



Beetle borings in wood with host response in early Permian conifers from Germany

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Abstract

Wood boring represents a common feeding and survival strategy in several lineages of beetles. The larvae of wood-boring beetles hatch and excavate tunnels in wood during their development. The origin and evolutionary history of this life habit, however, remain poorly understood to date, as the fossil record is scarce. We present new silicified conifer wood specimens containing complex borings from the lowermost Permian Manebach Formation of the Thuringian Forest Basin in central Germany and the lower Permian Donnersberg Formation of the Saar–Nahe Basin in southwestern Germany. Additionally, this distinctive type of wood boring is recorded from the Carboniferous/Permian of the Czech Republic, Poland and China. For these borings, the new fodinichnion or agrichnion *Pectichnus multicylindricus* igen. et isp. nov. is established. It is characterised by several parallel cylindrical tunnels in a longitudinal arrangement, branching from a tangential primary tunnel oriented perpendicularly. The borings contain frass as coprolites made up of undigested wood cells. The conifer trees responded to the borings with callus production that subsequently filled or enclosed the tunnels. This is the earliest record of this specific life habit of ancient insects. The novel wood-boring strategy required structural modification and physiological adaptation; it probably emerged when insect diversity expanded considerably as terrestrial environments changed dramatically.

Keywords Wood boring · Coleoptera · Conifers · Wound response · Bioerosion · Permian

Introduction

Wood boring is a specific life habit that occurs in several extant groups of terrestrial arthropods, among them detritivorous oribatid mites and numerous insect families (e.g., Vité 1952; Hickin 1963; Solomon 1995; Kellogg and Taylor

2004; and references therein). In modern terrestrial ecosystems, several major and many minor lineages of coleopterans (beetles) are one of the predominant groups amongst arthropod wood borers (e.g., Johnson and Lyon 1991; Solomon 1995; Krantz and Walter 2009). Comparisons with modern representatives indicate that most of the Paleozoic wood borings were produced by oribatid mites, which can be traced back to the Devonian (Labandeira et al. 1997). Although

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borings in the Late Carboniferous cordaitan root *Premnoxylon* from Lewis Creek of the United States have been considered to be produced by ancestral beetles (Cichan and Taylor 1982; Scott and Taylor 1983), the small (up to 75 μm long) ellipsoidal coprolites contained in the borings appear to be too small for all known beetle families.

To date, the earliest known beetle wood borings were documented in middle Permian conifer wood from Tikhie Gory, Russia (Naugolnykh and Ponomarenko 2010). From the late Permian, beetle wood borings have been reported from glossopterid tree axes of South Africa (Zavada and Mentis 1992) and conifer wood from Antarctica (Weaver et al. 1997). Some complex wood borings attributed to polyphagous beetles have recently been recognised in conifer wood from North China (Feng et al. 2017). They demonstrate complex dietary changes during the development of the beetle larvae and provide a unique glimpse into the early evolution of insect farmers and subsociality.

In this contribution, we describe new fossil material from the lower Permian of Germany showing similar structures to the North China wood borings. The findings not only represent the oldest evidence of wood-boring beetles but also shed new light on the evolution of insect life habits and the plant–beetle co-evolutionary history.

Geology, materials and methods

The wood specimens described in this study were collected from two early Permian localities (Fig. 1), i.e. (1) the lowermost Permian Manebach Formation at Crock locality in the Thuringian Forest Basin, Thuringia State, central Germany; and (2) the lower Permian Donnersberg Formation at Winnweiler locality in Rhineland-Palatinate State, southwestern Germany, respectively.

The fossil site Crock is situated ca. 10 km southeast of Schleusingen, in the South of Thuringia (Feng et al. 2015). Historically, there were several coal mines producing anthracite coal from the lower Permian of Crock. Crock is the only known locality within the Thuringian Forest Basin yielding lower-ranked coals that proved useable for cuticle maceration (Kerp and Barthel 1993). Although there is a long history of both fossil collecting and palaeobotanical research in the Thuringian Forest Basin (Barthel 2003, 2004, 2005, 2006, 2007, 2008), fossil wood has been reported only occasionally (Barthel et al. 2010). Several new types of fossil wood have recently been described in detail from Crock (Witter et al. 2011), including a specialised feeding trace of oribatid mites preserved in a conifer wood (Feng et al. 2015).

The specimen described from Crock was found in coarse-grained alluvial fan deposits exposed on the slopes of the

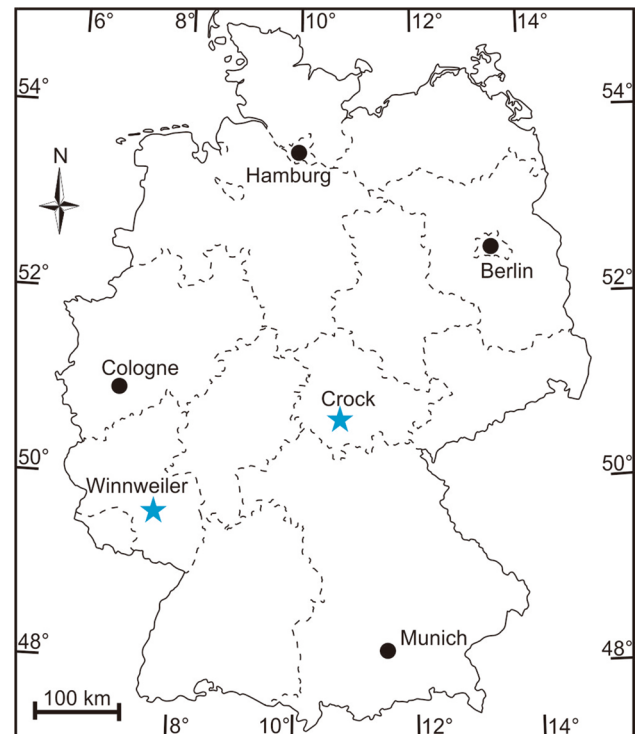


Fig. 1 Geographic map showing the fossil localities (asterisks) of early Permian wood borings in Germany

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 lower to middle Permian (Cisuralian) strata of the Thuringian Forest Basin. These wood-containing basal alluvial fan deposits are overlain by coal-bearing, fine-grained clastic sequences, which have been assigned to the Manebach Formation (Lützner et al. 2012). The stratigraphic level of the fossil wood locality in the basal Rotliegend strata is early Asselian.

Fossil wood from the Winnweiler site has been attracting scientific attention since the previous century (e.g., Schuster 1908). This may be due to the fact that large numbers of fossil wood specimens are being exposed on the surface. The exact stratigraphic origin of the wood-bearing horizon remained uncertain for a long time, although the plant assemblage represents an early Permian xeromorphic upland vegetation, which is predominated by diverse cordaitaleans and conifers due to the impression and petrified wood fossils (Gothan 1905; Noll et al. 2005; Noll 2012).

Petrified wood from Winnweiler is parautochthonously embedded in volcanoclastic deposits of the Wingertsweilertshof Subformation, belonging to the middle to upper portion of the Donnersberg Formation (Lorenz and Haneke 2004). This subformation is characterised by alluvial fans, and braided and meandering river deposits, including

associated floodplains, within the half-graben of the Saar–Nahe Basin (Haneke et al. 2012). The Donnersberg Formation comprises voluminous subvolcanic, effusive, pyroclastic and epiclastic rocks, representing persistent synsedimentary volcanism during the Artinskian (Lorenz and Haneke 2004). The Winnweiler sediments are derived from the Donnersberg eruptive centre 6 km to the north-east, and consist of stacked debrites representing repeated deposition by mass flows and hyperconcentrated flows within ephemeral channels. Silicified wood of varying size, fragmentation and preservation occurs at the top of the non-stratified debrites roughly or not aligned (Trümper et al. 2018). Medium- to small-scale cross-bedded sandstones and siltstones at the top of the channel fills contain plant fossils as imprints and indicate gradually, but rapidly declining sediment contents and flow velocities following the mass flows.

The majority of secondary xylem fragments investigated from Winnweiler are of the pycnoxylic type, which is best referred to the genus *Agathoxylon* Hartig (Rößler et al. 2014). However, some specimens with sclerenchyma nests in the pith can be assigned to the *Tyloedendron*-type conifers (Noll and Wilde 2002). All of the wood samples including thick woody trunks, side branches and roots in this locality commonly exhibit distinct growth rings that resulted from regular climatic fluctuations. The growth rings show notable ring boundaries and a small amount of latewood. This type of growth ring coincides with the type 1 growth rings in the contemporaneous Chemnitz fossil lagerstätte (Luthardt et al. 2017), and thus probably corresponds to the regular sunspot activities during the early Permian (Luthardt and Rößler 2017).

The bored wood collected at Crock and Winnweiler was ground and polished for detailed examination. Photographs were produced with a Nikon Eclipse ME600 transmitted light microscope and a Nikon SMZ1500 stereoscopic light microscope. Images were taken on both microscopes, which were equipped with a Nikon DS-5M-L1 digital camera. Composite images were stitched using Adobe® Photoshop® CS5 Extended program software. The specimens are stored at the Museum für Naturkunde Chemnitz (MfNC), Germany, labelled as K6674, K6675, K6676 and K6677 for Winnweiler specimens, and K6678 for the Crock specimen.

Ichnotaxonomy

Ichnofamilia **Talpinidae** Wisshak, Knaust et Bertling, 2019
Ichnogenus ***Pectichnus*** nov.

Type ichnospecies *Pectichnus multicylindricus*. igen. et isp. nov.

Etymology. Latinised after the Classic Greek *pektos* = combed and *ichnos* = trace.

Diagnosis. Single horizontal tangential gallery in bark/wood, secondarily branching off in longitudinal tunnels at right angles corresponding to the host axis.

Pectichnus multicylindricus isp. nov.

Figures 3, 4, 5, 6

Holotype. MfNC-K6674 (Figs. 5a, g–h, 6a–c, f–j).

Etymology. Latin *multus* = many; *cylindrus* = cylinder.

Diagnosis. *Pectichnus* with equally-spaced, parallel secondary cylindrical tunnels gradually merging into the secondary xylem and longitudinally extending from the main gallery at the interface of bark and secondary xylem.

Locality and horizon. Winnweiler, Rhine-Palatinate State, southwestern Germany; Donnersberg Formation, Rotliegend, Asselian, early Permian.

Additional material. The new ichnotaxon includes specimens from the lower Permian of Germany (MfNC-K6675: Fig. 6f; MfNC-K6676: Figs. 5b, 6d; MfNC-K6677: Figs. 5c, 6e, and the holotype), the upper Permian of North China (YKLP20008, YKLP20009, YKLP20010: Fig. 2a), and the Carboniferous/Permian transition of Paczków–Pilce, Poland (coll. Sandra Niemirowska, Warsaw, no. 264: Fig. 2b) and Sestajovice, Czech Republic (coll. Niemirowska, no. 2992: Fig. 2c).

Description. The specimens from the Shitanjing Coalfield, Ningxia Huizu Autonomous Region, Northwest China, consist of axes of the conifer *Ningxiaites specialis* Feng 2012. They are permineralised by silica and were found in the Sunjiagou Formation of Changhsingian, late Permian, age. The beetle–plant interactions, including distinctive galleries and tunnels inside the tree tissues, have been described in detail by Feng et al. (2017). Five sequential phases in the life cycle of wood-boring beetles were recognised by the authors. Two series of borings, one comprising 11 subsidiary cylindrical tunnels (and an associated triangular callus), another showing lateral borings embedded in wood (Fig. 2a).

The conspicuous wood-boring pattern was also recognised in two Late Carboniferous or early Permian specimens in the collection Niemirowska. No. 264 from Poland shows borings with 11 subsidiary tunnels (Fig. 2b); No. 2992 from the Czech Republic (Fig. 2c) shows borings with eight subsidiary tunnels. Wound reaction tissue in both specimens indicates that the host trees were alive. It has filled in the tunnels but, nevertheless, preserved their shape. This response

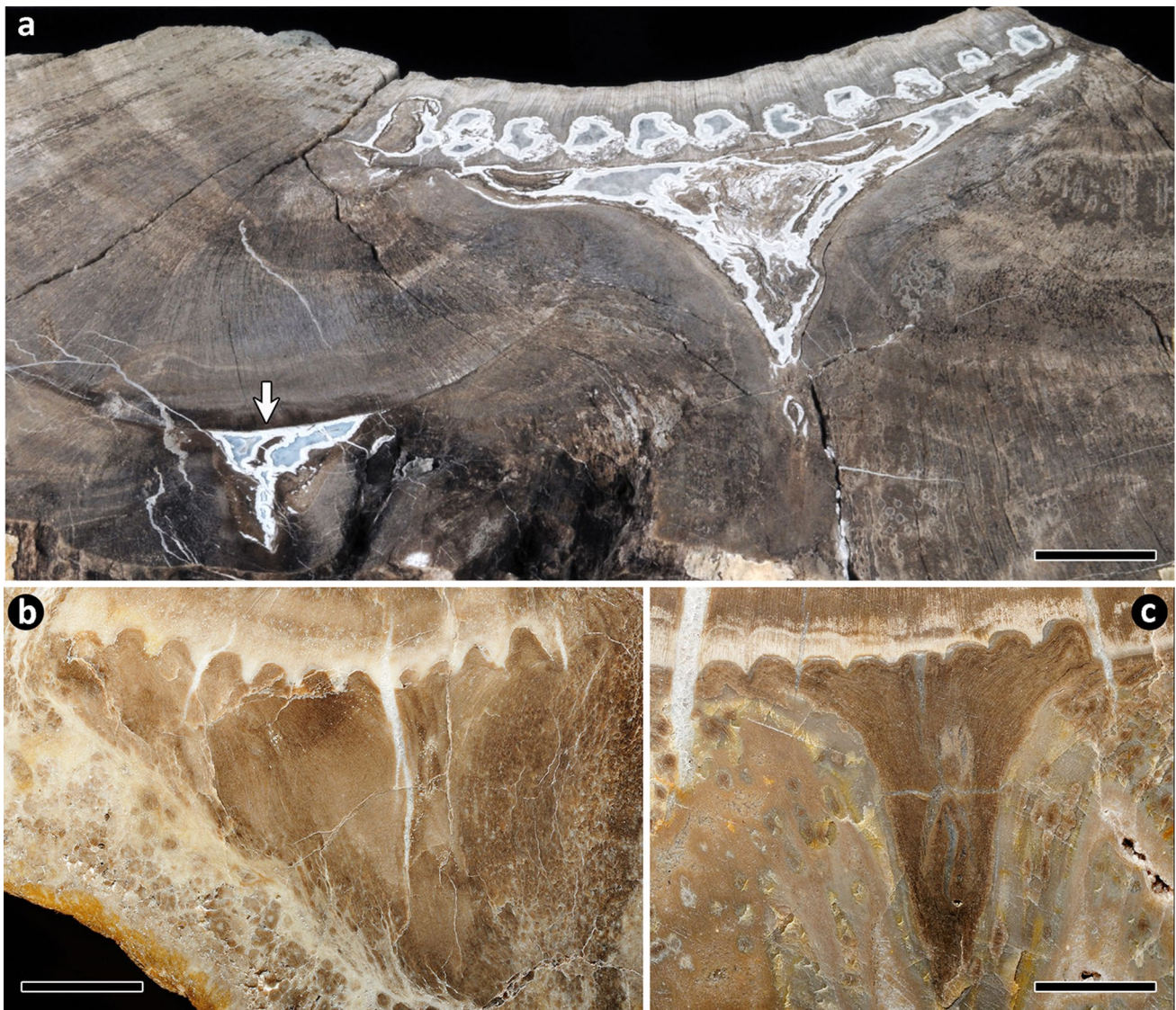


Fig. 2 Fossil conifer wood with beetle borings from the Carboniferous–Permian of China, Poland and Czech Republic. **a** Cross-section of a conifer wood from the upper Permian of Northwest China (for details see Feng et al. 2017), showing two series of borings comprising 11 subsidiary tunnels and an associated triangular callus (upper right), the arrow indicating lateral borings embedded in wood. Palaeobotanical Collections of the Institute of Deep Time Terrestrial Ecology, Yunnan University, China, catalogue number YKLP20010, scale

bar=10 mm; **b** cross-section of a conifer wood from the Carboniferous/Permian transition of Poland, gravel pit in the area Paczków–Pilce. It shows a series of wood borings with 11 subsidiary tunnels. Private collection of Sandra Niemirowska, Warsaw, No. 264, scale bar=10 mm; **c** cross-section of a conifer wood from the Carboniferous/Permian transition of Czech Republic, gravel pit near Sestajovice. It shows wood borings with eight subsidiary tunnels. Private collection of Sandra Niemirowska, Warsaw, No. 2992, scale bar=10 mm

does not constitute a part of the diagnosis, as embedment structures are not trace fossils (Bertling et al. 2006).

The wood specimen from Crock consists of a wedge-shaped fragment of secondary xylem, ca. 30 mm in thickness (Fig. 3a). The pycnoxylic secondary xylem is exclusively composed of thick-walled tracheids and parenchymatous ray cells (Fig. 3b). Tracheids are circular to sub-circular in cross-section and have uniseriate and biseriate bordered pits contiguously arranged on the radial tracheid walls (Fig. 3c). The cross-fields generally display one or two large, simple pits

in each field (Fig. 3d). Fungal-decayed structures have not been recognised in the wood. The wood anatomical characteristics indicate that the host plant is a *Zalesskioxylon*-type conifer. It bears 15 tunnels, including 13 longitudinal tunnels and two tangential tunnels (Fig. 3a, arrows). The longitudinal tunnels formed a boring series tangentially arranged in a single growth ring. The tunnels are circular to somewhat polygonal (commonly hexagonal) in cross-section, and up to 3.5 mm in diameter (Fig. 4a–c). The interval distance between adjacent tunnels is relatively stable, measuring from

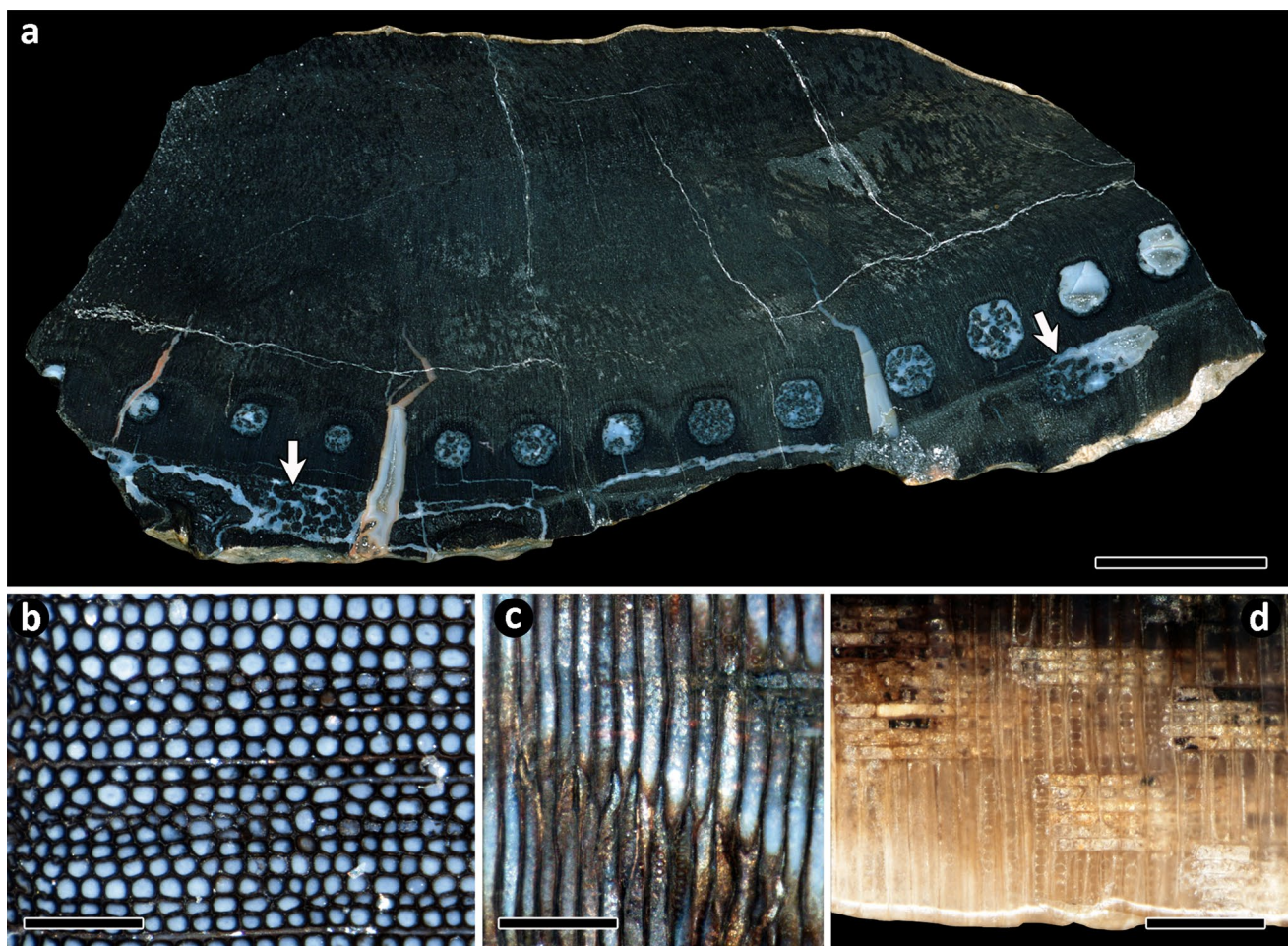


Fig. 3 Fossil conifer wood with *Pectichnus multicylindricus* igen. et isp. nov. from the lowermost Permian of Crock, Manebach Formation, Thuringian Forest Basin, central Germany. **a** Overview of specimen K6678 showing 13 longitudinal tunnels and two tangential tunnels (arrows), scale bar = 10 mm; **b** cross-section showing circular to

sub-circular outlines of tracheids, and the procumbent parenchymatous rays, scale bar = 200 µm; **c** radial longitudinal section showing uni- to biseriate bordered pits on the radial tracheid walls, scale bar = 200 µm; **d** radial longitudinal section showing large, simple pits in the cross-fields, scale bar = 200 µm

2.2 to 4 mm. It appears that the diameter of the tunnels is gradually increasing from one end to the other in the boring series, while the outline of the tunnel cross-sections changes from circular to polygonal. Although the borings are incompletely preserved, in longitudinal section the tunnel tapers conspicuously (Fig. 4d, arrow). Additionally, the longitudinal section exhibits a roughened inner surface of the tunnels and a jagged appearance, with plant debris occurring in the tunnel lumen (Fig. 4e). The tangential borings show almost the same diameters as the longitudinal ones (Fig. 4f).

Both the longitudinal and tangential borings are infilled with large coprolites (Fig. 4a–c, f). They are spheroidal to indistinctly shaped with diameters varying from 0.2 to 1.1 mm (av. 0.5 mm, $n=55$). The coprolites are formed by masses of undigested plant tissues (Fig. 4g, h). In some cases, fragments of tracheids and rays can be recognised in

the coprolite matrix. Some tangential borings show wound reaction with contorted wood tissue (Fig. 4i, arrow).

Four wood specimens have been collected at the Winweiler site. Three of them were examined in closer detail (Fig. 5a–d): pith, primary xylem and secondary xylem of the specimens are well preserved and reveal anatomical features. The wood is characterised by a large pith with sclerenchyma nests (Fig. 5d, e). The primary xylem is of the endarch maturation type. Tracheid elements of the primary xylem have annular, helical to scalariform thickenings from the protoxylem to metaxylem (Fig. 5f). The secondary xylem is pycnoxylic and exclusively comprises tracheids and rays (Fig. 5g). Circular bordered pits are contiguously arranged in uniseriate rows on the radial tracheid walls, or very rarely, partially biseriate. When biseriate, the pits are in alternate and opposite arrangements (Fig. 5h, arrows). Parenchymatous rays are commonly

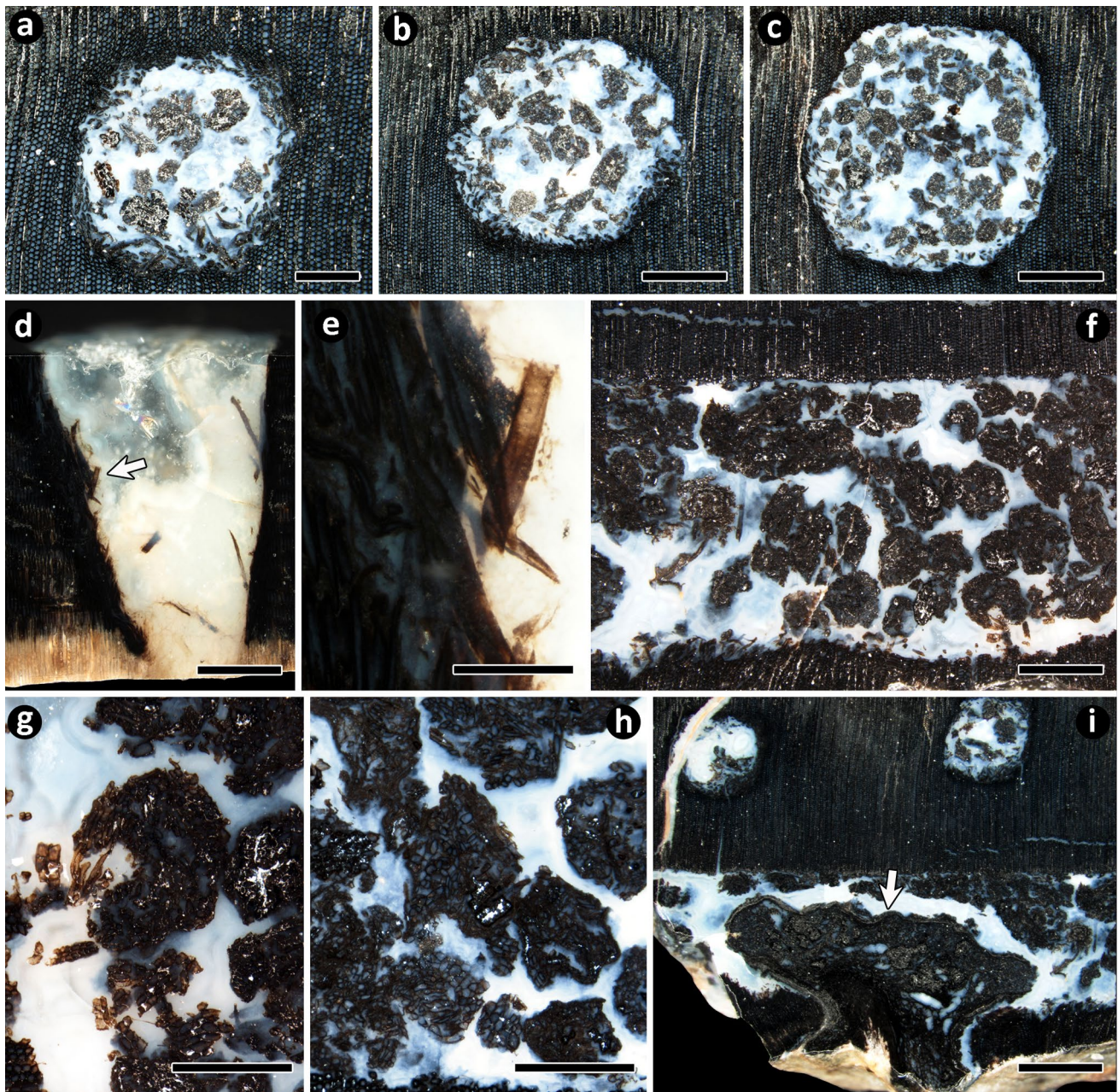


Fig. 4 Fossil conifer wood specimen K 6678 with *Pectichnus multicylindricus* igen. et isp. nov. from the lowermost Permian of Crock, Manebach Formation, Thuringian Forest Basin, central Germany. **a–c** Cross-sections of the longitudinal tunnels, showing circular and hexagonal outlines, scale bars=500 μ m, 1 mm, 1 mm; **d** longitudinal section of a tunnel, note the narrowing end, scale bar=1 mm; **e** detail

of **(d)** showing the roughened inner surface of the tunnel with wood fragments, scale bar=250 μ m; **f** tangential tunnel showing large coprolites, scale bar=1 mm; **g** and **h** coprolites in the borings, note the undigested wood tissues, scale bars=500 μ m; **i** tangential tunnel, arrow indicates impinging wood originated from lateral growth of the host plant, scale bar=2 mm

uniseriate (Fig. 5i). The host is thus identified as *Tylocladon*-type conifer, which is common at Winnweiler (Noll 2012). Structures indicating fungal decay have not been recognised in the wood.

A complete boring series possessing six parallel tunnels is well preserved in one specimen (Fig. 5a), while the borings in the other specimens are incompletely preserved

(Fig. 5b–d). Structurally, the Winnweiler borings are identical to the longitudinal borings from Crock, which run in one single growth ring. The cylindrical tunnels are (sub) circular in cross-section and have an average diameter of 5 (3.5–6.5) mm. A longitudinal section shows that the tunnel is up to 40 mm long.

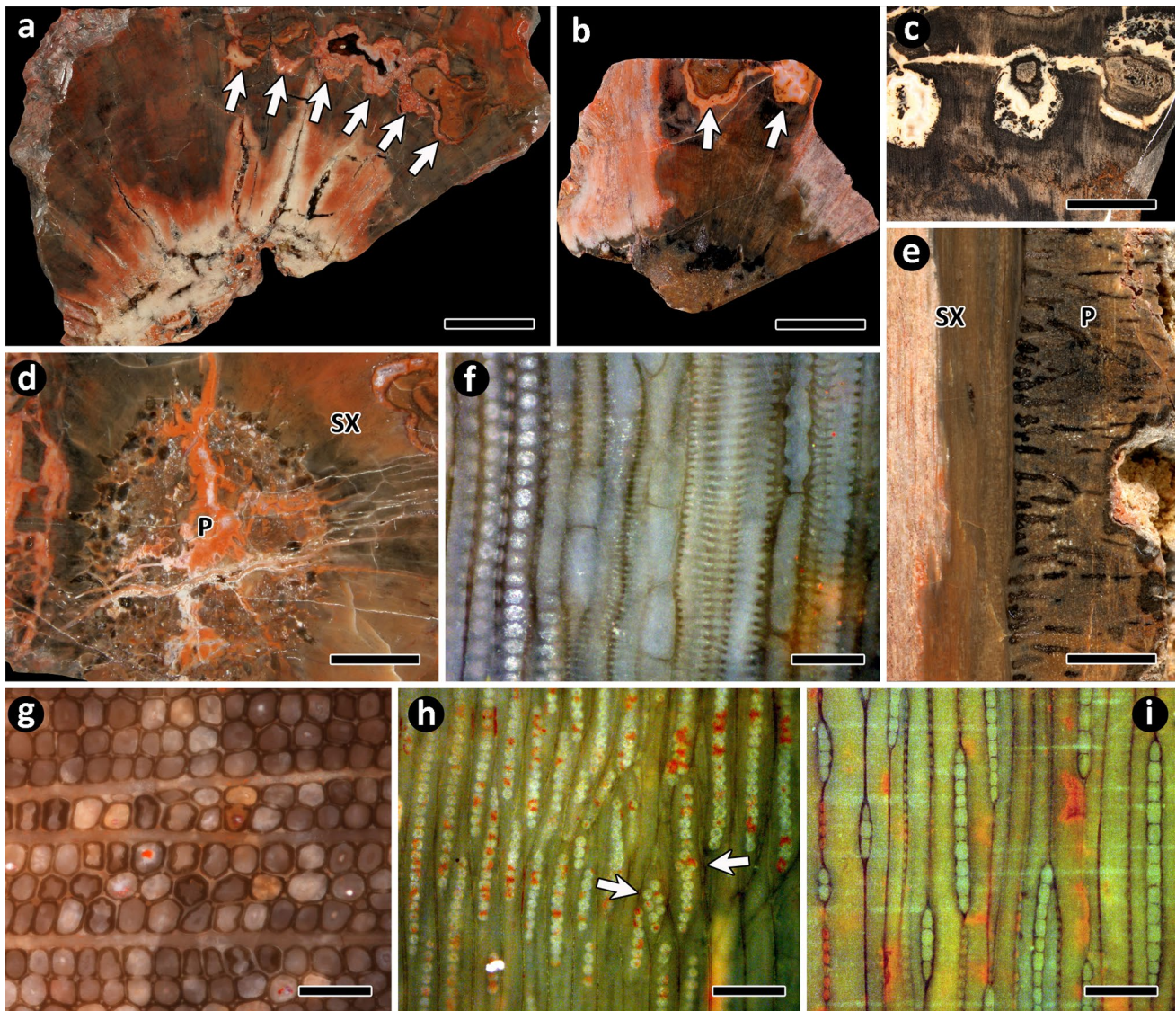


Fig. 5 Fossil conifer wood with *Pectichnus multicylindricus* igen. et isp. nov. from the lower Permian Donnersberg Formation of Winnweiler, Saar-Nahe Basin, southwestern Germany. **a** Overview of the holotype K6674, arrows indicate six longitudinal tunnels, scale bar=10 mm; **b** specimen K6676, arrows indicate two longitudinal tunnels, scale bar=5 mm; **c** specimen K6677 showing three longitudinal tunnels, scale bar=5 mm; **d** cross-section of K6675 showing large pith (P) and secondary xylem (SX), scale bar=10 mm; **e** longitudinal section of K6676, note the sclerenchyma nests in the pith (P)

and the pycnoxylic secondary xylem (SX), scale bar=5 mm; **f** radial longitudinal section of the primary xylem of K6676, showing the helical to scalariform thickenings from the protoxylem to metaxylem, scale bar=50 µm; **g** cross-section of the holotype K6674 showing circular to sub-circular outlines of tracheids, and the procumbent parenchymatous rays, scale bar=100 µm; **h** radial longitudinal section of the holotype K6674, arrows indicating the alternate and opposite radial tracheid pits, scale bar=100 µm; **i** tangential longitudinal section of K6676 showing the uniseriate rays, scale bar=100 µm

Large, spheroidal to amorphous coprolites are commonly present in the borings. Serial transverse sections of the borings reveal that wound reaction tissues gradually enclosed or filled the borings from the marginal tunnels to the central ones (Fig. 6a–c, arrows). Wound-induced tissues completely filling the tunnels are seen in both their cross and longitudinal sections (Fig. 6d, arrows). The reaction tissue eventually enveloped the boring series, characterised by a thick response wood, which originated from lateral growth of the

host plant (Fig. 6e, f): Many parenchyma cells surround the borings (Fig. 6g). The contorted impinging wood in the borings possesses intricate bark structures (Fig. 6h). A most likely wound-induced epicormic shoot on the wood surface (Fig. 6j) is recognised close to the borings (Fig. 6i, arrows), originating from ray-derived traumatic parenchyma.

Remarks. The early Permian borings from central and southwestern Germany are arranged in parallel series of up to

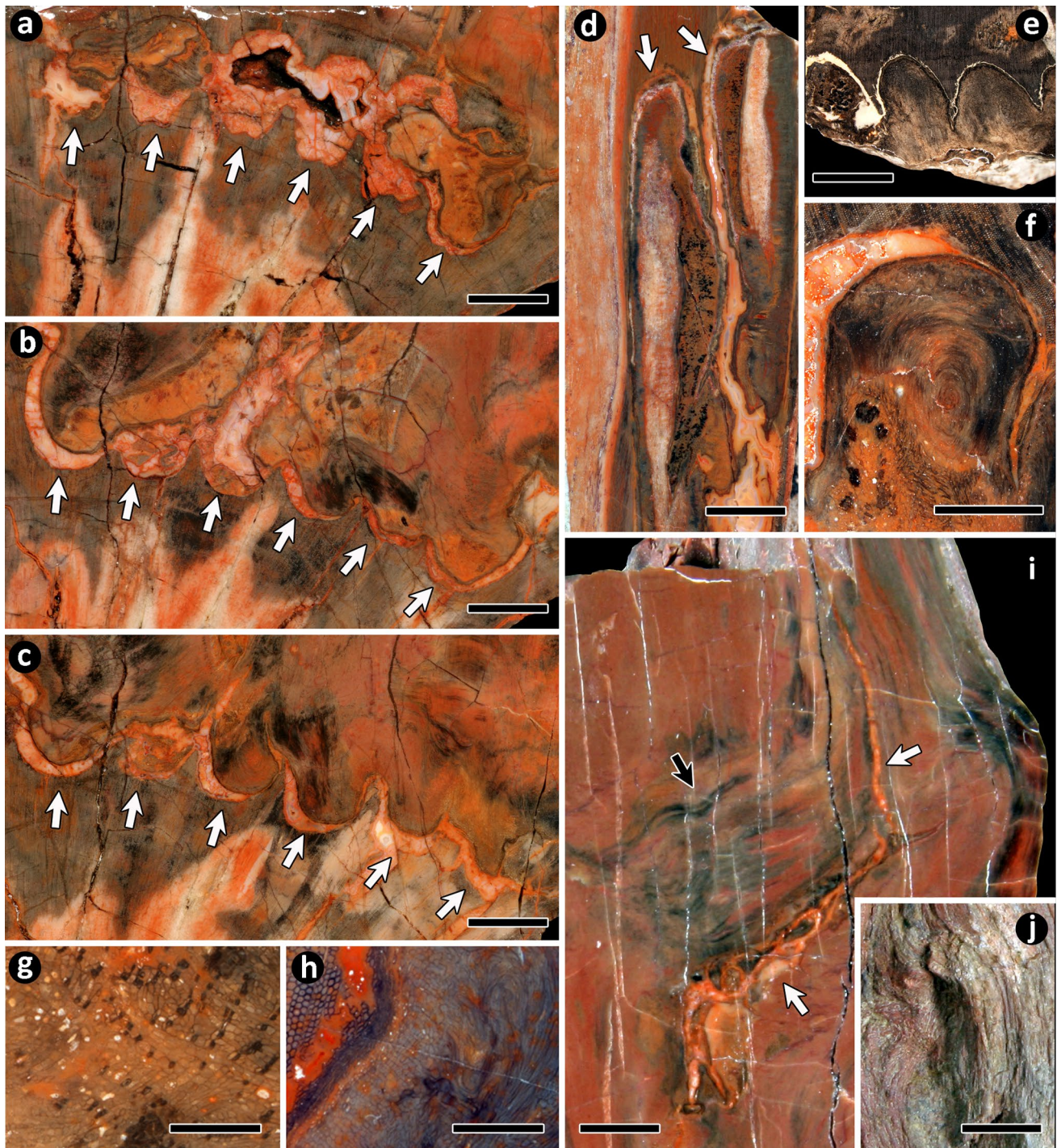


Fig. 6 Fossil conifer wood with *Pectichnus multicylindricus* igen. et isp. nov. from the lower Permian Donnersberg Formation of Winnweiler, Saar–Nahe Basin, southwestern Germany. **a–c** Serial cross-sections of the longitudinal tunnels (arrows) of the holotype K6674 showing the sequence of the wound reaction tissues into the tunnels, note the impingement initiating from the marginal tunnels, scale bars=5 mm; **d** longitudinal section of K6676 showing the tunnels (arrows), scale bar=5 mm; **e** cross-section of K6677 showing the tunnels enclosed by contorted reaction wood, scale bar=5 mm; **f**

enlargement of the tunnel (K6675) showing the complete impingement by reaction wood, scale bar=2 mm; **g** cross-section of the holotype K6674 showing the parenchyma cells surrounding the wound area, scale bar=500 μ m; **h** cross-section of the holotype K6674 showing the bark of the circumvallating reaction wood, scale bar=500 μ m; **i** longitudinal section of the holotype K6674, white arrows indicate a longitudinal tunnel, black arrow indicates an epicormic shoot, scale bar=5 mm; **j** scar with spindle-shaped callus on the wood surface (the holotype K6674), scale bar=5 mm

11 longitudinal tunnels; tangential tunnels are rarely seen. Due to the incompleteness of the specimens, the connection of both tunnel orientations remains somewhat obscure, although they occur very close to each other and possess similar diameters.

The brief review of bioerosion ichnotaxa by Wisshak et al. (2019) reveals that no similar structures have yet been described, let alone named. The ichnotaxonomical treatment of wood borings is yet in its infancy, and we encourage subsequent authors to formally describe their finds, following the path set by Wisshak et al. (2019) and respecting the rules of the International Code of Zoological Nomenclature (1999) and the widely accepted guidelines of Bertling et al. (2006).

Known stratigraphic and palaeogeographic distribution. Carboniferous–Permian of Europe (Germany, Poland and Czech Republic) and Asia (China).

Discussion

Producer affinity

The German borings frequently contain large coprolites and are distributed in the secondary xylem of the host conifers. Even if evidence of body fossils is lacking in this material, the position, tunnel geometry and coprolite dimension suggest that beetles produced these borings (see e.g. Vité 1952; Gullan and Cranston 2014). The material from the upper Permian of North China is better preserved, and it comprises body fragments of the producers (Feng et al. 2017), so the interpretation of the authors is followed here. The boring system appears to have been produced by an adult female beetle laying eggs in a tangential tunnel between wood and bark and by growing larvae feeding in longitudinal subsidiary tunnels inside the wood.

Probable beetle borings have been documented in fungus-infected conifer-like wood from the lower Kazanian, middle Permian, of Tatarstan, Russia (Naugolnykh and Ponomarenko 2010). They are principally oriented longitudinally, parallel to the wood axis, and are connected by short shafts of varying orientation. The authors suggest Permocupedidae as the most likely producers, but their material differs strongly from the one presented here. The adult body shape of this family seems to preclude that its members have produced *Pectichnus* (Feng et al. 2017). This points to the Tshekardocoleidae as potential tracemakers, as this is the only other beetle family known from the lower Permian (Ponomarenko 2003). The body fossil record is very likely

incomplete, however, so that other, yet unknown, insects may be the producers.

Ecology

The position, geometry, extent and sequence of borings within host plants reflect the consumption strategy of a wood-boring beetle (Gullan and Cranston 2014). Our material provides strong evidence for the consumption of different plant tissues during the beetles' ontogeny. Serial sections indicate that the longitudinal tunnels commenced close to the cambial layer of the conifer tree, but subsequently completely emerged into the secondary xylem, suggesting that the larvae may have consumed mainly wood tissues.

Tunneling wood represents a complex life strategy of insects, which effectively avoid predation and fungal parasites for their offspring (Raffa et al. 2015). Contrary to Nel et al. (2018), who claim that significant changes in mouthpart morphologies of insects cannot be recognised during the Late Carboniferous to middle Permian, the wood borings reported here imply a series of functional innovation, especially regarding mouthparts and cellulose digestion. Compared with other vegetative organs, wood is a relatively nutrition-poor food source. For this reason, approximately 10% of all extant insect wood borers accommodate intracellular endosymbionts in their gut cells or gut lumen (Schoonhoven et al. 2006). Cellulose-digesting microorganisms as gut symbionts not only help to digest cellulose but also enhance the nutritional quality of wood (Schowalter 2017). Gut mixing is especially important for digestion of cellulose and lignin into labile carbohydrates and concentration of nitrogen and other nutrients (Breznak and Brune 1994), which may fuel nitrogen fixation by microbes in xylophage guts (Nardi et al. 2002).

Among extant wood-boring insects, ectosymbioses are widespread as associations with microscopic fungi (e.g., Six 2012; Meurant 2017). These fungi degrade woody debris lodged in tunnels or the wood itself, thus providing the important service of cellulose degradation for the wood borers (Haack and Slansky 1987; Hernández-García et al. 2017; Birkemoe et al. 2018). Fossil evidence for the presence of cellulolytic fungi in wood borings demonstrates that obligate nutritional dependency on fungi of wood-boring beetles occurred already during the late Permian (Feng et al. 2017). The occurrence of fungal hyphae within borings suggests that those beetle occupants were probably early farmers, resembling modern bark beetles, macrotermite termites and attine ants (Farrell et al. 2001; Biedermann et al. 2009; Wilson and Nowak 2014). Features of fungal decay, however, have not been observed in the European Permian wood borings. This suggests that their producers possessed intestinal microbiomes for the digestion process rather than

being mycophagous. In this context, it is worth noting that wood decay structures were not observed in the early Permian oribatid mite borings from the Crock locality (Feng et al. 2015). The reason may be that fungal ectosymbionts had not been functionally adopted by the terrestrial arthropods during the early Permian.

On the other hand, it is hard to imagine that a beetle with mycophagous larvae (late Permian of China) should produce the same type of borings as a xylophagous representative (early Permian of Europe). In due course, the ichno-ethological classification remains somewhat uncertain: given the volumetric dominance of larval longitudinal tunnels with coprolites containing wood fragments, *Pectichnus* has largely to be regarded as a fodinichnion, although the tangential gallery bored by the mother beetle has calichnial quality. If the hyphae in the late Permian Chinese samples prove to be relics of ambrosia-type fungi, however, this would qualify the borings as agrichnia.

The parallel path of the tunnels described here is direct evidence for thigmotaxis of the beetle borers already developed in the earliest Permian. Larvae of extant bark beetles (Scolytidae) similarly avoid contact when jointly tunneling the wood substrates (Beaver 1974). Keeping the tunnels at a distance precludes intraspecific (conspecific) competition in the larval stages, thus effectively reducing the mortality of the population (De Jong and Grijpma 1986; Byers 1989; Kirkendall 1989; Legros et al. 2009).

Evolution

Crowson (1975) and Ponomarenko (2003) associate the origin of beetles with the breakdown of wood. Understanding the autecology of the *Pectichnus* producers therefore has implications not only for the assessment of biotic interactions in Permian terrestrial ecosystems but also for the co-evolutionary history of the associated organisms (cf. Labandeira 2013). Two conifer species are identified as host plants for the wood borers under discussion, indicating that the wood-boring habit developed as a rather broad trait. Given the wood and bark structures available as substrates for Late Paleozoic borers, it does not come as a surprise (a) to see conifer wood as the prime target of their attack, and (b) to register very few (if any) pre-Permian insect borings (Scott et al. 1992). On the other hand, the tunnel-enclosing sequence by reaction-wood circumvallation shows that the ancient conifers were well primed for the beetle's attack. It should be noted that the formation of an epicormic shoot in the traumatic area indicates an advanced physiological feature as wound response of the host plants (Decombeix et al. 2010, 2018), which is similar to modern conifers (Krokene 2015).

The diversity of herbivorous insects displays a dramatic expansion during the Late Carboniferous (Scott et al. 1992;

Labandeira and Currano 2013), in accordance with a series of significant geological events at that time (Montañez et al. 2016). The coprolites contained in wood borings in Carboniferous cordaitalean wood have previously been claimed as produced by ancestral beetles (Scott and Taylor 1983). Large coprolites and millipede larva, however, have been observed in the central pith cavity of the largest Permian calamite (*Arthropitys bistriata*) trunk from the Chemnitz fossil lagerstätte (Röbller et al. 2012). This indicates that wood-boring habits originated in a parallel and perhaps penecontemporaneous manner in various arthropod groups; it could plausibly be extended into the Carboniferous. For the time being, the earliest definitive beetle body fossils are early Permian in age (Ponomarenko 1963; Kukulová-Peck and Beutel 2012; Toussaint et al. 2017). In addition, probable beetle coprolites have been widely documented in a variety of Permian host plants (Weaver et al. 1997; D'Rozario et al. 2011), indicating a previous existence for some stem-group lineages of the Coleoptera (McKenna et al. 2015).

The sudden rise of insect diversity lead to interspecific competition for habitat niches and food sources; it may have resulted in stressful ecological conditions for the individual populations (Labandeira and Currano 2013; Nicholson et al. 2014; Dmitriev et al. 2018). Therefore, we propose that the wood-boring habit of beetles could have emerged under the combined pressure of insect expansion and dramatic environmental changes. The form of the boring system described herein and the behaviour indicated by it suggests that one of the earliest lineages of the Polyphaga, one of the four main beetle clades, was probably present prior to the Carboniferous–Permian transition.

Concluding remarks

Detailed analysis of wood borings from two early Permian conifer hosts provides the earliest direct evidence of secondary xylem utilisation by beetles. The novel feeding behaviour implied functional innovation in digestive adaptation. The boring pattern is highly distinctive and ichnotaxonomically established herein as *Pectichnus multicylindricus* gen. et isp. nov. Its stratigraphic and palaeogeographic distribution is enlarged considerably. As the host plants were still alive at the time of the beetle attack, they responded by subsequent fill and circumvallation of the borings as a wound reaction. This shows that physiological responses to borings were well established already at the beginning of the co-evolutionary history of wood-boring beetles and conifer trees.

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