

EVIDENCE OF ASCOMYCETE HYPHAE ON A PENNSYLVANIAN FERN COMPRESSION, CZECH REPUBLIC

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Abstract: The paper documented, branched hyphae preserved on the adaxial cuticle of pinnules of the Pennsylvanian leptosporangiate fern *Discosporopteris chlupatum* Pšenička *et al.* from the Whetstone Horizon, Radnice Member, Kladno Formation of the Pilsen Basin, Czech Republic. The hyphae occur as running structures on the leaf surface, show simple septa and lack clamp connections, consistent with an ascomycete affinity. Exceptional host-tissue preservation indicates rapid burial by volcanic ash and supports epiphyllous colonisation, most plausibly parasitic, although early saprotrophic colonisation cannot be excluded. This record expands the limited evidence of Paleozoic foliar fungi preserved as compressions and highlights the potential of volcanoclastic deposits for detecting plant–fungus associations.

Keywords: Fern leaves, hyphae, Asterinaceae, Carboniferous, compressions

INTRODUCTION

Fungi are considered important members of extant ecosystems. They are decomposers of organic matter, function as mutualistic symbionts and parasites of plants and animals, and demonstrate a wide array of co-evolutionary interactions among these organisms (Taylor & Taylor 1997). The oldest fungal structures have been discovered in 3000 Ma old palaeosols, which presumably contained algae and fungi in microbial mats (Mitchell *et al.* 2016 - 2400 Ma, Bengtson *et al.* 2017). The oldest unequivocal filamentous fungi are 850 Ma old, nevertheless phylogenetic analyses suggest that closely related unicellular organisms are much older (Berbee *et al.* 2017, McLoughlin 2017). The oldest fungi are preserved as non-septate hyphae and are believed to represent some type of reef saprophyte (Kobluk & James 1979, Taylor & Taylor 1997). Association of primitive plants with mycorrhizal fungi have been known since the Middle Cambrian (Horodyskyj *et al.* 2012). Fragmentary evidence of fungi on early land plants was

reported by Gensel *et al.* (2008) and Wellman (2014) from Ordovician (476–432 Ma). The oldest terrestrial fungi are described from Silurian and consist of hyphae and several spore types (Pratt *et al.* 1978, Sherwood-Pike & Gray 1985, Taylor *et al.* 1997). The most abundant findings of fungi originate from the Lower Devonian Rhynie Chert locality (410 Ma), UK (e.g., Krings & Taylor 2014a, Krings & Taylor 2014b, Krings *et al.* 2016). Abundant fungal remains are recognised on permineralised fossil plants, including well-preserved hyphae, appressoria and perithecia with ascospores (e.g., Krings *et al.* 2009, 2014a, Taylor *et al.* 2009). Globally, the oldest ascomycetes have been described from this unique locality (Taylor *et al.* 1999, Krings *et al.* 2014). Other plant remains associated with fungi included, for example glomeromycotean fungi (Krings *et al.* 2007) and Rhynia with sporocarps and spores (Karatygin *et al.* 2006; Krings *et al.* 2007a, 2014a, Taylor *et al.* 1999). Several studies focusing on Carboniferous permin-

eralisations included description of a new genus of basidiomycetes on fern wood (Dennis 1970), fruiting bodies and hyphae with clamp connections (Dennis 1976), and an endophyte on pecopterid pinnules (Krings *et al.* 2009).

Fungal remains are more common in the Mesozoic due to the better preservation of fungal tissues. Fossil fungi on leaves are also described from the Cretaceous and Cenozoic (e. g., Meschinelli 1898, Jasinski & Payette 2007, Krings *et al.* 2009). Nevertheless, well-preserved specimens that can be confidently assigned to major taxonomic groups are rare (Krings *et al.* 2009).

Although fungi are very important components of palaeoecosystems, their fossil record is infrequently recognised. One reason is that fungal bodies are formed by mycelium consisting of fragile hyphae that are sensitive to fossilization, except in coals where their remains are included as the maceral funginite and can be quite common (ICCP 2001). In Mesozoic and Palaeozoic coals and sediments, funginite is mainly represented by sclerotia-derived forms and different types of hyphae (e.g., Stach 1956, Hook & Hower 1988). In Tertiary and younger coal deposits, funginite consists mainly of roundish unicellular to multicellular oval forms. Funginite also occurs as tubular forms (hyphae) and as structured textures of thin tubes (mycelia, plectenchyma) (e.g., Hower *et al.* 2010, Hower *et al.* 2011). In recent sediments and peats, sclerotia can occasionally be observed with the naked eye (ICCP 2001, Thormann *et al.* 1999).

However, fungi preserved as compressions are very rare and exceptionally recognised. In general, compression fossils of fungi are still rare, are often misidentified due to complicated preservation, and can be easily overlooked by palaeobotanist and palynologist (Taylor *et al.* 1999). The rarity of fungal remains may also be affected by rapid burial of plants. In addition, fungal hyphae and other structures are usually microscopic and may therefore be easily overlooked. Although globally rare, occurrences of fossil fungi and their spores are of considerable interest. Plant-fungus associations can expand our knowledge of palaeoecology and palaeoenvironment (Taylor *et al.* 2014).

This study provides new information on hyphae found on the surface of pinnules of a Pennsylvanian fern of the genus *Discosoropteris* Pšenička *et al.* (Pšenička *et al.* 2022) from the Duckmantian of the Pilsen Basin, Czech Republic.

MATERIAL AND METHODS

An infected pinnule was macerated from a fertile frond of the holotype of *Discosoropteris chlupatum* (Pšenička *et al.* 2022) (Plate I, fig. A) from the Doubrava locality near Nýřany, from Pilsen Basin, Czech Republic (Whetstone Horizon of the Radnice Member, Kladno Formation, late Duckmantian). The pinnule was selected from the frond. Pinnules with cuticles and fungal fragments were isolated from the rock and macerated in 35% hydrofluoric acid for 24 h. Cuticles were macerated in Schulze's solution (KClO₃ dissolved in 40–70% HNO₃) for 5 to 25 min., subsequently washed in distilled water, and bleached in KOH (5%) to remove oxidation products. The cuticle were washed several times in distilled water, mounted in glycerine jelly on slides, and observed under an OLYMPUS BX50 microscope using Nomarski contrast; photographs were captured using an Olympus DP72 camera. Some samples were examined under SEM (including JEOL 6380LV, Institute of Geology and Paleontology, Faculty of Science, Charles University). Specimens F4 and slides are stored at the Centre of Palaeobiodiversity, West Bohemian Museum in Pilsen.

STRATIGRAPHY AND GEOLOGICAL BACKGROUND

The specimen was found in a waste dump of a small abandoned coal mine near Doubrava village located in SW part of the Pilsen Basin – one of late Paleozoic sedimentary basins in the Czech Republic (Figure 1). Deposition in the basin started during Middle Pennsylvanian and, with several gaps, continued until the early Permian (Opluštil *et al.* 2016). The basin fill is divided into four main lithostratigraphic units of formation status, some of which are further subdivided into members (Figure 2). The Bělka tuff, which preserves the hyphal remains, is an approximately 0.5 m thick volcanic ash bed in the lower part of the Whetstone Horizon – a succession of an *in situ* volcanic ash bed (Bělka) overlain by a redeposited “Whetstone” layer up to several metres thick, composed of redeposited volcanic ash mixed with siliciclastics. The Whetstone Horizon is sandwiched between the Lower and Upper Radnice coals. This extensively mined coal group occurs within the Lower Radnice Member, which forms the lower part of the Kladno Formation (Figure 2). The ra-



Figure 1. Late Paleozoic (Carboniferous and Permian) continental deposits in the Czech Republic. Indicated is a position of the Doubrava locality in the Pilsen Basin (PB) and position of the original volcanic centre of the Altenberg-Teplice Caldera (ATC). Abbreviations of the basins: M – Manětín, Ž – Žihle, R – Radnice, KR – Kladno-Rakovník, MR – Mšeno-Roudnice, ČK – Česká Kamenice, MH – Mnichovo Hradiště, KP – Krkonose-Piedmont, IS – Intra-Sudetic, B – Blanice.

dioisotopic age of magmatogenic zircons entombed in the Bělka tuff is about 314 Ma, corresponding to the Middle Pennsylvanian late Duckmantian substage (Opluštil *et al.* 2016). At that time, the Pilsen Basin and territory of the present-day Czech Republic were located at tropical latitudes within the Intertropical Convergence Zone on the eastern part of the supercontinent Pangea (Murphy *et al.* 2009).

Burial history of plant remains in the Bělka tuff bed

The position of the Bělka tuff bed in the roof of the Lower Radnice Coal suggests that volcanic ash buried the peat swamp and its vegetation almost instantaneously, possibly within hours to a few days (Figure 3). Excavations at several localities revealed an apparent contrast in the character of

the fossil record in the Bělka and Whetstone beds, allowing reconstruction of the burial history of the vegetation cover (e.g., Libertín *et al.* 2009, Opluštil *et al.* 2009, 2014). The Bělka bed contains uncharred plant remains of various sizes, including prostrate stems and branches up to several metres long, often bearing foliage. Coalified stems 1 cm to nearly 1 m thick preserved in an upright position and rooted exclusively in the roof of the Lower Radnice Coal indicate burial in growth position and represent peat-swamp vegetation. Some of these stems are several metres tall and extend from the Bělka into the overlying Whetstone (Figure 3). In contrast, the fossil record of the Whetstone consists mainly of small isolated allochthonous plant fragments concentrated in its lower part, as well as thin layers with abundant millimetre- to few centimetre-sized plant detritus.

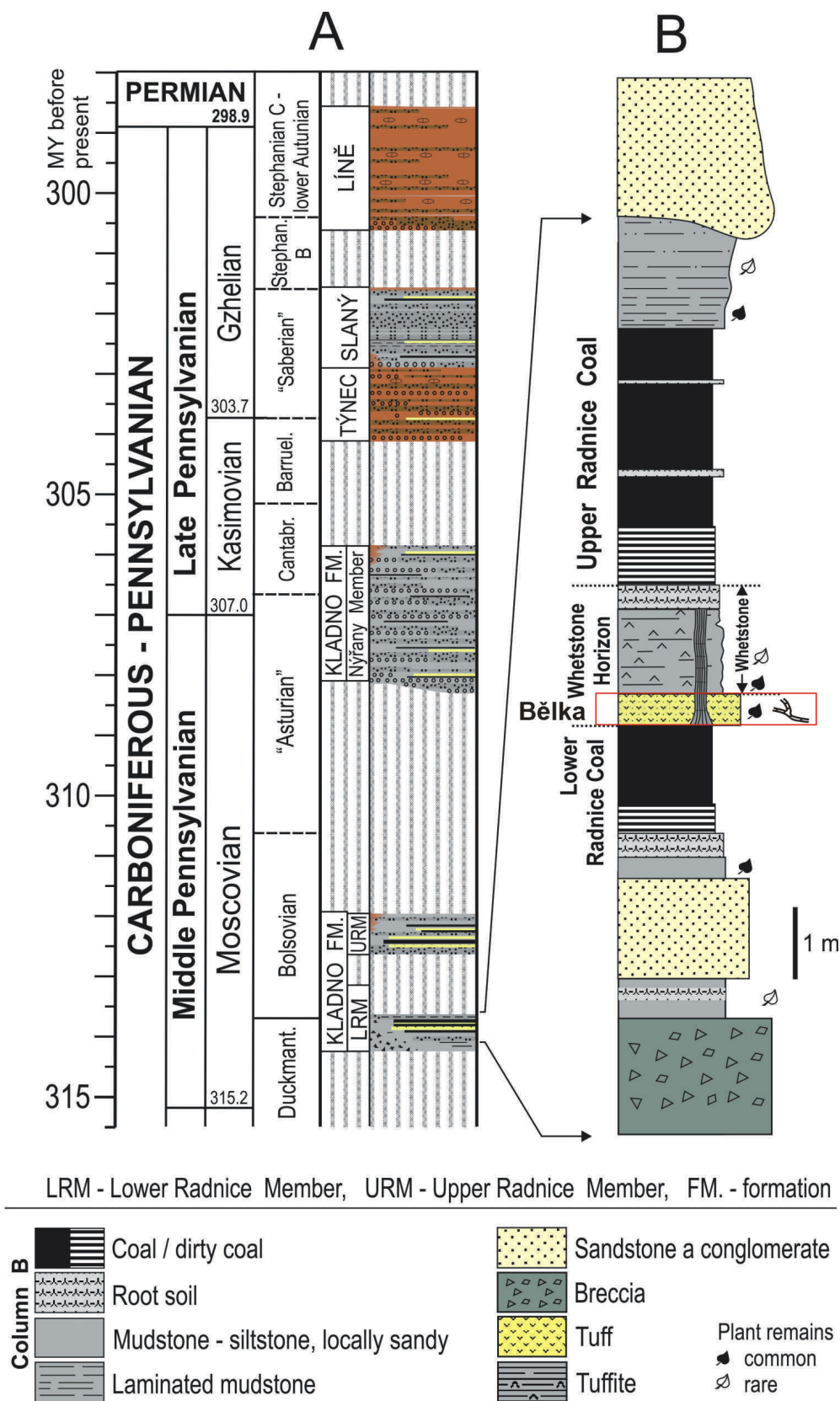


Figure 2. Sedimentary succession of the Pilsen Basin: A – Lithostratigraphic units of the Pilsen Basin plotted against the time axis. B – Detail stratigraphic section of the Lower Radnice Member with the Radnice coal group and the Whetstone Horizon sandwiched between them. Modified according to Bek et al. (2021)

The spatial distribution of plant remains in the Bělka bed is irregular in terms of density and taxonomic composition, thus reflecting the original structure and composition of the vegetation at the time of the volcanic eruption. Typically, foliage, fertile organs and fragments of branches are situated around their parent stems. In contrast, vertical distribution of plant remains within the Bělka bed is related to plant habit. As a result, tiny herbaceous plants forming the ground cover were buried first by the initial ash fall, and their remains occur in the basal few centimetres of the tuff bed. Thick arborecent lycopsid or cordaitalean branches are more common in the middle and upper parts of the Bělka tuff bed, together with plant remains of lianas buried later after the ash load overcome branch strength (Opluštil *et al.* 2009, 2014, Pšenička & Opluštil 2013). Field excavations as well as revision of plant fossils in historical collections have shown that the peat swamp of the Lower Radnice Coal was colonised mainly by tropical forest dominated by arborescent lycopsids and cordaitaleans, with shrubby and ground-cover storeys (Opluštil *et al.* 2007, Opluštil *et al.* 2014).

Common and diverse were also sphenopsids, ferns and pteridosperms.

RESULTS

Description and discussion

Fungal hyphae occur in the intercostal field of the thin adaxial cuticle of a sphenopterid pinnule of *Discosoropteris chlupatum* (Plate I, fig. A). The foliar epiphytic/parasitic fungus consists of septate hyphae 4 – 8 μm wide, with compartments between septa 21 – 25 μm long; the hyphae are thin-walled and show occasional irregular constrictions (Plate I, figs B – C). Hyphae may be unbranched or branched. Branches can be distinctly narrowed or approximately the same width as the hyphae from which they extend (Plate I, figs B – C). Narrowed branches are up to 4 μm wide. These types of hyphae represent typical running hyphae extending on the surface of fern leaves (Krings *et al.* 2011). It is possible that such hyphae later grew into the leaf by breaching the cuticle and epidermis using specific penetration structures.

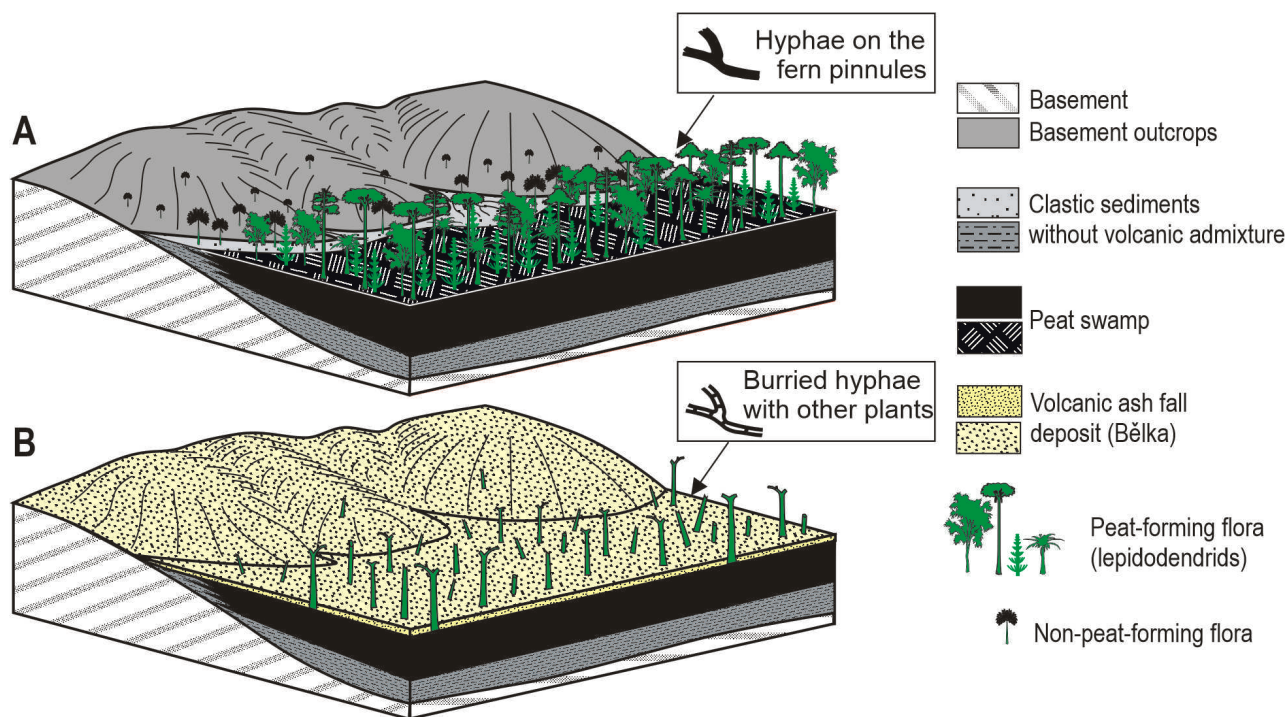


Figure 3. Modified according to Opluštil *et al.* (2014), A – intact coal forest colonizing peat swamp of the Lower Radnice Coal prior the volcanic eruption; B – damaged coal forest partly buried in volcanic ash early after the eruption.

The hyphae described herein represent a rare fossil record of fungi on leaves of land plants preserved as compression. Due to the presence of simple septa (without clamp connections), we interpret these remains as evidence of an epiphytic *in situ* ascomycete on a fern leaf of Pennsylvanian age preserved as a compression. The nature of the association between the fern and the fungal hyphae is not clear. Preservation of a single fungus on a pinnule, together with excellent cuticle preservation indicative of a living leaf, suggests a parasitic mode of life with epiphyllous colonisation. It cannot be stated with certainty that the leaf was not decomposing on the forest floor and colonized by a saprotrophic fungus. However, given the exceptionally good preservation of this true fern, we suggest that it was in fact parasitized. Comparable colonisation occurs in extant members of Erysiphales or Asterinales, both of which are obligate biotrophic parasites of vascular plants. However, the former group is believed to have evolved much later, in the Middle Cretaceous Period (Takamatsu 2013), and the latter is typically characterised by thick-walled, septate mycelium and specific infection apparatus (appressoria), which were not observed in our specimen. Similar Paleozoic hyphae were described by Krings *et al.* (2009) from the Grand-Croix locality in France (300 Ma). They detected a very similar branched hyphae colonizing endophytically pectopterid permineralized pinnules (see Krings *et al.* 2009, pl. I, fig. 3), supporting our interpretation that these structures belong to fungi rather than subaerial epiphytic filamentous algae, which may be relative-

ly common in extant tropical ecosystems (López-Bautista *et al.* 2006). The endophyte described by Krings *et al.* (2009) consists of septate hyphae 2 – 4 μm wide, thin-walled, with irregular constriction, unbranched or branched, and includes spherical-ovoid structures interpreted as possible conidia. In contrast, our septate hyphae are 4 – 8 μm wide (Plate I, figs B – C), and we have no evidence that they belong to an endophytic fungus. The small fern leaf described by Krings *et al.* (2009) contained septate hyphae, some with prominent swellings, extending through the hypodermis of the leaf. Because no host response was observed, it was not possible to determine whether the host was alive at the time of infection or already decaying, suggesting that the fungus may have represented a saprotroph (Krings *et al.* 2009). Nevertheless, our specimens of *Discosoropteris chlupatum* with hyphae are very nicely preserved (see in Pšenička *et al.* 2022) and allow detailed study of anatomy, epidermis, cuticles with stomata, annulate sporangia and *in situ* spores. Such exceptional preservation is rare in true ferns, indicating that burial must have occurred extremely rapidly. Therefore, as stated above, we assume that the preserved fungal species may have lived as an epiphyllous parasite. Alternatively, the fungus may have colonised the leaf as a saprotroph soon after leaf abscission and contributed to decomposition. Finally, we might have recorded a saprotrophic phyllosphere fungus whose activity is limited because such fungi disappear during the early stages of decomposition (Osono 2006).

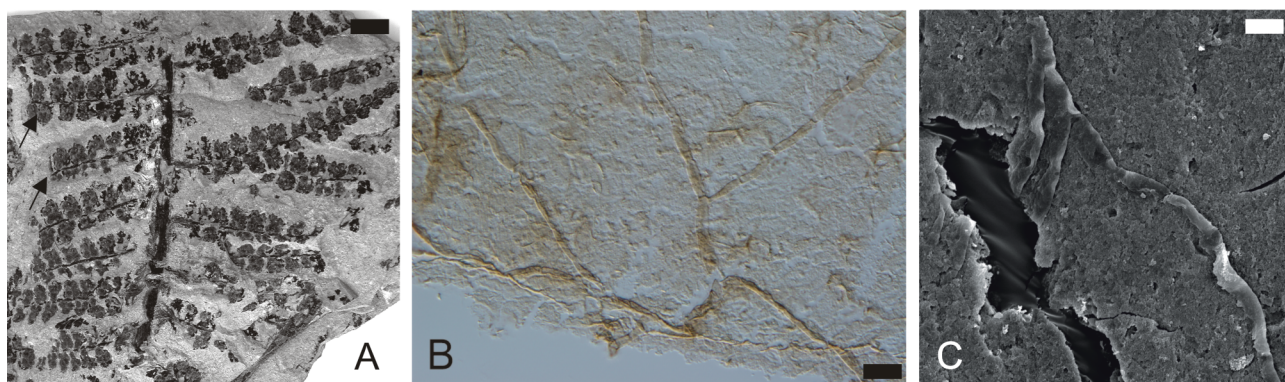


Plate I. *Discosoropteris chlupatum* Pšenička *et al.* (2022), holotype (F4), West Bohemia Museum in Pilsen, CZ. A – fertile frond that have been attacked by hyphae (arrow), scale bar 10 mm; B – fungal septate branched hyphae occurred in intercostal field of adaxial cuticle, scale bar 20 μm ; C – detail of septate hyphae under SEM observation, scale bar 10 μm .

Further Paleozoic studies of fungi associated with plants will provide more information about their environments. It is important to note that during the late Paleozoic there is evidence of numerous fungal interactions ranging from saprophytes to parasites and, in some cases, highly evolved and complex host responses preserved in permineralisations. There is no reason why such interactions should not also be preserved in compression fossils, and such remains should not be overlooked in order to gain as much information about paleoecology as possible. This preliminary research aims to demonstrate the presence of fossil fungi on the true fern in the Paleozoic and highlights the significance of their unique preservation.

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