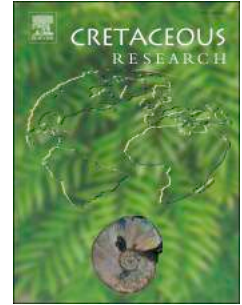# Journal Pre-proof

Brachyoxylon fossil woods with traumatic resin canals from the Upper Cretaceous Cerro Fortaleza Formation, southern Patagonia (Santa Cruz Province, Argentina)

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- Cosme F. Rombola prepared this manuscript, described and preliminary identified the fossil material, and wrote the first version.

- Carlos D. Greppi and Roberto R. Pujana supervised Cosme's work, discussed with him the wood anatomy, the taxonomy, and some aspects of the traumatic resin canals. In addition, Carlos D. Greppi made thin-sections of the fossil woods studied.

- Juan García Massini supervised Cosme's work and discussed with him all the aspects related to the traumatic resin canals.

- Eduardo S. Bellosi and Sergio A. Marenssi wrote the geological aspects and discussed some interpretations, particularly referred to the paleoclimatic inferences. In addition, Sergio A. Marenssi collected the samples in the field.

1 *Brachyoxylon* fossil woods with traumatic resin canals from the Upper Cretaceous Cerro

2 Fortaleza Formation, southern Patagonia (Santa Cruz Province, Argentina)

3

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16

ABSTRACT

18 Two silicified fossil woods from outcrops of the Cerro Fortaleza Formation (Campanian,

19 Upper Cretaceous) in Los Hornos Hill, Santa Cruz Province, Argentina are described. Based

20 on their anatomical characteristics, both specimens were assigned to a new species of the

21 fossil genus *Brachyoxylon* Hollick and Jeffrey, *B. patagonicum* sp. nov. They are

22 characterized by having distinct growth ring boundaries, absence of axial parenchyma,

23 uniseriate rays, mixed and uniseriate intertracheary radial pitting, and araucarioid cross-

24 fields with 1–8 circular half-bordered pits per cross-field. In turn, one specimen has three

25 rows of axial traumatic resin canals parallel to the growth rings were identified close to the

26 middle of the growth rings or close to the latewood. Approximately 45% of *Brachyoxylon*

27 species present traumatic resin canals, which suggests that they are a common feature of

28 this fossil genus. Alternatively, the specimen with the canals shows biological remains

29 (hyphae) and wood fungal degradation patterns, which may be thought as some of those of

30 possible organisms contributing to the formation of the resin canals. This record provides

31 fresh evidence attesting to the abundance and widespread distribution of Cheirolepidiaceae

32 in the Cretaceous of Patagonia.

33

34 *Keywords*. Wood anatomy; Conifer; Cheirolepidiaceae; South America; Austral Basin

35

36

37 **1. Introduction**

38

39   The Cretaceous was warmer and wetter compared to the Jurassic, probably because

40 the increase in atmospheric CO_2 and global changes in marine streams associated with the

41 rupture of Pangea (Arthur et al., 1988; Berner, 1990; Spicer and Corfield, 1992; Price et al.,

42 2013). This scenario favored the development and the diversification of the flora, even at

43 high latitudes, where numerous plan assemblages has been recorded (Passalia, 2004).

44   The flora of southern Patagonia was dominated during the Early Cretaceous by

45 conifers and ferns (Del Fueyo et al., 2007). Among the conifers, the most diversified groups

46 were the Cheirolepidiaceae and Podocarpaceae, whereas other groups of gymnosperms,

47 such as the Araucariaceae, cycads, bennettitaleans, and gingkoaleans were well

48 represented (Del Fueyo et al., 2007). Conifers formed tall forests in fluvial, lacustrine and

49 deltaic paleoenvironments, whereas ferns, pteridosperms, and smaller plants, such as

50 cycads and benettitaleans, developed in open areas (Del Fueyo et al., 2007). Early

51 angiosperms from the Barremian–Aptian represent a marginal group in fossil plant

52 assemblages (Archangelsky et al., 2009). However, Albian–Coniacian angiosperms were

53   much more diverse and abundant components of ancient ecosystems (Archangelsky et al.,

54   2009).

55   The paleobotanical record of Patagonia during the Cretaceous is based mainly on

56   palynological associations and fossil leaf remains (e.g., Del Fueyo et al., 2007; Prámparo,

57   2012; Prámparo et al., 2018; Romero et al., 2019). However, despite the abundance of

58   Cretaceous plant assemblages, studies on fossil woods are comparatively scarce and

59   focused mainly on the Early Cretaceous (e.g., Martínez and Lutz, 2007; Vera and Césari,

60   2015; Carrizo and Del Fueyo, 2015; Brea et al., 2016; Gnaedinger et al., 2017; Nunes et al.,

61   2018, 2019; Greppi et al., 2020, 2021). There are considerably fewer studies of conifer fossil

62   woods for the Late Cretaceous (Tortorelli, 1941; Nishida et al., 1992; Del Fueyo, 1998;

63   Martinez and Lutz, 2007; Pujana et al., 2007; Varela et al., 2016; Novas et al., 2019).

64   Assemblages of conifer and angiosperm fossil woods have been described from the Upper

65   Cretaceous Cerro Fortaleza and Puntudo Chico formations (Egerton et al., 2016; Vera et al.,

66   2019, 2020).

67   The Cheirolepidiaceae is one of the better represented conifer families in the

68   Mesozoic of Patagonia and it was most diverse and abundant during the Jurassic–

69   Cretaceous (Greppi et al., 2021). In Patagonia, the Cheirolepidiaceae apparently dominated

70   the canopy and formed monospecific or mixed forests with other conifers (e.g.,

71   Araucariaceae, Podocarpaceae) (e.g., Del Fueyo et al., 2007; Greppi et al., 2020, 2021).

72   *Classopollis* (Pflug) Pocock and Jansonius pollen grain of the Cheirolepidiaceae are

73   frequently found in association with *Classostrobus* Alvin, Spicer and Watson cones (e.g.,

74   Alvin et al., 1978; Axsmith et al., 2004; Rothwell et al., 2007; Hieger et al., 2015). In addition,

75   several fossil leaf (e.g., *Pseudofrenolopsis* Nathorst, *Brachyphyllum* Brongniart, *Hirmeriella*

76   Hörhammer, and *Tomaxellia* Archangelsky) are usually found in organic connection with

77   male cones with *Classopollis* pollen grains or by the presence of this pollen grain genus

78   dispersed in the sediments (e.g., Archangelsky, 1968; Alvin et al., 1978; Barbacka et al.,

79 2007; Du et al., 2013). *Brachyoxylon* is a fossil wood genus usually related to the

80 Cheirolepidiaceae (Alvin et al., 1981). *Pomperaugoxylon* Hickey, Hu and Skinner from the

81 Triassic of USA, is another fossil wood genus related to this extinct conifer family, and one

82 of the oldest of the family (Hickey et al., 2011). *Telephragmoxylon* Torrey, another fossil wood

83 genus related to the Cheirolepidiaceae (Iamandei et al., 2005), is not validly published

84 because it does not comply with the International Code of Botanical Nomenclature (Philippe

85 and Bamford, 2008).

86   Resin canals (=ducts) are postcambial tubular structures produced by the division of

87 groups of contiguous cells (schizogenesis) (Brown et al., 1949). Axial (=vertical) and

88 horizontal (=radial) resin canals in secondary xylem (wood) can be normal (=constitutive) or

89 of traumatic origin (Esteban et al. 2003). Axial resin canals in secondary xylem occur, in

90 conifers, mainly in certain extant Pinaceae and also more rarely in extant Cupressaceae

91 (Holden, 1913; Bailey and Faull, 1934; Hudgins et al 2004; IAWA Committee, 2004;

92 Vazquez-González et al., 2020). When horizontal resin canals occur, they always appear

93 inside the rays (Esteban et al., 2003; IAWA Committee, 2004).

94   The presence of traumatic resin canals (TRC) in conifer fossil wood, in secondary

95 xylem, has been documented from the Late Triassic to the Late Pleistocene, mostly in the

96 Northern Hemisphere. Fossil wood genera related to the Pinaceae (*Cedroxylon* Kraus,

97 *Keteelerioxylon* Shilkina, *Lariciaxylon* Greguss, *Piceoxylon* Gothan, *Pinoxylon* Knowlton,

98 *Protocedroxylon* Gothan, *Protopiceoxylon* Gothan, and *Lesbosoxylon* Süss and Velitzelos)

99 more commonly have TRC than fossil genera of other conifer families (e.g., Shimakura,

100 1937; Blokhina et al., 2006; Blokhina and Afonin 2009; Selmeier and Grosser, 2011; Ding et

101 al., 2016; Sakala et al., 2018; Akkemik et al., 2020). Also, TRC were described in fossil

102 genera related to the Taxodiaceae (*Glyptostroboxylon* Süss and Velitzelos, *Oguraxylon*

103 Nishida and *Taxodioxylon* Hartig), and to a lesser extent to the Cupressaceae (*Sequoioxylon*

104 Torrey) (e.g., Nishida, 1974; Süss and Velitzelos, 1997; Oh et al., 2011; Afonin, 2013).

105   Presence of TRC was described in *Agathoxylon* Hartig from the Upper Cretaceous of Egypt,

106   but these are not clearly observable in the original publication (Youssef et al., 2000).

107   In this contribution, we describe in detail two fossil wood specimens attributable to

108   the Cheirolepidiaceae collected from Los Hornos Hill (southwestern Santa Cruz Province,

109   Argentina) in sediments of the Cerro Fortaleza Formation (Upper Cretaceous). These are

110   compared to similar conifer woods and the TRC are described and discussed.

111

112   **2. Geological setting**

113

114   The Austral-Magallanes Basin, in southern South America, contains a nearly

115   continuous record of Middle Jurassic–Cenozoic deposits (Quattrocchio et al., 2006;

116   Schwarz et al., 2011), which were deposited during three main tectonic stages: a rift stage

117   (Late Jurassic), a thermal subsidence stage (Early Cretaceous), and a foreland stage

118   (Aptian–Miocene) (Biddle et al., 1986; Robbiano et al., 1996; Cuitiño et al., 2019). The infill

119   of the basin during the Late Cretaceous is represented by a regressive sequence that

120   allowed for the progradation of continental deposits to the southeast (Spalletti and Franzese,

121   2007).

122   The Cerro Fortaleza Formation corresponds to the foreland stage. It was defined by

123   Arbe and Hechem (1984) and extends along the margins of the La Leona and Turbio rivers,

124   Hondo Canyon and the lower reach of the Guanaco River (Kraemer and Riccardi, 1997). It

125   is equivalent to the ''Dinosaurs Beds'' or the ''Pari Aike Beds'' (Feruglio in Fossa Mancini et

126   al., 1938; Feruglio, 1944), to the Chorrillo Formation (e.g., Leanza, 1972; Furque, 1973,

127   Nullo et al., 1981; Oviedo, 1982; Novas et al., 2019), and to the Pari Aike Formation (e.g.,

128   Riccardi and Rolleri, 1980; Kraemer and Riccardi, 1997; Novas et al., 2002). Varela (2015)

129   mapped these Cretaceous dinosaur-bearing beds in the area of the Viedma Lake (including

130   Los Hornos Hill) as the Mata Amarilla Formation, but we consider that this unit is not exposed

131 in this area, and we prefer to separate the Cerro Fortaleza and the Mata Amarilla formations

132 as different stratigraphic units. Consequently, Sickmann et al. (2018) correlate some

133 deposits previously assigned to the Cenomanian Mata Amarilla Formation (e.g., Riccardi

134 and Rolleri, 1980; Varela et al., 2012) with the Cerro Fortaleza Formation. The Cerro

135 Fortaleza Formation rests in concordance on the marine sandstones of the La Anita

136 Formation and is unconformably covered by the La Irene Formation (Macellari et al., 1989;

137 Kraemer and Riccardi, 1997).

138   The Cerro Fortaleza Formation is poorly consolidated and greenish gray in color. It

139 consists predominantly of lenticular beds of cross-bedded sandstones (fluvial channel

140 deposits), interbedded with tabular beds of laminated tuffaceous mudstones, carbonaceous

141 claystones and siltstones, very weakly-developed paleosols and volcanic ash deposits

142 (Novas et al., 2002; Egerton et al., 2016). In the upper section, which includes the studied

143 woods, the fine-grained deposits (floodplain facies) are prevalent. Channel bodies are wider

144 than in the lower section, show lateral accretion surfaces and frequently include dinosaur

145 remains and large fossil trunks (Novas et al., 2002). The Cerro Fortaleza Formation records

146 the fluvial sedimentation in a coastal plain during a regressive phase. The marine

147 intercalations at the base and towards the south indicate a transitional environment in this

148 sector of the basin (Novas et al., 2002). Sedimentological features suggest a southwestern

149 oriented meandering fluvial system, with extended and poorly-drained floodplains (Maceralli

150 et al., 1989; Novas et al., 2002; Egerton et al., 2016; Sickmann et al., 2018).

151   From the paleontological point of view, the Cerro Fortaleza Formation contains

152 marine and continental invertebrates (Riccardi and Rolleri, 1980; Oviedo, 1982; Arbe and

153 Hechem, 1984; Sickman et al., 2018), marine trace fossils (Sickmann et al., 2018), marine

154 and continental phytoplankton (Oviedo, 1982; Povilauskas et al., 2006) and other

155 palynomorphs (Oviedo, 1982; Archangelsky in Riccardi 1984; Povilauskas et al., 2006),

156 plant remains (trunks and leaves) (Riccardi and Rolleri, 1980; Arbe and Hechem, 1984;

157   Maceralli et al., 1989; Kraemer and Riccardi, 1997; Villar de Seoane in Novas et al., 2002;

158   Povilauskas et al., 2006; Egerton et al., 2016; Sickmann et al., 2018; Tettamanti et al., 2018),

159   as well as marine (Sickmann et al., 2018) and continental vertebrates (e.g., Feruglio, 1944;

160   Arbe and Hechem, 1984; Novas et al., 2002, 2004, 2008; Marenssi et al., 2003; Ezcurra et

161   al., 2010; Lacovara et al., 2014; Sickmann et al., 2018).

162   The age of the Cerro Fortaleza Formation was inferred from its stratigraphic

163   relationship with the underlying La Anita Formation, dated as Campanian based on marine

164   invertebrates (Riccardi, 1983; Maceralli, 1988) and detrital zircon ages (Sickmann et al.,

165   2018, 2019); and by the Maastrichtian age of the overlying La Irene Formation according to

166   its to stratigraphic position and palynological content (Maceralli et al., 1989; Kraemer and

167   Riccardi, 1997; Povilauskas et al., 2008). Recently, Sickmann et al. (2018), using U-Pb data

168   on detrital zircons (76.2 $\pm$ 1.6 Ma and 78.4 $\pm$ 2.4 Ma), suggested a Campanian age for the

169   Cerro Fortaleza Formation in the area between the Viedma Lake and Argentino Lake.

170

171   **3. Material and methods**

172

173   Two fossil woods were collected from Los Hornos Hill, upper section of the Cerro

174   Fortaleza Formation (49°49'47" S, 72°06'56" W; Fig. 1), Santa Cruz Province by SAM in

175   2003. This locality is now known as "Bosque Petrificado La Leona" (La Leona Petrified

176   Forest), and is a tourist attraction. The specimens are silicified secondary xylem and are

177   housed in the paleobotany collection of the Museo Provincial Padre Jesús Molina (MPM PB)

178   in Río Gallegos, Santa Cruz Province, Argentina, under accession numbers 18277 and

179   18278. We prepared thin sections (transverse, TS; tangential longitudinal, TLS; radial

180   longitudinal, RLS) in the Museo Argentino de Ciencias Naturales (MACN) following standard

181   techniques (Hass and Rowe, 1999). Thin sections bear the specimen number followed by a

182   lowercase letter. Slides were examined using light microscopy (Leica DM2500 and DM500)

183 and the photographs were taken with a Leica DFC295 and ICC50HD digital cameras. Both

184 specimens were observed with scanning electron microscopy (Philips XL30 of MACN) after

185 being gold-coated. At least 20 measurements were taken for each character. Measurements

186 are expressed as the weighted mean of both specimens followed by the range and weighted

187 mean standard deviation (sd) in parentheses.

188 The descriptive terminology is based on the recommendations of the IAWA

189 Committee (2004). For the generic classification of the woods, we followed the key proposed

190 by Philippe and Bamford (2008). Indices for measuring and quantifying the intertracheary

191 radial pitting arrangement (Cp and Si) are those of Pujana et al. (2016). Si = 1.00 indicates

192 that all the intertracheary pits are uniseriate, Si > 1.00 indicates that there are two- or more-

193 seriate pits, Cp = 0% that no pits touch and Cp = 100% that all pits touch (Pujana et al.,

194 2016). We replaced the term used by Philippe and Bamford (2008) ''oculipores'' with half-

195 bordered pits.

196

197 **4. Systematic paleontology**

198

199 Fossil genus *Brachyoxylon* Hollick and Jeffrey, 1909.

200 Type species. *Brachyoxylon notabile* Hollick and Jeffrey, 1909, p. 54, pl. 13, figs. 2–6, pl. 14,

201 fig. 2.

202

203 *Brachyoxylon patagonicum* sp. nov. Rombola, Greppi and Pujana

204 Fig. 2–5

205

206 *Derivation of the name*. The specific epithet refers to Patagonia, the region where the

207 material was recovered.

208 *Holotype*. MPM PB 18277 (2 TS, 3 RLS, and 1 TLS).

209   *Paratype*. MPM PB 18278 (2 TS, 2 RLS, and 1 TLS).

210   *Type locality*. Los Hornos Hill, Santa Cruz Province, Argentina.

211   *Stratigraphic horizon*. Cerro Fortaleza Formation (Upper Cretaceous).

212   *Diagnosis*. Secondary xylem composed of tracheids and rays. Growth ring boundaries

213   distinct, latewood with 1–4 rows of tracheids. Intertracheary radial pitting mixed and

214   exclusively uniseriate. Cross-fields with usually 1–8 half-bordered, mostly contiguous and

215   alternate, pits per cross-field (araucarioid cross-fields). Rays uniseriate, height medium.

216   Horizontal and end walls of ray parenchyma cells smooth. Axial parenchyma absent.

217

218   *Description*. MPM PB 18277 (Fig. 2A) was taken from a tree that had a minimum diameter

219   of 20 cm, and MPM PB 18278 from a tree of minimum diameter of 26 cm and is laterally

220   compressed (Fig. 2B). In specimen MPM PB 18277 a branch scar is observed, that

221   apparently departed ca. 90º from the trunk (Fig. 2A). Thin sections were made in the outer

222   portion of both specimens, (i.e., 8–13 cm from the center).

223   Pycnoxylic secondary xylem with distinct growth ring boundaries, latewood with 1–4

224   rows of tracheids (Fig. 3A–B). Growth ring width is difficult to measure because of the

225   presence of false rings. Clearly identified growth rings have a width of ca. 1100–2800 μm.

226   Cells are roundish to polygonal as seen in transverse sections (Fig. 3B–C). Intertracheary

227   pitting on radial walls is mixed, uniseriate (Si = 1.00), mostly contiguous (Cp = 68.9%) (Fig.

228   3D–E, Fig. 4A–B). Intertracheary radial pits are roundish and 13.8 μm (10.6–17.2, sd = 1.4)

229   μm in vertical diameter (Fig. 3D–E, Fig. 4A–B). Tracheid tangential diameter is 26.4 (17.1–

230   34.8, sd = 4.3) μm and radial diameter is 29.6 (21.1–37.5, sd = 4.2) μm in the earlywood

231   and 16.3 (10.6–18.4, sd = 2.7) μm in the latewood (both diameters measured in transverse

232   section). Pits on tangential walls were not observed. Cross-field pitting is araucarioid with

233   2.8 (1–8) contiguous half-bordered pits per cross-field (Fig. 3G, Fig. 4C). Cross-field pits are

234   circular with the border wider than the aperture (cupressoid) and 7.6 (4.0–10.9, sd = 1.5) μm

235   in vertical diameter (Fig. 3G, Fig. 4C). Rays are homocellular, with horizontal and end walls

236   of ray parenchyma cells smooth (Fig. 3F). Many ray cells and occasionally some tracheids

237   near the rays have dark contents, probably resiniferous (Fig. 3B–C). Average ray height is

238   medium; 5.6 (1–18, sd = 3.9) cells high and 128 (23–376, sd = 76) µm. Rays are exclusively

239   uniseriate (Fig. 3H–I), and have a frequency of 6.5 (4–10, sd = 1.4) rays per mm.

240   There are numerous traumatic resin canals (TRC) in specimen MPM PB 18277.

241   These are arranged concentrically forming tangential rows (parallel to the growth rings) and

242   only interrupted by the rays (Fig. 5A–C). The position in the growth ring is difficult to establish,

243   because of the presence of false growth rings, but they seem to be in the middle of the ring

244   or close to the latewood. There are rows of TRC in two successive growth rings, one of them

245   laterally faint (Fig. 5A). There is one more row of TRC in another section of the wood (Fig.

246   5B). TRC are radially elongated, 127 (92–158, sd = 16) µm x 98 (56–134, sd = 33) µm as

247   seen in transverse sections (Fig. 5C–D). They have one or two layers of subsidiary cells, 2–

248   5 cells wide (Fig. 5D–F). The subsidiary cells are sub-rectangular to sub-squarish as seen

249   in transverse sections (Fig. 5C–D), radially elongated, 21 (14–31, sd = 5) µm x 42 (16–98,

250   sd = 21) µm; they are 33 (14–67, sd = 13) µm high and are thick-walled (walls are thicker

251   than the lumen and ca. 8–11 µm in thickness) in longitudinal section (Fig. 5F). Epithelial cells

252   were not observed.

253   Specimen MPM PB 18277 (the one with TRC) shows decay of the wood. At lower

254   magnification it is possible to identify large areas of the woody tissue in transverse and

255   longitudinal sections with highly deformed cells partial or completely disconnected from

256   neighboring cells due to degradation of the middle lamella (Fig. 6A, B). In other areas of the

257   wood, the cells do not show any structural changes of the wall layers and have opaque

258   compounds in the cell lumens (Fig. 6C). In those cells in which the middle lamella is

259   selectively degraded, it is possible to identify hyphae in the cell lumen (Fig. 6D). The hyphae

260 have hyaline walls, a diameter of ca. 3–8 μm, and transverse septa (Fig. 6D, E). In some

261 cases, hyphae branches dichotomously (Fig. 6F)

262

263 *Comparisons with fossil woods.* These two woods are characterized by: (1) distinct growth

264 ring boundaries, (2) absence of axial parenchyma, (3) mixed tracheid radial pitting, (4)

265 uniseriate radial pitting, (5) uniseriate rays, and (6) araucarioid cross-fields with 1–8 circular

266 half-bordered pits per cross-field. These characteristics match *Brachyoxylon* following

267 Philippe and Bamford (2008).

268 Hollick and Jeffrey (1909) included fossil woods in *Brachyoxylon* with the following

269 characters: tracheid radial pits not all alternate or flattened, but more frequently rounded and

270 not contiguous, normal resiniferous canals absent (only TRC) and cross-fields araucarioid.

271 This fossil genus is characterized by a mixed type of radial pitting, generally circular uni- to

272 multiseriate radial pits, araucarioid cross-fields and predominantly uniseriate rays (Bamford

273 and Philippe, 2001; Philippe and Bamford, 2008).

274 *Agathoxylon* and *Shimakuroxylon* Philippe, Boura, Oh and Pons resemble

275 *Brachyoxylon* in having araucarioid cross-fields, but they differ mainly by the radial pits

276 arrangement. *Agathoxylon* has araucarian radial pits that, according to Philippe and

277 Bamford (2008), is when more than 90% of pits on the radial wall of tracheids are contiguous

278 with neighbouring pits. In this state pits are often somewhat flattened and when multiseriate

279 are always alternately arranged. *Shimakuroxylon* has at least 10% of radial pits of the

280 japonicum type, which is opposite to slightly sub-opposite and mutually flattened pits, which

281 gives them a squarish outline (Philippe et al., 2014). Two more genera have mixed radial

282 pitting like *Brachyoxylon*, but cupressoid cross-fields: *Zonaloxylon* Grauvogel-Stamm,

283 Mayer-Berthaud and Vozenin-Serra, and *Protocupressinoxylon* Eckhold. This cupressoid

284 cross-field type has spaced half-bordered pits, mostly ordered and never clearly alternate

285   (Philippe and Bamford, 2008); alternatively, cross-fields with continuous, unordered, and

286   often alternate, half-bordered pits (araucarioid) characterize *Brachyoxylon*.

287   *Brachyoxylon patagonicum* was compared to most similar species of *Brachyoxylon*

288   in Table 1. According to Philippe et al. (2014) and Iamandei et al. (2018), the following

289   species should not be included in *Brachyoxylon*: *B. boureauii* Serra, *B. desnoyersii*

290   Lemoigne, *B. nipponicum* Nishida, *B. nonakai* Yamazaki and Tsunada, *B. orientale* Serra

291   and *B. urkutense* Greguss.

292   It is worth to mention that *B. raritanense* Torrey from the Upper Cretaceous of North

293   America shares most of the diagnostic characteristics with *B. patagonicum* (absence of axial

294   parenchyma, radial pits uniseriate and mixed, uniseriate rays, and araucarioid cross-fields

295   with ca. 1–8 pits per cross-field). However, *B. raritanense* is characterized by its indistinct

296   (or absent) growth ring boundaries (Table 1). Torrey (1923) described poorly marked growth

297   rings for this species, sometimes delimited by a slight narrowing of tracheids, but he

298   indicated that they could be false rings. In the Cerro Fortaleza specimens, the growth rings

299   boundaries are distinct; these are delimited by a few cells (1–4 rows of flattened and

300   thickened tracheids). *B. patagonicum* could be included in *Brachyoxylon* sp. cf. *B. currumilii*

301   described by Vera et al. (2019) from Patagonia, since it shares all the diagnostic characters

302   with it, and differs only by the presence of axial parenchyma in the holotype described by

303   Bodnar et al. (2013). *B. patagonicum* also shares most of its characters with *Brachyoxylon*

304   *trautii* (Barale) Philippe, including the presence of false rings and resiniferous tracheids.

305   However, in *B. trautii* cross-fields usually have more pits, and growth rings are 95% false

306   according to Philippe (1995).

307   Traumatic resin canals in *Brachyoxylon* cannot be considered of diagnostic value as

308   these are only secondary formed in response to biotic or abiotic elicitors (see discussion).

309

310   **5. Discussion**

311

312   *5.1 The Cheirolepidiaceae*

313

314   *Brachyoxylon* has been related to various conifer families including Araucariaceae,

315   Cupressaceae, and Protopinaceae (e.g., Hollick and Jeffrey 1909; Seward, 1919; Iamandei

316   and Iamandei, 2005). However, it is assumed to belong to the Cheirolepidiaceae based on

317   its frequent co-occurrence with other fossil genera assigned to this family (e.g., pollen, seed

318   cones, leaves) (Alvin et al., 1981; Alvin, 1982; Zhou, 1983; Machhour and Pons, 1992;

319   Rothwell et al., 2007; Limarino et al., 2012; Hieger et al., 2015). Patagonian records of this

320   fossil genus are mostly related to the Cheirolepidiaceae (Bodnar et al., 2013; Vera and

321   Césari, 2015; Greppi et al., 2020, 2021). However, *Brachyoxylon* is not the unique fossil

322   wood genus associated with this family, and other, such as *Telephragmoxylon*,

323   *Pomperaugoxylon*, and some species of *Protocupressinoxylon*, *Protopodocarpoxylon*

324   Eckhold and *Agathoxylon* have been also considered to be in this family (Harris, 1979; Alvin

325   et al., 1981; Zhou, 1983; Iamandei et al., 2005; Hickey et al., 2011).

326   This extinct family had a cosmopolitan distribution, mainly in low latitudes, from the

327   Late Triassic (e.g., Norris, 1965; Playford and Dettmann, 1965) to the Cretaceous-

328   Paleogene boundary (Barreda et al., 2012), showing greater diversity during the Jurassic–

329   Cretaceous (Alvin, 1982; Greppi et al. 2021). Fossils have been found in riparian

330   environments with marine influence to purely continental environments (Vakhrameev, 1970,

331   1981; Barnard and Miller, 1976; Batten, 1996). Cheirolepidiaceae were more common in

332   arid and semi-arid environments, in subtropical to tropical climates (Doyle et al., 1982;

333   Watson, 1988; Vakharameev, 1991; Abbink et al., 2004). However, its frequent presence

334   along with Araucariaceae in the same fossil assemblages indicates that the

335   Cheirolepidiaceae was also present in temperate climates (Vakharameev, 1981).

336   *Brachyoxylon* has been documented from the Permian to the Late Cretaceous, and

337   is more frequent in northern latitudes (e.g., the United States, Tunisia, Japan, Cambodia,

338   Thailand, France and Romania) than in Gondwana (Philippe et al., 2004). The affinity of

339   Permian *Brachyoxylon* spp. have been questioned (e.g., Kurtzawe and Merlotti, 2010;

340   Kurtzawe et al., 2012) based on the lack of enough diagnostic features to distinguish them

341   from other fossil woods with similar anatomy. In Argentina, it has been recorded from

342   sediments of the Lower–Middle Jurassic to the Upper Cretaceous of central and southern

343   Patagonia (Bodnar et al., 2013; Vera and Césari, 2015; Vera et al., 2019; Greppi et al., 2020,

344   2021).

345   Fossils of the Cheirolepidiaceae in Mesozoic paleofloristic associations in Patagonia

346   also include leaves (e.g., *Tomaxiella biforme* Archangelsky; Archangelsky, 1968), cones

347   (e.g., *Pararaucaria delfueyoae* Escapa, Cúneo, Rothwell and Stockey; Escapa et al., 2013)

348   and *Classopollis*-type pollen grains (e.g., Archangelsky et al., 1981; Archangelsky and

349   Archangelsky, 2004). The widespread occurrence of Cheirolepidiaceae in Jurassic and

350   Cretaceous deposits in Patagonia is consistent with the great diversity and abundance of

351   fossils and prominence of this family in a wide array of habitats with different ecological

352   requirements (Greppi et al., 2021). Based on the analysis of a palynological sequence from

353   the Paleocene that contains *Classopollis*-like pollen, some species of the family

354   Cheirolepidiaceae may have been early colonizers of disturbed environments (Barreda et

355   al., 2012).

356

357   *5.2 Cerro Fortaleza Formation paleobotany*

358

359   Egerton et al. (2016) described conifer and angiosperm fossil woods from the Cerro

360   Fortaleza locality (Fig. 1 in Egerton et al., 2016). Among the conifers, they described three

361   taxonomic units with mixed radial pitting: *Planoxylon* sp.*, Taxodioxylon* sp. 1, and

362 *Taxodioxylon* sp. 2. A specimen was assigned to *Planoxylon* sp. mainly because of the

363 presence of ray cell walls pitted or thickened (*Abietineentüpfelung).* These thickenings are

364 present on the transverse walls of the ray cells. This character is difficult to observe in the

365 microphotographs Fig. 4G–H of Egerton et al. (2016) and is the only character that

366 differentiates it from *Brachyoxylon patagonicum*. *Taxodioxylon* sp. 1 has, according to the

367 description, 2–6 pits per cross-field, but illustrations show that it frequently has one or two

368 (Fig. 6C–D in Egerton et al.*,* 2016), less than in *B. patagonicum*. In addition, *Taxodioxylon*

369 has axial parenchyma, and taxodioid cross-field pits (which are not clearly illustrated) that

370 are not observed in *B. patagonicum*. *Taxodioxylon* sp. 2 has axial parenchyma, sometimes

371 biseriate pits, and taxodioid cross-field pits (Egerton et al., 2016), which are characters that

372 have not been observed in *B. patagonicum*. In addition, Varela et al. (2016) assigned one

373 specimen (MPM PB 1568, pmLPPB1937) from Los Hornos Hill (in Mata Amarilla Formation,

374 suggested as equivalent to the Cerro Fortaleza Formation) to *Podocarpoxylon garciae* Del

375 Fueyo*,* but the specimen was not illustrated.

376   Pollen grains and microplankton palynomorphs were described from the middle and

377 upper levels of the Puesto La Asunción of the Cerro Fortaleza Formation (Oviedo, 1982).

378 Archangelsky in Riccardi (1984) recognized tricolporate, triporate and tricolpate pollen

379 grains (angiosperms) in deposits along the eastern bank of the La Leona River on Cerro

380 Fortaleza. Povilauskas et al. (2006) also described a palynoflora to the south of Viedma

381 Lake and close to the La Leona River. These authors highlighted the presence of spores of

382 bryophytes and ferns, pollen grains of gymnosperms and angiosperms, and colonies of

383 *Pediastrum* Meyen, and sparse microplankton. However, they mentioned that the recovered

384 palynomorphs are not diagnostic indicators of the age of the deposits.

385   Finally, there are a few mentions of fossil leaf fragments, which are poorly preserved

386 and could not be identified (Riccardi and Rolleri, 1980; Arbe and Hechem, 1984; Maceralli

387 et al., 1989; Kraemer and Riccardi, 1997; Tettamanti et al., 2018). In addition, Villar de

388   Seoane in Novas et al. (2002) reported the presence of poorly preserved imprints of cycads

389   and conifers from Los Hornos Hill.

390

391   *5.3 Growth ring boundaries*

392

393   The study of growth rings contributes to infer the paleoclimate and the

394   paleoenvironmental characteristics of ancient ecosystems (Creber and Chaloner, 1984;

395   Francis, 1984; Francis and Hill, 1996; Morgans et al., 1999). The presence of distinct growth

396   ring boundaries indicates seasonality, whereas their absence indicates lack of climatic

397   seasons (Creber, 1977; Brison et al., 2001; Pujana et al., 2007, 2020). The fossil woods

398   recovered from Los Hornos Hill locality have distinct growth ring boundaries, suggesting

399   seasonality.

400   The growth ring width in fossil woods has been used as an indicator to characterize

401   the growing season (Fritts, 1976). The development of growth rings depends fundamentally

402   on environmental factors (e.g., temperature, rainfall, available water, among others), which

403   may vary depending on the year (Fritts, 1976). Wide rings indicate rapid growth, which is

404   typical of favorable environmental conditions, whereas narrower rings in the same taxa of

405   similar ontogenic age represent slower growth, and unfavorable environmental conditions

406   (Fritts, 1976). Based on the width of the growth rings, *B*. *patagonicum* shows a growth of ca.

407   3.2 mm of annual diameter and a maximum of 5.6 mm (average growth ring width is 1.6 mm

408   and the widest is 2.8 mm). This indicates that they would have grown more than the global

409   mean ring width of the extant conifers, estimated at approximately 1.1 mm (Falcon-Lang,

410   2005).

411   A minimum age, based on the width of the rings and the diameter, was estimated for

412   the specimens of *B. patagonicum* of ca. 70 years. Based on the diameter of the specimens,

413   and using the formulae of Niklas (1994) and Mosbrugger et al. (1994), we can infer that the

414   woods were part of trees of ca. 10–20 m of height. Consequently, the studied specimens

415   were mature trees.

416

417   *5.4 Traumatic resin canals*

418

419   Traumatic resin canals (TRC) may be formed in the secondary xylem on extant

420   conifers, as in Pinaceae and a few Cupressaceae and some Taxodiaceae, and also in the

421   phloem and primary xylem, as in Araucariaceae (Hudgins et al., 2004; Krokene et al., 2008).

422   TRC originate in genera of the Pinaceae that also have normal resin canals (*Cathaya* Chun

423   and Kuang, *Keteleeria* Carrière, *Larix* Mill, *Nothotsuga* Hu, *Picea* Link, *Pinus* Linneo and

424   *Pseudotsuga* Carrière), as well as in those that lack them (*Abies* Mill, *Cedrus* Trew,

425   *Pseudolarix* Gordon and *Tsuga* Carrière) (IAWA Committee, 2004; Esteban, 2020). In turn,

426   TRC have been cited in some Cupressaceae (*Sequoia* Endlicher, *Metasequoia* Hu and

427   Cheng, *Sequoiadendron* (Lindley) Buchholz, *Microbiota* Komarov and *Tetraclinis* Masters)

428   that lack normal resin canals (Jeffrey, 1903; Bailey and Faull, 1934; Benkova and

429   Schweingruber, 2004; Esteban et al., 2015; Vazquez-González et al., 2020). TRC can be

430   both axial and horizontal (IAWA Committee, 2004). The uniseriate layer of cells adjacent to

431   the resin canal is called the epithelium, whereas the remaining parenchyma and chain

432   tracheids outside the epithelium are the subsidiary cells (Wiedenhoeft and Miller, 2002).

433   Apparently, in *B. patagonicum* only subsidiary cells preserved their structure.

434   TRC originate in response to various biotic (e.g., attacks by pathogenic insects or

435   fungi) or abiotic disturbances, such as fire and frost damage and geomorphological events

436   (e.g., avalanches, rock falls or floods) (Franceschi et al., 2002; Hudgins et al., 2004; Krokene

437   et al., 2008).

438   TRC are produced in the same way as normal axial canals, by schizogenesis

439   between incipient epithelial cells when they are still close to the cambial zone and are

440   sometimes surrounded by parenchymal cells filled with grains of starch and phenolic

441   compounds (Krokene et al., 2008). When the inducing stimulus for the formation of TRC is

442   strong, it can produce a complete tangential ring as occurs in fir (Christiansen et al., 1999)

443   and apparently as in *B. patagonicum*. The occurrence of discrete tangential rows,

444   concentrically arranged parallel to the growth rings in the secondary xylem in *B.*

445   *patagonicum* is similar to how these are formed after a traumatic stimulus, as in Pinaceae,

446   Cupressaceae and Taxodiaceae (IAWA Committee, 2004; Esteban, 2020). On the other

447   hand, in other genera (*Abies*, *Tsuga*, *Cedrus* and *Pseudolarix*) TRC are formed mainly in

448   the vicinity of the wounds (Bannan, 1936; Wu and Hu, 1997).

449   In addition to the presence of a series of conspicuous tangential rows of TRC in *B.*

450   *patagonicum*, their irregular contours are also consistent with a traumatic origin (IAWA

451   Committee, 2004). Moreover, the presence of unaltered cells with lumens blocked by

452   opaque compounds in areas of the fossil woods also with presence of fungal hyphae may

453   be interpreted as a chemical response by the host. (Otjen and Blanchette, 1982, 1984). This

454   evidence and the presence of TRC in the analyzed wood could indicate possible natural

455   defensive barriers against invasive fungi (Otjen and Blanchette, 1982; Krekling et al., 2004;

456   Krokene et al., 2008). Alternatively, the TRC may been formed as response to abiotic factors,

457   such from breakage of windblown branches and trunks.

458   About 45% of the species of *Brachyoxylon* have one or more rows of TRC, which is

459   a frequent characteristic of this fossil genus (e.g., Torrey, 1923; Iamandei and Iamandei,

460   2005; Iamandei et al., 2018; Jiang et al., 2020). Presence of TRC was documented in

461   *Telephragmoxylon,* another fossil genus related to Cheirolepidiaceae (Torrey, 1921;

462   Iamandei et al., 2005). The size and shape of the TRC in *Brachyoxylon* are very similar in

463   many of the species of the genus, and they are also usually arranged in tangential rows as

464   in *B. patagonicum* (e.g., *B. comachense* Torrey, *B. lagonense* (Laudoueneix) Duperón-

465   Laudoueneix, *B. woodworthianum* Torrey and *B. zhouii* Jiang, Wu, Tian, Wan and Xie).

466 However, sometimes TRC are significatively bigger (*B*. sp. Oh, Kim, Paik, Lim) or smaller

467 (*B*. *avramii* Iamandei and Iamandei, and *B*. *notabile*) than in *B*. *patagonicum*. These

468 differences may correspond to a greater or lesser biosynthesis of resin and energy invested

469 by the plant at the time of generating a defensive barrier, as it occurs in extant conifers

470 (Arbellay et al., 2014). Higher resin levels are related to an increase in the size of canals,

471 whereas lower levels correspond to canals of increasingly lower sizes (Arbellay et al., 2014).

472 Finally, there are some species such as *B*. *holbavicum* Iamandei, Iamandei and Grădinaru

473 and *B*. *saurinii* Boureau and Serra that present isolated TRC (Boureau and Serra, 1961;

474 Iamandei et al., 2018).

475 In extant conifer woods, TRC are mainly distributed in the latewood; although, in

476 some species they show up in the earlywood (Esteban et al., 2003). It is difficult to determine

477 the position of the TRC identified in *B*. *patagonicum* because of the presence of false growth

478 rings. However, they apparently develop in the middle of the ring or close to the latewood.

479

480 **6. Conclusions**

481

482 A new species, *Brachyoxylon patagonicum* is described. This has distinct growth ring

483 boundaries, uniseriate radial pitting, araucarioid cross-fields, uniseriate rays, and lacks axial

484 parenchyma.

485 One specimen has well-preserved axial TRC ordered in tangential rows. Formation

486 of the TRC may have been triggered by abiotic factors, such as breakage from windblown,

487 or else, that they may have formed as a response to a biotic trigger, in which case presence

488 of fungal remains and decay patterns may have been involved in it.

489 This record is consistent with the abundance and diversity of the Cheirolepidiaceae

490 in the Cretaceous of Patagonia, and adds an example that showsthe presence of traumatic

491 resin canals, as is in other previously described *Brachyoxylon*.

492

Acknowledgments

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947

948 **Table 1.** Comparison of *Brachyoxylon patagonicum* with other species of *Brachyoxylon* with

949 distinct to indistinct (not absent) growth ring boundaries, uni- to biseriate radial pitting, and

950 exclusively or predominantly uniseriate rays. Abbreviations: GRB = Growth ring boundary;

951 IPS = Intertracheary pitting seriation; PxCF = Pit per cross-field; RS = Ray seriation; RH =

952 Ray height [cells]; AP = Axial parenchyma; C = Crassulae; TRC = Resin canal; D = Distinct;

953 I = Indistinct; A = Absent; P = Present; ? = doubtful/unknown. Bold letter indicates

954 coincidences with *Brachyoxylon patagonicum*. All the authorities' citations are in the

955 references.

956

957 **Fig. 1.** Map showing the fossiliferous locality (green star).

958

959 **Fig. 2.** The two specimens studied. A, MPM PB 18277 with a branch scar, that apparently

960 departed ca. 90º from the trunk. Scale bar: 2 cm. B, MPM PB 18278 laterally compressed.

961 Scale bar: 2 cm.

962

963 **Fig. 3.** *Brachyoxylon patagonicum* sp. nov. A, distinct growth ring boundaries (transverse

964 section, TS). MPM PB 18277 (b) Holotype. Scale bar: 500 µm. B, detail of distinct growth

965 ring boundaries showing two or three rows of flattened tracheids (TS). MPM PB 18277 (b)

966 Holotype. Scale bar: 200 µm. C, ray cells (white arrowhead) and some tracheids (yellow

967 arrowhead) near the rays with dark, probably resiniferous, contents (TS). MPM PB (a) 18277

968 Holotype. Scale bar: 100µm. D, uniseriate mixed radial pitting and a tracheid with

969 resiniferous content (arrowhead) (radial longitudinal section, RLS). MPM PB (e) 18277

970 Holotype. Scale bar: 50 µm. E, uniseriate mixed radial pitting (RLS). MPM PB (j) 18278

971 Paratype. Scale bar: 50 µm. F, homocellular rays, with horizontal and end walls of ray

972 parenchyma cells smooth (RLS). MPM PB (d) 18277 Holotype. Scale bar: 50 µm. G, cross-

973 fields (RLS). MPM PB 18277 (d) Holotype. Scale Bar: 20 µm. H, uniseriate rays (tangential

974 longitudinal section, TLS). MPM PB 18277 (f) Holotype. Scale bar: 200 µm. I, uniseriate rays

975 with resiniferous content (arrowhead) (TLS). MPM PB 18277 (f) Holotype. Scale bar: 100

976 µm.

977

978 **Fig. 4.** *Brachyoxylon patagonicum* sp. nov. A–B, uniseriate mixed radial pitting (scanning

979 electron microscopy, SEM). MPM PB 18277 Holotype (A) and MPM PB 18278 Paratype (B).

980 Scale bars: 20 µm. C, cross-fields (SEM). MPM PB 18277 Holotype. Scale bar: 20 µm.

981

982 **Fig. 5.** Traumatic resin canals (TRC) of the specimen MPM PB 18277. A, two rows of TRC

983 in the secondary xylem (arrowhead) (transverse section, TS) (b). Scale bar: 1000 µm. B, a

984 row of TRC in another section of the wood (arrowhead) (TS) (a). Scale bar: 1000 µm. C,

985 detail of the row of TRC (TS) (a). Scale bar: 200 µm. D, detail of two TRC (TS) (a). Scale

986 bar: 100 µm. E, TRC and rays (radial longitudinal section, RLS) (e). Scale bar: 200 µm. F,

987 detail of a TRC (RLS) (e). Scale bar: 50 µm. Abbreviations: rc= resin content, sc= subsidiary

988 cell, t= tracheid and r= ray.

989

990 **Fig. 6.** Fungal evidence of the specimen MPM PB 18277. A, highly deformed and degraded

991 cells in transverse section (TS). Note how the middle lamella between neighboring cells was

992 completely removed (red arrowheads) (a). Scale bar: 50 µm. B, cells partially disconnected

993 by dissolution of the middle lamella (red arrowheads) in radial longitudinal section (RLS) (e).

994 Scale bar: 50 µm. C, cells without structural alteration and lumens blocked by opaque

995 substances (TS) (a). Scale bar: 50 µm. D, cells partially disconnected and degraded with

996 the presence of hyphae in their lumens (green arrowheads) and in the area where the middle

997 lamella was consumed (white arrowhead) (TS) (a). Scale bar: 20 µm. E, hypha with

998 transverse septa (yellow arrowhead) (RLS) (c). Scale bar: 10 µm. F, dichotomous branching

999 hypha (purple arrowhead) (TS) (a). Scale bar: 20 µm.

| Fossil species	Age	Country	GRB	IPS	PxCF	RS, RH	AP	C	TRC	Other differences with *B. patagonicum*
B. comanchense Torrey 1923	Cretaceous	USA	**D**	**1(2)s**	Up to 12	1s, 1–6	**A**	?	**P**	Radial pits on large tracheids often horizontally elongate. Pith with sclerenchyma
B. cristianicum Iamandei, Iamandei and Grădinaru 2018	Lower Jurassic	Romania	**D**	1–2s	**1–6**	1(2)s, 1–20	P	**A**	A	
B. currumilii Bodnar, Escapa, Cúneo and Gnaedinger 2013	Early–Middle Jurassic	Argentina	**D**	**1(2)s**	4–11	1s, 1–10	P	**A**	A	
B. eboracense (Holden 1913) Philippe 2002	Jurassic	England	**D**	1–2s	numerous	1s, low	**A**	**A**	A	Bars of Sahnio, undetailed description
B. holvavicum Iamandei, Iamandei and Grădinaru 2018	Lower Jurassic	Romania	**I–D**	1(2)s	**1–6(9)**	1–2s, 1–25	**A**	**A**	**P**	
B. liebermannii Philippe 1995	Jurassic	France	I	**1s**	5–12	1s, low	**A**	**A**	A	
B. notabile Hollick & Jeffrey 1909	Late Cretaceous	USA	**D**	1–2s	5–11	1s, 1–8	**A**	P	**P**	Crassulae
B. nummularium (White 1908) Kurzawe, Iannuzzi and Merlotti 2012	Permian	Brazil	I	1–2s	**1–6**	1(2)s, 1–39	**A**	**A**	A	
B. raritanense Torrey 1923	Cretaceous	USA	I?	**1s**	**1–9**	**1s, 1–15**	**A**	**A**	A	Indistinct (or absent) growth ring boundaries
B. serrae Philippe, Suttethorn and Buffetaut, 2011	Early Cretaceous	Thailand	**D**	1–2s	5–16	**1s, 1–15**	**A**	**A**	**P**	
B. trautii (Barale 1981) Philippe 1995	Middle Jurassic	France	**I–D?**	**1(2)s**	4–9	**1s, 1–10**	**A**	**A**	A	Numerous (at least 95%) false rings
***Brachyoxylon patagonicum* sp. nov.**	Late Cretaceous	Argentina	**D**	**1s**	**1–8**	1s, 1–18	**A**	**A**	**P**	
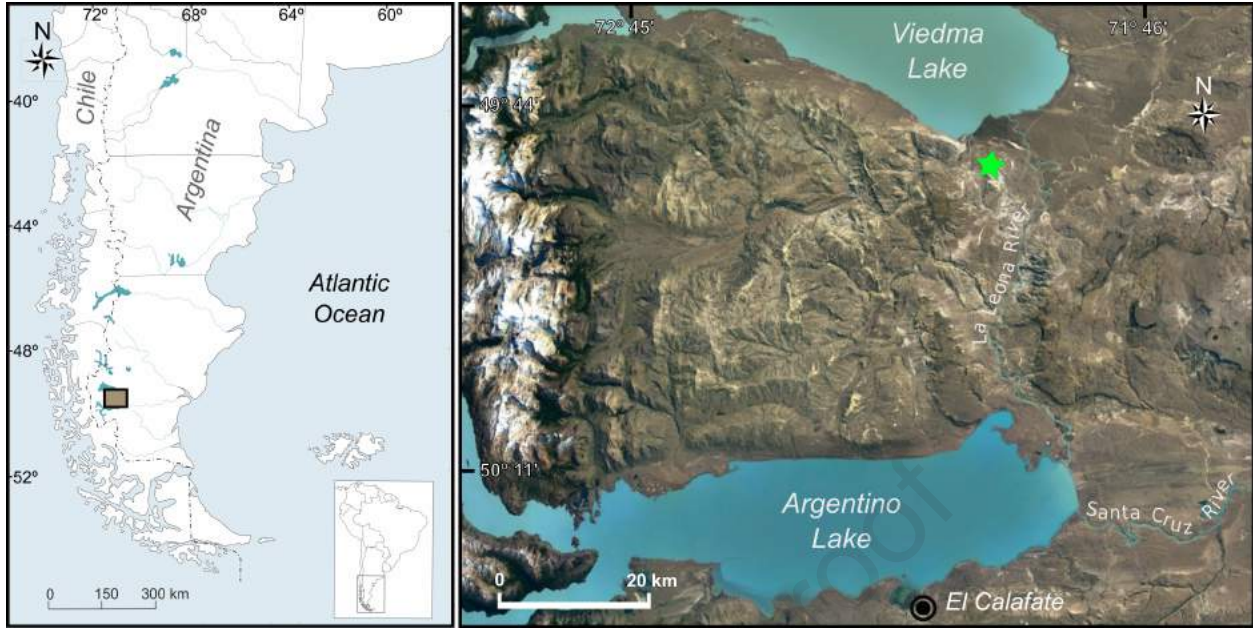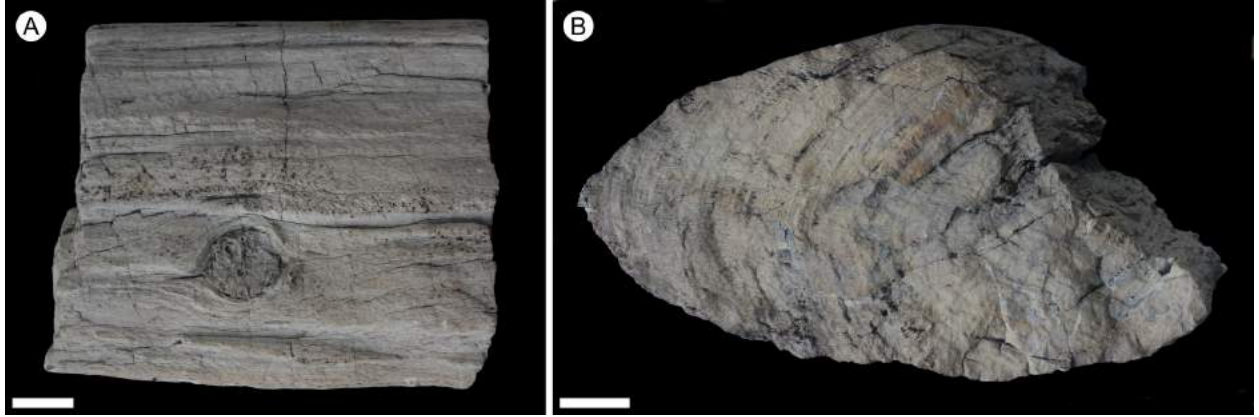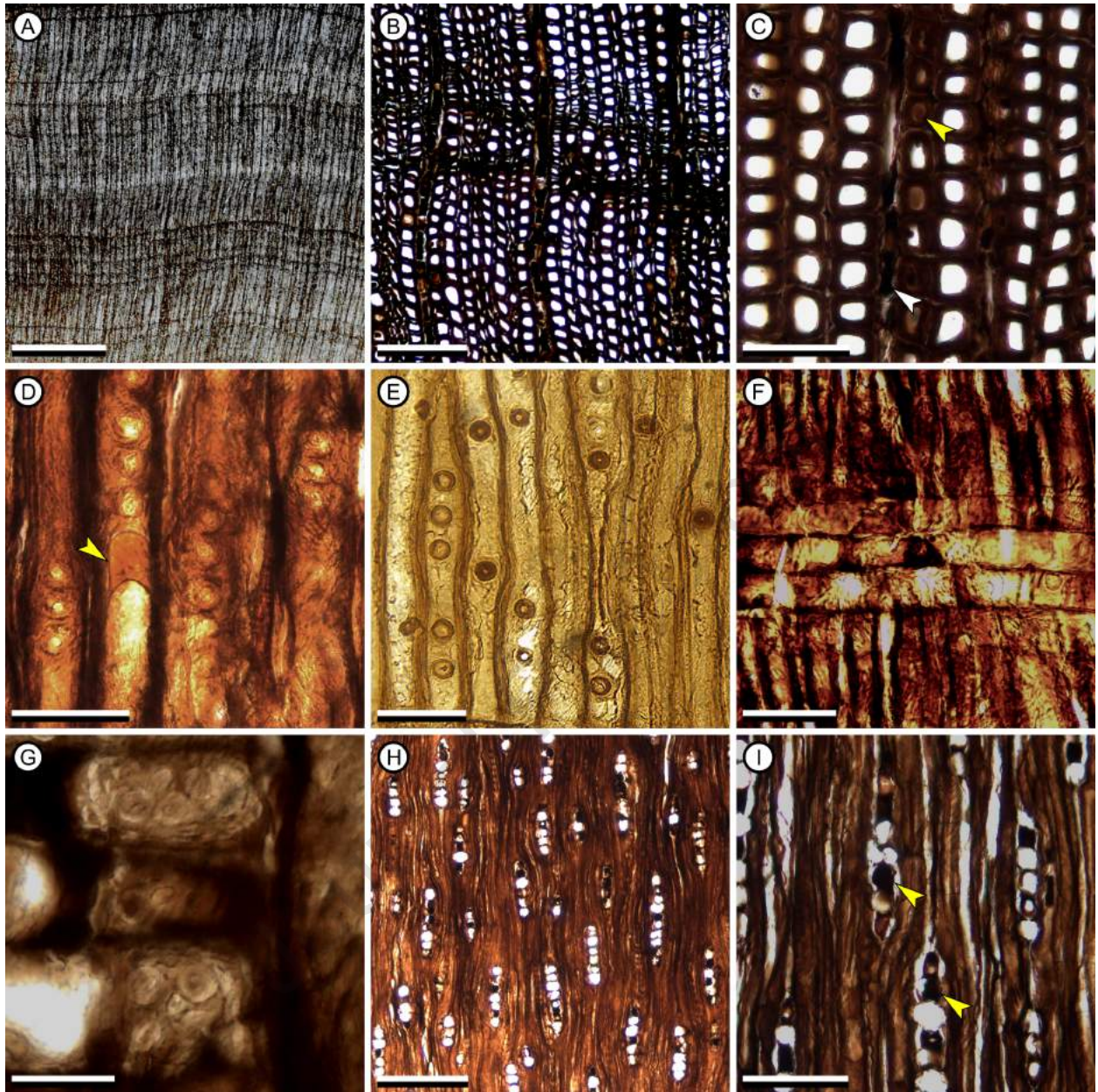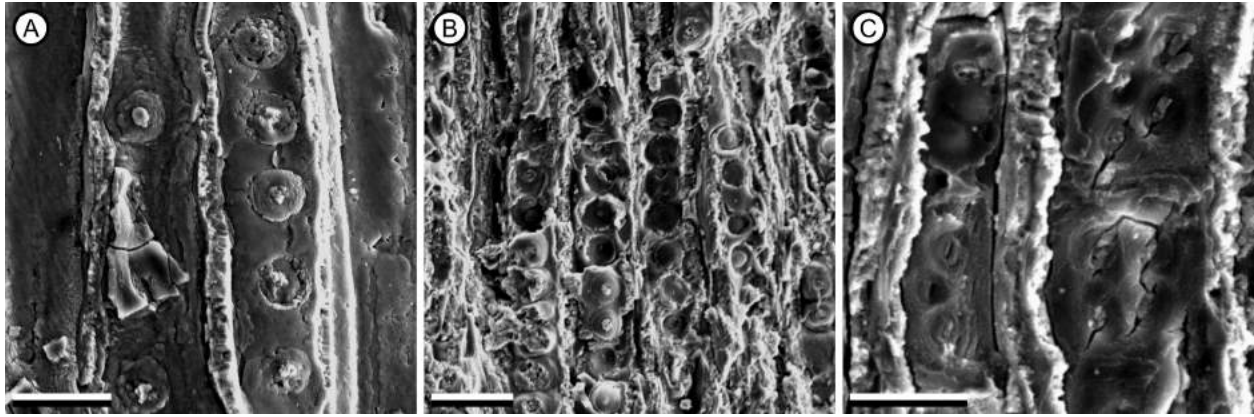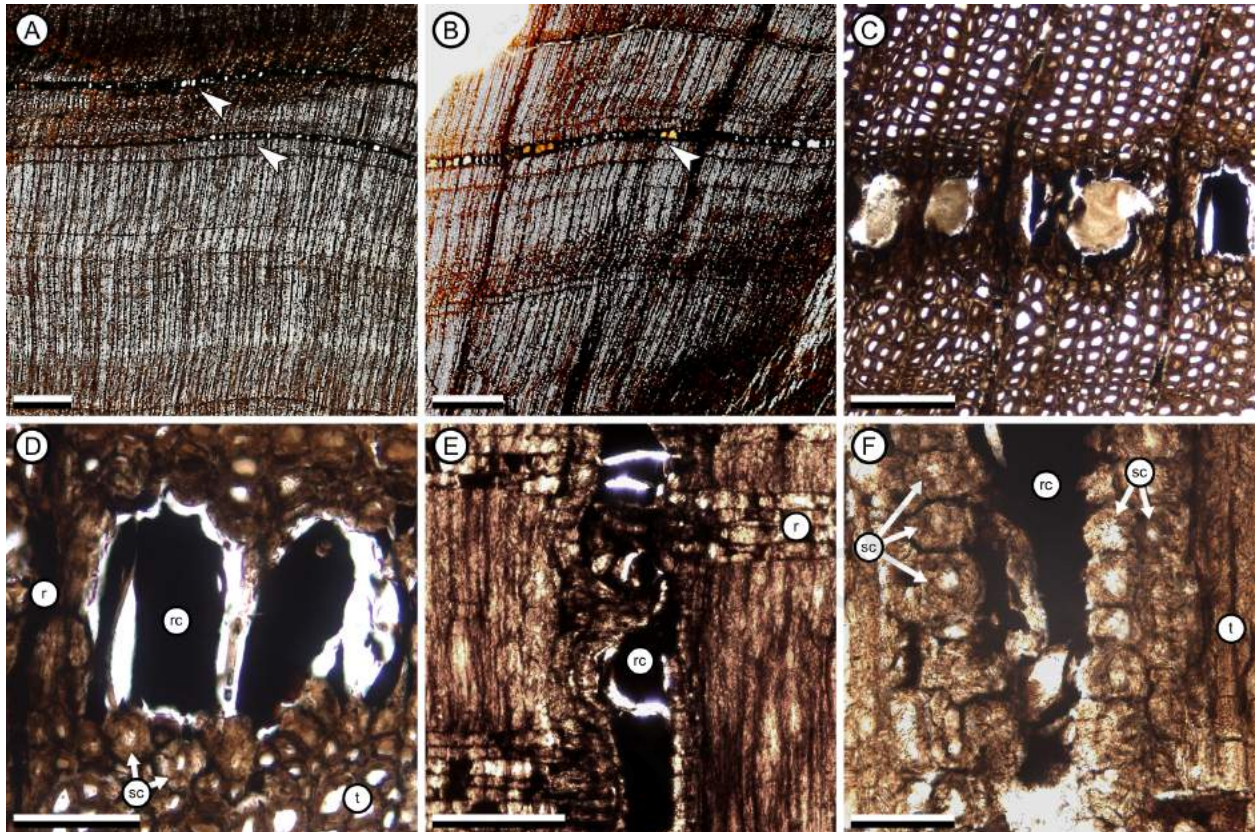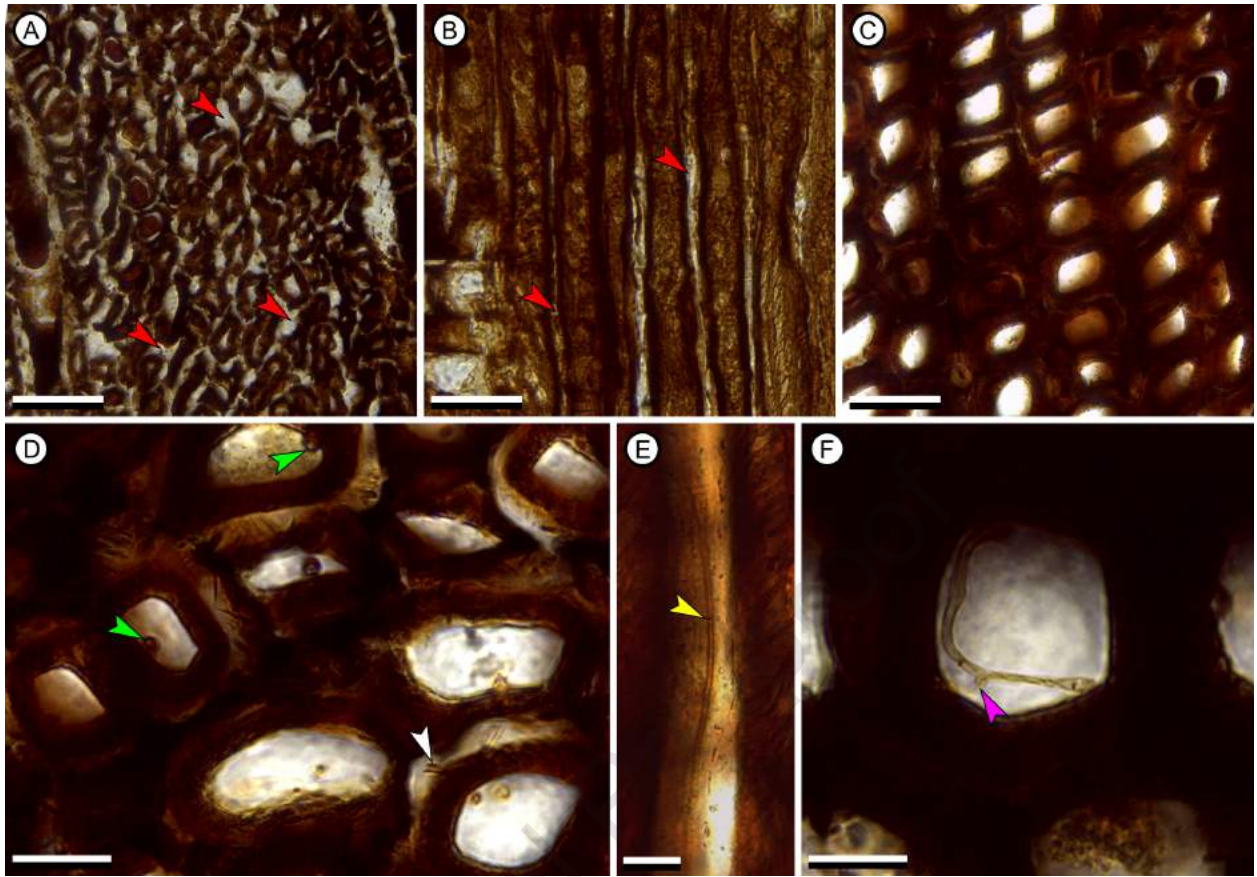
Highlights

Two specimens of fossil woods were collected from the Cerro Fortaleza Formation (Upper Cretaceous of Patagonia).

A new species of *Brachyoxylon* is proposed.

One specimen has very well-preserved traumatic resin canals arranged in three tangential rows.

This record adds to the abundance of Cheirolepidiaceae in the Creataceous of Patagonia.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: