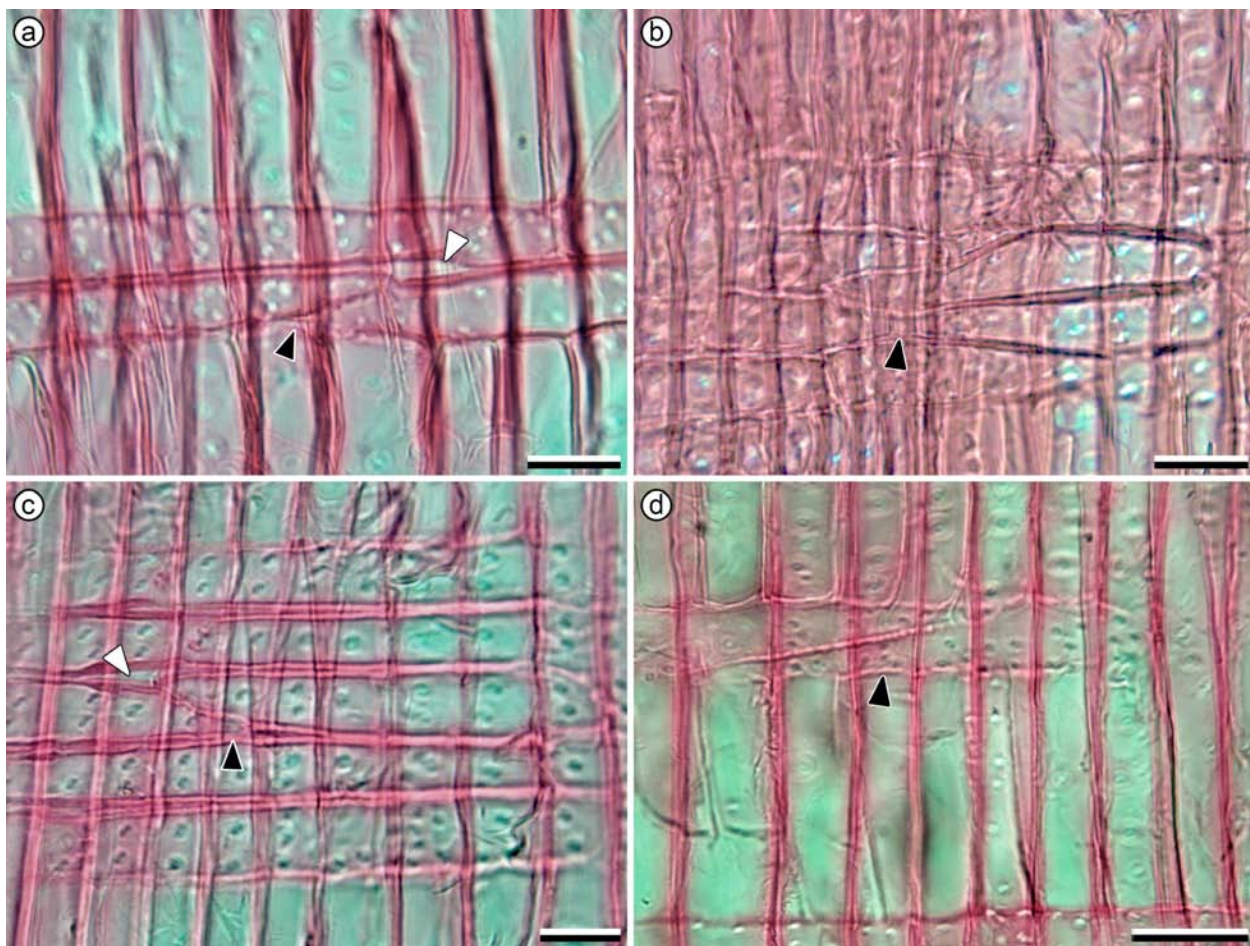




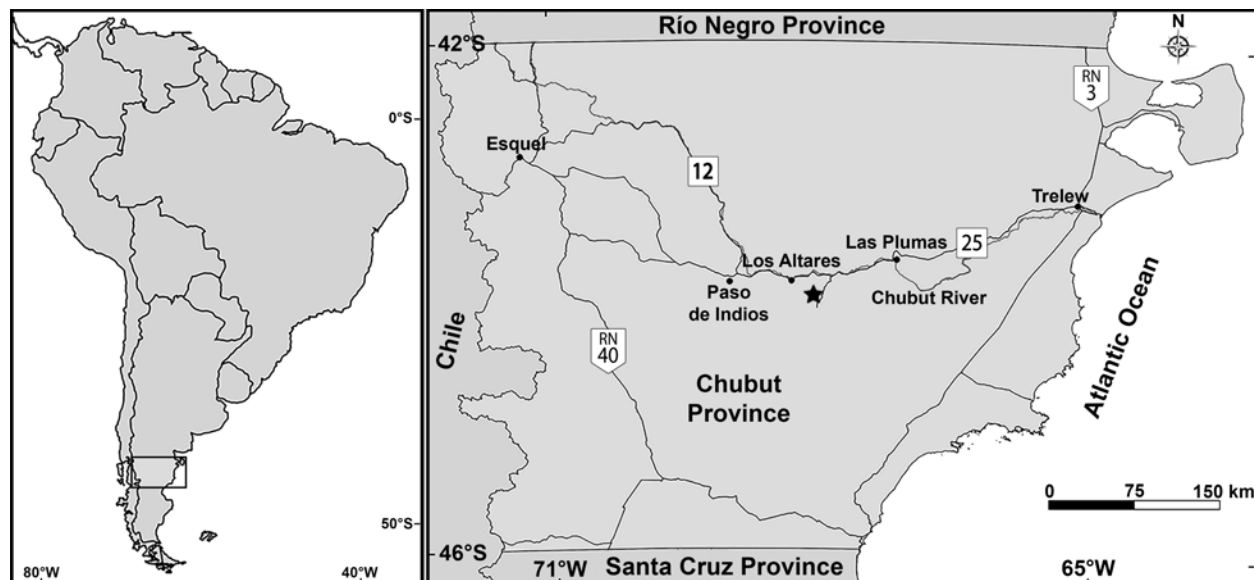








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	GD	GR	ATS	ATRP	CT	ATTP	AP	APW	APA	RW	RH	RPEW	RPHW	IN	RPR	CFPT	CFPN	RT
<i>Actinostrobus</i>	Australia	Well-defined	polygonal	Uniseriate (biseriate)	Absent or present	(present)	present	smooth	(Diffuse) tangentially zonate (marginal)	uniseriate	1-15	smooth	unpitted	absent	Present	cupressoid	2 - 6 (8-10)	absent
<i>Athrotaxis</i>	Tasmania	Well-defined	polygonal	Uniseriate (biseriate)	Absent	present	present	smooth	(Diffuse) tangentially zonate (marginal)	Uniseriate partially biseriata	1-15	smooth or (nodular)	unpitted	absent	Present	cupressoid	1-2	absent
<i>Austrocedrus 11</i>	Argentina Chile	Well-defined	polygonal	Uniseriate (biseriate)	absent	present	present	smooth	diffuse	Uniseriate and partially biseriata	1-15	smooth	unpitted	present	present	cupressoid	1 - 4 (6)	absent
<i>Callitris</i>	Australia, Tasmania New Caledonia	Slightly defined	Circular or polygonal	Uniseriate (biseriate)	Present	Absent (present)	present	Smooth or nodular	(Diffuse) tangentially zonate (marginal)	Uniseriate and partially biseriata	1-15 (30)	smooth	Pitted or unpitted	absent	present	cupressoid	1 - 4	absent
<i>Calocedrus</i>	USA, China, Thailand Birmanian Laos Vietnam	Well or slightly defined	polygonal	Uniseriate (biseriate)	absent	present	present	nodular	Diffuse, tangentially zonate or marginal	Uniseriate and partially biseriata	1 - 15	Smooth or nodular	Pitted or unpitted	present	absent	cupressoid	1 - 5 (7)	absent
<i>Chamaecyparis</i>	USA, Japan Taiwan	Well defined	Circular or polygonal	Uniseriate	absent	Absent or present	Absent or present	Smooth or nodular	Diffuse or tangentially zonate	Uniseriate and partially biseriata	1 - 15	Smooth or nodular	Pitted or unpitted	Absent or present	absent	Cupressoid or taxodioid	1 - 4 (8)	Absent or present
<i>Cryptomeria</i>	Japan	Well defined	polygonal	Uniseriate (biseriate)	absent	present	present	Smooth or nodular	Diffuse, tangentially zonate or (marginal)	uniseriate	1-30	smooth	unpitted	present	present	Cupressoid and taxodioid	1-2	absent
<i>Cunninghamia</i>	China Taiwan Vietnam	Well defined	polygonal	Uniseriate (biseriate)	absent	present	present	Smooth (nodular)	diffuse	Uniseriate and partially biseriata	1-15	Smooth (nodular)	unpitted	absent	absent	taxodioid	1-4	absent
<i>Cupressus</i>	temperate regions of Northern hemisphere	Well or slightly defined	Circular or polygonal	Uniseriate	absent	present	Scarce or present	Smooth or nodular	Diffuse, tangentially zonate or marginal	Uniseriate and partially biseriata	1 - 15 (55)	Smooth or nodular	Pitted or unpitted	present	present	cupressoid	1 - 4 (8)	Absent or present
<i>Diselma</i>	Tasmania	Well defined	polygonal	Uniseriate	absent	present	present	nodular	Diffuse or tangentially zonate	Uniseriate	1 - 10 (12)	Smooth or nodular	unpitted	present	absent	cupressoid	1 - 2 (3 - 5)	absent
<i>Fitzroya</i>	Argentina Chile	Well defined	polygonal	uniseriate	absent	present	present	(Smooth) or nodular	Diffuse or tangentially zonate	Uniseriate	1- 15	Smooth or nodular	Pitted or unpitted	present	present	cupressoid	1 - 4 (8)	Absent or (present*)
<i>Fokienia</i>	China, Laos Vietnam	Well defined	polygonal	Uniseriate (biseriate)	absent	present	present	Smooth or nodular	(Diffuse) tangentially zonate or (marginal)	Uniseriate and partially biseriata	1- 15 (24)	smooth	(Pitted) or unpitted	present	absent	cupressoid	1 - 3 (6)	absent
<i>Glyptostrobus</i>	China, Vietnam	Well defined	polygonal	Uniseriate (biseriate)	absent	present	present	nodular	Diffuse, tangentially zonate or (marginal)	Uniseriate	1-20 (30)	smooth	unpitted	present	present	Cupressoid and taxodioid	1 - 4	absent
<i>Juniperus</i>	Northern hemisphere	Well defined	Circular or polygonal	Uniseriate (biseriate)	absent	present	Scarce or present	Smooth or nodular	Diffuse, tangentially zonate or marginal	Uniseriate and partially biseriata	1 - 14 (24)	Smooth or nodular	Pitted or unpitted	present	present	Cupressoid	1 - 4 (6)	absent
<i>Libocedrus</i>	New Zealand New Caledonia	Well or slightly defined	polygonal	Uniseriate (biseriate)	absent	Absent (present)	present	Smooth or nodular	Diffuse, tangentially zonate or marginal	uniseriate	1-15	Smooth	unpitted	absent	present	cupressoid	1 - 4 (11)	absent
<i>Metasequoia</i>	China	Well defined	polygonal	Uniseriate (biseriate)	absent	present	present	Smooth or nodular	Diffuse	Uniseriate and partially biseriata	1-15 (30)	Smooth	(Pitted) or unpitted	present	absent	cupressoid and taxodioid	1 - 2	absent
<i>Microbiota</i>	Siberia	Well defined	polygonal	Uniseriate	absent	present	present	Smooth or nodular	tangentially zonate or (marginal)	Uniseriate	1-15	Smooth	(Pitted) or unpitted	absent	absent	cupressoid	1 - 2	absent
<i>Neocallitropsis</i>	New Caledonia	Slightly defined	Circular or polygonal	Uniseriate Biseriate (multiseriate**)	absent	present	Absent or scarce	smooth	diffuse	uniseriate	1- 15	smooth	unpitted	absent	absent	cupressoid	1 - 2 (4 - 6)	absent
<i>Papuacedrus</i>	New Guinea Maluku Islands	Slightly defined	polygonal	Uniseriate (Biseriate)	absent	present	present	Smooth	diffuse	Uniseriate and partially biseriata	1 - 15	smooth	unpitted	present	present	cupressoid	1-2 (4 - 6)	absent

<i>Pilgerodendron</i>	Argentina Chile	Well defined	polygonal	Uniseriate	absent	present	present	Smooth or nodular	Diffuse or tangentially zonate	Uniseriate and partially biseriate	1- 10 (15)	Smooth	unpitted	present	absent	cupressoid	1 - 3 (4 - 6)	absent
<i>Platycladus</i>	China Manchuria	Well defined	polygonal	Uniseriate (Biseriate)	absent	present	present	nodular	tangentially zonate or marginal	Uniseriate	1- 15	smooth	unpitted	present	absent	cupressoid	1 - 4	absent
<i>Sequoia</i>	USA	Well defined	polygonal	Uniseriate Biseriate	absent	present	present	Smooth or nodular	Diffuse (marginal)	Uniseriate and partially biseriate	1- 15 (30)	Smooth or (nodular)	(Pitted) or unpitted	present	absent	Cupressoid and taxodioid	1 - 2	Absent or present***
<i>Sequoiadendron</i>	USA	Well defined	polygonal	Uniseriate (Biseriate)	absent	present	present	Smooth or nodular	Diffuse or marginal	Uniseriate and partially biseriate	1- 30	smooth	Pitted or unpitted	absent	present	Cupressoid and (taxodioid)	1 - 2	absent
<i>Taiwania</i>	Taiwan China	Well defined	polygonal	Uniseriate Biseriate	absent	present	Scarce or present	Smooth	Diffuse or tangentially zonate	Uniseriate and partially biseriate	1- 20	smooth	unpitted	present	present	Cupressoid	1 - 2	absent
<i>Taxodium</i>	USA, Mexico	Well defined	polygonal	Uniseriate Biseriate	absent	present	present	(Smooth) nodular	Diffuse or tangentially zonate	Uniseriate and partially biseriate	1- 30	smooth	(Pitted) unpitted	absent	present	Cupressoid and taxodioid	1 - 4	absent
<i>Tetraclinis</i>	Spain Morocco Algeria Tunisia	Well defined	polygonal	Uniseriate (Biseriate)	absent	present	present	smooth	Diffuse, tangentially zonate or marginal	Uniseriate and partially biseriate	1- 17	smooth	unpitted	absent	present	Cupressoid	1 - 4	absent
<i>Thuja</i>	USA, Canada China, Corea Japan	Well defined	polygonal	Uniseriate (biseriate)	absent	present	Absent (present)	Smooth or nodular	Diffuse or marginal	Uniseriate	1- 18	smooth	Pitted or unpitted	present	present	Cupressoid and taxodioid	1 - 4 (8)	absent
<i>Thujopsis</i>	Japan	Well defined	polygonal	Uniseriate (biseriate)	absent	present	present	nodular	Diffuse, tangentially zonate or marginal	Uniseriate and partially biseriate	1 - 15 (24)	smooth	(pitted) or unpitted	absent	present	cupressoid	1 - 2 (4)	Absent or present**
<i>Widdringtonia</i>	Malawi, Mozambique, Zimbabwe South Africa	Slightly defined	polygonal	uniseriate (biseriate)	absent	present	present	smooth	Diffuse, tangentially zonate or marginal	Uniseriate and partially biseriate	1- 17 (35)	smooth	unpitted	Absent	absent	cupressoid	1 - 2 (3 - 4)	absent
<i>Austrocupressinoxylon</i>	Argentina	Well defined	Circular or polygonal	Uniseriate (biseriate)	absent	present	present	smooth	diffuse	Uniseriate	1-11	Smooth or nodular	Pitted or unpitted	Present	present	Cupressoid and araucarioid	1-10	present

	TTS	RTP	TTP	AP	CF	RPH W	RPEW	RT	RC	DC	Age	Area
<i>Agathoxylon</i> Hartig 1848	-	Araucarian	Absent / Present	Present	Araucarioid	-	-	Absent	Absent	-	Triassic, Jurassic, Cretaceous and "Tertiary"	Widespread
<i>Baieroxylon</i> Greguss 1961	-	Mixed	-	Present	Araucarioid	-	-	Absent	Absent	-	Permian, Triassic, Jurassic, Cretaceous	Europe, Asia, South America
<i>Brachyoxylon</i> Hollick et Jeffrey 1909	-	Mixed	Absent/ Present	Absent	Araucarioid	-	-	Absent	Present in traumatic wood	-	Permian, Triassic, Jurassic, Cretaceous	Widespread
<i>Callitrixylon</i> Privé & Boureau	Circular	Abietinean	Absent	Present	Cupressoid	Smooth or pitted	Smooth	Present	Absent	Callitroid thickenings	"Tertiary"	Europe
<i>Chamaecyparixylon</i> Chudajberdyev in Vakhrameev et al. 1958	Polygonal	Abietinean	Present	Present	Cupressoid	Smooth	Smooth	Absent	Absent	-	Cenozoic	Occidental Europe and ex URSS
<i>Cupressinoxylon</i> Göpper nom. cons. Bamford et al. 2002	Circular / Polygonal	Abietinean	Present in some species	Abundant	Cupressoid	Smooth	Smooth	Absent	Absent	-	Triassic, Jurassic, Cretaceous and Tertiary	Widespread
<i>Juniperoxylon</i> Houlbert in Lecointre emend Kräusel 1949	Variable	Abietinean	Present	Present	Cupressoid or taxodioid	Smooth or nodular	Smooth, sometimes with indentures	Present	Absent	<i>juniperoid pitting</i>	Triassic?, Cretaceous and Tertiary	Europe
<i>Libocedroxylon</i> Greguss 1967	Polygonal	Abietinean	Present	Abundant	Cupressoid or taxodioid	Nodular	Nodular	Absent	Absent	-	"Tertiary"	Occidental Europe
<i>Podocarpoxyton</i> Gothan 1906	-	Abietinean	-	Present	Podocarpooid	Smooth	Smooth	Absent	Absent	-	Permian, Triassic, Jurassic, Cretaceous, Cenozoic	Widespread

<i>Protochamaecyparixylon</i> Giraud in Giraud & Hankel 1985	Polygonal	Mixed	Absent	Scarce	Cupressoid	Smooth	Smooth	Absent	Present in traumatic wood	-	Triassic, Jurassic	Chile, Tanzania
<i>Protojuniperoxylon</i> Eckhold 1921	Polygonal	Mixed	Absent	Scarce	Cupressoid	Nodular	Nodular, with indentures	Present	Absent	<i>juniperoid pitting</i>	Triassic, Cretaceous	South America, Europe
<i>Taxaceoxylon</i> Krausel et Jain 1964	-	Abietinean	-	Absent	Cupressoid	-	-	-	Absent	spiral thickenings present in tracheids	Triassic, Jurassic, Cretaceous, Cenozoic	North America, India, Japan, Argentina
<i>Tetraclinoxylon</i> Grambast 1951	Circular	Abietinean	Absent	Present	Cupressoid	Smooth	Smooth	Absent?	Absent?	-	"Tertiary"	Europe
<i>Thujoxylon</i> Unger in Endlicher 1842	Polygonal	Abietinean	Sometimes present	Absent or scarce	Cupressoid sometimes taxodioid	Smooth	Smooth with indentures	Absent	Present or absent	-	Cenozoic	North America, Europe
<i>Widdringtonoxylon</i> Greguss 1967	Polygonal	Abietinean	Absent	Present	Cupressoid	Smooth	Smooth	Absent	Absent	-	"Tertiary"	Europe
<i>Austrocupressinoxylon</i> gen. nov.	Circular / Polygonal	Abietinean	Present	Present	Cupressoid and araucarioid	Smooth or slightly nodular	Smooth with indentures	Present	Absent	-	Cretaceous	South America