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A Permian nurse log and evidence for facilitation in high-latitude *Glossopteris* forests.

Short title: Facilitation in Permian high-latitude forests

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The biology of trees that grew in high-latitude forests during warmer geological periods is of major interest in understanding past and future ecosystem dynamics. As we study the different plants that composed these forests, it becomes possible to make comparisons with ecosystem processes that occur today. Here we describe a silicified late Permian (Lopingian) glossopterid (seed fern) trunk from Skaar Ridge, central Transantarctic Mountains, Antarctica, with evidence of glossopterid rootlets growing into its wood. The specimen is interpreted as a nurse log similar to those seen in some extant forests. Together with evidence of glossopterid roots growing within the lacunae of older roots, this new specimen suggests the existence of facilitative interactions among the glossopterid trees that dominated the high-latitude forests of Gondwana during the late Permian. More generally, the existence of self-facilitation might

have favoured the expansion of glossopterids within various environments, especially those at high paleolatitudes, during the Permian icehouse to greenhouse transition.

Large woody debris in the form of tree stumps, fallen trunks, large branches and roots make up 5–15% of plant biomass in extant natural forests. They serve as habitat and a source of nutrients for a variety of organisms (Harmon *et al*. 1986). In particular, they offer a specific microhabitat that facilitates the germination and growth of seedlings of certain species of trees ("nurse log" interaction, Fig. 1A-C). Fossils of young roots that were growing into wood have been reported from Paleozoic and younger deposits. Fairon-Demaret *et al.* (2003) described, for example, rootlets growing inside conifer trunks in a 55 Ma old *in situ* forest in Belgium. Césari *et al.* (2010, 2012) reported a similar situation in a much older, ca. 300 Ma old, *in situ* forest in Argentina. Both forests were monospecific and grew on periodically waterlogged soils (Fairon-Demaret *et al.* 2003; Césari *et al.* 2010, 2012). This evidence indicates that the evolution of the nurse log syndrome and its paleoenvironmental contexts can be studied in the fossil record. One of the limitations to this type of investigation, however, is that root anatomy is very conservative. This makes it challenging to assess the exact affinities of the fossil roots unless there is evidence that only one taxon was present, i.e., *in situ* monospecific forests, such as those mentioned above. It is especially challenging in the case of roots with little or no secondary growth that cannot be identified based on wood characters. As a result, the affinities of most of the plants that produced the roots seen in fossil wood specimens remain unknown.

During the Permian, the warming of the global climate from icehouse to extreme hothouse conditions allowed trees to colonize high latitudes and establish forests well beyond the polar circle (Taylor *et al.* 2000; Cantrill & Poole 2012). Fossils from these regions yield insights into the diversity and biology of the trees growing in these ecosystems with no modern analogue, i.e., warm polar forests with a strongly seasonal light regime (e.g., Creber 1990; Francis 1994; Taylor & Ryberg 2007; Gulbranson *et al.* 2014; Slater *et al.* 2015; Miller *et al.* 2016). In the Late Permian, the high-latitude forests of the Southern Hemisphere were largely dominated by trees belonging to an extinct order of seed plants, the Glossopteridales (Cúneo *et al.* 1993; Anderson *et al.* 1999; Taylor *et al.* 2009). Glossopterid trees produced very distinctive roots assigned to the genus *Vertebraria* Royle that are characterized by wood with conspicuous lacunae formed by a discontinuous cambium in the first seasons of growth (Neish *et al.* 1993; Decombeix *et al.* 2009). This unusual anatomical feature has important functional implications (Decombeix & Rowe 2018) and makes glossopterid roots very easy to recognize from those of any other plant if wood is present.

Here we illustrate young glossopterid roots growing through the wood of an older glossopterid trunk. Combined with previous evidence of glossopterid roots growing in the lacunae of older roots, this new fossil suggests the existence of facilitation mechanisms between glossopterids trees growing at a same locality. We discuss the possible advantages of this type of interaction in the high-latitude forests of the Permian of Gondwana.

Material and Methods

The specimen described in this paper is preserved in permineralized peat collected from Skaar Ridge, Beardmore Glacier area, central Transantarctic Mountains, Antarctica (84° 49919.10S, 163°20928.00E; elevation: 2289 m; Fig. 2A). The plant remains found in the peat blocks are largely dominated by glossopterid organs. Wood, bark, *Vertebraria* roots, and *Glossopteris* leaves are the most common. The permineralized peat occurs within the Buckley Formation, which also includes sandstones, siltstones, shales, and coals that were deposited in braided stream systems. The formation is considered to be late Permian (Lopingian) in age, based on palynomorphs and associated compression fossils (Farabee *et al.* 1991). At the time, the Beardmore Glacier area was located well within the southern polar circle, at an estimated paleolatitude of around 75° S (Torvisk & Cocks 2013, Fig. 2B).

The specimen was cut into three slabs and 11 thin-sections were prepared from one of them at UMR AMAP, Montpellier, following the standard method (Hass & Rowe 1999). Images were taken using ArchiMed software (Microvision Instruments, Evry, France) with Sony XCD-U100CR digital cameras attached to an Olympus SZX12 stereomicroscope and to an Olympus BX51 compound microscope. Figs. 3A and 3B were created from six to ten photos using the focus-stacking feature in ArchiMed.. Figs. 4A and 4B are focused stacks of four photos each, also processed in ArchiMed. Images of extant nurse logs (Fig. 1) were taken with a Canon PowerShot A1000 IS. Plates were composed with Adobe Photoshop version 21.0.1 (Adobe Systems, San José, California, USA). Transformations made in Photoshop included cropping, rotation, and adjustment of exposure, contrast, and colour balance when needed. The specimen and corresponding slides are housed in the Division of Paleobotany collections, Biodiversity Institute, University of Kansas, Lawrence, under specimen number #17,918 and slide accession numbers 30,762–30,772.

Description

General aspect

The preserved portion of the trunk is about 5 cm in diameter and 7 cm long. The central part is not present and the configuration of the rings indicates that the specimen represents the outer part of a larger trunk (Fig. 3A), with a diameter that can be estimated from the direction of tracheid files to be over 20 cm. The fossil trunk is covered on one side by a thin layer of plant fragments, including at least one *Vertebraria* root (Fig. 3B).

Longitudinal sections through the trunk show several small roots coming from this layer and penetrating the wood of the trunk (Fig. 3B, 3D, 3F). In transverse section, numerous rootlets are visible (Fig. 3A, 3C, 3E). They are mostly found close to the boundary of growth rings. In some cases, several rootlets are present in a hole with a relatively clearly delimited border that might be a gallery created by arthropods, fungi, or previous roots (e.g. Fig. 3C, Fig. 3E, left; Fig. 4H). In most cases, however, the close association of the rootlet tissues with those of the trunk and the distortion and compression of the trunk's wood around the roots indicate that they are growing in the confines of the wood tissue, compressing it laterally as they grow (e.g., Fig. 3C, Fig. 3E, right; Fig. 4C–G).

Trunk anatomy and affinities

The wood is composed of tracheids and parenchymatous rays. Several conspicuous growth ring boundaries can be observed, each marked by a very small number of cells with a smaller radial diameter (Fig. 3A, 3E, 4B). Six rings are preserved; they range 5–10 mm in width. Tracheids are square to polygonal in transverse section, 22–44 µm in radial diameter and 21.5–38.5 µm in tangential diameter (n=30) (Fig. 3A). In tangential section, rays are uniseriate and low, 1–6 cells high ; individual ray cells measure 20–32 × 9–19 µm (n=30). In radial section, tracheid walls have multiseriate circular to oval bordered pits 2.7–7 µm in diameter that can be in an alternate or opposite arrangement, or, in some cases, form groups of a few pits (Fig. 4A, 4B). This wood anatomy with distinct growth rings, square to rectangular tracheids in transverse section, small uniseriate rays, a mixed pitting (alternate, opposite, and in groups), and small crowded cross-field pits is typical of the morphogenus *Australoxylon* (Marguerier 1973). Based on the similarity of the wood with other trunks (Decombeix *et al.* 2010: fig. 4C, 2016: fig. 2E–H) and still more with large *Vertebraria* roots (Decombeix *et al.*

2009: fig. 3D, F) from the same locality, we infer this is a glossopterid trunk. *Australoxylon*-type wood has also been described for *Vertebraria* roots and associated trunks from other localities of Gondwana (Weaver *et al.* 1997 and references therein).

Rootlet anatomy and affinities

The rootlets range in size from less than 200 µm to a few millimetres in diameter (Figs. 3, 4C–G). They commonly have only primary growth and show various protoxylem configurations with 2–6 protoxylem strands (Fig. 4C–G). The inner part of the cortex of the young roots is absent in many specimens and might correspond to an aerenchymatous layer. The outer cortex is composed of 3–5 layers of well-preserved parenchyma cells. A small number of roots produce some wood and show the conspicuous star-shape of young *Vertebraria* roots with secondary growth (Fig. 4G), indicating that at least some, if not all of the rootlets belong to glossopterids.

Fungal activity

The trunk contains a few decay pockets (Fig. 4H “P”) that are lenticular, spindle-shaped to lacriform .They are relatively small 8–420 µm in transverse section and 180–900 µm in longitudinal section. There are no cellular contents or fungal remains within the pockets. A few vegetative hyphae are scattered throughout the wood. The hyphae are 0.7–4 µm thick, irregularly septate, typically straight but form cruciform to Y-branching (Fig. 4I–J). There are small spherical bodies ca. 5 µm in diameter that co-occur with the hyphae and may be fungal spores, small tyloses, or preservational artefacts (Fig. 4I). Although the pockets are smaller, their shape and associated fungal remains are like the white pocket rot described in other glossopterid specimens from Skaar Ridge (15–18 mm in diameter) (Stubblefield & Taylor 1986; Harper *et al.* 2017).

Discussion

Nurse log

The presence in Antarctic deposits of glossopterids trunks up to 50–60 cm in diameter indicate that at least some representatives of this genus were relatively large trees, with reconstructed heights of 20–30 meters (e.g., Cantrill & Poole 2012; Gulbranson *et al.* 2012; Miller *et al.* 2016). The unusual secondary growth of the roots allows their affinities to be determined easily, making it possible to study the taxa involved in plant-plant interactions even on autochthonous fossils, such as those from Skaar Ridge. We interpret the presence of *Vertebraria* roots growing in the trunk as evidence that it acted as a nurse log for young glossopterids. Today, this type of interaction is important for the establishment of tree seedlings in boreal (Hofgaard 1993), temperate (Christie & Armesto 2003; Harmon & Franklin 1989; Lusk & Ogden 1992), and tropical forests (Lack 1991; Sanchez *et al.* 2009). The *Picea sitchensis-Tsuga heterophylla* temperate rainforests of the Olympic Peninsula, Washington state, USA, represent an extreme example with 88–97% of the tree seedlings growing on such logs (McKee *et al.* 1982) (Fig. 1A, 1C). Other cases in which the seedlings of canopy trees establish preferentially on wood have been reported in temperate forests of New Zealand (e.g., Lusk & Ogden 1992), in South American *Nothofagus* forests (e.g., Veblen *et al.* 1979), in old growth boreal and sub-alpine forests of Japan (Narukawa *et al.* 2003), and in boreal conifer forests of Sweden (e.g., Hofgaard 1993).

Because decaying wood is relatively poor in nutrients, several hypotheses have been proposed for the establishment of trees on fallen logs and other coarse woody debris. Possible advantages include the absence of the deep litter layer that could prevent the rooting of seedlings with a small radicle, reduced competition with understory plants (especially for light), absence of soil pathogens, absence of cover seedlings or allelopathic substances produced by other plants, a better aeration in waterlogged areas, a different availability of nutrients and of symbiotic fungi, and a reduced animal browsing (e.g. Harmon & Franklin 1989). Decayed wood also has the ability to store water (Harmon *et al*. 1986). Finally, wood-decaying fungi might also positively influence the establishment of tree seedlings on nurse logs (Fukasawa 2012). It is very likely that the importance of these factors varies between geographic and climatic areas, and between tree taxa. In the *Picea sitchensis-Tsuga heterophylla* temperate rainforests of the Olympic Peninsula mentioned earlier, Harmon and Franklin (1989) showed, for example, that competition with mosses and herbaceous plants on the forest floor was the probable cause of the very high number of tree seedlings growing on woody debris. In Hawaiian montane forests with waterlogged soil, the proportion of young trees established on logs is higher than in better drained sites (Santiago 2000), suggesting that the logs provide better substrate conditions in terms of aeration and/or oxidation-reduction potential. There is also evidence that in waterlogged environments large woody debris can be used by already established trees. For example, tupelos (*Nyssa*) growing in swamps send their roots into decaying logs and stumps, up to 2–3 feet (0.6–0.9 m) above the soil or water level according to Lemon (1945). Although it is impossible to test the different factors that might have influenced their growth, the glossopterid trees from Skaar Ridge were probably growing in a swampy area of the floodplain, which led to the formation of the peat (Taylor *et al.* 1989). Interestingly, the late Carboniferous–early Permian nurse logs described by Cesari *et al.*

(2010, 2012) occurred in a forest with periodically waterlogged soils and those reported by Fairon-Demaret *et al.* (2003) were growing in a swampy lowland habitat, with irregular events of water stress. The nurse tree syndrome has thus probably occurred through geological time in fossil forests growing in waterlogged conditions. There is, however, a preservation bias towards this type of environment (e.g. Martin-Closas & Gomez 2004), so it is possible that nurse logs existed in other types of forests also.

Despite the presence of fungal hyphae, the good preservation of the wood and the small size of the pocket rot pockets in the trunk compared to other specimens from Skaar Ridge suggest that the wood was in an early stage of decay. This provides evidence that the trunk was not deeply buried in the peat but was still indeed on the surface when it was colonized by the roots. It is also interesting to note that no mycorrhizal fungi were observed in the small rootlets within the nurse log although they are known to occur in the glossopterid roots from Skaar Ridge that grew directly inside the peat (Harper *et al.* 2013). Mycorrhizal colonization is critical for seedling growth, especially under stressful conditions (Smith & Read 2008), and individuals that are unable to form mycorrhizae typically have a higher mortality risk (Onguene & Kuyper 2002). Mycorrhizal fungi can also help young seedlings in nurse logs to extract sufficient nutrients from rotting wood (Harmon *et al.* 1986; Baier *et al.* 2006). A possible explanation for their absence in this case is that the ambient environment in the log may have been too acidic because of the wood-rotting fungi (Mallik 2003) ; in extant ecosystems, there is evidence that the decay process can soften the wood substrate for root penetration, but also change the pH and nutrient availability (Maser & Trappe 1984; Fukasawa 2012). Alternatively, mycorrhizae may have not established at the time of preservation or were not preserved.

Other evidence of facilitation between glossopterids

In the permineralized peat from Skaar Ridge and other comparable localities, rootlets are very abundant in the lacunae formed in the wood of older *Vertebraria* specimens (e.g., McLoughlin 1992: pl. 10 figs 2–5; Decombeix *et al.* 2009: figs. 2G, 8D). These rootlets commonly have only primary growth and cannot be assigned with certainty to the glossopterids. However, as in the trunk described previously, some specimens with secondary growth display the typical *Vertebraria* structure. The fact that the young glossopterid roots are more frequent in the lacunae of older roots than in in their wood suggests that the lacunae were easier to grow in and/or provided better conditions in terms of substrate aeration. In any case, this difference supports the observations made on extant plants that the main cause of root growth in coarse woody debris is not the use of nutrients from decaying wood.

Slater *et al.* (2015, p. 1454) noted that “Dense horizontally extensive *Vertebraria* root mats may [also] have helped to stabilise the glossopterid trees in poorly cohesive waterlogged soils by intermeshing with the roots of neighbouring trees.” Our work on the mechanical properties of *Vertebraria* roots indicates that they were probably well adapted for growth and anchoring in a heterogeneous matrix, such as the one formed by a peat rich in old *Vertebraria* roots (Decombeix & Rowe 2018). Thus, it is possible that the presence of glossopterid roots had positive feedbacks on neighbouring glossopterid trees at two different levels: (1) by helping in soil stabilisation at the scale of the stand and (2) by providing an ideal substrate for the development of new rootlets. This type of positive niche construction is, for example, also observed among Salicaceae growing in extant riparian ecosystems (Corenblit *et al.* 2018).

Facilitation between glossopterid trees and the high latitude environment

Facilitative interactions are encounters between organisms that benefit at least one of the participants and cause harm to neither (Stachowicz 2001). In extant ecosystems, facilitation increases with increasing stress and appears particularly important at upper physiological limits (e.g., Choler *et al.* 2001; Callway *et al.* 2002; He *et al.* 2013; Anthelme *et al.* 2014). Facilitation may, in some cases, ease range expansion and it might have favoured the expansion of glossopterids across Gondwana during the Permian, including the rapid colonisation of high-latitude environments following the late Paleozoic deglaciation (Isbell & Cúneo 1996).

To date two morphospecies of *Glossopteris* leaves have been recognized in the peat from Skaar Ridge, *G. skaarensis* and *G. schopfii*, suggesting the presence of at least two "whole-plant" species (Pigg 1990). Other organs are more difficult to segregate into multiple species and the number of glossopterid species that produced the *Vertebraria* roots observed in the peat and woody debris remains uncertain. There is, however, enough evidence to support facilitation among glossopterid taxa, at a conspecific or congeneric level. In extant ecosystems, conspecific facilitation is rare but it occurs in low diversity, stressful environments (e.g., Eränen & Kozlov 2008; Fajardo & McIntire 2011; Cavieres & Peñaloza 2012), where it can lead to the formation of dense populations. The Permian peat flora from Skaar Ridge is species-poor. Mosses, lycopsids, and ferns are each represented by a single species (Smoot & Taylor 1986; Galtier & Taylor 1994; Ryberg *et al.* 2012). Sphenophytes have not been identified, although they co-occur with *Glossopteris* in many plant assemblages from Antarctica and the rest of Gondwana (Cúneo *et al.* 1993; Anderson *et al.* 1999; Prevec *et al.* 2009; Slater *et al.* 2015). Evidence of non-glossopterid seed plants in the peat from Skaar Ridge is also scarce. Cordaite and conifer remains have not been identified in the peat although, like the sphenophytes, they are known to occur in late Permian deposits of

Antarctica (e.g., Cúneo *et al.* 1993). Non-*Vertebraria* gymnosperm roots are also present in the Skaar Ridge peat (Decombeix *et al.* 2009) but very rare and of diminutive size. Likewise, the large bark fragments that occur abundantly in some peat blocks are all anatomically similar. Such low diversity mire communities dominated by glossopterid trees and with an understory of moss and small-sized ferns, lycophytes, and sphenophytes are documented extensively in Upper Permian high latitude deposits (Cúneo *et al.* 1993; Slater *et al.* 2015; McLoughlin *et al.* 20119; May *et al.* 2019 and references in these papers). A recent analysis of two *in situ* glossopterid forests at Lamping Peak, about 100 km from Skaar Ridge (Fig. 2A), estimated the living, above-ground biomass at 146 to 400 Mg.ha^{-1} (depending on the method used) and the basal area 65–80 $\text{m}^2.\text{ha}^{-1}$ (Miller *et al.* 2016). These values fall within the range of estimates for some mature temperate rainforests of Australia, Europe, and North America (e.g., Balian *et al.* 2005; Keith *et al.* 2009; Jacob *et al.* 2013; Ximenes *et al.* 2018). Combined with previous data on growth ring anatomy (Creber 1990; Francis 1994; Taylor & Ryberg 2007), these results show that the productivity of late Permian high-latitude glossopterid forests was similar to modern forests in temperate regions. Our new specimen shows that some plant-plant facilitative interactions were also similar.

Accumulated evidence indicates that the glossopterid trees that dominated the late Permian high latitude forests had a thick insulating bark at least at the base of the tree (Decombeix *et al.* 2016), the ability to produce epicormic shoots (Decombeix *et al.* 2010), various leaf habits (deciduous and evergreen, Gulbranson *et al.* 2014), endomycorrhizal associations (Harper *et al.* 2013), and a unique type of root system (Decombeix & Rowe 2018). Although none of these characters in itself is linked to growth at high latitudes, they suggest that these trees could tolerate stressful conditions (for example in terms of temperature range) and colonize diverse environments. The Antarctic glossopterids grew not only in peat swamps, but also on seasonally dry, sandy floodplains (Cúneo *et al.* 1993; Isbell & Cúneo 1996). Our new data of nurse log strategy and facilitation between the roots suggest that positive interactions among glossopterids growing at the same locality could also have favoured their expansion and dominance at high latitudes by a process similar to positive niche construction in extant ecosystems (Laland *et al.* 2016). On the other hand, the low diversity and importance of self-facilitation might have made these forests more susceptible to catastrophic collapse if a tipping point for glossopterid survival was reached, as happened across Gondwana at the end of the Permian (Mays *et al.* 2020; Vajda *et al.* 2020 and references therein).

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FIGURE LEGENDS

Fig. 1. Extant examples of nurse logs in a temperate rainforest, Olympic Peninsula, WA, USA. (A) Seedlings growing on a fallen log. Note the absence of seedlings on the surrounding forest floor.

(B) Colonnade, i.e., old trees still aligned following the pattern of the log they grew on.

(C) Tree growing on a still-upright decaying stump.

Fig. 2. (A) Location of Skaar Ridge (red dot) and other main Permian-Triassic fossil plant sites in the region (black dots) (modified from Collinson and Elliot, 1984).

(B) Position of the Central Transantarctic Mountains in the late Permian (from Torvisk & Cocks 2013)

Fig. 3. General aspect of the trunk with rootlets in transverse (A, C, E) and longitudinal (B, D, F) sections

(A) Transverse section of the logshowing numerous rootlets (arrows) and one gallery (G) inside the wood, mostly along the growth ring boundaries. Slide 17918-C2-2-2. Scale bar = 3 mm.

(B) Longitudinal section showing some peat (P) with abundant plant remains on top of the trunk (T), a *Vertebraria* root cut in longitudinal section (V), and rootlets growing inside the wood (arrows), mostly along the growth ring boundaries. Slide 17918-C1-2-4. Scale bar = 3 mm.

(C) Enlargement of a transverse section, showing various rootlets isolated or in groups growing inside the wood. Slide 17918-C2-1-3. Scale bar = 1 mm.

(D) Enlargement in longitudinal section showing the peat (P), a layer of degraded wood (D), and trunk wood (T) with rootlets penetrating along the ring boundaries. Slide 17918-C1-2-2. Scale bar = 1 mm.

(E) Detail of a transverse section showing on the left, part of a large gallery filled with plant remains including rootlets and on the right, an isolated rootlet with four protoxylem strands. Note the distorted wood cells around the rootlet. Slide 17918-C2-2-2. Scale bar = 0.5 mm

(F) Detail of a longitudinal section showing a rootlet growing vertically inside the wood. Slide 17918-C1-2-2. Scale bar = 0.5 mm

Fig. 4. Detail of the trunk wood, root anatomy, and evidence of fungal activity.

(A) Radial sections of the trunk wood showing the low rays and radial pits arranged in groups on the wall of the tracheids. Slide 17918-C1-2-2. Scale bar = 100 µm.

(B) Radial section of the trunk at the level of a growth ring boundary showing low rays and alternate, opposite, and grouped pitting on the tracheids. Slide 17918-C1-2-2. Scale bar = 100 µm.

(C) Young diarch root in the wood. Note empty inner cortex (IC). Slide 17918-C2-2-1. Scale bar = 200 µm.

(D) Young root with three or four protoxylem strands. Note empty inner cortex (IC) and compressed trunk wood around it. Slide 17918-C2-2-3. Scale bar = 200 µm.

(E) Young root in the wood in oblique section. Slide 17918-C2-2-1. Scale bar = 200 µm.

(F) Young root in the wood. Slide 17918-C2-2-1. Scale bar = 200 µm.

(G) Young root with six protoxylem strands and some development of the secondary xylem forming six "arms." Slide 17918-C2-1-1. Scale bar = 1 mm.

(H) Remains of several rootlets within a hole in the trunk. Note clean borders and lack of compressed trunk wood around the structure and evidence of pocket rot (P) on the right. Slide 17918-C2-2-3. Scale bar = 500 µm.

(I) Fungal hypha (arrows) crossing tracheids in the wood of the trunk. Slide 17918-C2. Scale bar = 10 µm.

(J) Fungal hypha with Y-branch (arrows) in the wood of the trunk. Slide 17918-C2. Scale bar = 10 µm.