



## Arbuscular mycorrhizal fungi in a voltzialean conifer from the Triassic of Antarctica



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### ABSTRACT

Mycorrhizas are intimate mutualistic relationships between plants and fungi that represent an integral component of ancient and extant ecosystems. These symbioses have been established for at least 400 million years and are found in numerous fossil plant groups, including early land plants, seed ferns, and cordaitaleans. In modern ecosystems, it is common for different types of mycorrhizas to occur within a single plant; however, fossil evidence of this is exceedingly scarce. A vesicular–arbuscular mycorrhiza is described in *Notophytum krauselii* (voltzialean conifers) based on permineralizations from the Middle Triassic of Antarctica. This symbiosis occurs in young non-nodular roots and is characterized by fungal hyphae, vesicles, and arbuscules within a discrete zone of the root cortex. Together with the mycorrhizal root nodules described previously for *N. krauselii*, this discovery represents only the second record of multiple types of mycorrhizae occurring within the same fossil plant, and provides important information on the system of interactions that may have allowed voltzialean conifers to survive in an extreme paleoenvironment.

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### 1. Introduction

Belowground ecosystems incorporate highly integrated components that form complex and dynamic communities. For example, in forest ecosystems there are just as many abiotic and biotic interactions within the rhizosphere as there are above ground (Fitter et al., 2005; Wang and Qiu, 2006). Among these diverse rhizosphere interactions are mycorrhizal symbioses, the mutualistic relationship between a fungus and plant in which both partners benefit from the exchange of nutrients (Simard and Durall, 2004). This ancient intimate relationship has been suggested as a necessary preadaptation that made it possible for plants to colonize the terrestrial realm (Pirozynski and Malloch, 1975; Simon et al., 1993; Fitter et al., 2005; Bonfante and Selosse, 2010). Today, mycorrhizal associations are common among a large majority (i.e., an estimated >80%) of extant plant families, and include most bryophytes, lycophytes, pteridophytes, gymnosperms, and angiosperms (Simard and Durall, 2004; Wang and Qiu, 2006). Plant–fungal relationships closely resembling extant mycorrhizas with regard to structure and morphology have also been reported in several extinct lineages and species of plants, e.g., early land plants (rhyniophytes), arborescent lycopsids, seed ferns, cordaitaleans, (e.g., Remy et al., 1994; Krings et al., 2007;

Strullu-Derrien et al., 2009; Krings et al., 2011; Harper et al., 2013), and fossil representatives of living plant groups, including conifers and flowering plants (e.g., LePage et al., 1997; Stockey et al., 2001; Beimforde et al., 2011).

Triassic permineralized peats from the central Transantarctic Mountains of Antarctica have preserved an exceptionally diverse assemblage of fossil fungi, including a putative trichomycete (White and Taylor, 1989a), a basidiomycete (Osborn and Taylor, 1989), several examples of zygomycetous fungi (White and Taylor, 1989b; Krings et al., 2012), fungal “sporocarps” (White and Taylor, 1989c), and possible saprotrophic fungi in reproductive structures (Bergene et al., 2013). Moreover, glomeromycotan fungi involved in endomycorrhizal associations were reported in the cycad *Antarcticycas schopfii* (Stubblefield et al., 1987a,b; Phipps and Taylor, 1996), and mycorrhizal root nodules in narrow rootlets of the voltzialean conifer *Notophytum krauselii* (Schwendemann et al., 2011). The latter taxon is among the most completely known anatomically preserved plants of the Triassic paleoecosystems in Antarctica (Bomfleur et al., 2013). It can be viewed as a model system for studies of paleoecology in Triassic Gondwanan ecosystems due to its abundance, distribution throughout Gondwana, and known descriptions of the morphology and anatomy of roots, stems, branches, trunks (i.e., *N. krauselii*; Meyer-Berthaud and Taylor, 1991, 1992), leaves (i.e., compressions: *Heidiphyllum elongatum*, permineralizations: *Notophytum* leaves; Anderson, 1978; Axsmith et al., 1998), reproductive structures, i.e., seed cones (*Telemachus* sp.

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and *Parasciadopitys aequata*; Yao et al., 1993; Escapa et al., 2010), pollen cones (*Switzianthus* sp.; Anderson and Anderson, 2003; Bomfleur et al., 2011), and bisaccate pollen of the *Alisporites* type (e.g., Yao et al., 1993), as well as microbial associations (e.g., Bomfleur et al., 2013).

In this study we report a vesicular–arbuscular endomycorrhiza (VAM or AM) that occurs in non-nodular roots of *N. krauselii*. The fungal partner spreads through the intercellular system of the outer and middle root cortex and consists of aseptate hyphae, thin-walled vesicles, and intracellular arbuscules within a discrete zone of the host cortex. The discovery of an AM in addition to the mycorrhizal root nodules in *N. krauselii* is important because it provides evidence that different types of endomycorrhizal associations occurred within Antarctic voltzialean conifers. The mycorrhizal systems (simultaneously or alternately) may have contributed to the system of adaptations that enabled these plants to survive in a high-latitude peat-forming environment as has been suggested of this part of the Antarctic continent during the Triassic.

## 2. Geological setting, material, and methods

### 2.1. Geological setting

The fossils occur in permineralized (silicified) peat from the Fremouw Formation in the central Transantarctic Mountains of Antarctica (Taylor et al., 1986; Cúneo et al., 2003; Faure and Mensing, 2010). The Fremouw Formation is a 620–750 m thick siliclastic succession deposited by low sinuosity, braided streams (Faure and Mensing, 2010). The fossils occur within several allochthonous clasts that are at approximately the same stratigraphic level within a trough-crossbedded, medium-grained, greenish-gray volcanoclastic sandstone. Permineralized peat is found at a single level at the Fremouw Peak locality, approximately 30 m below the top of the formation. Blocks of peat were likely rafted into their current position during a flooding event that caused them to be stranded on sand bars prior to permineralization (Taylor et al., 1989) and isolated into individual lenses within the outcrop. The peat was silicified after burial in its current position and the age of the fossil plants within the peat is equivalent to the surrounding clastic sediments, i.e., fluvial sandstone, which also contains trunks of wood of equivalent age to the peat (Decombeix et al., 2014). The silica source for the permineralization is interpreted to be the result of the dissolution of siliceous, volcanic detritus that was abundant in the upper Fremouw Formation. The peat and surrounding material have been dated as early Middle Triassic (Anisian) based on palynomorphs and nearby vertebrate fossils (Farabee et al., 1990; Hammer, 1990; Sidor et al., 2008; Faure and Mensing, 2010).

### 2.2. Material

The peat blocks used in this study contain abundant components attributable to the voltzialean conifers, including axes of *N. krauselii* (Plate I, 1) characterized by eustelic woody stems, roots of *N. krauselii* characterized by a distinctive *phi* layer suggesting that the plants may have grown in a fluctuating water table environment (Millay et al., 1987; Taylor and Ryberg, 2007), permineralized *N. krauselii* leaves (Plate I, 2), numerous *Alisporites* pollen grains (Plate I, 3), and ovules of *Parasciadopitys* (Plate I, 4).

Fossil roots in general are difficult to identify at any systematic level because the characters used to define them are relatively uniform. However, *N. krauselii* roots and aerial axes/stems do share several anatomical features that make it possible to assign the roots with confidence to the stems, which in turn are correlated with other vegetative and reproductive organs (e.g., Meyer-Berthaud and Taylor, 1991; Escapa et al., 2011).

The thin sections prepared for this study are composed almost entirely of roots in various planes of section, which provide the opportunity to examine slightly different stages of development and to

compare the anatomical features with those roots described previously and assigned to *N. krauselii* (Meyer-Berthaud and Taylor, 1991, 1992; Bomfleur et al., 2013). This also makes it possible to trace the distribution of the fungus within the roots and to analyze where it occurs within the tissue systems. Mature roots contain a distinct zone of primary xylem, well-defined endodermis, secondary xylem, cortical tissues, and a poorly preserved and locally difficult to discern epidermis (Plate I, 5). Mature roots, however, are rarely encountered in the peat blocks relative to the smaller, immature rootlets lacking secondary xylem. The smaller rootlets occur singly or in distinct clusters (Plate I, 6), vary from 0.5 to 5 mm in diameter with most between 1 and 2.2 mm; some are sectioned in a way to show well-defined apices. Generally, the stele of these rootlets is poorly preserved, but the endodermis is present; the cortex of smaller rootlets is approximately 4–6 cell layers thick, and appears similar to that in mature roots; the epidermis is difficult to discern.

### 2.3. Methods

Fossil specimens were initially prepared according to standard acetate peel techniques utilizing hydrofluoric acid (Joy et al., 1956; Galtier and Phillips, 1999) to survey the material for fungi, including roots that may show evidence of mycorrhizal colonization. For promising specimens standard thin sections were prepared (Hass and Rowe, 1999), but with the following modifications. Pieces of peat were mounted on microscope slides using Hillquist 2-part A-B epoxy compound and cut with a Buehler Petrothin® thin-sectioning machine to a thickness of ~250 µm. The wafer was then ground to a thickness of ~50–65 µm and analyzed using a Leica DM5000B transmitted-light compound microscope. Digital images were taken with a Leica DC500 digital camera attachment and minimally processed using Adobe Photoshop CS6 Version 13.0 x64 (©1990–2012, Adobe Systems). When suitable specimens were identified, multiple micrographs of the same specimen were recorded at different focal planes and compiled to produce composite images (e.g., Bercovici et al., 2009). The images were stacked in Adobe Photoshop CS6 and specific areas were modified to reveal the complete three-dimensional image as seen in the thin sections. Several images were also digitally focal stacked using Helicon Focus software (Method B, Radius 8, Smoothing 4) in order to study intricate areas of the specimens (e.g., Saupe and Selden, 2009). Measurements were taken using ImageJ 1.48b software (Abràmoff et al., 2004). Specimens and slides are deposited in the Paleobotanical Collections, Natural History Museum and Biodiversity Institute, University of Kansas (KUPB) under specimen accession numbers 26590, 30000–30007.

## 3. Results: fungi in *N. krauselii*

More than 50 young *N. krauselii* rootlets have been discovered that are characterized by a distinct, continuous zone of apparently more opaque cells positioned in the cortex approximately 3–4 cell layers below the epidermis. This zone is 2–5 cells thick and can readily be recognized in both transverse (Plate I, 7) and longitudinal sections (Plate I, 8) because of the concentration of fungi.

This zone within the root cortex appears more opaque because it is densely packed with multi-branched intracellular arbuscules attached to intercellular trunk hyphae, and sparsely dispersed vesicles positioned terminally on parental (branch) hyphae (Plate II, 8). Prominent hyphae (~7 µm in diameter) are perpendicular, septate, and ramify throughout the zone (Plate II, 1). It is interesting to note that evidence of this fungus has not been found in any cells of the stele, the cortical tissues outside of the distinct zone, epidermis, or in the surrounding matrix. However, a few rootlets host other hyphae that are generally larger (~15 µm diameter) (Plate II, 2). These hyphae have not been found attached to vesicles or arbuscules, and likely represent another fungus present in the rootlet or represent trunk hyphae from which smaller lateral hyphae branch to

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