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A specialized feeding habit of Early Permian oribatid mites

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ABSTRACT

Oribatid mites (Acari: Oribatida) are very diverse and important detritivorous and fungivorous micro-arthropods in modern forest ecosystems. Although the fossil record of oribatid mites can be traced to the Early Devonian, the paleoecology of oribatid mites during the deep geological past remains poorly understood. Remarkably good preservation of tunnel networks in a permineralized conifer wood specimen is described from the Early Permian of Germany. This fossil provides evidence for four aspects of oribatid mite feeding habits. First, there is preferred consumption of the more indurated tissues from growth-ring cycles. Second, tracheids were targeted for consumption. Third, feeding on tissues resulted in fecal pellet accumulations at the bottoms of tunnels. And fourth, the absence of feeding on ambient decomposing fungi such as necroses and rots, but rather the processing of pristine plant tissues, indicate the presence of a self-contained, microorganismic gut biota. These rather specialized feeding habits allowed oribatid mites a prominent role in the decomposition of digestively refractory plant tissues in Early Permian ecosystems.

1. Introduction

Oribatid mites (Acari: Oribatida) are a very diverse group of small, detritivorous and fungivorous arthropods (Schatz and Behan-Pelletier, 2008; Walter and Proctor, 2013). They are a dominant component of the microarthropod fauna in most forest ecosystems (Behan-Pelletier et al., 2008), and are speciose and numerically dominant in temperate forest canopies (Behan-Pelletier and Walter, 2000). Body-fossil records indicate that oribatid mites were present during the expansion of Early Devonian terrestrial ecosystems some 410 million years ago (Norton et al., 1988), but little is known of their paleoecological history (Labandeira, 1998, 2007). Oribatid mite borings and their typically co-occurring coprolites are observed worldwide in Late Paleozoic silica permineralized or petrified woods, as well as in plant tissues preserved in chert or carbonate permineralized coal balls (Labandeira et al., 1997; Rößler, 2000), and consequently provide a basis for understanding their relationships to their abiotic and biotic environments. Although coprolite dimensions within tunneled tissues have been used to determine fossil oribatid mite morphotypes (Feng et al., 2010, 2012), their feeding habits, including detritivory, are poorly understood.

Here, we describe distinctive oribatid mite borings contained in a specimen of exceptionally well-preserved conifer wood from the Early Permian Manebach Formation near Crock village, in Thuringia State, Germany. The borings are rectangular or sub-rectangular in transverse section, with smooth interior walls filled with small, ovoidal to sub-spheroidal coprolites. The borings occur amid tracheid elements and are bordered by rays, indicating that the mites preferred to feed on lignified cells and avoided fleshier parenchymatous cells.

2. Material and methods

A permineralized wood specimen containing three-dimensional networks of borings with infilled coprolites was obtained from the Early Permian Manebach Formation of Crock, a small village located ca. 10 km southeast of Schleusingen, in the south of the Thuringia State, Germany.

Historically, there were several coal mines in Early Permian strata producing anthracite coal near Crock. Crock is the only known locality within the Thuringian Forest Basin providing lower ranked coals that would allow for maceration (Kerp and Barthel, 1993). Although there is a long history of fossil collection and paleobotanical research in the Thuringian Forest Basin (Barthel, 2009), formally mentioned fossil woods have been only occasionally reported. Recently, Witter et al. (2011) described in detail several new finds of fossil woods from Crock.

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The wood described from Crock is found in coarse-grained alluvial fan deposits that crop out on the surfaces of slopes of Irmelsberg Hill. These sediments from the southwestern part of the so-called Schleusingen marginal zone belong to the southernmost occurrence of the Rotliegend Group, consisting of Early to Middle Permian strata within the Thuringian Forest Basin. These wood-containing basal, alluvial-fan strata were overlain by coal-bearing, fine-grained clastic sequences that were assigned to the Manebach Formation. The stratigraphic level for the fossil wood locality is comparable with basal Rotliegend strata of Asselian age, and is located within the Manebach Formation sequence of the Thuringian Forest Basin (Lützner et al., 2012).

The Late Paleozoic continental succession of the Thuringian Forest Basin is 5–6 km thick and consists of eleven formations from the lowermost Stephanian C representing the Late Pennsylvanian, to the Upper Rotliegend of the Middle Permian (Lützner et al., 2012). Chert and fossil wood fragments commonly are encountered in the Early Permian Manebach Formation, which consists of gray conglomerates, sandstones, mudstones and locally intercalated coal seams (Barthel et al., 2010).

Permineralized woods containing borings and coprolites collected from Crock were sectioned for detailed examination. Thin sections from transverse, tangential and radial planes of wood were prepared as follows. First, a specimen was sectioned to an appropriately thin wafer with a diamond saw, of which the upper surface was ground using a grinding wheel with carborundum grit in a decreasing series of #240, #400 and #800 grade sizes. The smooth upper surface was attached to a glass slide with Buehler EpoThin™ Epoxy Resin (20-8140-032) and EpoThin™ Epoxy Hardener (20-8142-016), and the exposed surface was subsequently ground to a thickness of 30–50 μm.

Photographs were taken with a Nikon Eclipse ME 600 transmitted light microscope and a Nikon SMZ 1500 stereoscopic light microscope. Images were taken on both microscopes, which were equipped with a Nikon DS-5M-L1 digital camera. Composite images were stitched

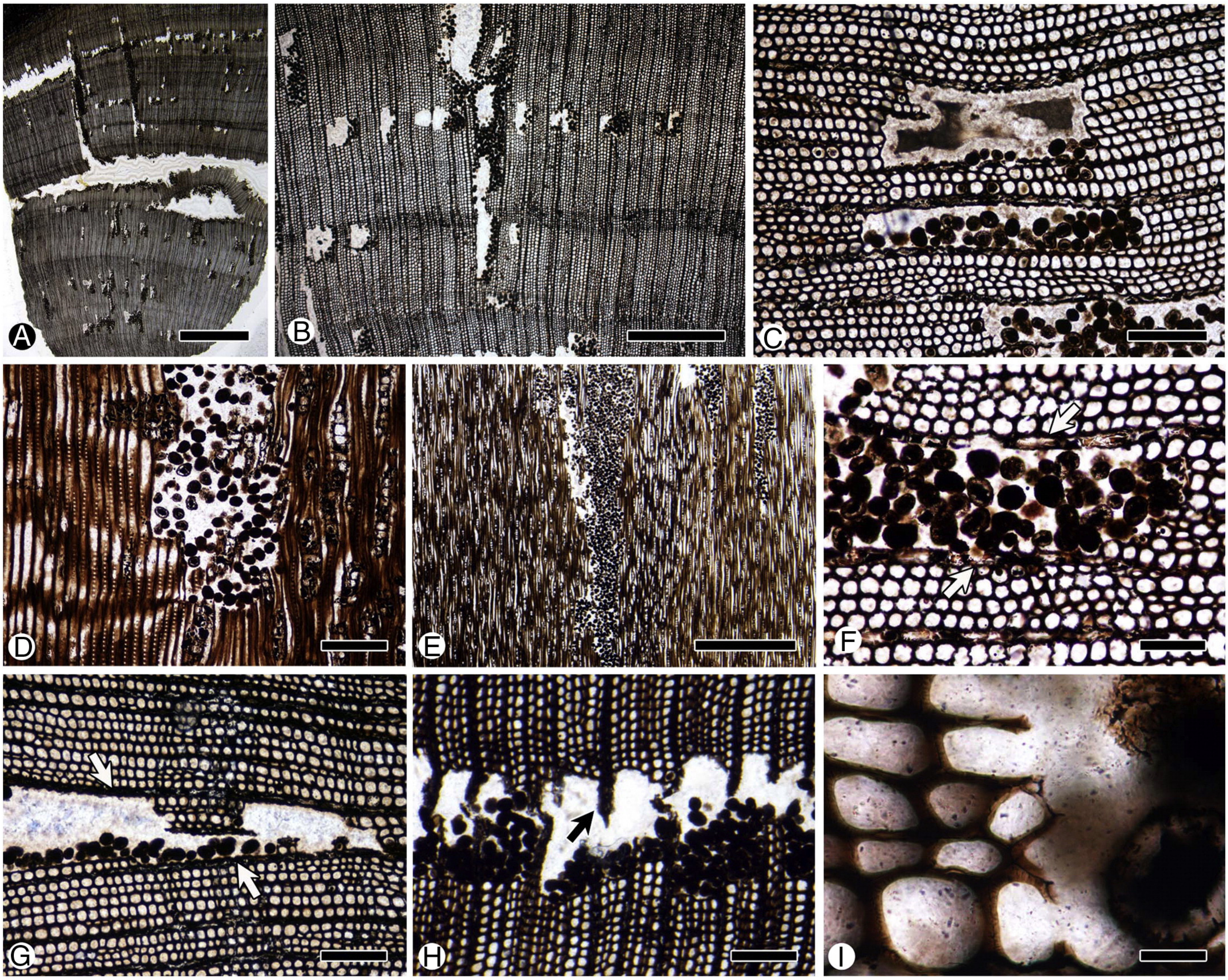

Fig. 1. Oribatid mite borings and coprolites preserved in gymnospermous wood from the Early Permian Manebach Formation, Germany. (A) — Transverse section (TS) showing the concentrically arranged bands of borings in secondary xylem, scale bar = 3 mm. (B) — TS, borings restricted to growth rings, occasionally intersecting several growth rings, scale bar = 1 mm. (C) — TS, rectangular or sub-rectangular outlines of borings with effaced margins and right-angle wall junctures, scale bar = 200 μm. (D) — Longitudinal radial section, effaced inner-wall surfaces and truncated bottoms of the borings, scale bar = 200 μm. (E) — Longitudinal tangential section, borings vertically extend along the wood axis, scale bar = 1 mm. (F) — TS, borings bordered by ray cells; arrows indicate ray cells, scale bar = 100 μm. (G) — TS, long borings bordered by single rows of ray cells (arrows), scale bar = 200 μm. (H) — TS, discontinuous rays (arrow) locally projecting into an excavated area, scale bar = 200 μm. (I) — TS, displaying incompletely attacked tracheid elements at the tunnel edge and the succeeding undamaged tracheid elements with intact cell walls, scale bar = 25 μm.

using Adobe Photoshop CS5 Extended program software. The specimen and thin sections are stored at the Museum für Naturkunde Chemnitz, in Germany, labeled as K6024 Crock001.

3. Results

3.1. Borings and coprolites

The wedge-shaped wood fragment is ca. 25 mm in diameter and 55 mm long, and represents a portion of the secondary xylem cylinder. Ten bands of borings were observed in transverse section (Fig. 1A). The borings are concentrically arranged and are oriented parallel to the growth rings that are typically separate from one another and restricted to distinctive bands. A few large borings radially intersect with up to four growth rings (Fig. 1B). The borings generally are very close to growth boundaries or rarely occur in the central region of the growth rings (Fig. 1B). In transverse section, the pronounced outlines of the borings are rectangular or sub-rectangular with smooth inner-margin surfaces and squared-off corners (Fig. 1C). In longitudinal section, tunnel bottoms are truncated (Fig. 1D). Borings are 0.11–0.53 mm wide (tangential) and 0.21–1.6 mm long (radial) in transverse sections. Longitudinal sections of borings extend vertically for more than 3 mm along the direction of the stem axis to form long, tubular tunnels (Fig. 1E).

The borings predominantly occur among tracheid elements and are bordered by ray cells (Fig. 1F, arrows). Even for radially extended borings in transverse section, the tunnels are continuously constrained by single rows of ray cells (Fig. 1G, arrows). Parenchymatous rays occur commonly between adjacent borings. However, in extensively bored regions, discontinuous rays locally project into the excavated area to varying degrees (Fig. 1H, arrow), which may be caused by lateral damage. Both incompletely consumed tracheid elements at the tunnel edge and the succeeding undamaged tracheid elements show intact cell-wall structures, including a middle lamella and a primary and a secondary wall that include the S1 to S3 layers (Fig. 1I). No evidence of fungal saprophytism has been recognized, such as cell wall separation, apposition features or conspicuously thickened wall corners.

Often filled to capacity, the borings contain dark ovoidal to sub-spheroidal coprolites (Fig. 2A). Only digested material is contained within the coprolites, as they lack recognizable plant tissue (Fig. 2B). Coprolites are 23–64 μm long × 19–55 μm wide. Cross sections of coprolites commonly reveal a continuous outer rind and a compressed central

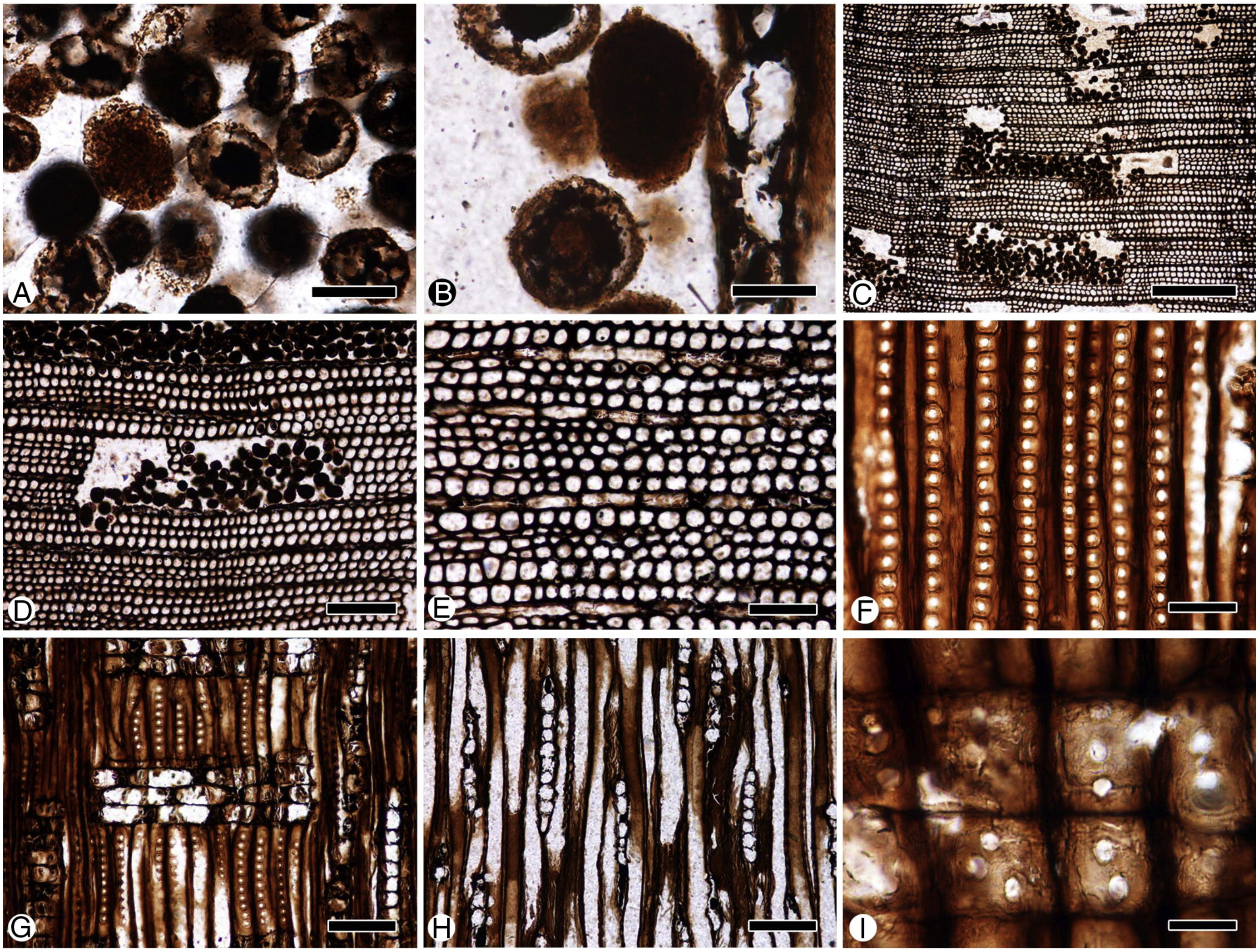

Fig. 2. Oribatid mite borings and coprolites preserved in gymnospermous wood from the Early Permian Manebach Formation, Germany. (A) — Ovoidal to sub-spheroidal dark coprolites within borings, commonly characterized by a continuous outer shell and compressed central core, scale bar = 50 μm. (B) — Close-up of coprolites, note no recognizable plant tissue, scale bar = 25 μm. (C) — Transverse section (TS), coprolites lying at the bottoms of borings, scale bar = 500 μm. (D) — TS, coprolites lying at the bottoms of borings, scale bar = 200 μm. (E) — TS, host wood consisting only of tracheids and rays, scale bar = 100 μm. (F) — Longitudinal radial section (LRS), unseriate bordered pits on the radial walls of tracheids, scale bar = 50 μm. (G) — LRS, brick-like rays, scale bar = 100 μm. (H) — Longitudinal tangential section, uniseriate rays, scale bar = 100 μm. (I) — LRS, cupressoid type pits in cross-fields, scale bar = 25 μm.

core (Figs. 2A and 2B), perhaps resulting from desiccation. The coprolites conspicuously lie at the tunnel bottoms, providing a top-down orientation of the borings (Figs. 2C and 2D).

3.2. Host plant

The host plant is well-preserved with anatomical detail, revealed in the secondary xylem, although the pith and the primary xylem are not preserved. Growth rings with considerably narrow latewood are clearly present (Fig. 1B). The transition from earlywood to latewood is more or less gradual. Structurally uniform secondary xylem consists only of thick-walled tracheids and parenchymatous rays (Fig. 2E). Circular pits with small round apertures are uniseriate, rarely biseriate, and are contiguously arranged on the radial walls of the tracheid elements (Fig. 2F). Rays are composed of brick-like, thin-walled cells (Fig. 2G), which are arranged in uniseriate or partially biseriate rows (Fig. 2H). Cross-fields display one to four cupressoid-type pits (Fig. 2I). The host plant is identified as *Araucaria*-like wood, a common gymnospermous fossil-genus in the Late Paleozoic of Euramerica (Röβler et al., 2014).

4. Discussion

Among modern detritivorous, terrestrial invertebrates, oribatid mites are very common wood-borers. Oribatid mites typically produce excavations less than 1 mm in diameter and deposit small fecal pellets (Wallwork, 1976; Labandeira et al., 1997), that are nearly identical to those from the Early Permian Manebach Formation. No evidence of body fossils was found in the specimen, although tunnel geometry and coprolite dimension suggest that oribatid mites were the most probable culprit.

Fossil borings in woody stems attributed to an oribatid mite origin generally are round in their transverse sections and typically are distributed irregularly along woody axes (Zhou and Zhang, 1989; Goth and Wilde, 1992; Labandeira et al., 1997; Kellogg and Taylor, 2004; Feng et al., 2010; Slater et al., 2012). In addition to a distinctive rectangular shape and distributional pattern in our material, the borings are restricted to areas possessing highly lignified tracheids; parenchymatous rays are avoided. The specimen indicates a preferential feeding habit that was confined and channeled by parenchyma cells and other impediments such as growth rings. In extensively excavated areas, the borings are connected but partially separated by rays.

The distribution pattern of borings is uniform and largely constrained by the boundaries of growth rings. Superficially similar distribution patterns of borings have been documented in *Araucarioxylon*-type wood from the Middle Triassic and Middle Permian of Antarctica (Stubblefield and Taylor, 1986; Slater et al., 2012) and the Late Permian of Australia (McLoughlin, 1992). In these occurrences, fungal hyphae displayed infective external signs that were recognized in the host plants. These borings in fossil woods from Gondwana are interpreted as a result of pocket rot from various fungi (Labandeira and Prevec, 2014). However, saprophytic features such as cell-wall delamination and apposition features were not recognized in our material. Likewise, there is no evidence of broader fungal infection in the tissue, eliminating the possibility that the oribatid mites were feeding on fungi in rotting wood.

The density of tracheid elements in latewood is much higher than that in earlywood. Consequently a more effective feeding strategy for the mite would be to preferentially attack the higher lignified latewood rather than earlywood. The distinct distribution of the banded borings likely represents a specialized feeding habit in this particular lineage of Permian mites.

Spindle-shaped borings containing coprolites have been reported in Late Permian woods of *Australoxylon mondii* from the Antarctic Bainmedart Coal Measures (Weaver et al., 1997). These wood borings regularly occur as bands and are restricted to latewood. Although our borings also occur as bands that parallel growth rings, they can be present either adjacent to growth boundaries or rarely in a central region between adjacent dormant tissues. The larger diameter of the Antarctic borings suggests that they were made by small beetles (Weaver et al., 1997; Slater et al., 2012).

Recently, a gymnospermous wood, *Septomedullopitys szei*, possessing spindle-shaped cavities in the secondary xylem, has been reported from the Late Permian of eastern Xinjiang, northwestern China (Wan et al., 2014). These cavities are free of cellular debris and, irregularly distributed, and were interpreted as white-rot fungal damage (Wan et al., 2014). Notably, both oribatid mite coprolites and fungal hyphae were found in some branched borings in *S. szei* wood (Wan et al., 2014). It appears that the damage in *S. szei* wood represent a complex tritrophic association among the host plant, invasive fungi and trophically connected arthropods.

Information pertaining to the specific feeding habits of arthropods is critical for a thorough understanding of biotic interrelationships in these Late Paleozoic terrestrial ecosystems (Scott, 1980; Scott and Taylor, 1983; Shear and Kukalová-Peck, 1990; Scott et al., 1992). Also important for characterizing early arthropod–plant relationships (Labandeira, 2007) are features such as top-down indicators from coprolites in tunnels, reported in *Shenoxylon mirabile*, from a Late Permian conifer (Feng et al., 2010, 2011). A similar coprolite distribution pattern in our study indicates that the dead tissues of horizontally positioned, fallen trunks housed a decomposer community consisted largely of oribatid mites with very specific feeding habits.

5. Conclusion

Borings and coprolites in an *Araucaria*-like wood from the Early Permian Manebach Formation of Germany suggest an arthropod–plant association that previously has not been documented. The principal arthropod food source consisted of lignified tracheid elements. Recognition of this specialized detritivore relationship contributes to a better understanding of the importance of Paleozoic, oribatid mites life-habits.

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