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Bark anatomy of Late Permian glossopterid trees from Antarctica

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15 **Abstract**

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3 16 The Glossopteridales are an extinct group of seed plants that dominated Gondwanan floras
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5 17 during the Permian. Their remains are found across a wide range of habitats and
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8 18 paleolatitudes, and it is particularly interesting to understand the anatomical characteristics
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10 19 that might have enabled such an extensive distribution. Here, we document for the first
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12 20 time the bark anatomy of high-latitude glossopteridalean trees using peels and thin-sections
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14 21 made from a Late Permian trunk from Skaar Ridge, Antarctica. The bark is 3 cm thick. The
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16 22 secondary phloem is composed of sieve cells, axial and ray parenchyma, and fibers
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18 23 arranged in discontinuous unicellular tangential layers. The outer bark is a rhytidome, with
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20 24 numerous alternating layers of periderm and non-conducting secondary phloem showing
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22 25 some proliferation of the axial parenchyma. Successive periderms mostly run parallel to
23
24 26 the cambium, with some longitudinal undulation and rare connections between two
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26 27 periderms. A similar anatomy was observed in bark fragments found isolated in the matrix
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28 28 or closely associated with large glossopterid stems or roots. The anatomy of the Skaar
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30 29 Ridge specimens shows that Antarctic Glossopteridales had a relatively thick, probably
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32 30 stringy bark. The retention of a significant amount of insulating dead bark tissue on the
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34 31 trunk likely provided protection of the cambium, conducting secondary phloem, and
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36 32 potential latent buds against biotic and abiotic environmental hazards (fire, frost, scalding,
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38 33 insects, etc.) and may have contributed to the extensive paleolatitudinal distribution of the
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40 34 Glossopteridales during the Permian.
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52 36 **Key words** paleobotany; Paleozoic; high-latitude; Glossopteridales; secondary xylem;
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54 37 secondary phloem; rhytidome.
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INTRODUCTION

The Glossopteridales are a group of seed plants of Permian and possibly Triassic age (Taylor *et al.* 2009 and references therein). Their distinctive leaves (*Glossopteris*), roots (*Vertebraria*), and reproductive structures have been reported from all parts of Gondwana, i.e., the southern continents of today. The importance of the group is three-fold. First, from an historical perspective, the distribution of *Glossopteris* leaves across Africa, Australia, Antarctica, India, and South America provided significant support in the early XXth century to the continental drift theory (Wegener 1915) and the reconstruction of the supercontinent Gondwana. From an evolutionary perspective, the reticulate leaves of the glossopterids have sometimes been compared to those of the dicotyledons and their complex reproductive structures to the angiosperm carpel, (e.g., Plumstead 1956; Stebbins 1974; Retallack & Dilcher 1981; Taylor & Taylor 1992). Finally, from a paleoecological perspective, the glossopterids appear as a major component of Permian ecosystems in Gondwana. Their abundant remains document an extensive paleolatitudinal distribution, from temperate to periglacial climatic zones (McLoughlin 2011 and references therein). In addition, the Glossopteridales are found in various depositional environments, from peatlands to well-drained environments, lakes, and even uplands (e.g., Cúneo *et al.* 1993). This distribution is particularly interesting in that it provides an example of a woody Paleozoic taxon adapted to a very large range of environmental conditions. In particular, the Glossopteridales rapidly colonized the high latitudes of Gondwana as the ice sheets retreated during the end-Permian (Isbell & Cuneo 1996). While today the tree line is at 64°- 72°N, the greenhouse climate of the end-Permian allowed glossopteridalean trees to form forests at latitudes above 75°S, and probably up to 85°S (Grunow 1999; Scotese 2002). There, they grew under a more extreme light regime than any extant tree, with 4-5 months of perpetual light in summer and darkness in winter.

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63 Anatomically preserved fossils of Glossopteridales from such high paleolatitudes offer
64 us unique insights into the biology of these plants (Pigg & Nishida 2006; Slater *et al.* 2015).
65 In the last decade, well-preserved specimens from Antarctica have in this way provided
66 details on tree growth and productivity in warm polar forests (Taylor & Ryberg 2007; Miller
67 *et al.* 2016), on the anatomy and development of the unusual *Vertebraria* root system
68 (Decombeix *et al.* 2009), on the ability of the glossopterids to produce epicormic shoots that
69 could regenerate their crown (Decombeix *et al.* 2010a), and on the co-occurrence of
70 deciduous and evergreen species (Gulbranson *et al.* 2014). In addition, information on
71 glossopterid interactions with arthropods (Slater *et al.* 2012) and fungi (Harper *et al.* 2013)
72 gradually allows us to understand the Permian high-latitude forests as complex ecosystems.

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73 In this paper we focus on an important aspect of glossopterid vegetative anatomy that
74 has not been studied in detail: their bark. While this tissue is rarely preserved in the fossil
75 record, it can provide significant taxonomic and physiological information. Among its many
76 roles, the bark of seed plants contains the secondary phloem, which redistributes
77 photosynthates, hormones, and other essential components through the plant. The dead tissues
78 of the outer bark protect the functioning part of the secondary phloem and the vascular
79 cambium against biotic and abiotic hazards. A small amount of preserved secondary phloem
80 was reported in the stem *Glossopteris skaarensis* (Pigg & Taylor 1993) and in *Vertebraria*
81 roots from Skaar Ridge (Decombeix *et al.* 2009). However in both cases only a few layers of
82 the tissue were present and the composition and organization of the tissue were unclear. Here,
83 we describe well-preserved bark associated with glossopterid remains occurring in Late
84 Permian silicified peat from the Central Transantarctic Mountains. This new information is
85 placed in the context of bark evolution in seed plants and of the biology of high-latitude
86 Glossopteridales.

89 *Geographical and geological settings*

90 The specimens described in this paper occur in silicified peat blocks from the Skaar
91 Ridge locality, Beardmore Glacier region, Central Transantarctic Mountains, Antarctica (Fig.
92 1A; 84°49919.10S, 163° 20928.00E; elevation: 2,289 m). These peat blocks occur within the
93 Buckley Formation of the Beacon Supergroup. A Late Permian age has been assigned to the
94 Buckley Formation based on palynomorphs and associated floras (Farabee *et al.* 1991). The
95 reconstructed position of the locality for the Late Permian is well within the southern polar
96 circle (Fig. 1B) and it corresponds to some of the highest paleolatitudes at which the
97 Glossopteridales were growing.

98 *Assignment of the specimens to the glossopterids*

99 Fragments of gymnosperm bark are moderately common within peat blocks from
100 Skaar Ridge, and all the observed specimens show the same anatomy. The Skaar Ridge flora,
101 like nearby compression floras (Cúneo *et al.* 1993), is largely dominated by unquestionable
102 remains of the glossopterids such as *Glossopteris* leaves, *Vertebraria* roots, and reproductive
103 structures (Taylor & Taylor 1990). However, other gymnosperm taxa also may have been
104 present. There are, for example, rare occurrences in the peat of gymnosperm roots with a non-
105 *Vertebraria* anatomy (Decombeix *et al.* 2009). In addition, different morphogenera of stems
106 have been reported from the Permian of Antarctica (e.g., Maheshwari 1972; Decombeix *et al.*
107 2012) and it is unknown whether all belonged to the glossopterids. To take into account this
108 uncertainty, we looked for bark that would be more closely associated with glossopteridalean
109 remains. The key specimen presented in this paper corresponds to a trunk with the
110 *Australoxylon*-type of wood typically found in glossopterid stems and roots (e.g. see
111 illustrations and discussions in Mussa 1978; Neish *et al.* 1993; Decombeix *et al.* 2009, 2010;

112 Weaver *et al.* 1997; Prasad & Chandra 1978; Bamford 1999). A sector of the trunk has 2.5 to
113 3 cm of bark still attached. The cambial zone is partly preserved, providing unequivocal
114 evidence that similar bark fragments found around large woody stems and roots or fragmented
115 in the matrix do indeed belong to the glossopterids. The following description is based on this
116 single specimen as it is the best preserved, but observation of additional material shows a
117 similar anatomy. This includes isolated bark fragments from the silicified peat, another, less-
118 well preserved trunk with attached bark (specimen #16,494), and a large *Vertebraria* root with
119 a thick layer of bark tissue on its periphery (specimen #13,686).

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121 *Preparation of the specimens*

122 The silicified peat blocks containing the bark remains were etched for 3-4 min in 49%
123 hydrofluoric acid and serial cellulose acetate peels were made using the standard technique
124 (Galtier & Phillips 1999). Selected peels were mounted in Eukitt (O. Kindler, Freiburg) on
125 microscope slides for observation. Because of unequal preservation in the bark, thin-sections
126 (Hass & Rowe 1999) in the transverse and longitudinal planes were also prepared in order to
127 obtain thicker sections with a better preservation of the most fragile cell walls. Observations
128 and photography were conducted using Sony XCD-U100CR digital cameras attached
129 respectively to an Olympus SZX12 stereomicroscope and to an Olympus BX51 compound
130 microscope. Images were captured using Archimed software (Microvision Instruments, Evry,
131 France) and plates were composed with Adobe Photoshop CS5 version 12.0 (Adobe Systems,
132 San José, California, USA). Transformations made in Photoshop include cropping, rotation,
133 and adjustment of brightness and contrast for the whole image. Average measurements are
134 given for n=30. The trunk, peels, and slides are deposited in the Paleobotanical Collections,
135 Natural History Museum and Biodiversity Institute, University of Kansas (KUPB), under the
136 specimen accession number 15,508 and slide accession numbers 30,267--30,274; 30,273; 30,

1 277, and 29,976--29,978. Additional specimens prepared for this study are deposited under
2 138 the specimen accession numbers 13,686 and 16,494 and slide accession number 30,275.
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6 7 140 *Nomenclature*

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9 141 The term bark is used here as defined by Esau (1965, p. 272) to include all the tissues
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11 142 located outside the vascular cambium, i.e., secondary phloem, primary phloem (if still
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13 143 present), primary cortex (if still present), and periderm. "Inner bark" is used to designate the
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15 144 tissues located between the cambium and the innermost periderm and "outer bark" to
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17 145 designate all tissues located beyond that innermost periderm.
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23 24 147 RESULTS

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26 148 The amount of preserved secondary xylem is a little more than 7 cm in width (Fig. 2A,
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28 149 B). The central portion of the trunk is not present and, based on the slight curvature of the
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30 150 growth ring boundaries, the complete trunk was considerably larger. The secondary xylem is
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32 151 typically of the *Australoxylon* type (Marguerier 1973): distinct growth rings (Figs. 2C), square
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34 152 to rectangular tracheids in transverse section, low and uniseriate rays (Fig. 2D), small and
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36 153 crowded cross-field pits, and three types of radial pitting on the tracheid walls (araucarioid,
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38 154 abietinean, and conspicuous arrangements in groups of 2-5 pits) (Figs. 2E-H). The attached
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40 155 bark can be up to 3 cm thick (Figs. 2A, B). The inner bark consists of secondary phloem with
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42 156 discontinuous layers of fibers that are one cell thick radially. The outer bark is of the
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44 157 rhytidome type, with alternating layers of periderm and non-conducting secondary phloem
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47 158 (Fig. 3A). Numerous successive periderms are preserved in the trunk. In transverse section,
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49 159 they mostly run parallel to the cambium and rarely curve inwards and connect to the previous
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51 160 periderm layer (Fig. 3A). In longitudinal section, the periderms also remain mostly parallel to
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53 161 one another but have a slightly undulated outline (Figs. 2B, 3B).
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162 The cambial zone is poorly preserved (Figs. 2I, 3C). The inner bark is approximately
1 400 μm thick and composed of secondary phloem containing sieve cells, axial and ray
2 163 parenchyma, and fibers (Figs. 3A-E). Poor preservation makes it difficult to delimit the
3 164 boundary of the conducting part of this tissue. Like the secondary xylem rays, the phloem rays
4 165 are uniseriate and a few cells high (Fig. 3G). Phloem ray cells are 20-23 μm high and 13-16
5 166 μm wide in tangential section and are procumbent in radial section. In transverse section, the
6 167 fibers have a rectangular shape, with a tangential diameter of 21-51 μm (average 37 μm) and
7 168 a radial diameter of 11-29 μm (average 21 μm); their wall thickness is 3-18 μm and the lumen
8 169 is oval to slit-like. Fibers are moderately abundant and they tend to form discontinuous layers
9 170 that are only one cell thick in radial direction. (Figs. 3D, E, I). In some well-preserved areas,
10 171 fibers have been observed very close to the cambium (Fig. 3C) and it is hypothesized that they
11 172 were part of the conducting phloem and not the result of a later thickening of thin-walled
12 173 cells.
13 174

175 Axial parenchyma cells are isodiametric and range from 14-55 μm in diameter (Figs.
16 3D-H). It must be noted that the axial parenchyma is badly preserved in the innermost part of
17 176 the secondary phloem (Fig. 3C) and that measurements were taken beyond the first periderm,
18 177 when these cells might have already increased in diameter. Indeed, between the successive
19 178 periderms, the non-conducting secondary phloem shows a proliferation of the axial
20 179 parenchyma that tends to disorganize the layers of fibers. In addition, most parenchyma cells
21 180 in the non-conducting secondary phloem show some degree of wall disintegration which
22 181 gives the tissue a slightly spongy aspect (e.g. Fig. 3I). While this might be an artifact of
23 182 preservation, it has been observed in all studied bark fragments from Skaar Ridge and the
24 183 occurrence of such a spongy bark is well-documented in some extant trees such as *Eucalyptus*
25 184 (Chattaway 1953). Poor preservation of the inner bark prevented us from observing in detail
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186 the characteristics and distribution of sieve cells but their presence is indicated by the
187 occurrence of elongated thin-walled cells in the inner layers of the rhytidome (Fig. 3F).

188 The successive periderms are located 0.2 mm to 1.5 mm apart (commonly around 500-
189 700 μm in the inner part). The outer periderms are more spaced than the inner ones, likely due
190 to the proliferation of the secondary phloem parenchyma. Periderm layers are 25-35 μm thick
191 in transverse section (Fig. 3I). Each one is marked by 3-5 cells that are extremely flattened in
192 the radial plane and have dark, slightly thickened walls (Figs. 3H, I). The successive
193 periderms mostly run parallel to the cambium. They very rarely curve inwards and connect to
194 the previous periderm layer in transverse section. (Fig. 3A).

DISCUSSION

Evolutionary context

198 In plants with a bifacial vascular cambium (lignophytes, Kenrick & Crane 1997), the
199 bark tends to separate from the wood cylinder at the level of the cambium. As a result, fossil
200 lignophyte axes are often found in a decorticated state and the number of taxa to which we
201 can compare the bark anatomy of the glossopterid trunk from Skaar Ridge is limited.
202 The secondary phloem anatomy seen in the glossopteridalean trunk from Antarctica, with
203 axial parenchyma, sieve cells, and discontinuous layers of fibers is an organization first
204 documented in the Late Devonian progymnosperm (*Archaeopteris/Callixylon*, Decombeix &
205 Meyer-Berthaud 2013) and still present in some extant gymnosperms, for example in the
206 Cupressaceae (e.g., Den Outer 1967). Better-preserved specimens are needed, however, to
207 analyze this tissue in more detail, especially regarding the characters of the sieve cells.

208 Among fossil lignophytes for which axes with the bark still attached have been found
209 and studied, few show a rhytidome type of outer bark. However, there is good evidence that
210 the formation of a rhytidome existed relatively early in seed plant evolution. The oldest

211 examples are found in arborescent seed plants of Early Carboniferous age. A first type is
212 found in a Tournaisian tree from Australia, characterized by a 1.5 cm thick bark (Decombeix
213 2013). The secondary phloem contains conspicuous bands of fibers that are several cells in
214 radial thickness. At least four sequent periderms were observed within this fossil trunk. They
215 are not parallel to one another and tend to connect often, which suggests that this bark was
216 shed as small scales. In *Stanwoodia kirktonensis* from the Viséan of Scotland, the periderm
217 also forms relatively small scales (Galtier & Scott 1991). A major difference is that the
218 phloem fibers do not form thick tangential layers but are isolated or in discontinuous, one-cell
219 thick layers. A rhytidome outer bark was also reported in other Early Carboniferous
220 arborescent seed plants of Viséan-Serpukhovian age, including *Eristophyton beinertianum*
221 (Scott 1902), *Eristophyton fasciculare*, (Galtier *et al.* 1993), and *Endoxylon zonatum* (Scott
222 1924). Among Late Carboniferous plants, the only detailed report of a rhytidome bark is in
223 the Cordaitales. Taylor (1988) described layers of periderm in *Cordaixylon* that are curved
224 and overlapping, which also suggests the formation of scales. Degani-Schmidt and Guerra-
225 Sommer (2016) recently reported well-preserved secondary phloem attached to *Agathoxylon*
226 charcolified wood from the Permian of Brazil. The affinities of the specimens are thought to
227 be either with the Glossopteridales or the Cordaitales. The secondary phloem is composed of
228 sieve cells in tangential layers alternating with mixed rows of fibers and axial parenchyma ;
229 the outer organisation of the bark is unknown (Degani-Schmidt & Guerra-Sommer 2016).

230 The Mesozoic fossil record contains a few examples of well-preserved rhytidomes in
231 conifers. This includes (1) *Araucarioxylon arizonicum* from the Triassic of the USA that is
232 characterized by curving lenses of sequent periderms (Ash & Savidge 2004), (2)
233 *Telemachus/Notophytum krauselii* from the Triassic of Antarctica, which has several
234 successive concentric layers of periderm (Meyer-Berthaud & Taylor 1991; Bomfleur *et al.*
235 2013), and (3) *Taxodioxylon gypsaceum* from the Cretaceous of Canada (Ramanujam &

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236 Stewart 1969). Apart from conifers, Artabe *et al.* (1999) reported a rhytidome in the
237 corystosperm *Rhexoxylon brunoi* from the Triassic of Argentina but did not illustrate
238 anatomical details. The existence of a rhytidome in the Antarctic corystosperm *Kykloxylon*
239 *fremouwensis* was hypothesized by Decombeix *et al.* (2010b) but currently remains equivocal.
240 The relatively small number of reports on rhytidome type bark in the fossil record is probably
241 due to the fact that although this type of bark is often preserved, it is found detached from the
242 parent plant and affinities are uncertain. In the case of the glossopterids, isolated fragments of
243 bark have been reported previously at localities such as Skaar Ridge or in the Prince Charles
244 Mountains (Slater *et al.* 2015) but this is the first time that anatomy has been studied from
245 bark still attached to a stem.

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247 ***Outside aspect of the bark in the Antarctic glossopterid tree***

248 The well-preserved bark remains reported in this study allow us to have a better idea
249 of the external features of the bark of the Skaar Ridge glossopterid trees. A first set of
250 information is provided by the shape of the sequent periderms. Their undulated aspect in
251 longitudinal section suggests the presence of shallow (ca. 5 mm) horizontal furrows. In extant
252 trees such horizontal furrows can be found all over the trunk (e.g. *Leucadendron argenteum*,
253 Proteaceae) or they can be limited to a portion of the trunk, usually in the oldest parts.
254 Fragments of bark found isolated in the peat do not always show this longitudinal undulation
255 so the second option is much more likely. The regular concentric organization of the
256 periderms in transverse section suggests that the oldest bark did not form longitudinal
257 furrows. Finally, the infrequent connection between two successive periderms rules out that
258 the bark detached as small scales.

259 A second indication on the external aspect of the bark is provided by the anatomy of
260 the non-conducting phloem trapped between the layers of periderm: relatively loose and with

261 small tangential layers of fibers. Extant trees in which non-conducting phloem fibers are
262 arranged in thin layers tend to have a stringy bark, versus a rough bark that results when fibers
263 are organized in thick multicellular layers or blocks (Roth 1981). Good examples of extant
264 species that have a bark anatomy comparable to our Permian specimen are *Libocedrus*
265 *bidwillii* (Chan 1985) and *Fitzroya cupressoides* (De Magistris & Castro 2001) in the
266 Cupressaceae. Similarities include (1) a secondary phloem with layers of fibers that are only
267 one cell thick and often discontinuous, (2) proliferation of the axial parenchyma in the non-
268 conducting phloem, (3) numerous thin periderms that are only a few cells in thickness, (4)
269 dead periderms and phloem retained as successive sheets on the trunk and forming a
270 rhytidome several centimeters in thickness (Chan 1985; De Magistris & Castro 2001).
271 *Fitzroya cupressoides* typically has a stringy bark with a fibrous aspect that can be 3-9 cm in
272 thickness (De Magistris & Castro 2001). *Libocedrus bidwillii* has a 5-10 cm thick bark that is
273 exfoliated as thin fibrous strips. We hypothesize that the trunk from Skaar Ridge had a
274 comparable external aspect. It must, however, be noted that young axes or more distal parts of
275 the trunk might have had a smoother bark, as such a variation is often seen in extant trees
276 (e.g., Roth 1981).

277 While secondary phloem anatomy is relatively consistent within a plant genus, the
278 anatomy and thickness of the rhytidome can be highly variable, as exemplified in *Quercus*
279 (Graça & Preira 2004; Sen *et al.* 2011; Quilhó *et al.* 2013) or *Eucalyptus* (Chattaway 1953). It
280 is thus impossible at this stage to know whether all species of glossopterids had similar bark
281 or if there were differences in anatomy and/or thickness between taxa, habitats, or
282 paleolatitudes. Further finds of well-preserved glossopterid bark from other localities will
283 hopefully answer this question.

284
285 ***Ecological implications***

286 The occurrence of a rhytidome that is several centimeters in thickness provides
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2 287 important information in understanding the biology of glossopterid trees. This relatively thick
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5 288 and insulating bark would offer good protection of the vascular cambium from biotic and
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7 289 abiotic hazards.

9 290 The glossopterids from Skaar Ridge grew during a period of extreme hothouse where
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12 291 the global temperature is estimated between 23° and 28°C, with an average temperature at the
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14 292 pole thought to have been above 0°C, versus -50°C today (Scotese 2015). Thus despite the
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17 293 high paleolatitude at which they grew (75-85°S), these trees likely experienced some frost but
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19 294 no extremely cold temperatures during the growing season. The presence in the Central
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22 295 Transantarctic Mountains of forests with large-leaved trees and significant productivity (e.g.,
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24 296 Taylor *et al.* 1992, Cúneo *et al.* 1993; Miller *et al.* 2016) supports this idea of a cold but
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27 297 temperate climate. No frost rings were observed in the wood of glossopterid trunks from
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29 298 Skaar Ridge (Taylor & Ryberg 2007), but it is possible that this is in part due to the insulation
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32 299 provided by their bark. A thick insulating bark would have also protected the cambium from
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34 300 overheating during the permanent exposure to sunlight that the tree received during the
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36 301 summer months, and from sunscald in spring and fall. Sunscald damage occurs when part of
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39 302 the trunk is exposed to intense sunlight on cold days and suffers from repeated freeze/thaw
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41 303 episodes (Harvey 1923). Sunscald does not kill the trees but can provoke serious damage to
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44 304 the cambium and increases the susceptibility to pathogen attacks. At the high-latitude where
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46 305 the Skaar Ridge glossopterids were growing, the risk of sunscald might have been high in
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49 306 spring and fall, particularly when the deciduous trees were leafless and the canopy did not
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51 307 shade the trunks.

53 308 A thick bark is also known to protect the cambium from fire damage. There is good
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56 309 evidence that wildfires occurred commonly throughout Gondwana in the Permian, including
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58 310 in high-latitude plant communities (Jasper *et al.* 2013). The occurrence of charcoal layers
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1 311 containing abundant remains of *Vertebraria* roots, *Australoxylon* wood, and *Glossopteris*
2 312 leaves in Middle Permian deposits from the Prince Charles Mountains (Slater *et al.* 2015)
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4 313 support the idea that high-latitude glossopterid forests were subject to frequent wildfires.
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6 314 Although no analyses have been conducted yet, some layers of permineralized peat collected
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8 315 at Skaar Ridge contain dispersed plant fragments that are much darker than the surrounding
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10 316 material and might correspond to charcoal/fusain (R. Serbet 2015 pers. com.)
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14 317 In addition to protecting the cambium and conducting secondary phloem against frost
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16 318 or heat damage, a thick bark would have also protected epicormic buds such as the ones
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18 319 documented in some of the Skaar Ridge trees (Decombeix *et al.* 2010a). As in extant trees it
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20 320 would also have offered protection against insects and fungi that are known to have occurred
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22 321 in these high-latitude forests (e.g., Kellogg & Taylor 2004; Slater *et al.* 2012; Harper *et al.*
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24 322 2015, in press)
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28 323 When added to other characteristics, such as the ability to regenerate their crown via
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30 324 epicormic sprouts (Decombeix *et al.* 2010a), a diverse leaf habit (Gulbranson *et al.* 2014), or
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32 325 an hydraulic system adapted to limit risks of embolism (Wilson *et al.* 2014), the possession of
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34 326 a thick insulating bark would have surely provided advantages to the glossopterids during
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36 327 their conquest of high-latitude environments during the Permian. The same anatomical
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38 328 characters that suggest a resistance to frost also provide resistance to drought and fire and may
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40 329 have contributed to the success of the group in a variety of habitats and paleolatitudes.
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2 337 University of Montpellier (UM); <http://amap.cirad.fr/>.

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503 **FIGURE LEGENDS**

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5 505 **Figure 1.** Position of the locality today and during the Late Permian -- A: Map of Antarctica,
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7 506 the star indicates the position of Skaar Ridge. Modified from Cantrill and Poole 2013. -- B:
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9 507 Latest Permian paleogeographic reconstruction showing climatic zones, latitude of the
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11 508 occurrence of Glossopteridales, and the position of the locality at that time (star; modified
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14 509 from Gulbranson *et al.* 2014).
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19 511 **Figure 2.** General aspect, wood and cambial anatomy-- A: General aspect of specimen
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21 512 #15,508 viewed in transverse section and showing a portion of bark (B, double-headed
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24 513 arrows) still attached to the secondary xylem (X2). Scale bar = 10 mm.-- B: General aspect of
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26 514 the specimen in longitudinal section showing the wood (X2), cambial region (C), and bark (B)
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28 515 with an undulated outline. Scale bar = 10 mm. -- C: Transverse section of secondary xylem
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30 516 with three growth-ring boundaries. Slide 30,270 (15508-Cside 3 β). Scale bar = 100 μ m. -- D:
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32 517 Low and uniseriate secondary xylem rays in tangential section. Slide 30,272 (15508-D3 α).
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34 518 Scale bar = 50 μ m.-- E: Radial section of secondary xylem with mixed radial pitting and
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36 519 cross-field pitting (arrow). Slide 30,267 (15508-Btop 1 α). Scale bar = 50 μ m.-- F: Detail of
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38 520 tracheid pitting. Slide 30,267 (15508-Btop 1 α). Scale bar = 25 μ m.-- G: Detail of tracheid
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40 521 pitting. Slide 30,267 (15508-Btop 1 α). Scale bar = 25 μ m.-- H: Detail of tracheid. Slide
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42 522 30,272 (15508-D3 α). Scale bar = 25 μ m.-- I: Cambial zone (Ca) and innermost secondary
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44 523 phloem (Ph2) in transverse section. Slide 30,269 (15508-Cside 1). Scale bar = 50 μ m.
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53 525 **Figure 3.** Bark anatomy. The cambium is located towards the bottom on all transverse
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55 526 sections and on the left on all longitudinal sections.-- A: General view of the bark in
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58 527 transverse section showing the layers of secondary phloem (Ph2) and several successive
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528 periderms (Pe). The asterisk (left) indicates a connection between two layers of periderm.
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2 529 Slide 30,269 (15508-Cside 1). Scale bar = 250 μm . -- B: General view of the bark in
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5 530 longitudinal section showing the layers of secondary phloem (Ph2) and several successive
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7 531 periderms (Pe). Slide 30,273 (15508-D3 β). Scale bar = 250 μm -- C: Transverse section of
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9 532 cambial zone (Ca) and innermost secondary phloem (Ph2) with only fibers preserved. Slide
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11 533 30,269 (15508-Cside 1). Scale bar = 50 μm . -- D: Transverse section of the bark beyond the
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13 534 first layer of periderm showing successive layers of periderm (Pe) and non-conducting
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15 535 secondary phloem with fibers (Ph2). Slide 30,269 (15508-Cside 1). Scale bar = 100 μm . -- E:
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17 536 Detail of the same region in D showing two successive layers of periderm (Pe) and the
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19 537 secondary phloem (Ph2). Note the expanded outline of the axial parenchyma cells in the
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21 538 phloem. Slide 30,269 (15508- Cside 1). Scale bar = 50 μm . -- F: Longitudinal section of the
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23 539 secondary phloem in the outer bark. Slide 30,273 (15508-D3 β). Scale bar = 30 μm . -- G:
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25 540 Longitudinal section of the secondary phloem in the outer bark showing expanded axial
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27 541 parenchyma cells, a small uniseriate ray in tangential view (R) and part of a fiber (F). Slide
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29 542 30,273 (15508-D3 β). Scale bar = 50 μm . -- H. Longitudinal section in the outer bark showing
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31 543 the radially flattened, thicker-walled cells of a periderm layer. Slide 30,273 (15508-D3 β).
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33 544 Scale bar = 50 μm . -- I. Transverse section in the outermost part of the bark showing the
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35 545 secondary phloem with expanded and degraded axial parenchyma cells and some fibers, as
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37 546 well as a layer of periderm (Pe) with radially flattened dark cells. Slide 30,271 (15508-Cside
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39 547 2). Scale bar = 100 μm
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