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1 **Anatomy and affinities of permineralized gymnospermous trunks with preserved bark**
2 **from the Middle Triassic of Antarctica.**

3
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10
11 **Abstract**

12 Permineralized gymnosperm axes with pycnoxylic wood from the Middle Triassic Fremouw
13 Formation of the Central Transantarctic Mountains, Antarctica, are assigned to the
14 corystosperms (seed ferns) and conifers. Both groups have been previously described from this
15 formation based on juvenile stems with attached leaf bases and decorticated trunks. Here we
16 describe large axes with preserved bark from the Fremouw Peak permineralized peat locality.
17 The specimens are characterized by a small parenchymatous pith with clusters of sclereids, a
18 thick cylinder (> 10 cm) of pycnoxylic wood, and 1–2 cm of bark containing distinctive clusters
19 of sclereids and a complex system of cortical vascular bundles. Comparison with axes previously
20 described from the Middle Triassic of Antarctica shows that the new specimens are most similar
21 to *Kykloxylon*, a corystosperm genus based on young stems bearing *Dicroidium* leaves, and with
22 a portion of axis previously described as *Rhexoxylon* like. We suggest that both the new
23 specimens and the *Rhexoxylon*-like axis represent proximal parts of a *Dicroidium/Kykloxylon*
24 plant that possibly had a fluted trunk base, and we discuss the problem of delimiting features in
25 corystosperm axes.
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27 **Key words:** corystosperms; bark; stem anatomy; extraxylary tissues; Middle Triassic; Antarctica
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1. Introduction

Evidence of forest growth in Antarctica during the Triassic consists of *in situ* stumps and scattered woody axes, some preserved in permineralized peat. Paleogeographic reconstructions (e.g., Parrish, 1990) and tree-ring data (Taylor and Ryberg, 2007) indicate that these trees were growing in a temperate high-latitude environment characterized by a strongly seasonal light regime. Continued investigations of early Middle Triassic permineralized peat from Fremouw Peak in the Central Transantarctic Mountains have revealed that almost all major groups of Triassic gymnosperms were able to grow in these unusual conditions (see list in Taylor and Ryberg, 2007). Anatomically preserved stems include the cycad *Antarcticycas*, reconstructed as a small plant with a short upright or possibly subterranean stem (Smoot et al., 1985; Hermsen et al., 2009) and axes with a significant amount of pycnoxylic wood. Among the later, young stems or branches with attached leaf bases have been assigned to the conifers and seed ferns, specifically the podocarps (*Notophytum*, Meyer-Berthaud and Taylor, 1991) and corystosperms (*Kykloxylon*, Meyer-Berthaud et al., 1993). The affinities of large pieces of wood found at Fremouw Peak are, however, more problematic. *In situ* decorticated stumps of *Jeffersonioxylon* from contemporaneous or slightly younger deposits of nearby Gordon Valley were initially compared to the podocarps based on wood anatomy (Del Fueyo et al., 1995). The presence of leaf mats of the corystosperm morphogenus *Dicroidium* Gothan in the rocks which contained the stumps, however, led Cúneo and his collaborators (2003) to assign the wood to the corystosperms. In addition to these specimens, the outer part of a large axis with dissected secondary xylem from Fremouw Peak has been compared to *Rhexoxylon* Bancroft (Taylor, 1992). This genus, which is documented in Triassic–Lower Jurassic localities of South America and southern Africa (e.g., Walton, 1924; Archangelsky and Brett, 1961; Anderson and Anderson, 1983; Artabe et al., 1999; Bodnar, 2008), is traditionally assigned to the corystosperms based on co-occurrence with *Dicroidium* foliage in the Ischigualasto Formation of Argentina (Archangelsky, 1968).

In order to elucidate the affinities of the permineralized trees from the Fremouw Peak locality and to compare them in more detail to taxa found elsewhere in Gondwana, we searched for specimens providing additional anatomical information. In this report, we describe portions of trunks with well-preserved bark tissues. The presence of bark, which is rarely preserved in fossils, provides new information on the anatomy of these trees and allows for a more detailed comparison, especially with previously described juvenile axes from the Triassic of Antarctica. The term bark is used here, as defined by Esau (1965, p. 272), to include all the tissues located outside the secondary xylem, i.e., secondary phloem, primary phloem (if present), primary cortex (if present), and periderm. The epithet extraxylary is used here to designate structures located outside the secondary xylem but not part of the bark as defined above, i.e., vascular bundles.

2. Material and methods

The specimens were collected from a col on the north side of Fremouw Peak in the Beardmore Glacier area, Transantarctic Mountains, Antarctica (84°17'41" S, 164°21'48" E). They occur within the upper Fremouw Formation in permineralized peat, which is regarded as early Middle Triassic based on palynomorphs (Farabee et al., 1990). The specimens are silicified

73 and were studied using the cellulose acetate peel method (Galtier and Phillips, 1999) after the
74 polished surface was etched for 2–3 min in 49% hydrofluoric acid. Some of the peels were
75 scanned at 1200 dpi using a flatbed Epson Perfection V750 Pro scanner. Selected portions of
76 peels were also mounted on microscope slides with Eukitt® medium for microscopic observation
77 and photography. Cell and tissues measurements were made using Wright Cell Imaging Facility's
78 ImageJ software (Rasband, 1997–2009). Unless specified in the text, averages correspond to a
79 minimum of 50 measurements. Some images are composites of several photos in different focal
80 planes created with the Stack Focuser plug-in of ImageJ; these are indicated in the figure
81 explanations. Specimens are deposited in the Paleobotanical Collections, Natural History
82 Museum and Biodiversity Institute, University of Kansas, under specimen numbers 10442,
83 10673, 10808, 11700, 11773, 15801, 15830, 15904 and slide accession numbers 24012-24013
84 and 26538-26554.

85 86 **3. Description**

87 The specimens range from 2-15 cm long and 3-19 cm in diameter. They have a thick cylinder of
88 pycnoxylic secondary xylem surrounded by 1–2 cm of bark containing distinctive clusters of
89 thick-walled cells and vascular strands. All but one specimen consist of the external portion of
90 large woody axes with their central part (pith and primary xylem) missing (Plate I, 1, 2). The
91 specimen preserved in peat block 10,808 represents a portion of a branching axis and provides
92 some information on the anatomy of the pith.

93 94 **3.1. Secondary xylem (Plate I)**

95 In the largest specimen, the amount of preserved secondary xylem is up to 10 cm in thickness
96 and is slightly wedge shaped in cross section (Plate I, 1, 2). The tissue is composed exclusively
97 of tracheids and narrow, parenchymatous rays (Plate I, 3). Numerous growth rings are present,
98 each characterized by a small number of latewood tracheids. These show no significant increase
99 in cell wall thickness compared to the earlywood tracheids, but are narrower in radial diameter
100 (Plate I, 3). In some cases, the secondary xylem contains a so-called abnormal ring, characterized
101 in transverse section by the presence of several discontinuous radial layers of parenchymatous
102 tissue (Plate I, 4). These layers can occur within a typical growth ring, which indicates that they
103 may have formed during the growing season.

104 One of the specimens (15,830) also includes parenchymatous sectors that interrupt the
105 secondary xylem cylinder (Plate I, 1, 2, 5). The anatomy of these regions is comparable to that of
106 the inner bark (see §3.2.) and consists of parenchymatous tissue containing scattered groups of
107 thick-walled cells and small wedge-shaped vascular bundles with secondary growth (Plate I, 5).
108 Most of the bundles have the same general orientation as the trunk, i.e., vertical, but a few follow
109 a more oblique course. On both sides of the parenchymatous sectors, the secondary xylem of the
110 trunk forms small wedges that extend in toward the parenchymatous interruption (Plate I, 5). In
111 cross section, growth rings also appear curved inward on both sides of the parenchymatous
112 sector (Plate I, 5).

113 Secondary xylem tracheids are square to polygonal in cross section and about 38 µm in
114 diameter (Plate I, 3). They have 1–3 rows of bordered pits on their radial walls (Plate I, 6) and up
115 to 4 rows on the largest tracheids. Pits are circular when uniseriate, but hexagonal and crowded

116 when bi- or multiseriate. They are about 13 μm in diameter ($n=25$) and have a small (2–5 μm)
117 circular to elliptical aperture (Plate I, 6). Rays are uniseriate (Plate I, 7), rarely partly biseriate,
118 and a few cells high (<10). In tangential section, ray cells are rectangular in the center and
119 rounded to pointed at the top and bottom of the rays; they measure 31 x 52 μm . Cross-field
120 pitting usually consists of several small, circular-to-oval pits (Plate I, 6, 8, arrowheads). Cross-
121 field pits with horizontally elongated apertures are present in some cases (Plate I, 9).

122 123 **3.2. Bark (Plate II, III)**

124 The bark is characterized by the presence of conspicuous groups of thick-walled cells and a thin,
125 sinuous periderm (Plate II, 1, Pe). The area immediately external to the secondary xylem,
126 corresponding to the location of the vascular cambium and the youngest secondary phloem, is
127 typically crushed or incompletely preserved (Plate II, 2, 3). The organization of old secondary
128 phloem is clearly seen in some specimens (Plate II, 4). In transverse section, it is possible to
129 recognize radially aligned thin-walled cells (Plate II, 4, t), most likely corresponding to the sieve
130 cells and phloem parenchyma, as well as uniseriate parenchymatous rays (Plate II, 4, r) and
131 conspicuous groups of polygonal thick-walled cells (Plate II, 2, 4, asterisk). The thin-walled cells
132 have an average diameter of 46 μm in transverse section and are elongated in longitudinal
133 section (Plate II, 3). The thick-walled cells form ovoid clusters that average 200–250 μm in
134 diameter (range 50–400 μm). Individual cells in the clusters are isodiametric (Plate II, 2–4) and
135 characterized by polylamellate walls; they most likely represent sclereids (Parameswaran, 1980).
136 The sclereids range from 20–120 μm (average 60 μm) in diameter and have walls up to 27 μm
137 thick; primary pitting is visible in some cells. In areas where there are no extraxylary vascular
138 bundles, clusters of sclereids occur in a somewhat regular arrangement and are visible extending
139 outward to the periderm (Plate II, 5). In some specimens (e.g., 15,830; 11,700) there are no
140 sclereid clusters in the inner bark, but they are present and regularly arranged in the outer bark.

141 The outermost region of the bark consists of a thin periderm that can show a very
142 irregular course in cross section, most likely linked to the production of lateral organs (Plate I, 1–
143 2; Plate II, 1, 6). The periderm has a relatively constant thickness of about 700 μm and is
144 composed of up to 40 layers of radially aligned, thin-walled cells that are rectangular in cross
145 section and about 15 x 30 μm (Plate II, 5, 6). In several specimens, areas with an anatomy
146 similar to that of the bark and delimited by the same type of periderm are visible around the
147 specimens (Plate II, 6). These could either indicate the production of several layers of periderm
148 or the presence of the base of lateral organs that remained attached to the trunk. Because all the
149 specimens represent only small sectors of trunks, it is not possible to determine accurately the
150 anatomy and course of these putative lateral organs.

151 Vascular bundles with both secondary xylem and phloem occur in the bark and can vary
152 in diameter (Plate I, 2; Plate II, 6, arrowhead; Plate III, 1); many are wedge shaped in transverse
153 section (e.g., Plate II, 6, upper arrowhead). Secondary xylem is usually eccentric, i.e., much more
154 developed on one side of the bundle (Plate II, 6), but in a few instances is equally developed on
155 the two sides (Plate III, 1). The secondary xylem of these bundles is comparable in anatomy to
156 that of the trunk. A lacuna or a zone of crushed opaque tissue outside the centrifugal xylem
157 generally indicates the location of the secondary phloem (Plate III, 1). The orientation of the
158 bundles in relation to that of the trunk is variable. For example, in specimen 15,830 most bundles

159 have more extensive development of secondary tissues on the side located toward the center of
160 the trunk, while in specimen 15,904 most bundles have a larger amount of secondary tissue on
161 the side that is away from the center of the trunk. In a given transverse section, most bundles are
162 oriented parallel to the vertical axis of the trunk, but a few appear in longitudinal section, running
163 perpendicularly or obliquely. In some cases the bundles are branching within the bark.
164

165 **3.3. Axis center**

166 Specimen 10,888 represents a portion of a branching stem and is the only example where
167 the center of an axis has been observed. The specimen has a wood and bark anatomy comparable
168 to the others, but includes a portion of pith tissues about 255 x 112 μm wide in the center (Plate
169 III, 2, Pi). The pith is composed of two types of cells, parenchyma cells that are poorly preserved
170 or absent, and clusters of thick-walled sclereids 20–50 μm in diameter (Plate III, 2, asterisks).
171 The secondary xylem forms a single solid cylinder around the pith, which indicates that its
172 development was only centrifugal.
173

174 **4. Affinities**

175 Three groups of gymnosperms have been recognized in the permineralized peat from the
176 Fremouw Peak formation: cycads, conifers, and corystosperms (seed ferns). In order to clarify
177 the affinities of the new specimens, we provide here a comparison with stem morphogenera of
178 these three groups previously described from this formation. A least two other gymnosperm
179 groups have been reported in compression floras from the Triassic of Antarctica, the peltasperms
180 and ginkgoaleans (e.g., Escapa et al, 2010b). However, there is no information on the anatomy of
181 peltasperm stems in general, and the specimens do not show any characters indicating
182 ginkgoalean affinities such as heterogeneity of secondary xylem tracheid diameter (e.g., Scott et
183 al., 1962).

184 **4.1. Cycadophytes**

185 The new specimens from the Fremouw Formation are characterized by a combination of
186 a thick cylinder of pycnoxylic wood and parenchymatous bark with regularly arranged clusters
187 of sclereids, as well as many vascular bundles that extend through the bark. The significant
188 amount of parenchyma in the bark and the apparently complex arrangement of extraxylary
189 bundles are somewhat similar to that of the cycadophytes. In both Cycadales and Bennettitales,
190 however, stems typically exhibit only a narrow cylinder of secondary xylem compared to the
191 width of the pith and cortex, a different configuration from that of the new Fremouw Peak axes.
192 A few cycadophytes, however, produce a relatively large cylinder of wood; e.g., the extant cycad
193 *Dioon spinulosum* can produce up to 10 cm of wood (Chamberlain, 1911). *Antarcticycas* is
194 currently the most completely known fossil gymnosperm from the Fremouw Formation, with
195 anatomically preserved stems, roots, leaves, cataphylls, and possible male cones (Smoot et al.,
196 1985; Hermsen et al., 2009). All known *Antarcticycas* stems are small and only a few
197 centimeters in diameter. Despite a somewhat similar appearance due to the width of the cortex
198 and the sinuous periderm, *Antarcticycas* stems are easily distinguished from the new specimens
199 by several features. These include the large parenchymatous pith, manoxylic secondary xylem,
200 different anatomy of the secondary phloem, including the absence of clusters of sclereids, the
201 presence of girdling leaf traces, and the presence of conspicuous mucilage canals in the pith and

202 cortex in *Antarcticycas* (Smoot et al., 1985). Since all or some of these characters are also found
203 in other cycads, it is highly improbable that the new Fremouw specimens represent a cycad.
204

205 4.2. *Conifers and corystosperms*

206 Stem morphogenera of these two groups present numerous similarities and are thus considered
207 here together. A discussion on the difficulty of distinguishing some fossil conifer and
208 corystosperm stems is provided in the next section (§5).
209

210 4.2.1. *Notophytum* (conifer)

211 *Notophytum krauselii* is represented in the Fremouw permineralized peat by roots, young
212 stems, and large decorticated axes exceeding 20 cm in diameter. This plant is assigned to the
213 conifers based on the anatomy of the secondary xylem and of the leaves attached to young stems
214 (Meyer-Berthaud and Taylor, 1991); it has been suggested that the leaves correspond to the
215 compression foliage taxon *Heidiphyllum* (Axsmith et al., 1998; Escapa et al., 2010a). The pith of
216 *Notophytum* is exclusively composed of parenchyma cells, while the new specimens also have
217 clusters of sclereids. Secondary xylem tracheids of *Notophytum* typically have a single row of
218 circular pits on the radial walls and when biseriate, the pits are either opposite or alternate.
219 Cross-field areas consistently show one to four, usually two large (7 x 12–24 µm), oval-to-
220 rectangular simple pits. This differs from the specimens described in this paper, which
221 commonly have 2–3 rows of radial pits and cross-field areas with numerous small, circular-to-
222 elongate pits. The secondary phloem of *Notophytum* is composed of multiseriate bands of sieve
223 cells alternating with uni- to biseriate bands of parenchyma cells (Meyer-Berthaud and Taylor,
224 1991). Some of the older stems also have multiseriate bands of fibers, an organization that differs
225 from the new specimens where the only recognizable thick-walled cells occur as clusters of
226 sclereids. Finally, the periderm in *Notophytum* consists of large polyhedral cells with thickened
227 walls (Meyer-Berthaud and Taylor, 1991).
228

229 4.2.2. *Jeffersonioxylon* (corystosperm)

230 Trunks of *Jeffersonioxylon gordonense* from the Gordon Valley (Del Fueyo et al., 1995)
231 are up to 60 cm in diameter. They occur rooted in shales containing mats of *Dicroidium*, a
232 typical corystosperm leaf morphogenus (Cúneo et al., 2003). *Jeffersonioxylon* trunks are
233 decorticated and variably compressed and, as a result, only their secondary xylem anatomy is
234 known. Rays are mostly uniseriate and low, a condition found in all the non-cycad gymnosperms
235 described to date from the Fremouw peat. Tracheid radial pitting in *Jeffersonioxylon* consists of
236 one or two rows of pits in opposite or alternate arrangement. Cross-field pitting has been
237 described as generally consisting of one or two circular to ovate pits, although some cross fields
238 can contain up to four pits (Del Fueyo et al., 1995, fig. 15). Since the number of pits in a given
239 cross field can depend on the diameter of the tracheid, the exact number is perhaps not a useful
240 systematic character. Nevertheless cross-field pits of *Jeffersonioxylon* are smaller than the ones
241 observed in the new specimens, which are only 3–5 µm in diameter. The limited number of
242 characters available for comparison between *Jeffersonioxylon* and the new specimens prevents
243 further assessment.
244

245 4.2.3. *Kykloxylon* (corystosperm)

246 Young stems of *Kykloxylon fremouwensis* are assigned to the corystosperms based on the
247 mode of production of leaf traces in the stems and anatomy of the leaves; leaves are those of
248 *Dicroidium fremouwensis* from the same locality (Pigg, 1990; Meyer-Berthaud et al., 1992,
249 1993). *Kykloxylon* stems possess a parenchymatous pith containing secretory cavities and
250 sclerotic nests comparable to the clusters of sclereids observed in the new trunks. The secondary
251 xylem of *Kykloxylon* is characterized by tracheids with 1–3 rows of opposite-to-alternate pits on
252 their radial walls, a configuration which is also similar to the new trunks with preserved bark.
253 *Kykloxylon* has 3–9 pits in the cross fields; pits are oval to elongate and range from 7 x 10 µm to
254 10 x 25 µm, an arrangement and size comparable to that observed in the wood of the new trunks.
255 The secondary phloem of *Kykloxylon* contains sieve cells and uniseriate parenchymatous rays
256 (Meyer-Berthaud et al., 1993). There are conspicuous sclerotic nests in the pith, and sclereid
257 clusters in the cortex and leaf bases of *Kykloxylon* that are similar in size and structure to those in
258 the stems described here. Another similarity can be seen in the periderm of *Kykloxylon*, which
259 consists of numerous radial rows of rectangular thin-walled cells. Thus, *Kykloxylon* appears to be
260 the taxon that most closely resembles the new specimens. One distinct difference is the absence
261 of secretory cavities which are typically found in several corystosperms organs from the
262 Fremouw permineralized peat deposit, including *Kykloxylon* stems and leaf bases (Meyer-
263 Berthaud et al., 1993), *Dicroidium fremouwensis* foliage (Pigg, 1990), *Pteruchus fremouwensis*
264 pollen organs (Yao et al., 1995) and *Umkomasia resinosa* cupulate organs (Klavins et al., 2002).
265 It is possible that the secretory cavities are a feature of young organs, i.e. short shoots, leaves and
266 reproductive organs. For example, juvenile shoots and twigs of the extant silver birch (*Betula*
267 *pendula*) have resinous glands that are replaced by bark cells at the end of the growing season
268 (Lapinjoki et al., 1991). Since several types of compressed *Dicroidium* foliage are recognized in
269 Antarctica (e.g., Boucher et al., 1993; Escapa et al., 2010b), an alternative hypothesis is that
270 there were several slightly different stems that bore this foliage morphotaxon.

271
272 4.2.4. *Rhexoxylon*-like specimen of Taylor (1992) (?corystosperm)

273 While *Rhexoxylon* is known from Africa and well documented in South America, only a
274 fragmentary specimen from Antarctica has been compared to this genus (Taylor, 1992). The
275 Antarctic specimen consists of the outer portion of a large axis with pycnoxylic secondary xylem
276 forming wedges separated by parenchymatous tissue. The secondary xylem has cross-field areas
277 with 2–6 small simple pits about 7 µm wide. The lack of data on the primary tissues prevented a
278 more detailed comparison of the specimen with *Rhexoxylon*, a genus characterized by medullary
279 vascular bundles and centripetal secondary growth (e.g., Archangelsky and Brett, 1961). The
280 extraxylary tissues in the *Rhexoxylon*-like axis from Antarctica include a zone more than 1 cm
281 thick composed of parenchymatous ground tissue containing vascular strands (Plate III, 3). In
282 cross section, the specimen has a layer of periderm (370–860 µm wide) that follows a sinuous
283 path and is composed of thin-walled cells. Poorly preserved areas delimited by the same type of
284 periderm are present in the outer part of the specimen and may represent the base of lateral
285 organs. Although clusters of sclereids were not observed in the inner part of the bark, they are
286 present in at least one of these external zones (Plate III, 3).

287 The new specimens from Fremouw Peak share numerous characters with this
288 *Rhexoxylon*-like axis, including the anatomy of the secondary xylem and extraxylary tissues, and
289 the presence of parenchymatous sectors in the wood with anatomy comparable to that of the
290 bark. To date no axis with a typical *Rhexoxylon* stele (i.e., containing medullary bundles and
291 both centrifugal and centripetal secondary growth) has been found in the Triassic permineralized
292 peat from Antarctica. A small number of gymnosperm axes from Fremouw Peak show slight
293 development of centripetal secondary xylem (A.-L.D, personal observation); however, they lack
294 perimedullary bundles and clearly differ from *Rhexoxylon* and from the new specimens,
295 including in their bark anatomy. Currently, the most parsimonious hypothesis is that both the
296 *Rhexoxylon*-like specimen of Taylor (1992) and the new specimens described in this paper
297 represent the same arborescent taxon with corystosperm affinities. This plant type is
298 characterized by trunks with a woody cylinder that may be dissected in its outer part but is more
299 similar to *Kykloxylon* than to *Rhexoxylon* in stelar organization. It is possible that the
300 *Rhexoxylon*-like specimen from Fremouw Peak represents growth after some type of wounding
301 or part of a trunk with a fluted base. Fluted trunks are formed by the unequal production of
302 secondary xylem around the circumference of the axis caused by a local reduction or absence of
303 cambial activity (Schweingruber, 2007, p. 22–25). This phenomenon is well documented in
304 extant trees such as the dawn redwood (*Metasequoia glyptostroboides*), and has also been
305 reported in some fossil conifers (e.g., Falcon-Lang et al., 2004, p. 55). The unequal cambial
306 activity has been linked to mechanical and physiological constraints (e.g., Day, 1964), although a
307 genetic component is apparently present in at least some species, such as the common lime (*Tilia*
308 *x vulgaris*, Pigott, 1992). The hypothesis that the so-called *Rhexoxylon*-like specimen from
309 Antarctica represents part of a wounded or fluted trunk would explain its co-occurrence with
310 axes that share numerous anatomical characters but in which the wood cylinder is complete or
311 less dissected. In the case of a fluted trunk, these axes would represent higher portions of the
312 trunk and branches; alternatively they could indicate the existence of a variation in trunk
313 development within the same morphotaxon.

314 315 4.3. *Other corystosperm stems with preserved bark*

316 Bark tissues have been described in detail in only a few corystosperms. The presence of a
317 thick cortex containing vascular strands as well as sclerotic nests and/or secretory cells has been
318 documented in several species of *Rhexoxylon*. In *R. africanum* from southern Africa (Bancroft,
319 1913; Archangelsky and Brett, 1961), the cortex is over 1 cm thick and contains sclerotic nests
320 and vascular strands. *Rhexoxylon piatnitzkyi* occurs in the Upper Triassic (Carnian) Ischigualasto
321 Formation of Argentina and possesses a cortex containing vascular strands and "cysts," the latter
322 term designating parenchyma cells with dark contents (Archangelsky and Brett, 1961).
323 Specimens of *R. cortaderitaense* are known from the Middle Triassic Cortaderita Formation of
324 San Juan Province, Argentina. These stems have a well-preserved cortex that is 1–3 cm wide and
325 composed of parenchyma containing idioblasts, probable sclerotic nests, and regularly arranged
326 structures described as vascular strands (Bodnar, 2008). *Rhexoxylon brunoi* (Upper Triassic Los
327 Colorados Formation, Argentina) is described as including a rhytidome-like cork layer up to 2
328 cm thick that contains quadrangular or rectangular suberized cells (Artabe et al., 1999), but no
329 detailed illustration of this tissue was provided. As far as we are aware, there is no detailed

330 description of the cortex available for other corystosperm axes (e.g., *Elchaxylon*, *Tranquiloxyton*,
331 *Cuneumxylon*).
332

333 **5. Distinguishing corystosperm and conifer stems**

334 Conifers and corystosperms co-occur in numerous Triassic localities throughout
335 Gondwana. Both groups include large trunks with well-developed pycnoxylic wood, so
336 distinguishing them solely based on the anatomy of decorticated axes can be problematic.
337 Indeed, similar features of the primary and secondary vascular system can be found in Triassic
338 conifer and corystosperm stems, and there are examples of taxa initially described as conifers
339 that have been reassigned to the corystosperms, e.g., *R. cortaderitaense* (Bodnar, 2008), which
340 was previously assigned to *Protophyllocladoxylon* Kräusel. *Rhexoxylon* Bancroft clearly differs
341 from contemporaneous conifers by its mesarch primary xylem maturation, complex system of
342 perimedullary bundles, and development of centripetal and centrifugal secondary xylem and
343 phloem (e.g., Walton, 1924; Archangelsky and Brett, 1961). Other genera more recently included
344 in the corystosperms, however, have endarch primary xylem maturation and lack perimedullary
345 bundles, e.g., young stems of *Kykloxylon* from Antarctica (Meyer-Berthaud et al., 1993) and late
346 Middle Triassic *Cuneumxylon* trunks from the Paramillo Formation of Argentina (Artabe and
347 Brea, 2003). As far as wood anatomy is concerned, stems currently assigned to the
348 corystosperms possess secondary xylem with uniseriate rays and 1–3 rows of pits on the radial
349 wall of tracheids, a configuration that also occurs in numerous taxa of Mesozoic conifers (e.g.,
350 Philippe and Bamford, 2008). Araucarioid and podocarpoid types of cross-field pitting have been
351 described in taxa assigned to both groups. *Rhexoxylon africanum* has only one large pit in each
352 cross field, but there is significant variation in both shape and number of cross-field pits within
353 the genus *Rhexoxylon* (see Artabe and Brea, 2003, table 2).

354 A component of the problem of distinguishing corystosperm and conifer stems comes
355 from the differential weight given by authors to various sets of anatomical characters.
356 Corystosperms have been defined based on foliage and reproductive structures (family
357 Corystospermaceae of Thomas, 1933; Corystospermales of Taylor et al., 2009). Corystosperm
358 stems can thus be defined as stems bearing *Dicroidium* foliage, *Pteruchus* pollen organs, or
359 *Umkomasia* ovulate structures. However, the different organs are typically found detached in the
360 fossil record or are attached but preserved in compression, so the stem anatomy remains
361 unknown (Axsmith et al., 2000; Anderson et al., 2008). The assignment to the corystosperms of
362 anatomically preserved axes from Antarctica is based on association with *Dicroidium* leaf mats
363 in the case of *Jeffersonioxylon* trunks (Cúneo et al., 2003). In the case of *Kykloxylon*, the
364 evidence is much stronger, based on the presence of attached leaf bases with an anatomy similar
365 to *Dicroidium* leaves, especially the presence of diagnostic secretory cells in the cortex of stems,
366 leaf bases, and leaves (Pigg, 1990; Meyer-Berthaud et al., 1992, 1993). The assignment of
367 *Rhexoxylon* stems to the corystosperms is based on their repeated association with compressed
368 *Dicroidium* leaves in the Ischigualasto Formation of Argentina (Archangelsky, 1968). Although
369 Archangelsky and Brett (1961) described the presence of a complex leaf base in *R. pianitzkyi*, no
370 clear anatomical connection between *Rhexoxylon* and *Dicroidium* has ever been conclusively
371 demonstrated in silicified specimens. Consequently, the only stem attached to *Dicroidium*-like

372 foliage with anatomy is *Kykloxylon*, and the similarities of the new trunks described in this paper
373 to this genus are a good indication of their corystosperm affinities.

374 Artabe and Brea (2003) base their concept of corystosperm stems on the presence of
375 anomalous secondary growth (see also Axsmith et al., 2007; Artabe and Brea, 2007 for a
376 discussion of this concept), because *Rhexoxylon*, the first genus of stems assigned to the group,
377 has a dissected cylinder with both centripetal and centrifugal secondary xylem present in each
378 segment of the stele, as well as perimedullar bundles. Centripetal secondary xylem has also been
379 described in *Elchaxylon* (Artabe and Zamuner, 2007) from the Upper Triassic of Mendoza
380 province, Argentina, although in this taxon, the centrifugal secondary xylem is a continuous
381 cylinder. Two other South American genera, *Cuneumxylon* (Artabe and Brea, 2003) and
382 *Tranquiloxyton* (Herbst and Lutz, 1995), have been included in the corystosperms based on the
383 existence of so-called anomalous secondary development. This includes unequal activity of the
384 vascular cambium around the circumference of the stem, which produces a fluted axis, and the
385 presence of supernumerary cambia producing included phloem. Both characters are present in
386 *Cuneumxylon*, while *Tranquiloxyton* only shows unequal activity of the cambium. Artabe and
387 Brea (2003) did not consider *Kykloxylon* in their synthesis on corystosperm stems because of its
388 solid cylinder of wood. However, *Kykloxylon* was described from young stems (1–5 years old)
389 and in *Cuneumxylon*, for example, the first supernumerary cambium occurs after the formation
390 of 6 cm of wood (Artabe and Brea, 2003). If peculiarities of secondary growth that might occur
391 later in development are not considered, it might be hypothesized that *Tranquiloxyton* and
392 *Cuneumxylon* have more in common with *Kykloxylon* and the new Antarctic specimens than with
393 *Rhexoxylon*. In particular, these three taxa all lack perimedullary bundles and any form of
394 centripetal secondary growth, as well as having primary xylem maturation that is endarch instead
395 of mesarch. In addition, both *Cuneumxylon* and the Antarctic specimens have secondary xylem
396 that displays several cross-field pits instead of 1–3 large pits as in *Rhexoxylon*. If placed on the
397 two conjectural corystosperm phylogenetic trees of Bodnar (2008), which are mostly based on
398 secondary growth characters, the new Antarctic specimens would be grouped either with
399 *Tranquiloxyton* and *Cuneumxylon* (Bodnar, 2008, fig. 10A) or with *Kykloxylon* in the group with
400 "normal cylinder axes" (Bodnar, 2008, fig. 10B). Whether the so-called "non-anomalous"
401 secondary growth of the new axes, *Kykloxylon*, *Tranquiloxyton*, and *Cuneumxylon* results from a
402 loss of characters present in *Rhexoxylon* (as suggested by Bodnar) or is in fact primitive remains
403 to be tested.

404

405 **Conclusion**

406 Two types of *Dicroidium* plants have been proposed: (1) a *Dicroidium/Rhexoxylon* plant
407 with a tree fern-like habit (Petriella, 1978), based on the association of *D. zuberi* foliage and *R.*
408 *piatnitzkyi* stems in the Ischigualasto Formation of Argentina (Archangelsky, 1968), and (2) a
409 *Dicroidium/Kykloxylon* plant in Antarctica with a solid cylinder of pycnoxylic wood and foliage
410 that was probably seasonally deciduous, i.e., a more conifer-like habit (Meyer-Berthaud et al.,
411 1993, Taylor et al., 2006). The presence of large axes in the permineralized peat from Fremouw
412 Peak that share numerous anatomical characters with *Kykloxylon* supports the idea that this
413 genus represents the distal part of an arborescent plant that bore *Dicroidium* leaves and had a
414 stelar organization different from *Rhexoxylon*. In this context, it is interesting to note that

415 according to Anderson and Anderson (1983, p. 69), *Rhexoxylon* has never been found associated
416 with *Dicroidium* in southern Africa and that the similarity between some corystosperm and
417 conifer stems can complicate reconstructions based on associated organs. Additional data on
418 gymnosperm stems from the Triassic of Gondwana, especially dealing with the anatomy of the
419 bark and lateral organs, will be necessary to provide a more accurate definition of corystosperm
420 stem anatomy and to more fully understand the diversity of stem types that bore *Dicroidium*
421 foliage.

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- 541
- 542

543

544 **Figure legends**

545 **Plate I.** Trunks with preserved bark from the Middle Triassic of Antarctica: general aspect (1-2)
546 and secondary xylem anatomy (3-9). Center of the trunk is toward the bottom in all transverse
547 sections. Legend: Pe: periderm, T: parenchymatous sectors in wood, X2: secondary xylem, *:
548 cluster of sclereids.

549 1: Transverse section of specimen 15,830. Scanned peel 15,830 C #1; scale bar = 2 cm.

550 2: Line drawing of the specimen in Fig. 1 in transverse section showing secondary xylem (X2),
551 extraxylary tissues (grey area) with cortical vascular bundles of various sizes (black) and
552 periderm (Pe), and two parenchymatous sectors (T) in the secondary xylem. Scanned peel 15,830
553 C #1; scale bar = 2 cm.

554 3: Transverse section through portions of two growth rings showing ring boundary. Note that
555 latewood tracheids (arrowhead) show reduced radial diameter but similar wall thickness to
556 earlywood tracheids. Slide 26538 (peel 15,830 A2bot #3a); scale bar = 200 μ m.

557 4: So-called abnormal growth ring in transverse section containing disorganized growth and
558 parenchyma cells. Slide 26538 (peel 15,830 A2bot #3a); scale bar = 250 μ m; focused stack of
559 three images.

560 5: Parenchymatous sector (T) partially dividing the woody cylinder as viewed in transverse
561 section. Note the presence of clusters of sclereids (*) and that the secondary xylem and the
562 growth rings are curved inward on either side of the sector. Slide 26539 (peel 15,830 A2bot #5);
563 scale bar = 2.5 mm.

564 6: Oblique radial section showing multiseriate pitting on the radial wall of tracheids and cross-
565 field pitting (arrowheads). Slide 26542 (peel 15,830 A side); scale bar = 100 μ m.

566 7: Low uniseriate rays and inter-tracheid pitting (arrowhead) in tangential section. Slide 26544
567 (peel 15,904 E #1 β); scale bar = 100 μ m.

568 8: Detail of cross field with several small circular pits (arrowheads) in radial section. Slide 26542
569 (peel 15,830 A side); scale bar = 25 μ m.

570 9: Detail of cross field with elongated pits in radial section. Slide 26547 (peel 15,904 E #2 β);
571 scale bar = 25 μ m; focused stack of three images.

572

573 **Plate II.** Trunks with preserved bark from the Middle Triassic of Antarctica: bark anatomy.
574 Center of the trunk is toward the bottom in all transverse sections. Legend: P2: old, probably
575 non-functioning, secondary phloem, Pe: periderm, r: root, T: parenchymatous sectors in wood,
576 X2: secondary xylem, *: cluster of sclereids.

577 1: Transverse section of etched surface of specimen showing the secondary xylem, secondary
578 phloem with conspicuous groups of thick-walled cells (darker spots), and periderm (Pe).
579 Specimen 10,673 Btop; scale bar = 1 cm.

580 2: Secondary xylem, cambial zone, and young phloem (double-headed arrow), and inner part of
581 the old secondary phloem in transverse section; slide 26554 (peel 10,673 Btop #2); scale bar =
582 200 μ m.

583 3: Secondary xylem, cambial zone, and inner part of the old secondary phloem in oblique radial
584 section. Note elongate cells in the secondary phloem (bottom center). Slide 26547 (peel 15,904 E
585 #2 β); scale bar = 200 μ m.

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586 4: Detail of inner part of old secondary phloem in transverse section showing thin-walled cells (r,
587 sieve elements or parenchyma), a ray (r), and sclereids. Slide 2655426547 (peel 10,673 Btop #2);
588 scale bar = 100 μ m.

589 5: Outer region of the bark in transverse section showing regularly arranged groups of sclereids
590 within the outermost secondary phloem (thin-walled cells) and the inner part of the periderm
591 (Pe). Note that the expansion of the dark cells in this region mostly disrupts the radial
592 arrangement of the cells. Slide 26554 (peel 10,673 Btop #2); scale bar = 200 μ m.

593 6: Outer region of a specimen in transverse section showing the sinuous course of the periderm
594 (folded on itself at the bottom left), two large vascular bundles (arrowheads), and young roots (r)
595 in the matrix outside the bark. Slide 26546 (peel 15,904 E #2 α); scale = 2.5 mm.

596
597 **Plate III.** Trunks with preserved bark from the Middle Triassic of Antarctica (1–2) and specimen
598 described as *Rhexoxylon* like (Taylor 1992) from the same locality (3). Center of the trunk is
599 toward the bottom in all transverse sections. Legend: Pe: periderm, Pi: pith, T: parenchymatous
600 sectors in wood, X2: secondary xylem, *: cluster of sclereids.

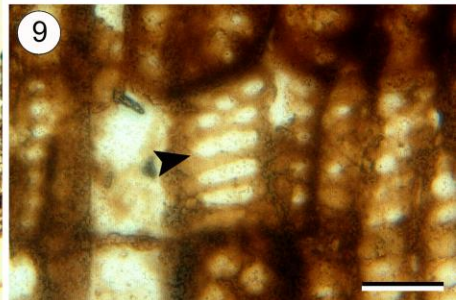
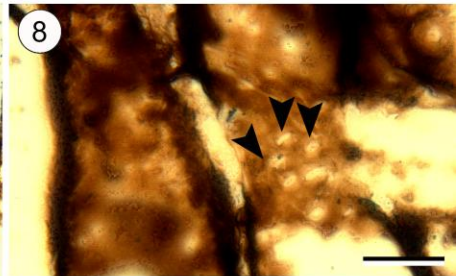
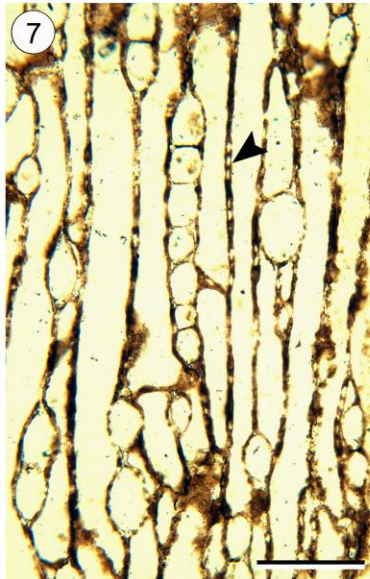
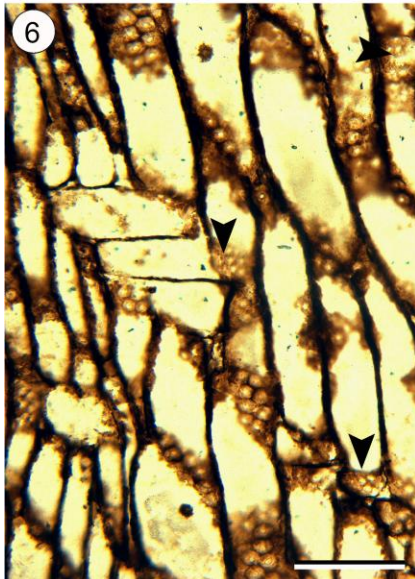
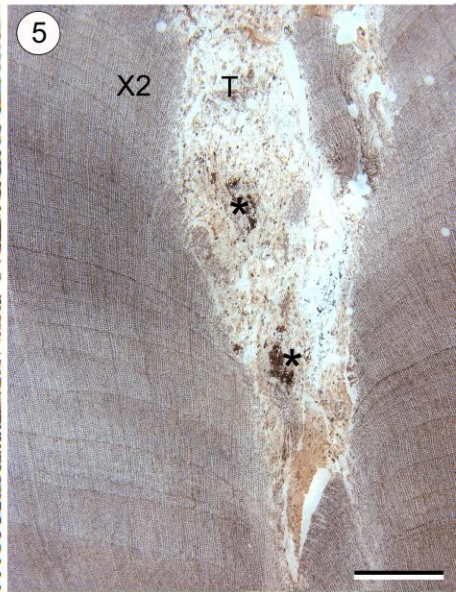
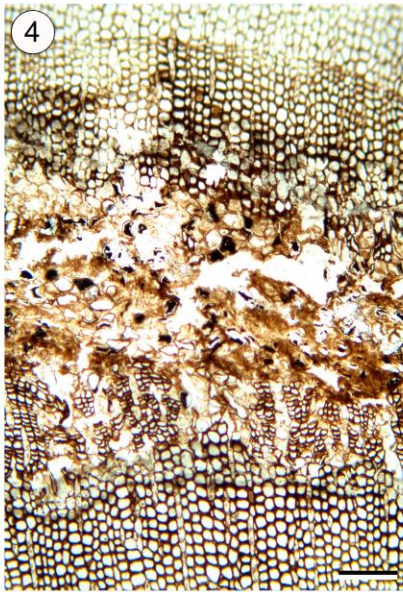
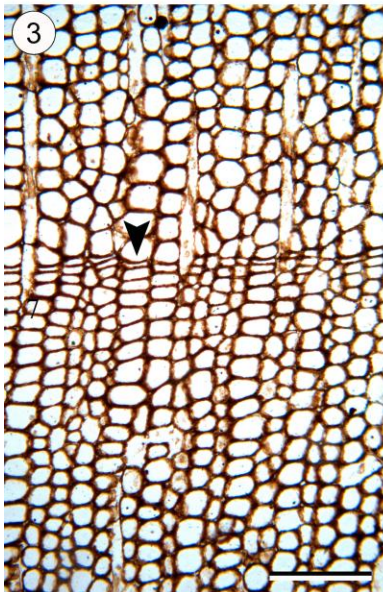
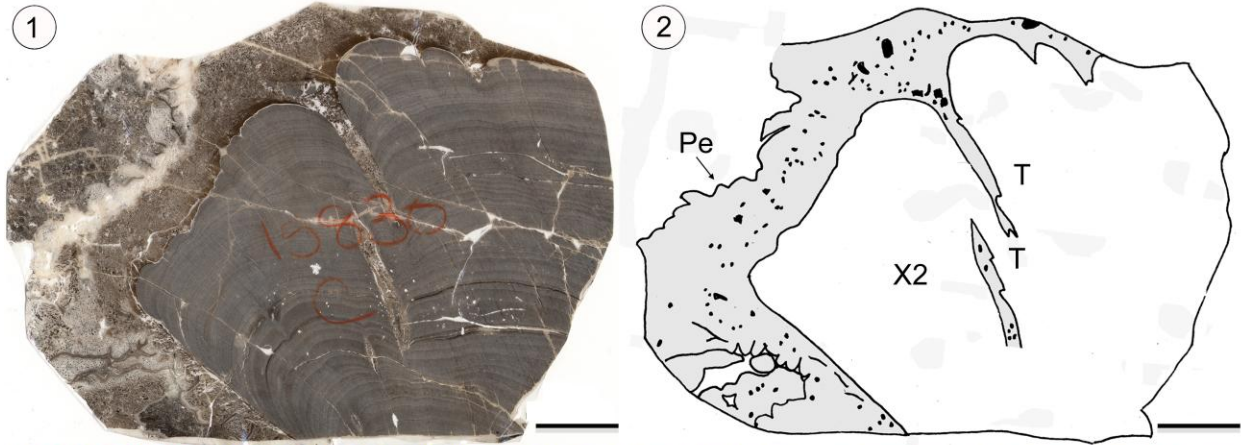
601 1: Detail of medium-sized cortical bundle in transverse section with secondary tissues developed
602 on two sides. The possible remains of the crushed secondary phloem (brown material, lower
603 right) are present outside the wider portion of secondary xylem. Slide 26549 (peel 11,700 B #1);
604 scale bar = 250 μ m.

605 2: General view of pith (Pi) in branching axis in transverse/oblique section; note clusters of
606 sclereids. Slide 26552 (peel 10,888 D #1); scale bar = 1 mm.

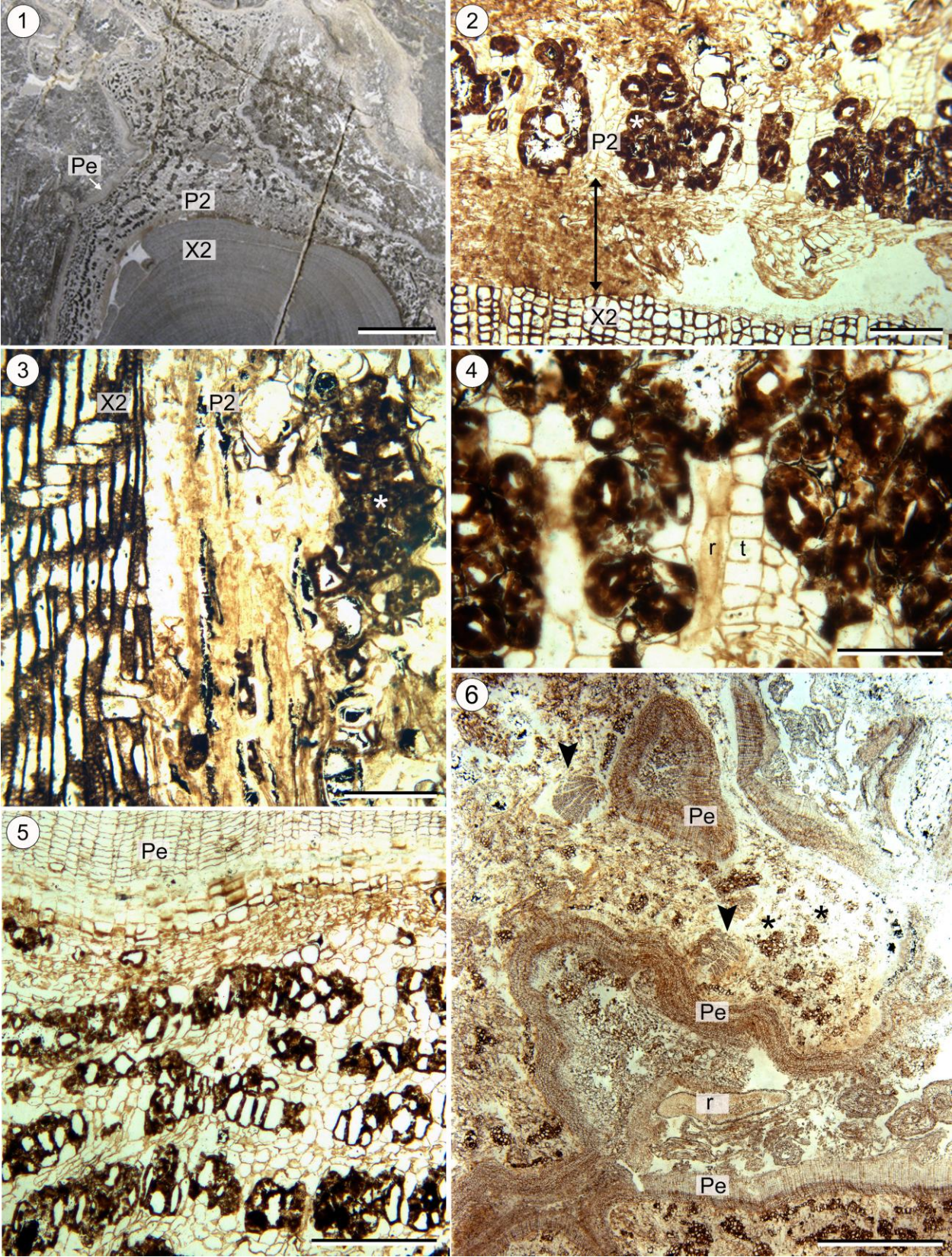
607 3: Outer part of the *Rhexoxylon*-like axis described by Taylor (1992) showing the wedge-shaped
608 secondary xylem (X2) interrupted by a parenchymatous sector (T). The bark contains extraxylary
609 vascular bundles (two are indicated by arrowheads), and a zone delimited by a periderm that
610 might represent the base of a lateral organ. Note the clusters of sclereids in this zone. Scan of
611 peel 11,314 D1top #1; scale bar = 500 μ m.

612
613

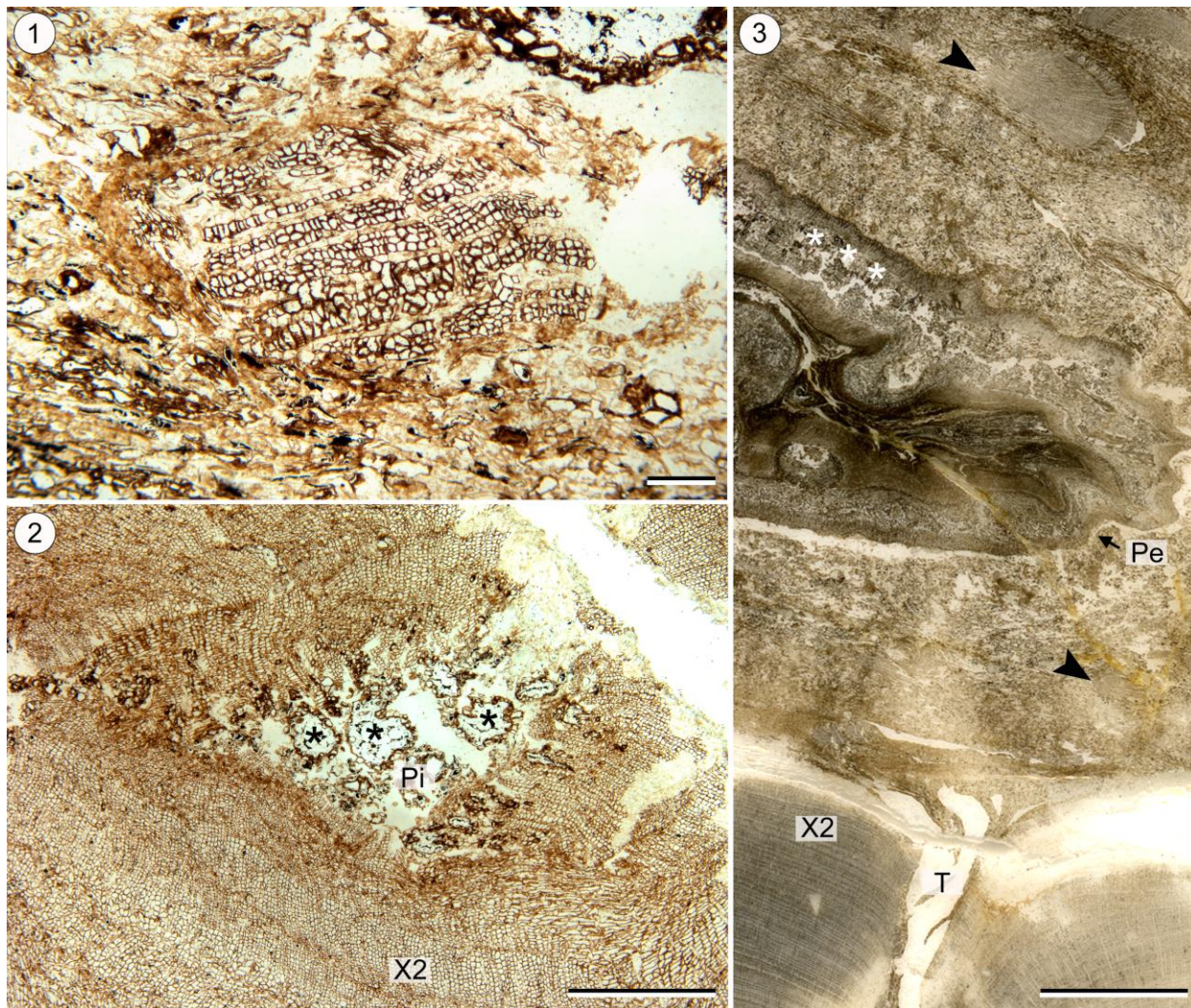
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