Ancient Basidiomycota in an extinct conifer-like tree, *Xenoxylon utahense*, and a brief survey of fungi in the Upper Jurassic Morrison Formation, USA

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Abstract.—Although the well-known Upper Jurassic Morrison Formation has yielded abundant fossil plants for nearly a century, relatively little is known about fossil fungi and their ecological relationships to the Morrison flora. The first mention of fungal decay in fossil wood was briefly made over three decades ago, and since then, a few more reports of fungal decay associated with Morrison plants have been published. However, up to now, detailed data on the fossil fungi themselves have not been given from the Morrison Formation. Here we describe in detail well-preserved fossil mycelia in a silicified log of *Xenoxylon utahense* Xie et Gee, 2021 from the Upper Jurassic Morrison Formation at Miners Draw, Blue Mountain, near Vernal in northeastern Utah, USA. The fungal hyphae are variable in form, ranging from straight to slightly curved to highly coiled to tubular; they measure ~1.53 μm in diameter and possess clamp connections, septa, and occasional bifurcations. The occurrence of clamp connections typical of living Basidiomycota indicates a taxonomic affinity to this division of fungi. On the basis of the patterns of wood decay in the *Xenoxylon* log, the fossil fungi are interpreted here as pertaining to saprotrophic, white-rot wood fungi. These fossil mycelia represent a new record of ancient Basidiomycota from the Upper Jurassic Morrison Formation and provide further evidence for plant–fungus interactions in Jurassic terrestrial ecosystems.

Introduction

Interactions between terrestrial plants and fungi can be traced back to the Early Devonian times, ca. 400 million years ago (Stubblefield et al., 1985; Taylor et al., 2015). One of the oldest occurrences was described by Kidston and Lang (1921) as fungi in the shoot cortex of *Aglaophyton major* (Kidston and Lang) Edwards, 1986 from the Lower Devonian Rhynie Chert in Scotland. However, fossil fungi in terrestrial plants are relatively poorly known throughout geological history. The scarcity of reports on plant–fungus interactions is likely due to the inconspicuous fungal decay patterns in ancient plants, the microscopic size of many fungi, and the type of preservation in fossil plants.

Fungal remains have been found associated with various types of plant preservation, ranging from leaf impressions and compressions to permineralized material. On impressions, it is extremely difficult to ascertain evidence of plant–fungus interactions, although various spots on some fossil leaves have been interpreted as fungal decay (e.g., Unger, 1841; Meschinelli,

1898). Compressions of both conifer and angiosperm foliage, however, have yielded evidence of multicellular epiphyllous fungi (e.g., Dilcher, 1963, 1965; Alvin and Muir, 1970; Iglesias et al., 2007; Ding et al., 2011; Bannister et al., 2016; Maslova et al., 2020). Permineralized plant remains have also yielded good fossil evidence of plant–fungus interactions (Taylor et al., 2015). In recent years, there has been an increasing awareness of fossil fungal remains, especially of wood-decay fungi in silicified woods (e.g., Pujana et al., 2009; Césari et al., 2012; García Massini et al., 2012; Harper et al., 2012, 2016; McLoughlin and Strullu-Derrien, 2016; Sagasti et al., 2019; Tian et al., 2020; Gee et al., 2022).

Here we report on permineralized wood with structurally preserved fungal hyphae in an Upper Jurassic log that was discovered in the Morrison Formation at Miners Draw in northeastern Utah, USA. The fossil log had recently been recognized as a new species of the enigmatic, conifer-like genus of *Xenoxylon*, *X. utahense* Xie et Gee, by Xie et al., 2021. The fungal decay patterns evident in the fossil wood, the structure of the fossil mycelia, and possible affinity of the ancient fungi are described and discussed here. Our finding sheds new light on plant–fungus interactions in the Morrison ecosystems during Late Jurassic times.
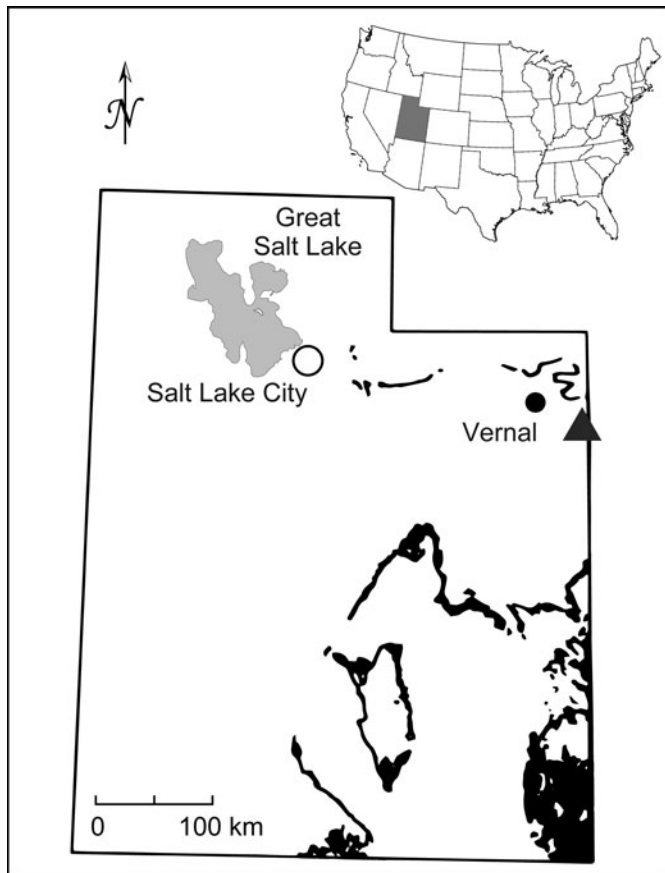
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Figure 1. Map of fossil locality (triangle) bearing the fossil log of *Xenoxylon utahense* in Miners Draw near Vernal (solid circle), Utah (dark gray in inset), USA, superimposed on the outcrops of the Upper Jurassic Morrison Formation (black). Morrison outcrop base map courtesy of Kenneth Carpenter.

Materials and methods

Evidence of fungal decay and the fungal remains themselves were found in a specimen of wood collected from a silicified log from the Upper Jurassic Morrison Formation in Miners Draw on Blue Mountain, about 30 km southeast of Vernal in Utah, USA (Fig. 1). At this site, the fossil wood-bearing strata occur as a series of light greenish-gray to brownish-gray, silty to very fine-grained sandstone with an exposed thickness of ~10 m (Fig. 2; Gee et al., 2019; Sprinkel et al., 2019). Stratigraphically, the strata pertain to the Salt Wash Member of the Upper Jurassic Morrison Formation, which represents a fluvial–lacustrine sedimentary environment at Miners Draw (Sprinkel et al., 2019).

Wood thin sections of the type specimen of *Xenoxylon utahense* (FHPR catalog number FHPR 11386, field specimen number 091119-8, thin sections of BMT-001b) were reinvestigated for fossil fungal remains in the wood tissue. The wood decay and fungal remains were studied with a Leica DM2500 compound photomicroscope (Leica Microsystems, Wetzlar, Germany) and subsequently measured and photographed with the aid of ImageAccess easyLab 7 software (Version 1992–2007, iMagic, Glattburg, Switzerland).
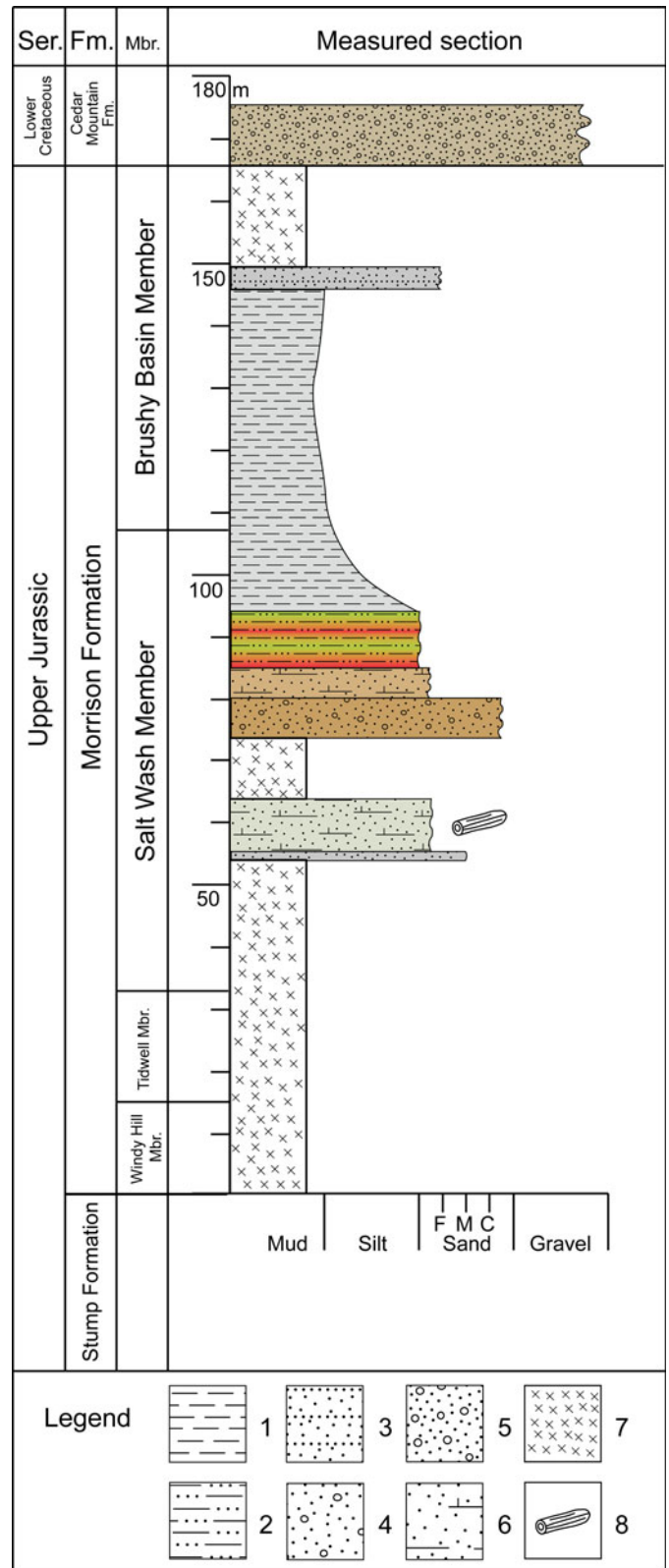

Figure 2. Lithostratigraphic column of the Upper Jurassic Morrison Formation in Miners Draw near Vernal, Utah, USA. Legend: (1) mudstone; (2) siltstone; (3) sandstone; (4) conglomeratic sandstone; (5) conglomerate; (6) silty sandstone; (7) covered and not measured outcrop; (8) fossil log. Section modified after Sprinkel et al. (2019).
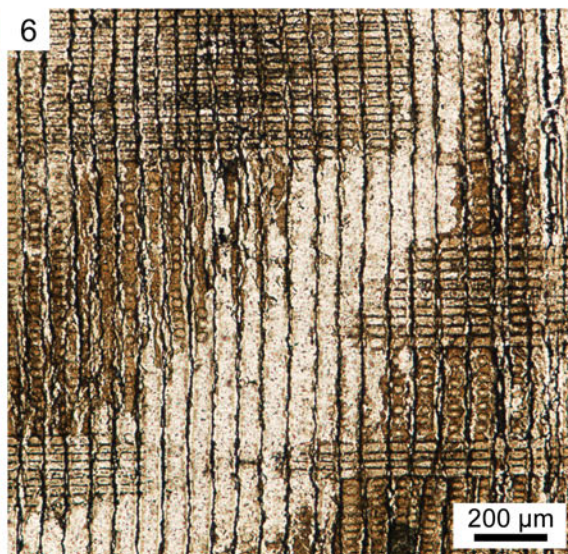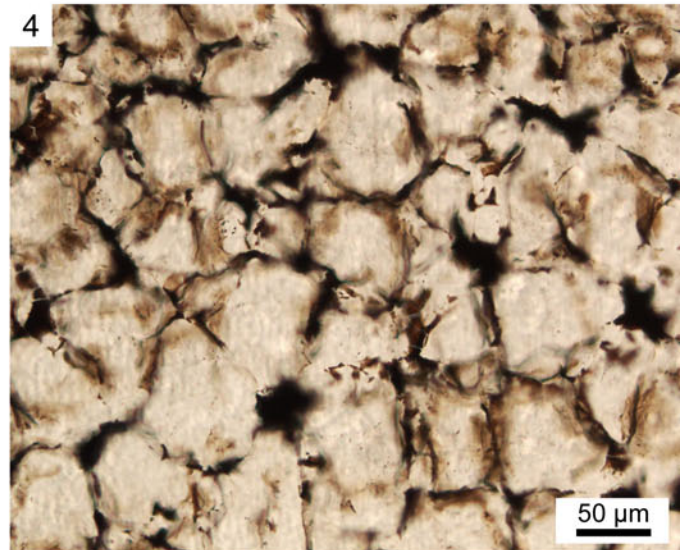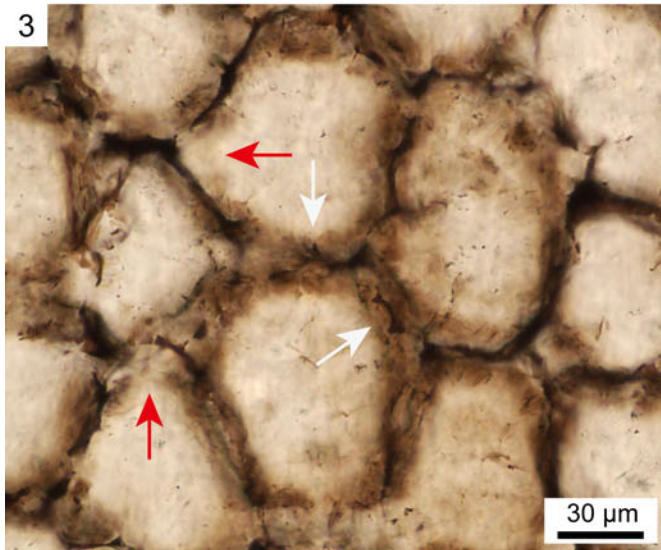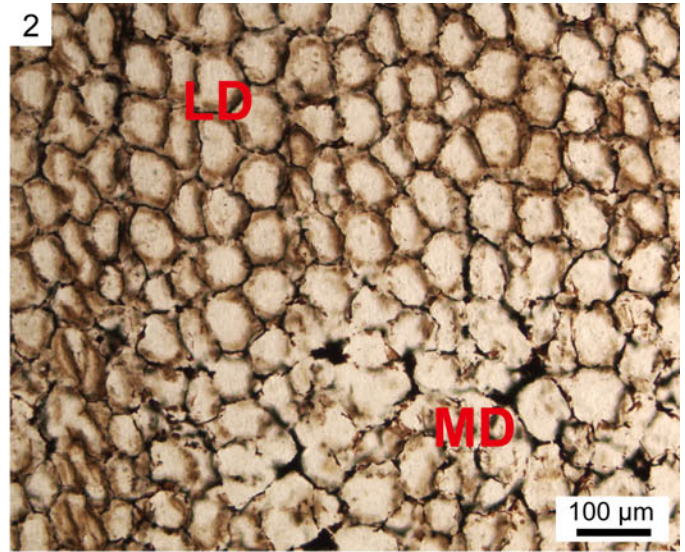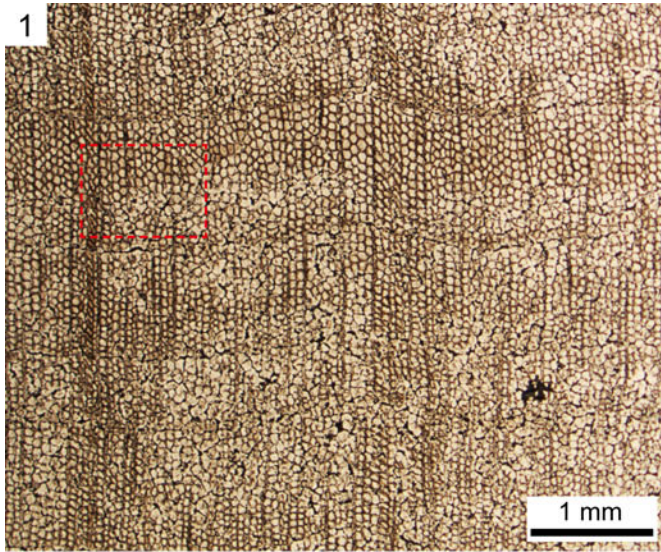
Figure 3. Specimen BMT-001b. Thin-section micrographs in transverse (**1–4**) and radial (**5–7**) sections of tree host *Xenoxylon utahense* Xie et Gee in Xie et al., 2021 from the Upper Jurassic Morrison Formation in Miners Draw, Utah, USA. (**1**) Overview of wood, showing several growth rings. (**2**) Close-up of (**1**) (area within red rectangle) showing details of the wood decay at different degrees of decay. LD = area with less decay; MD = more decay. (**3**) Close-up of (**2**) showing details in the area of less decay. Some parts of the cell walls remain more or less intact (white arrows), while other areas of the cell wall of the same tracheids are nearly completely degraded (red arrows). (**4**) Close-up of (**2**) showing extremely advanced disintegration of the tracheid cell walls in the area with more decay. (**5**) Overview of wood, in which the decolored zones appear as irregularly shaped bands or patches. (**6**) Close-up of (**5**) showing details of the decolored zones; the tracheid pitting on radial walls can no longer be observed in the decolored zone. (**7**) Close-up of (**6**) showing details of the fungal hyphae in the decolored tracheids (red arrow).

Repositories and institutional abbreviations.—Remnants of the wood specimens of *Xenoxylon* are deposited at the Utah Field House of Natural History State Park Museum (FHNHM), Utah, USA, under FHPR catalog number FHPR11386. Thin sections are housed and logged into the system at the University of Bonn in Bonn, Germany, as BMT-001a, BMT-001b, and BMT-001c.

Results

Tree host.—The fossil log at Miners Draw area was previously recognized as *Xenoxylon utahense* Xie et Gee by Xie et al., 2021, an extinct gymnosperm that may pertain to the extinct family Miroviaceae (cf. Nosova and Kiritchkova, 2008; Philippe et al., 2013). *Xenoxylon utahense* is a conifer-like wood dominated by tracheids and ray parenchyma that lacks axial parenchyma and resin canals. Tracheid pitting on radial walls is mostly uniseriate and strongly flattened. Crossfield pitting is fenestriform. Ray cells are mostly uniseriate, occasionally biseriate, homocellular, parenchymatous, with smooth and unpitted horizontal and end walls.

Wood decay and fungal body fossils.—In transverse section (Fig. 3.1–3.4), the tracheids show various stages of wood decay, such as the decomposition of the middle lamella and tracheid cell walls, as well as the separation of the individual cell wall layers. In areas with less decay (Fig. 3.2, marked LD, 3.3), some parts of the cell walls remain more intact (Fig. 3.3, white arrows) while other areas of the cell walls within the same tracheids show greater degradation (Fig. 3.3, red arrows). In zones with more decay (Fig. 3.2, marked MD, 3.4), the cell walls and middle lamella are almost completely disintegrated. In radial section, large, irregularly shaped zones of decay appear as decolored bands or patches (Fig. 3.5, 3.6). In these decolored zones, only the faint outlines of tracheid walls may be preserved, and the circular bordered pits on the radial walls of the tracheids can no longer be observed (Fig. 3.6). Fungal remains occur in abundance in these tracheids (Fig. 3.7, red arrow).

In radial section, the abundant fungal remains are represented by well-preserved mycelia composed of fungal hyphae. The fungal hyphae run more or less vertically through the tracheids (Fig. 4.1–4.7) but can also pass through the crossfields (Fig. 4.8), which illustrate that the hyphae had penetrated into the cell walls of the ray parenchyma. In the tracheid lumina, the fungal hyphae can be straight, lightly curved (Fig. 4), or highly coiled (Fig. 5.1, 5.2, 5.8, white arrow). The diameter of the hyphae ranges from 1.21 to 2.09 µm and measures 1.53 µm on average. The hyphae are tubular in morphology and smooth-walled (Figs. 4, 5). The crosswalls of the hyphae, also known as septa, can be observed in some hyphae and are

located near bifurcations (Fig. 5.3, arrowheads). A large number of typical clamp connections are present in the hyphae (Fig. 4.2, 4.3, red arrows; Fig. 5.4–5.9, red arrows). Bifurcations occur in some hyphae, sometimes in conjunction with a clamp connection (Fig. 5.4, 5.5, arrows).

Discussion

In the *Xenoxylon utahense* wood from Miners Draw under investigation here, there are multiple lines of evidence for fossil fungal decay (Figs. 3–5). On the tissue level, the preservation of the fossil wood is locally variable in its degree of decay. Particularly in radial section, the zones of decay are evident as irregularly positioned and shaped, decolored bands or patches (Fig. 3.5). In the decolored zones, the decay can be so advanced that only the faint outlines of the tracheid walls are preserved, and the outlines of the circular bordered pits can no longer be observed (Fig. 3.6). On the cellular level, there is also differential decay. In the areas showing less decay, some parts of the cell walls remain mostly intact, while other parts are more highly degraded (Fig. 3.1–3.3). In areas with cells with greater decay, there are varying degrees of decomposition of the middle lamina and tracheid cell wall (Fig. 3.3, 3.4).

Even more telling is the concrete and abundant evidence of the ancient fungus in the form of well-preserved mycelia (Figs. 3.7, 4, 5). The mycelia are represented by hyphae that not only extend through the tracheid cells but also pass through the crossfields into the ray parenchyma cells (Fig. 4.8). The hyphae are similar in their size and general morphology, although they can be straight, lightly curved, or highly coiled (Figs. 3.7, 4, 5).

While it is natural to expect some diagenesis to have affected wood preservation after 150 million years, it is the patchy and differential decoloration and decay in the wood tissue, along with the plenitude of fungal body fossils in the tracheid cells, that strongly point to ancient fungi as a major source of decay in this *Xenoxylon* tree. In living trees, selective delignification in wood and the cellular decomposition of the middle lamina and tracheid walls are strong indicators of white-rot fungi (Blanchette, 1991; Schwarze et al., 2000; Schwarze, 2007). Similar patterns of decay in fossil woods have also been attributed to white-rot fungi, such as examples from the Upper Devonian of North America (Stubblefield et al., 1985; Taylor et al., 2015), uppermost Permian of China (Wei et al., 2019), Paleozoic and Mesozoic of Antarctica (Stubblefield and Taylor, 1985, 1986; Harper et al., 2016), Jurassic of the Tibetan Plateau (Xia et al., 2020), Upper Jurassic of the western United States (Gee et al., 2022), Lower Cretaceous of northeastern Brazil (dos Santos et al., 2020) and northeastern China (Tian et al., 2020), and Eocene of southern Argentina (Pujana et al., 2009).
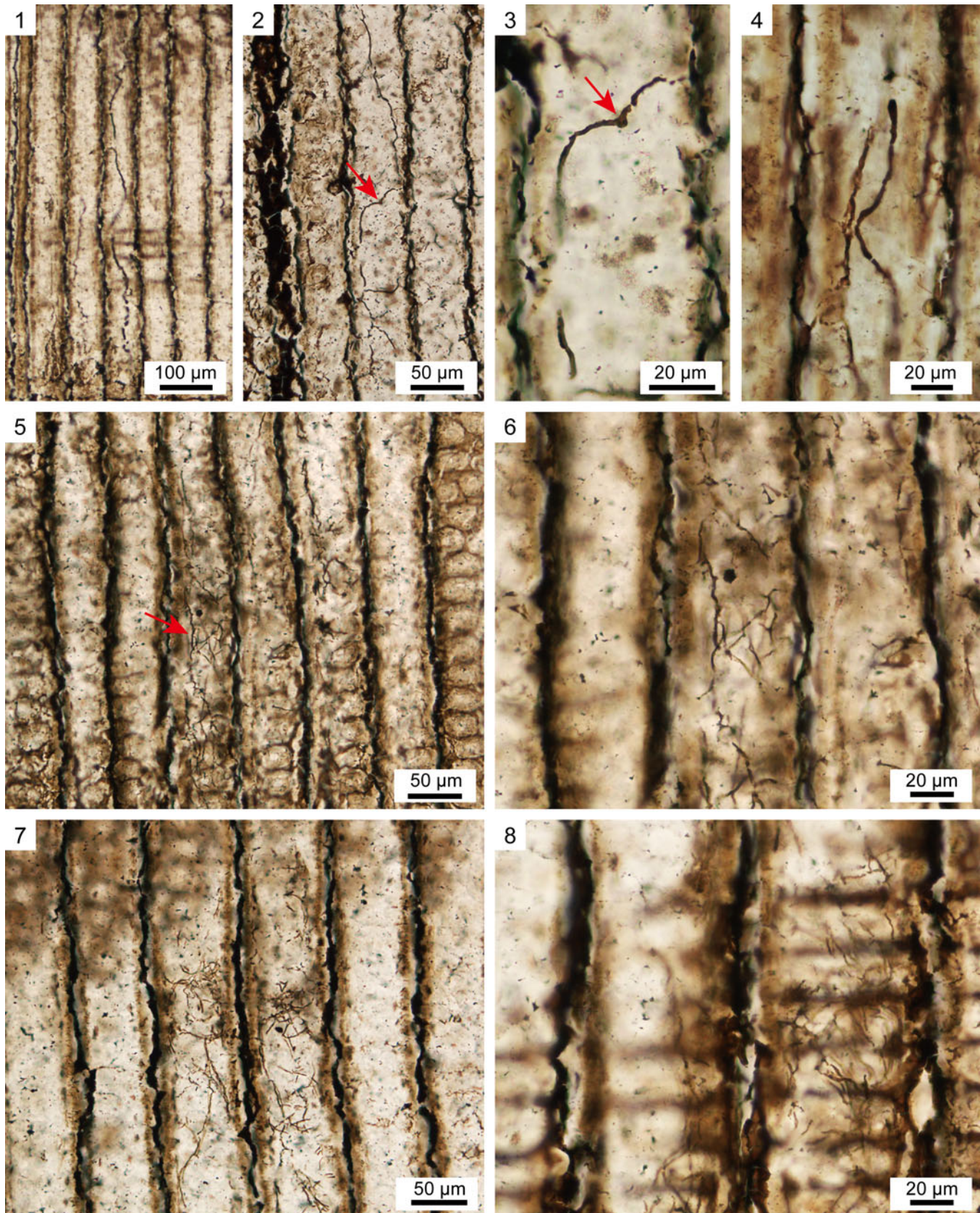
Figure 4. Specimen BMT-001b. Thin-section micrographs in radial section of *Xenoxylon utahense* with fungal hyphae. (**1**) Fungal hyphae passing through tracheid lumina. (**2**) Fungal hyphae growing along the tracheid walls, with a typical basidiomycetous clamp connection (red arrow). (**3**) Close-up of (**2**) highlighting the clamp connection (red arrow). (**4**) Fungal hyphae growing in the lumen of a tracheid. (**5**) Abundant fungal hyphae in tracheids (red arrow). (**6**) Close-up of (**5**) showing details of hyphae. (**7**) Another view of fungal hyphae, here in neighboring tracheids. (**8**) Fungal hyphae penetrating the crossfields between rays and tracheids.
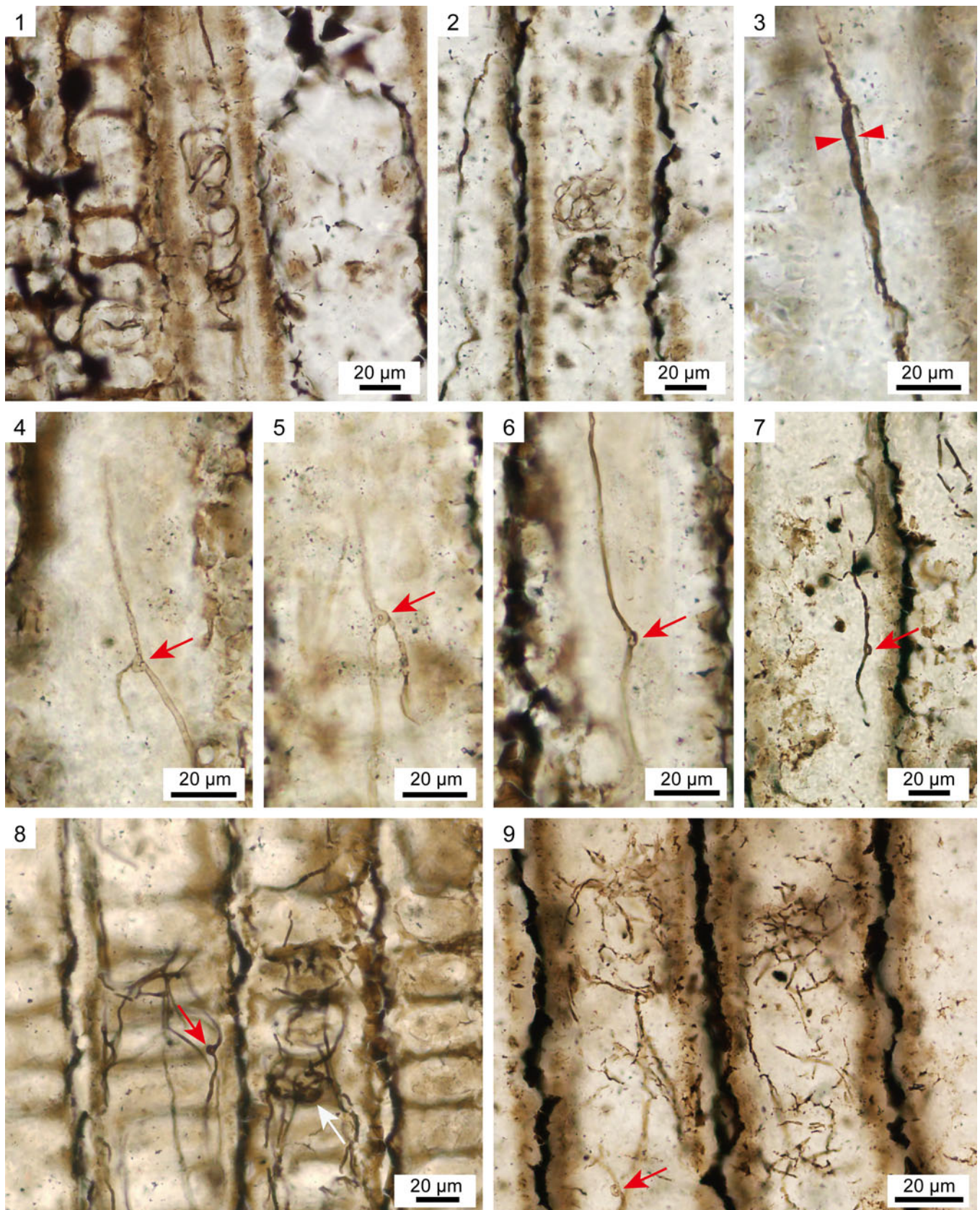
Figure 5. Specimen BMT-001b. Thin-section micrographs in radial section of *Xenoxylon utahense* with fungal remains. (**1, 2**) Highly coiled fungal hypha. (**3**) Septum (between arrowheads) in a fungal hypha. (**4–7**) Typical basidiomycetous clamp connections (red arrows), which are sometimes associated with a bifurcation of the hyphae. (**8**) Highly coiled fungal hyphae (white arrow) and clamp connection (red arrow). (**9**) A typical clamp connection (red arrow).

In recent wood that has been decayed by white rot, it has been observed that the fungal hyphae growing in the lumina of the tracheids produce decay enzymes that degrade the secondary wall of the tracheids during an early stage of simultaneous rot (Schwarze et al., 2000; Schwarze, 2007). Then, in a later stage, the primary and secondary walls of the tracheids, as well as the middle lamella, are partially broken down, which results in the tracheid wall being thinner, and individual tracheid cells become slightly separated from one another (Schwarze et al., 2000; Schwarze, 2007). These characters are well developed in the decayed areas of the *Xenoxylon* wood from the Morrison Formation, which show tracheids with the colonization by fungal hyphae and these various types of cell-wall alterations, including the local removal of the middle lamella, decomposition of the secondary wall of tracheids, and cell-wall separation. Hence, the sequence of damage observed in recent white-rot decay suggests that the wood decay in the *Xenoxylon* tree was preserved after it had reached an advanced stage of simultaneous white rot.

Probable affinity of the fungus in Xenoxylon utahense.—In general, the morphology of sexual reproductive organs is essential to the taxonomic identification of extant fungi. However, due to the scarcity of reproductive organs in fossil fungi and paleomycological studies, the systematic identification of fossil fungi is extremely difficult. Thus, the recognition of other diagnostic structural features has been recognized as a practical approach to identifying certain ancient fungi. For example, the structural character of clamp connections—a hyphal protrusion during cell division to maintain the binucleate (dikaryon) condition—is commonly used to identify fossil Basidiomycota in the absence of sexual reproductive structures (Krings et al., 2011; Taylor et al., 2015).

In the *Xenoxylon* wood from Miners Draw area, the affinity of the white-rot fungus to the Basidiomycota is strongly supported by the clamp connections and septa in the hyphae. The occurrence of fungal hyphae with clamp connections in silicified wood is not unusual in the fossil record. The oldest fossil record of fungal hyphae with clamp connections comes from the Carboniferous fern rachis *Botryopteris antiqua* Kidston, 1908 in France (Krings et al., 2011), although molecular clock analysis suggests that the first Basidiomycota originated during the Cambrian (Berbee and Taylor, 2001; Oberwinkler, 2012). Similar clamp connections have also been described from the Carboniferous of North America (Dennis, 1969, 1970), Lower Permian of North China (Wan et al., 2017), Triassic of Antarctica (Stubblefield and Taylor, 1986; Osborn et al., 1989), Jurassic of southwestern China (Feng et al., 2015), Jurassic of Argentina (Gnaedinger et al., 2015; García Massini et al., 2016), Lower Cretaceous of northeastern China (Hsü, 1953; Tian et al., 2020), Cretaceous of Mongolia (Krassilov and Makulbekov, 2003; Zhu et al., 2018), and Miocene of Argentina (Greppi et al., 2018).

Up to now, only three morphogenera have been established within fossil Basidiomycota on the basis of mycelia: *Palaeancistrus* Dennis, 1970, *Palaeofibulus* Osborn, Taylor, and White, 1989, and *Palaeosclerotium* Rothwell, 1972. The first genus, *Palaeancistrus*, is defined by septate fungal hyphae with clamp connections along with branching at mostly right angles (Dennis, 1970). The second genus, *Palaeofibulus*, is characterized by hyphal filaments with incomplete clamp connections (Osborn et al., 1989). The third genus, *Palaeosclerotium*, is recognized by fungal sclerotia, which are branched septate hyphae (Rothwell, 1972). However, when Singer (1977) reexamined the type specimen of *Palaeosclerotium*, he suggested that *Palaeosclerotium* shared affinities with the extant Ascomycota, an assessment that agrees with the conclusions of Dennis (1976). In the wood of *Xenoxylon* from the Morrison Formation described here, the occurrence of fossil mycelia with septate fungal hyphae and typical clamp connections best corresponds to the morphological features of *Palaeancistrus*.

Plant–fungus interactions in the Morrison Formation.—Abundant fossil plants have been reported from the Upper Jurassic Morrison Formation for nearly a century (e.g., Lutz, 1930); however, little is known from the ecological interactions between the Morrison plants and fungi. The first account of fossil fungi in a published paper is a short note referring to fungal remains observed in Morrison wood that neither included any illustrations (Tidwell, 1990) nor was followed up by a more detailed treatment.

White-rot decay similar to that described here in the *Xenoxylon utahense* wood has been recently described in the wood of a giant tree of *Agathoxylon hoodii* (Tidwell and Medlyn) Gee et al., 2019 from the Upper Jurassic Morrison Formation in Rainbow Draw near Dinosaur National Monument in Utah (Gee et al., 2022). The Rainbow Draw wood site is located only ~18 km in a straight line from the Miners Draw wood site; these fossil localities are considered stratigraphically equivalent to one another (Sprinkel et al., 2019), although different wood genera occur at each site (Xie et al., 2021; Gee et al., 2022). In the wood of the *Agathoxylon* log from Rainbow Draw, variable degrees of white-rot decay can be observed in neighbor cells. While the cell wall of a tracheid can appear seemingly intact, uniform, and dark in color, the cell walls of neighboring tracheids can appear to have lost color in only one small section or in the entire wall. In this particular *Agathoxylon* log, a sequence of events was reconstructed whereby the weakened and decomposed areas of wood tissue decayed by fungi facilitated the boring of large-diameter, vertical galleries by insects, most likely by beetle larvae (Gee et al., 2022).

More evidence for plant–fungus interactions in the Morrison Formation was described by Tidwell et al. (1998) as abundant small and star-shaped decayed areas in fossil conifer woods from the Mygatt–Moore Quarry (MMQ) in Colorado that is similar to damage caused by modern brown rot. In this case, it was commented that the fungus in MMQ woods is similar to *Stereum sanguionolentum* (Albertini and Schwein ex Fries) Fries, 1838 of the extant Stereaceae (Tidwell et al., 1998).

Beyond microscopic evidence of fungal decay, macroscopic characters have also been used to understand the relationship between plants and fungi in the Upper Jurassic Morrison Formation. For example, small to large cavities measuring 1–5 cm in diameter found in the heartwood of a fossil conifer wood from the Morrison Formation were subsequently interpreted as the infestation of the tree by fungi (Hasiotis, 2004). However, the maker of these cavities may still be open to interpretation because similar cavities can also be produced by beetles (e.g., Ponomarenko, 2003; Naugolnykh and Ponomarenko, 2010; Feng et al., 2017; Gee et al., 2022).

Thus, the new plant–fungus interaction described here in *Xenoxylon utahense* wood offers us additional evidence for understanding the complex network of interrelationships in the Upper Jurassic. However, for a deeper and more comprehensive knowledge of trophic interactions in Morrison ecosystems, further discoveries and research are needed. Other ecological interactions between Morrison plants and fungi, for example, mutualism, have not been documented; up to now, only saprotrophic or possible parasitic wood-decay fungi have been reported (Tidwell, 1990; Tidwell et al., 1998; Gee, 2015; Gee et al., 2022).

Wood decay patterns and saprophytic fungi.—In general, fungi are associated mainly with plants in three types of ecological interactions: parasitism, mutualism, and saprophytism (Newsham et al., 1995). Compared with parasitism and mutualism, saprophytism is the most common plant–fungus interaction (Schwarze et al., 2000; Schmidt, 2006) and plays a significant role in carbon recycling in ancient ecosystems (Stubblefield and Taylor, 1988; Taylor, 1993; Taylor and Krings, 2010; Taylor et al., 2015; Tian et al., 2021). For example, a fossil record of plant–fungus interactions from the Upper Devonian in Indiana, USA, was interpreted as saprophytism on the basis of wood-decay structures (Stubblefield et al., 1985).

In regard to saprotrophs, extant wood-decay fungi are separated into three primary types in modern woods according to their pattern of degradation process in wood: brown rot, white rot, and soft rot (Schwarze et al., 2000; Schwarze, 2007; Taylor et al., 2015), although some wood-decay fungi may also feed on living plants as parasites. Brown-rot and soft-rot fungi usually destroy the thick middle layer (S_2) of secondary cell wall of the tracheids first, whereas white-rot fungi, which are the only fungal group known to be capable of decomposing wood lignin, generally bleach the wood tissue by degrading lignin, cellulose, and hemicellulose (Blanchette, 1991; Schwarze et al., 2000). From the degradation sequence of wood polymers, two major patterns have been recognized in white rot: selective delignification and simultaneous rot (Adaskaveg and Gilbertson, 1986; Rayner and Boddy, 1988). Simultaneous rot occurs mainly in broad-leaved trees and seldom in conifers, while selective delignification occurs in both broad-leaved trees and conifers (Blanchette, 1991; Schwarze et al., 2000; Schwarze, 2007) and is characterized by a selective initial degradation of lignin and hemicellulose in the cell walls of tracheids. This initial stage is then followed by degradation of cellulose in the cell walls (Schwarze et al., 2000).

Conclusions

The occurrence of ancient Basidiomycota in an extinct conifer-like tree, *Xenoxylon utahense,* is described from the Upper Jurassic Morrison Formation at the Miners Draw area near Vernal in northeastern Utah. The fungal decay pattern is characterized by decolored, irregularly shaped zones or patches in the fossil wood, removal of the middle lamella, decomposition of the secondary wall in the tracheids, and separation of the tracheid wall layers, features that are characteristic of decay patterns observed in extant white rot. Abundant, well-preserved fungal hyphae

with typical clamp connections in the tracheids of the *Xenoxylon* wood are morphologically similar to those of the fossil white-rot genus *Palaeancistrus*. This new discovery represents a new Upper Jurassic record of the Basidiomycota in Utah, offers further evidence for paleomycological diversity in the Morrison Formation, and sheds greater light on plant–fungus interactions in Late Jurassic terrestrial ecosystems.

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