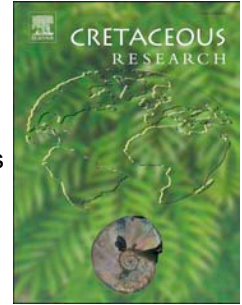# Accepted Manuscript

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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1   **A new cupressaceous wood from the Lower Cretaceous of Central Patagonia**

2   **reveals possible clonal growth habit**

3   Cristina I. Nunes[1,*], Josefina Bodnar[2], Ignacio H. Escapa[1], María A. Gandolfo[3], N. Rubén Cúneo[1]

4   [1]CONICET, Museo Paleontológico Egidio Feruglio, Av. Fontana 140, Trelew CP 9100, Chubut,

5   Argentina

6   [2]Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata,

7   Paseo del Bosque s/n, B1900FWA, La Plata, Buenos Aires, Argentina

8   [3]LH Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell

9   University, 410 Mann Library Building, Ithaca, NY 14853, U.S.A.

10   *Corresponding author; e-mail: cnunes@mef.org.ar

11   **ABSTRACT**

12   A new genus and species, *Austrocupressinoxylon barcinense*, based on remains of

13   cupressaceous wood is described for the Lower Cretaceous of central Patagonia, Argentina. The

14   studied specimens are silicified fragments of picnoxylic and homoxylic wood that exhibit a

15   combination of characters not previously reported, therefore a new genus is erected. The

16   characters are: 1- growth ring boundaries distinct, 2- transition from earlywood to latewood

17   gradual, 3- axial parenchyma diffuse,4- radial tracheid pitting predominantly abietinean,5-

18   cross-field pitting cupressoid, arranged in both cupressoid and araucarioid patterns, 6- rays

19   uniseriate heterocellular, 7- end and horizontal walls of ray parenchyma cells smooth or slightly

20   nodular, and 8- ray tracheids with smooth walls. The cross-field pitting patterns and the

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

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, Taiwanioideae, 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

3

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

4

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 Migdley, 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

2. Geological Setting

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

The Cerro Barcino Formation of the Chubut Group is composed of fluvial volcaniclastic sediments and comprises four members, from bottom to top: Puesto La Paloma, Cerro Castaño, Las Plumas and Puesto Manuel Arce (Figari et al., 2015; Rauhut et al., 2003; Umazano et al., 2017). The Cerro Castaño Member comprises sheet-to ribbon-channel sandstone bodies intercalated within tuffaceous and fine-grained sediments (Umazano et al., 2017). U-Pb dating of tuffs collected from an ash layer at the titanosaur excavation, a few meters below the plant horizon, indicates an age of ca. 101. 6 ± 0.11 Ma (late Albian, Early Cretaceous) for the Cerro Castaño Member (Carballido et al., 2017).

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

8

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 Phillipe and Bamford (2008) were followed. In

160 order to stimate 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 x $D^{0.430}$, 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.* Picnoxylic 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

12

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

14

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

15

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 *Podocarpoxylon*

292 (Podocarpaceae; see Pujana and Ruiz, 2017) and *Taxaceoxylon* (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 *Agathoxylon*,

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; Phillipe 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.* (Greguss, 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; Greguss, 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,

17

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. ducloixiana, 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). Althoug 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.

18

347

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 Antartic 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 *Carlquistoyxlon 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

Acknowledgments

427

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670

671   **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), Phillipe and Bamford (2008), Brea et al. (2009),

688   Pujana and Ruiz (2017).

689

690

691   **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 showin 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 ditinct, (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 possitions, in tracheid pits, (dissagregated 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.

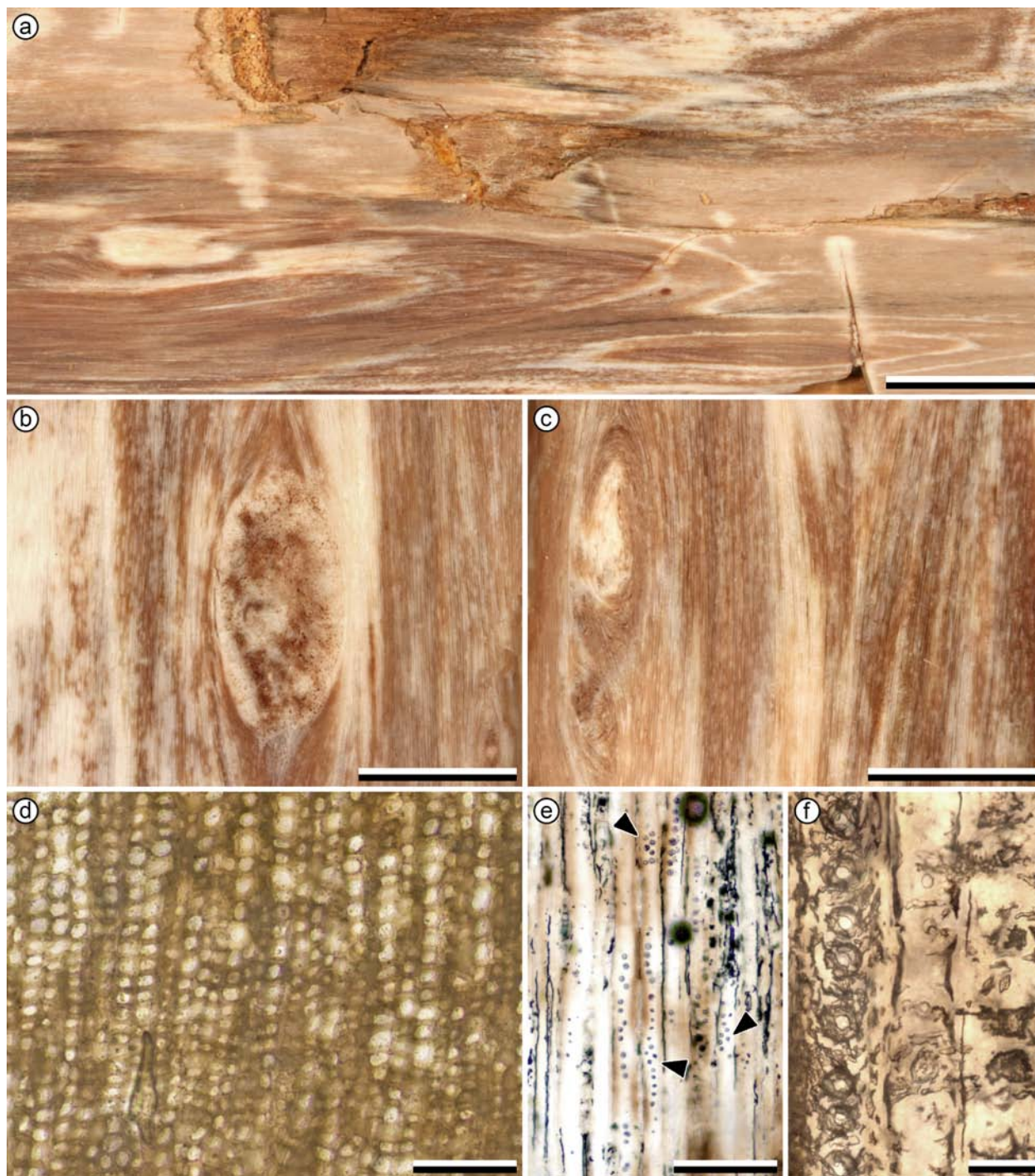732 **Figure 8.** Extant Cupressaceae heterocellular rays. -- a; b. Rays of *Pilgerodendron uviferum*.

733 Space whithin 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

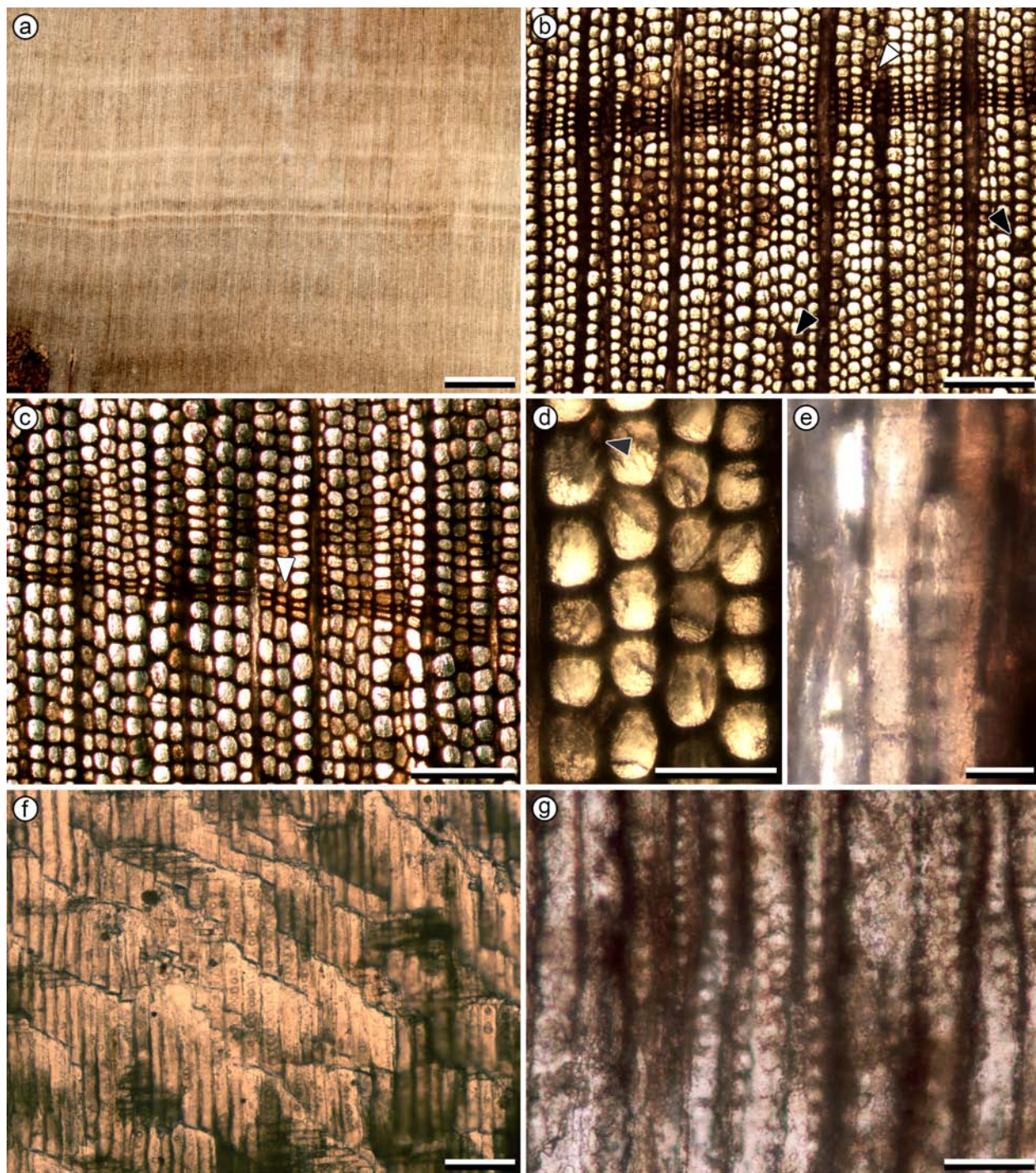735 slightly pitted walls (black arrow). -- Scale bar for a = 30 μm; for b and d = 60 μm; for c = 75 μm.
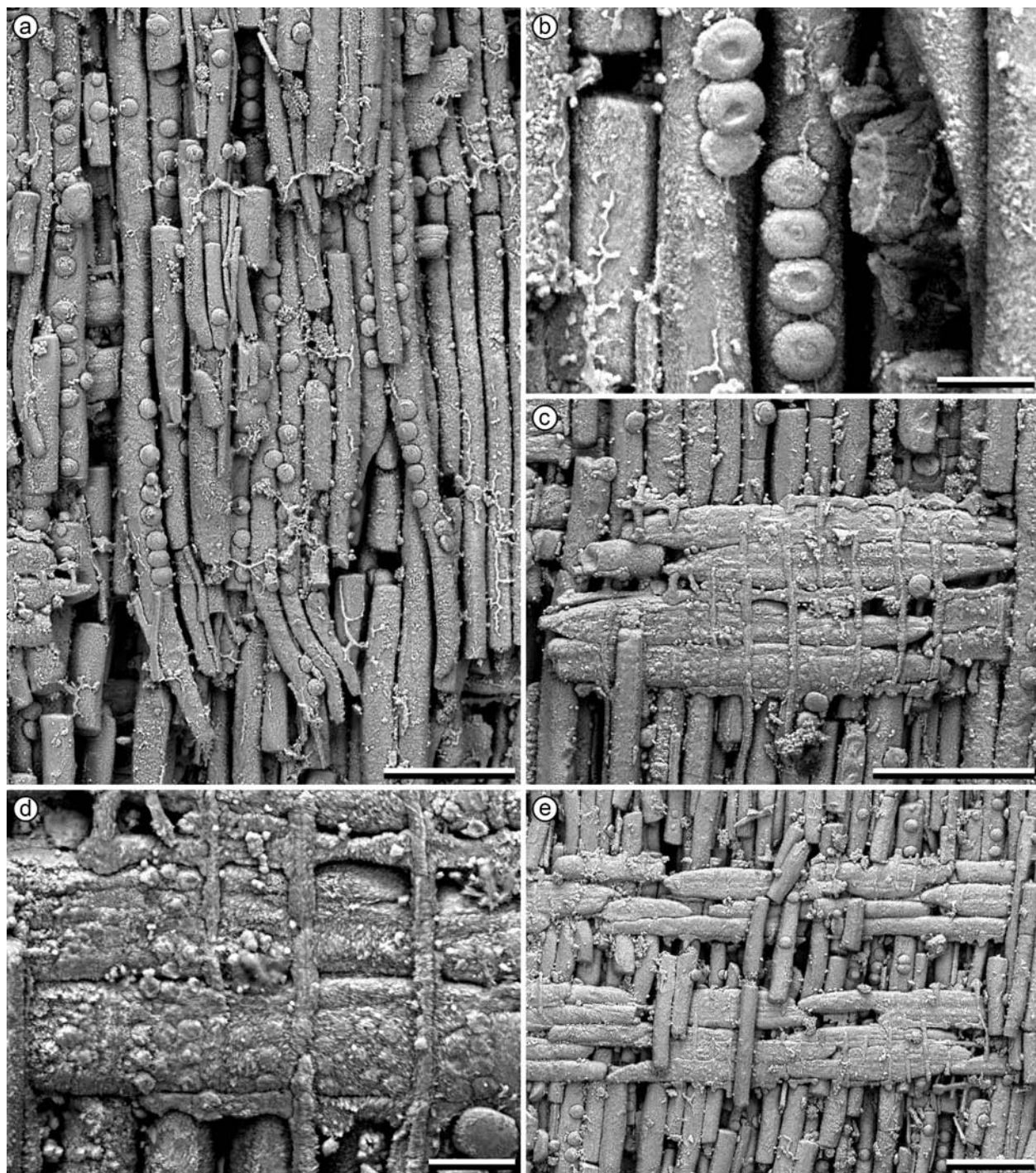
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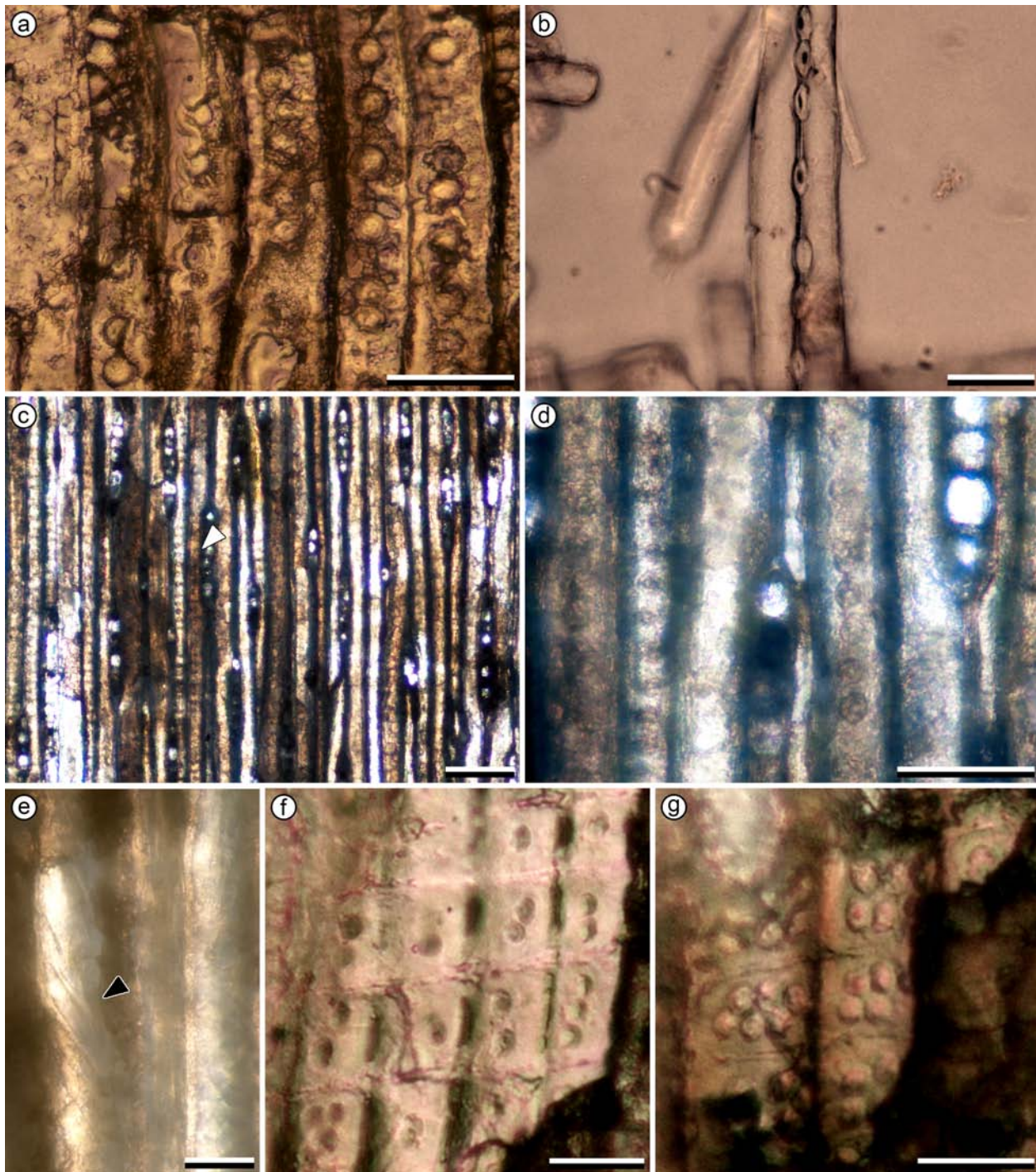
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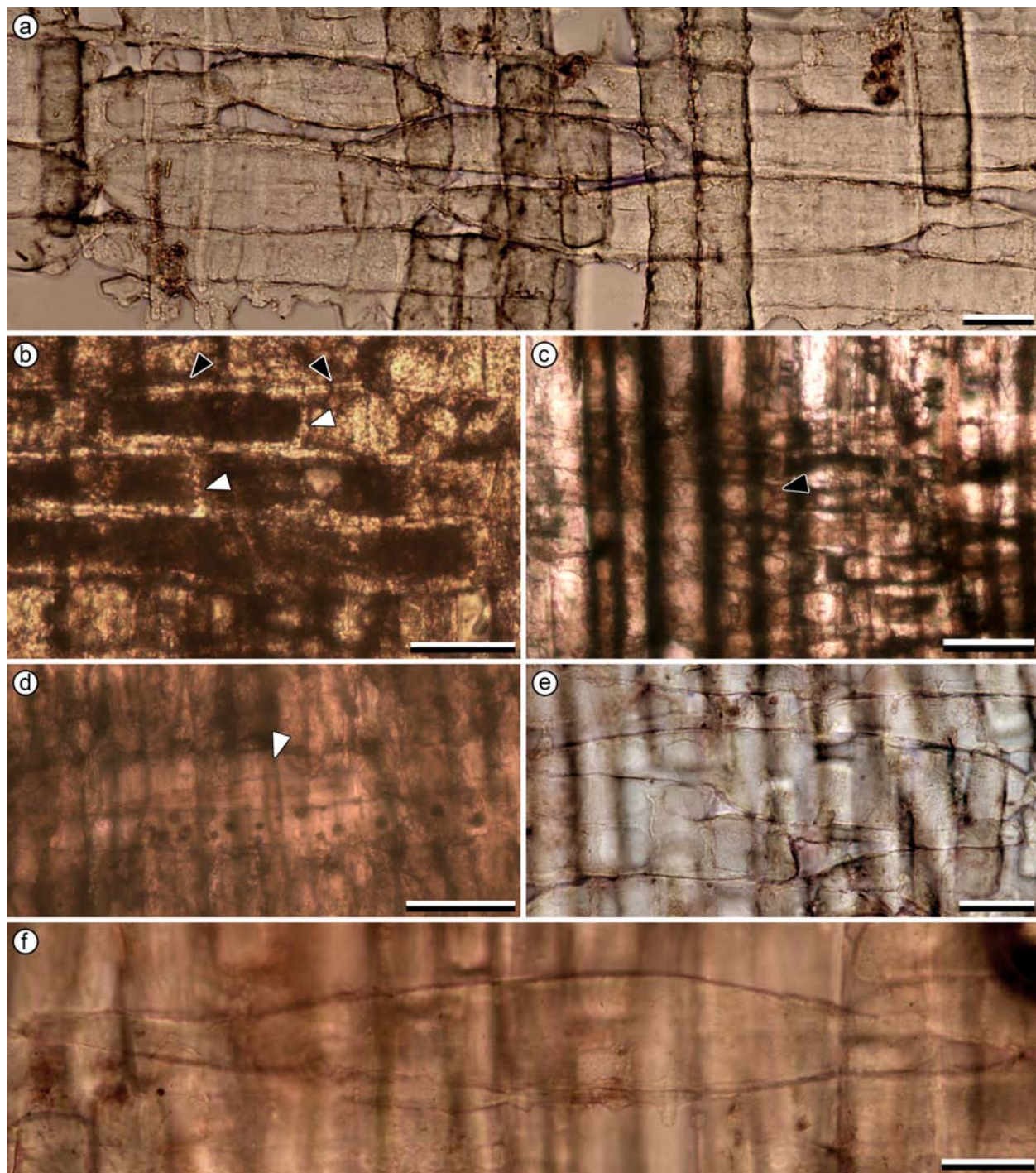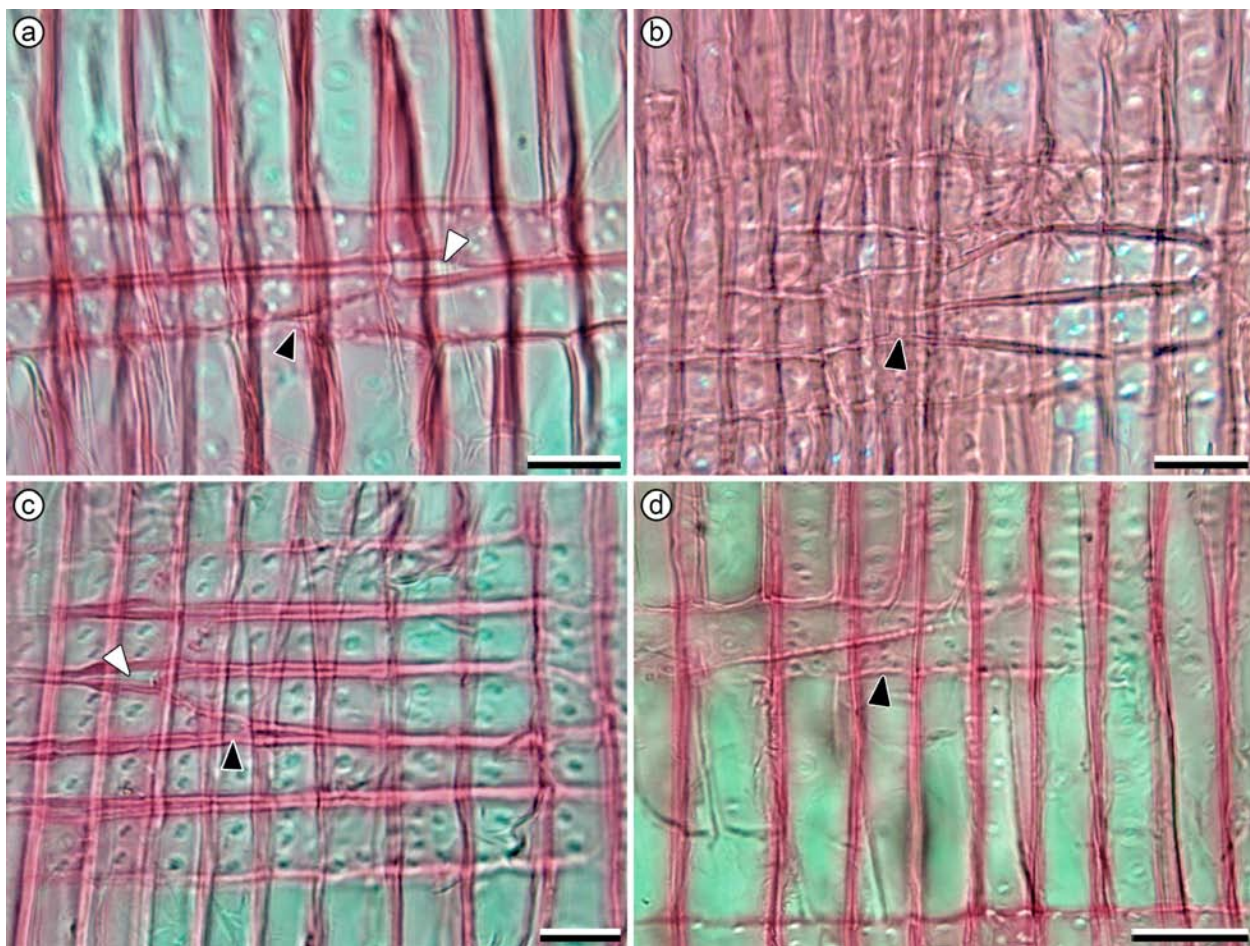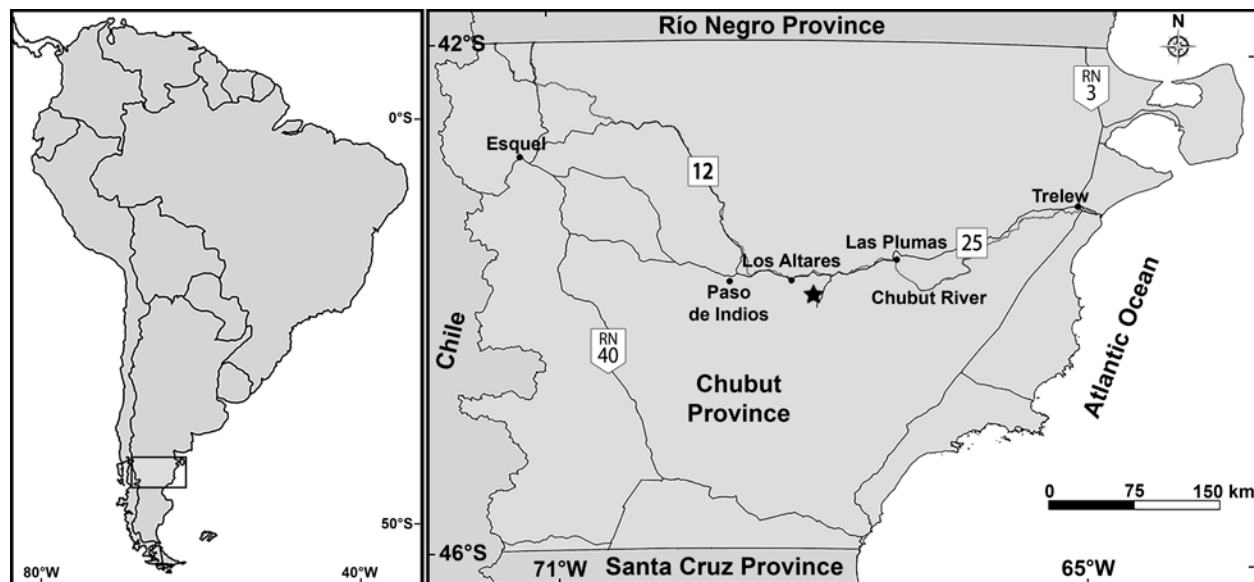
	GD	GR	ATS	ATRP	CT	ATTP	AP	APW	APA	RW	RH	RPEW	RPHW	IN	RPR	CFPT	CFPN	RT
Actinostrobus	Australia	**Well-defined**	polygonal	**Uniseriate (biseriate)**	Absent or present	(present)	present	smooth	(Diffuse) tangentially zonate (marginal)	uniseriate	1-15	smooth	unpitted	absent	Present	cupressoid	2 - 6 (8-10)	absent
Athrotaxis	Tasmania	**Well-defined**	polygonal	**Uniseriate (biseriate)**	Absent	present	present	smooth	(Diffuse) tangentially zonate (marginal)	Uniseriate or partially biseriate	1-15	smooth or (nodular)	unpitted	absent	Present	cupressoid	1-2	absent
Austrocedrus 11	Argentina Chile	**Well-defined**	polygonal	**Uniseriate (biseriate)**	absent	present	present	smooth	diffuse	Uniseriate and partially biseriate	1-15	smooth	unpitted	present	present	cupressoid	1 - 4 (6)	absent
Callitris	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 biseriate	1–15 (30)	smooth	Pitted or unpitted	absent	present	cupressoid	1 - 4	absent
Calocedrus	USA, China, Thailand Birmania Laos Vietnam	Well or slightly defined	polygonal	**Uniseriate (biseriate)**	absent	present	present	nodular	Diffuse, tangentially zonate or marginal	Uniseriate and partially biseriate	1 – 15	Smooth or nodular	Pitted or unpitted	present	absent	cupressoid	1 - 5 (7)	absent
Chamaecyparis	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 biseriate	1 - 15	Smooth or nodular	Pitted or unpitted	Absent or present	absent	Cupressoid or taxodioid	1 – 4 (8)	Absent or present
Cryptomeria	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
Cunninghamia	China Taiwan Vietnam	**Well defined**	polygonal	**Uniseriate (biseriate)**	absent	present	present	Smooth (nodular)	diffuse	Uniseriate and partially biseriate	1-15	Smooth (nodular)	unpitted	absent	absent	taxodioid	1-4	absent
Cupressus	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 biseriate	1 - 15 (55)	Smooth or nodular	Pitted or unpitted	present	present	cupressoid	1 - 4 (8)	Absent or present
Diselma	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
Fitzroya	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*)
Fokienia	China, Laos Vietnam	**Well defined**	polygonal	**Uniseriate (biseriate)**	absent	present	present	Smooth or nodular	(Diffuse) tangentially zonate or (marginal)	Uniseriate and partially biseriate	1- 15 (24)	smooth	(Pitted) or unpitted	present	absent	cupressoid	1 - 3 (6)	absent
Glyptostrobus	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
Juniperus	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 biseriate	1 – 14 (24)	Smooth or nodular	Pitted or unpitted	present	present	Cupressoid	1 - 4 (6)	absent
Libocedrus	New Zeland 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
Metasequoia	China	**Well defined**	polygonal	**Uniseriate (biseriate)**	absent	present	present	Smooth or nodular	Diffuse	Uniseriate and partially biseriate	1-15 (30)	Smooth	(Pitted) or unpitted	present	absent	cupressoid and taxodioid	1 - 2	absent
Microbiota	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
Neocallitropsis	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
Papuacedrus	New Guinea Maluku Islands	Slightly defined	polygonal	**Uniseriate (Biseriate)**	absent	present	present	Smooth	diffuse	Uniseriate and partially biseriate	1 –15	smooth	unpitted	present	present	cupressoid	1-2 (4 - 6)	absent

Genus	Distribution																	
Pilgerodendron	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
Platycladus	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
Sequoia	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***
Sequoiadendron	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
Taiwania	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
Taxodium	USA, Mexico	**Well defined**	polygonal	Uniseriate Biseriate	absent	present	present	(Smooth) nodular	Diffuse or tangentially zonate	Uniseriate and partially biseriate	1– 30	smooth	(Pitted)r unpitted	absent	present	Cupressoid and taxodioid	1 - 4	absent
Tetraclinis	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
Thuja	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
Thujopsis	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 unpited	absent	present	cupressoid	1 - 2 (4)	Absent or present**
Widdringtonia	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
Austrocupressinoxylon	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	RPHW	RPEW	RT	RC	DC	Age	Area
Agathoxylon Hartig 1848	-	Araucarian	Absent / Present	**Present**	Araucarioid	-	-	**Absent**	**Absent**	-	Triassic, Jurassic, Cretaceous and "Tertiary"	Widespread
Baieroxylon Greguss 1961	-	Mixed	-	**Present**	Araucarioid	-	-	**Absent**	**Absent**	-	Permian, Triassic, Jurassic, Cretaceous	Europe, Asia, South America
Brachyoxylon Hollick et Jeffrey 1909	-	Mixed	Absent/ Present	**Absent**	Araucarioid	-	-	**Absent**	**Present in traumatic wood**	-	Permian, Triassic, Jurassic, Cretaceous	Widespread
Callitrixylon Privé & Boureau	Circular	**Abietinean**	Absent	**Present**	Cupressoid	Smooth or pitted	Smooth	**Present**	**Absent**	Callitroid thickenings	"Tertiary"	Europe
Chamaecyparixylon Chudajberdyev *in* Vakhrameev et al. 1958	Polygonal	**Abietinean**	**Present**	**Present**	Cupressoid	Smooth	Smooth	Absent	**Absent**	**-**	Cenozoic	Occidental Europe and ex URSS
Cupressinoxylon 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
Juniperoxylon Houlbert *in* Lecointre *emend* Kräusel 1949	Variable	**Abietinean**	**Present**	**Present**	Cupressoid or taxodioid	**Smooth or nodular**	Smooth, sometimes with indetures	**Present**	**Absent**	*juniperoid pitting*	Triassic?, Cretaceous and Tertiary	Europe
Libocedroxylon Greguss 1967	Polygonal	**Abietinean**	**Present**	Abundant	Cupressoid or taxodioid	Nodular	Nodular	Absent	**Absent**	**-**	"Tertiary"	Occidental Europe
Podocarpoxylon Gothan 1906	-	**Abetinean**	-	Present	Podocarpoid	Smooth	Smooth	Absent	**Absent**	**-**	Permian, Triassic, Jurassic, Cretaceous, Cenozoic	Widespread

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