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Plant-arthropod and plant-fungus interactions in late Permian gymnospermous woods from the Bogda Mountains, Xinjiang, northwestern China

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ABSTRACT

Several lines of evidence of plant-arthropod and plant-fungus interactions are documented from the Wuchiapingian Wutonggou low-order cycle (approximate equivalent to the Wutonggou Formation) in Tarlong valley, southern Bogda Mountains, Xinjiang Uygur Autonomous Region, northwestern China. Fossil wood, *Septomedullopitys szei* Wan, Yang et Wang, contains differentially-damaged areas. Spindle-shaped pockets in the fossil wood occurring in the secondary xylem are commonly free of organic remains. They are comparable in appearance to modern white-pocket rot caused by fungi. The tracheid walls around the decomposed areas are degraded from the middle lamellae to outer layers. Abundant branching and septate fungal hyphae in the decayed areas, ray parenchyma and tracheid lumina indicate that fungi are responsible for the wood decay. These fungi are partially regarded as basidiomycetes because of the occurrence of clamp connections. According to the characteristic damages they caused to the host, ascomycetes are also viable candidates of the fungi because large parts of hyphae are without certain clamp connections. The other damaged excavations are branched and maze-like borings and galleries, which are filled with abundant fungal hyphae, cellular debris and spheroidal to ovoidal, dark-colored coprolites, ranging from 26 to 128 μm in diameter. The size, shape, and surface texture of these coprolites indicates that the coprolites are the feces of ancient oribatid mites. The fungal hyphae, coprolites, and degraded excavations in the pith of the late Permian wood suggest that wood-rotting and -boring were not limited to the xylem.

1. Introduction

Land plants and arthropods are two major macroscopic sources for biodiversity on the planet, and have historically provided the basic evolutionary history and ecological structure to continental ecosystems (Labandeira, 2006a). Plant-arthropod interactions are crucial to the evolution of terrestrial ecosystems (Labandeira, 1998a, 2006b, 2006a, 2006b). Once plants became established on the land, a number of plant-arthropod interactions evolved rapidly, having involved all the early plants (Labandeira, 2006b; Labandeira, 2007). Arthropod detritivores in Paleozoic terrestrial ecosystems have been recorded in both high-latitude and tropical terrestrial ecosystems from the late Silurian to the end of the Permian (Labandeira et al., 1997; Labandeira, 1998a, 1998b; Kellogg and Taylor, 2004; Feng, 2012; Feng et al., 2010, 2012, 2015; D'Rozario et al., 2011; Slater et al., 2012; Falcon-Lang et al., 2015). However, only few arthropod detritivores within gymnospermous woods have been reported from the middle-latitude areas in the same time period.

Similarly, fungi have had a long and complex geological history and played an important role in modern ecosystems (Taylor and Taylor, 1997; Taylor et al., 2009, 2014). Fungi are the major decomposers of higher plants in both modern (Otjen and Blanchette, 1982, 1984, 1985; Dighton et al., 2005) and ancient (Stubblefield and Taylor, 1986, 1988) ecosystems. The interactions between fungi and plants in terrestrial ecosystems have been well documented during the late Paleozoic (Dennis, 1970; Tiffney and Barghoorn, 1974; Pirozynski, 1976; Wagner and Taylor, 1981, 1982; Stubblefield and Taylor, 1986, 1988; Stubblefield et al., 1984, 1985a, 1985b; Hass et al., 1994; Taylor and Taylor, 1997, 2000; Krings et al., 2007, 2010, 2011, 2012). However, the reported plant-fungus interactions have been observed mainly

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from materials of Euramerica and Gondwana Floras, providing little information on the Angara Flora.

There are several investigations of plant-arthropod interactions in the Paleozoic of China. Studies of plant-arthropod interactions in the Paleozoic of China (Glasspool et al., 2003; Wang et al., 2009; Feng et al., 2010, 2012; D'Rozario et al., 2011; Feng, 2012) are purely based on materials from the Cathaysia Flora. China is the only country where the four major floras: Cathaysia, Angara, Euramerica and Gondwana, were developed during the Carboniferous and Permian (Shen, 1995). No fossil evidence of plant-arthropod interactions in the other three floras of China was reported. In addition, the records of fungus-plant association are rare in the Paleozoic of China (Wang, 1997).

In this study, we present evidence of the co-occurrence of fungal hyphae and arthropod coprolites are present in the late Permian gymnosperm wood *Septomedullopitys szei* Wan, Yang et Wang from southern Bogda Mountains in Xinjiang Uygur Autonomous Region, which is a part of the Angaran phytoprovince in the Permian (Fig. 1, A, B; Meyen, 1981, 1982, 1997; Sun, 1989). Extensive features of fungal decay and feeding behavior of oribatid mites are observed in the xylem tracheids and pith. Two distinctive types of damage to the wood are documented and attributed to the activities of wood-rotting fungi and oribatid mites. Results of this study provide additional information about the co-occurrence of plant-arthropod and plant-fungus interactions in the late Permian.

2. Geological setting, materials, and methods

The research area is located in the Tarlong-Taodonggou half graben, southern foothills of the Bogda Mountains, bordering the northwestern margin of the Turpan Basin, Xinjiang Uygur Autonomous Region, northwestern China (Fig. 1, A, B; Yang et al., 2007, 2010). The half graben was located at the easternmost Kazakhstan Plate in the Permian. (Fig. 1, C; Şengör and Nat'lin, 1996; Ziegler et al., 1997; Scotese, 2001; Yang et al., 2010). The uppermost Carboniferous to Lower Triassic sedimentary rocks in the half graben include conglomerate, sandstone, shale, and minor limestone and volcanic rocks deposited in fluvial, and lacustrine environments (Fig. 1, D; Yang et al., 2007, 2010). The permineralized stems of *Septomedullopitys szei* examined in current study were collected from a sandstone unit at the base of Wutonggou low-order cycle at the southwestern Tarlong Section (Wan et al., 2014; Fig. 1, D). The sandstone unit is on the top of a coarsening-upward shale-sandstone succession and has a concave erosional base. It was interpreted as a distributary channel fill on a deltaplain above the delta-front deposit (Yang et al., 2010). The age of the fossil-bearing interval is probably early Wuchiapingian, as determined from cyclostratigraphic correlation of the southwestern Tarlong Section with the northeastern Tarlong Section where three U-Pb zircon radiometric ages of the low-order cycle are available (Yang et al., 2010). The stems are parallel to the bedding plane, suggesting that they were transported from upstream or nearby interdistributary area and deposited in a distributary channel on the delta plain (Wan et al., 2014).

The fossil wood genus *Septomedullopitys* Lepekhina has been found only in the upper Permian of Angaran phytoprovince (Lepekhina and Yatsenko-Khmelevsky, 1966; Lepekhina, 1972). It is characterized by the combination of secretory ducts within the septate pith, endarch primary xylem and *Protophyllocladoxylon*-type secondary xylem. *S. szei* consists of reticulate pith with straight secretory ducts and several parenchymatous bands that are distinct from the Kuznetsk species (Wan et al., 2014). The characteristics of *S. szei* could be easily distinguished from other relative Palaeozoic pycnoxylic groups, including pteridosperms, and ginkgophytes. Cordaitaleans from Cathaysia and Euramerica Floras possess septate pith and endarch primary xylem which resemble *S. szei* (Wang et al., 2003; Hilton et al., 2009a,b; Taylor et al., 2009). However,

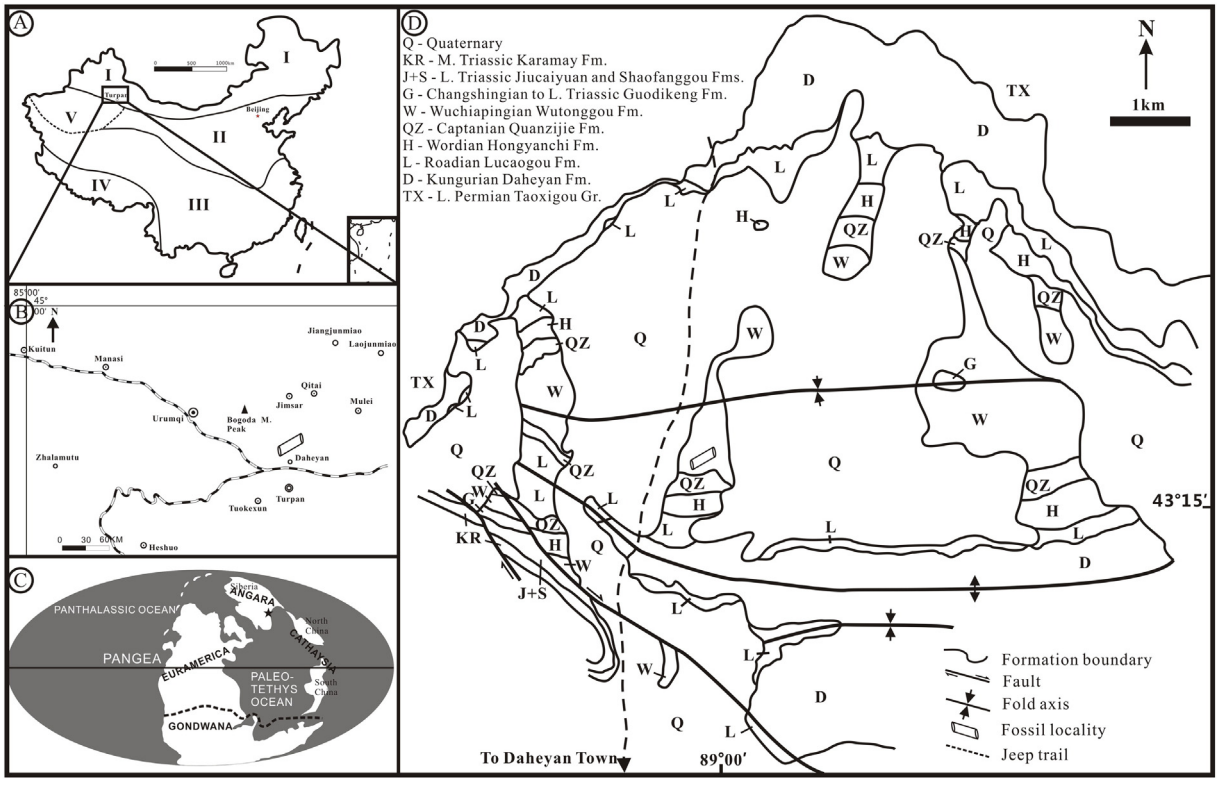

Fig. 1. Geographic and geologic maps of the research area. A) and B) Maps showing the location of the fossil stem of *Septomedullopitys szei* Wan, Yang et Wang. I - Angara province in the Junggar-Hinggan Region; II - Cathaysia-Euramerica-Angara mixed province; III - Cathaysia province; IV - Gondwana province; V - Angara province in Tarim Plate (Shen, 1995). The collection site is shown by the wood stem symbol in (B), which is in the Permian Angaran phytoprovince (Meyen, 1981, 1982, 1997; Sun, 1989). The collection site as shown by the wood stem symbol in (B) is ~12 km north of the town of Daheyan in the southern foothills of the Bogda Mountains, northwestern China. C) Paleogeographic map during late Permian showing the fossil site (star) in the easternmost Kazakhstan Plate at the mid-latitude NE Pangea. Modified after Scotese (2001). D) Geological map of the Tarlong-Taodonggou area showing the fossil collection site (wood stem symbol) in southwestern Tarlong. After Yang et al. (2010).