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FIRST EVIDENCE OF ARTHROPOD HERBIVORY IN CALAMITALEAN STEMS FROM THE PENNSYLVANIAN OF GERMANY

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Abstract: Arthropod borings are commonly described from pteridophyte and gymnosperm wood in the late Palaeozoic, but they are almost unknown from calamitalean stems. In this paper, a new type of boring in calamitalean stems from two German localities is reported. These are the mine dumps of Plötz near Halle (Saale), Saale Basin, (Wettin Subformation, Latest Pennsylvanian, Gzhelian, Stephanian C) and the Piesberg quarry near Osnabrück, Subvariscan Foreland Basin, (Osnabrück Formation, Middle Pennsylvanian, latest Moscovian, Asturian/Westphalian D). Most borings were found in marginal parenchyma of the internodes. They run longitudinally through the pith. The borings are preserved as three-dimensional casts that protrude on the surface of considerably compressed pith casts. This unique preservation of the boring casts required special taphonomic conditions, such as rapid burial coupled with different sediment infilling of the borings and the pith cavity, as well as anoxic conditions to prevent decomposition of the non-resistant parenchyma. Most borings are between 3 to 5 mm wide and contain two classes of invertebrate coprolites: the smaller coprolites are sub-spheroidal in shape and measure (37 to 74) x (37 to 63) µm in diameter. The larger coprolites are also sub-spheroidal and range between (88 to158) x (68 to 123) µm in diameter. The coprolites, the morphology of the borings, as well as the feeding strategy of the arthropods, suggest that the tunnel system was most likely produced by small millipedes (Myriapoda) and probably also visited by oribatid mites.

Key words: Late Carboniferous, Pennsylvanian, borings, calamitalean stem, plant-arthropod interaction.

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INTRODUCTION

Arthropods and plants play an essential role in terrestrial ecosystems, as they provided the basic organic constituents with extended evolutionary histories and ecological structures (Labandeira, 2006a). Since the earliest terrestrialisation in the latest Silurian/Early Devonian, plant-arthropod associations have been documented in the fossil record (e.g., Shear and Selden, 2001; Dunlop *et al*., 2003; Habgood *et al*., 2004; Labandeira, 2006a, b, 2007; Trewin and Kerp, 2017). According to Labandeira (2006a), four major herbivore expansions can be recognised.

The initial phase persisted from the latest Silurian to Late Devonian. Plant-arthropod associations of that period already comprised five main functional feeding groups: external feeding, piercing and sucking, palynivory, galling, as well as borings into the stems of primitive vascular plants and the cortical and medullary tissues of the basidiomycete fungus *Prototaxites* (Labandeira, 2006a, 2007; Labandeira *et al*., 2013). Herbivorous arthropods were myriapods, apterygotes (e.g., mites and, to a lesser extent, apterygote hexapods), and probably early pterygotes (Edwards *et al*., 1995, 2012; Labandeira, 2006a; Dunlop and Garwood, 2017).

With the diversification of the Palaeozoic flora and the appearance of more complex plant tissues such as roots, leaves, wood, and seeds, new types of herbivory evolved in a second phase, which occurred from the Late Mississippian to the end of the Permian (Labandeira, 2006a, 2007). This time interval, from which the fossils described in this paper derive, was characterised by the appearance of new, more complex, interactions between plants and arthropods. Six functional feeding groups can be distinguished: external foliage feeding, piercing and sucking, boring, oviposition, galling, and seed predation (Labandeira, 2006a). Among the various plant hosts, pteridophytes and basal gymnosperms were most frequently attacked by arthropods. The most abundant culprits were myriapods, and oribatid mites, as well as palaeopterous and neopterous insects (Scott, 1977; Baxendale, 1979; Chichan and Taylor, 1983).

Most common in the Palaeozoic fossil record, and documented from numerous localities, are different types of external-foliage feeding (skeletonisation, hole-margin, and surface feeding) as well as piercing and sucking (e.g., Labandeira and Phillips, 1996b; Adami-Rodrigues *et al*., 2004; Labandeira *et al*., 2007; Iannuzzi and Labandeira, 2008; Cariglino and Gutierrez, 2011; Labandeira and Currano, 2013; Pinheiro *et al*., 2015; Cariglino, 2018). Furthermore, galling became more abundant in the late Palaeozoic (e.g., Labandeira and Phillips, 1996a; Schachat *et al*., 2014; Belahmira *et al*., 2015; Marchetti *et al*., 2015; Schachat and Labandeira, 2015; Labandeira *et al*., 2016; Correia *et al*., 2020).

Oviposition evolved as a new strategy of reproductive behaviour of insects during the second phase. The earliest records of endophytic oviposition, i.e. the strategy of depositing eggs into dead or living plant tissue using the ovipositor, date back to the middle- to late Pennsylvanian (Béthoux *et al*., 2004; Laaß and Hoff, 2014; Wolterbeek, 2014; Wrede *et al*., 2019). Recently, Laaß and Hauschke (2019a, b) first reported clusters of circular insect eggs attached to the surface of plant foliage from the late Pennsylvanian of the Saale Basin in Germany, which they interpreted as the earliest evidence of exophytic oviposition in the fossil record.

Borings became more abundant and diverse during the Carboniferous and Permian, which was closely related to the development of massive trunks in several plant groups and the availability of new food resources, such as seeds, for the arthropod producers (Labandeira, 2006a). Most borings in Palaeozoic woods were reported from gymnosperms, pteridophytes and, to a lesser extent, from lycopsids. Essential information about borings can be obtained from the morphology of the tunnel networks, as well as from the content and dimensions of coprolites of the putative producers (Feng *et al*., 2017). Based on the study of invertebrate coprolite assemblages from the middle Pennsylvanian coal balls of Lewis Creek, Kentucky, Scott and Taylor (1983) distinguished three classes of coprolites, which, with slight modifications, were used to classify the borings in Palaeozoic woods from the Carboniferous to Triassic (see Appendix Tables 1–3).

The majority of borings from the late Palaeozoic to Triassic, which often contain small coprolites up to 120 to 150 µm in diameter, were probably produced by oribatid mites (see Appendix Table 1; e.g., Goth and Wilde, 1992; Scott *et al*., 1992; Labandeira *et al.,* 1997; Kellogg and Taylor, 2004; Feng *et al*., 2010a, 2012, 2015a, 2017; Feng, 2012; Slater *et al*., 2012; Wan *et al*., 2016; Wei *et al.,* 2019). In contrast, larger borings, sometimes filled in with medium-sized coprolites between 120 µm and 1 mm in diameter or with large coprolites of more than 1 mm in diameter, were often attributed to beetles, cockroaches or myriapods (see Appendix Tables 2, 3).

Borings in calamitalean stems are only rarely documented in the fossil record (see Appendix Tables 1 to 3, see also the review on herbivory on *Sphenophytes* by Correia *et al.,* 2020). Only a few borings in calamitalean stems have been reported from the late Palaeozoic. This is surprising, because calamite trunks commonly possess great richness in their parenchyma, which potentially represented a good food resource for arthropods (Rößler and Noll, 2006, 2010; Rößler *et al*., 2012a).

The first evidence of borings in a calamitalean stem comes from the Latest Gzhelian of Texas. It consists of a 2 mm long and 0.12 mm wide gallery and numerous 20 µm wide tunnels, which were situated either in the subcortex of the cortex or in fungal-laden wood (Xu *et al.*, 2018). These borings were described by the authors as a new damage type (DT284) and attributed to beetles (Archostemata).

The second record derives from the Late Pennsylvanian (Moscovian) of the United Kingdom and was described by Seward (1898), and Stopes (1907). It consists of a thin section of a calamitalean axis, which shows a boring through the xylem into the pith. According to Correia *et al.* (2020), the structures in question can also be assigned to DT284 and were probably produced by oribatid mites.

The third record of arthropod borings in calamitalean stems was described from the early Permian Petrified Forest of Chemnitz, Germany, and consists of a side branch of the calamite *Arthropitys bistriata* that was attacked by arthropods (Rößler *et al.,* 2012a, b). The ca. 2 cm wide pith cavity of this stem was almost completely filled in with very large invertebrate coprolites in the range between 1.4 mm to 2.8 mm × 2.0 mm to 5.8 mm in diameter, which were probably produced by myriapods (Rößler *et al.,* 2012a).

Similar large irregular cavities in the pith and the xylem filled in with plant debris and large invertebrate coprolites up to 3 mm in diameter were also reported from *Arthropitys*-type calamitalean stems from the Permian fossil forest of northern Tocantins, central-north Brazil (Rößler, 2006, fig. 8b, c; Neregato *et al*., 2017, pl. IX, figs 1, 2; Rößler *et al*., 2020).

In this paper, a new type of boring in calamitalean stems is described, which occurs in the Mid-Pennsylvanian Osnabrück Formation of the Piesberg quarry, Germany, and in the Latest Pennsylvanian Wettin Subformation of the Saale Basin, Germany (Fig. 1). At the same time, these are the first records of borings in calamitalean stems from both localities. We interpret this as an observation gap: from the Piesberg site, such borings are seen once in a while, but seldom collected.

GEOLOGICAL BACKGROUND

Localities

The pith cast of the calamitalean stem depicted in Figures 2, 3 derives from the Plötz mine dump (51°38′12.46″ N, 11°57′28.32″ E) of the former coal-mine district of Wettin-Löbejün-Plötz north of Halle (Saale), Saxony-Anhalt, Germany (Fig. 1A). The second and third specimens described in this paper (Figs 4, 5), were found in the Piesberg quarry (52°19′ 4.0″ N, 8°1′10.0″ E) near Osnabrück, Lower Saxony, Germany (Fig. 1A).

Wettin Subformation

The Plötz mine dump consists of material that derives from the coal-bearing sequence of the Wettin Subformation. Index fossils such as roachoid insects, branchiosaurid amphibians and conchostracans (Spinicaudata) suggest that the Wettin Subformation is of late Pennsylvanian age, Gzhelian, which corresponds to Stephanian C (Schneider *et al.*, 2005a, b; Schneider and Werneburg, 2012; Schneider and Scholze, 2018; Schneider *et al.*, 2020; Fig. 1B).

The Wettin Subformation is part of the Siebigerode Formation, which was deposited in the peri-montane Saale Basin in central Germany (Schneider *et al.*, 2005). The Siebigerode Formation comprises a 500 to 800 m thick red bed sequence, which consists of alluvial fan to alluvial plain and floodplain to lake facies associations (Schneider *et al.*, 2005; Trümper *et al.*, 2019a, b). The Wettin Subformation represents the grey-coloured and coal-bearing facies of the basin centre (Beyschlag and von Fritsch, 1899; Schneider and Gebhardt, 1993; Schneider *et al.*, 2005b; Schneider and Romer, 2010). The coal-bearing facies is dominated by siliciclastic fluvial sediments ranging from clay- and silt-stones to fine- and coarse-grained sandstones, which are intercalated by coal seams. As already pointed out by Laaß and Hauschke (2019a), the latter are covered by plant-rich roof shales of lacustrine origin. At Plötz, former mining activity mainly focused on the coal seam "Oberflöz". Accordingly, on the mine dump the fossil-rich material of the roof shale above the coal seam "Oberflöz" was typical. As will be discussed later, the lithology of the calamitalean pith cast from Plötz, particularly its high pyrite content, suggests that this fossil derived from the roof shale covering the "Oberflöz". Further details about the Siebigerode Formation, including the Wettin Subformation, were summarised by Schneider *et al.* (1995, 2005a, b), Schneider and Romer (2010), Laaß and Hoff (2014), Laaß and Hauschke (2019a) and Trümper *et al.* (2019a, b).

Osnabrück Formation

The pith casts of the calamitalean stems from the Piesberg quarry near Osnabrück (Figs 4, 5) are slightly older and derive from the Osnabrück Formation, which is of middle Pennsylvanian age, latest Moscovian, lower Asturian or Westphalian D (Fig. 1B). As detailed descriptions of the geology of this locality were already provided by Josten *et al.* (1984), David (1990), Brauckmann and Herd (2002), Jones and Glover (2005) and Köwing and Rabitz (2005) only few remarks are given here.

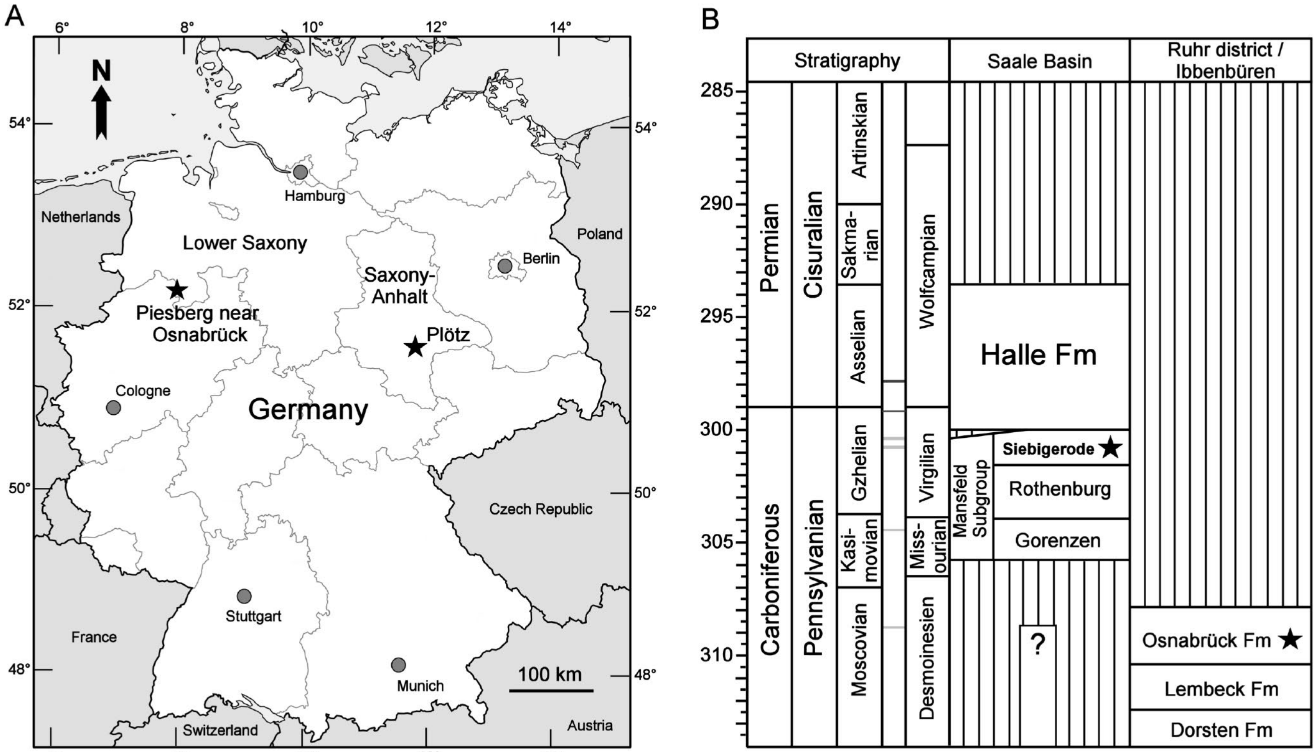

Fig. 1. Location and stratigraphy. **A.** Location of the localities Plötz near Halle (Saale), Saxony-Anhalt, and the Piesberg quarry near Osnabrück, Lower Saxony, Germany. **B.** Stratigraphy of both localities from which the fossils derive. The stratigraphic positions of the localities are marked by asterisks. Modified from Laaß and Hauschke (2019a) and Schneider *et al.* (2020).

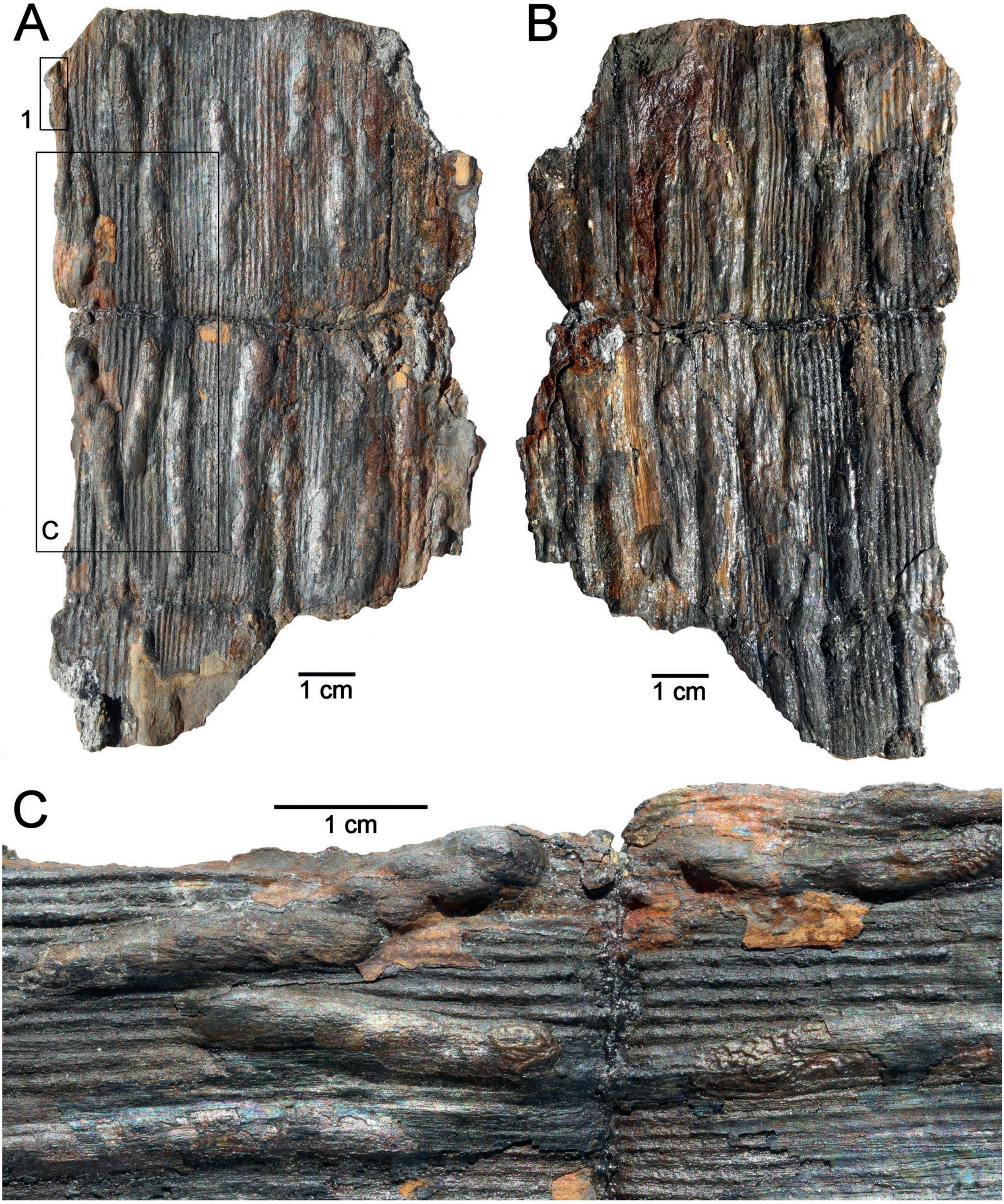

Fig. 2. Pith cast of a calamitalean stem (inventory number MAS Pal 1667) from the late Pennsylvanian of Plötz, Germany. **A.** Upper side of the endocast showing arthropod borings. Box “1”, see Figure 3. **B.** Underside of the endocast with arthropod borings. **C.** Enlargement of the region marked by the box in A. Note the wrinkles on the surface of the boring casts and the thin coaly layer, which partially covers the boring casts.

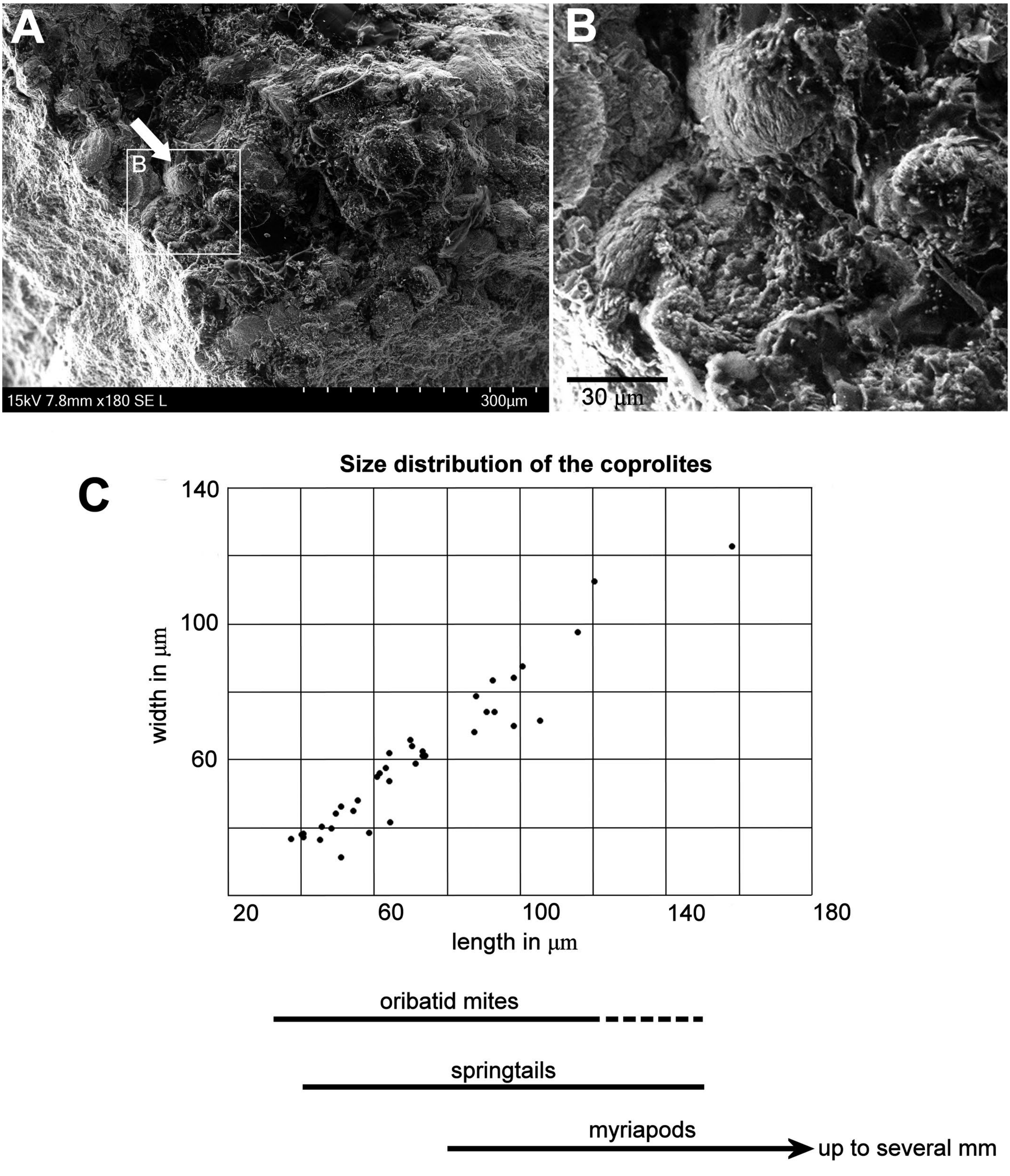

Fig. 3. Coprolites in the boring cast of the specimen from Plötz (inventory number MAS Pal 1667). The analysed boring cast is marked in Figure 2 by box “1”. **A.** SEM image of the coprolites. The arrow marks the coprolites, which were analysed by EDX. **B.** Enlargement of the region with three coprolites, which is marked in A by a box. Note the internal structure of the largest broken coprolite, which suggests that the coprolites consist of unidentifiable remains of possible plants. **C.** Diagram showing the size distribution of the coprolites compared with the size of faecal pellets of modern arthropods. Data used from Scott and Taylor (1983), Goth and Wilde (1992) and Labandeira *et al.,* (1997).

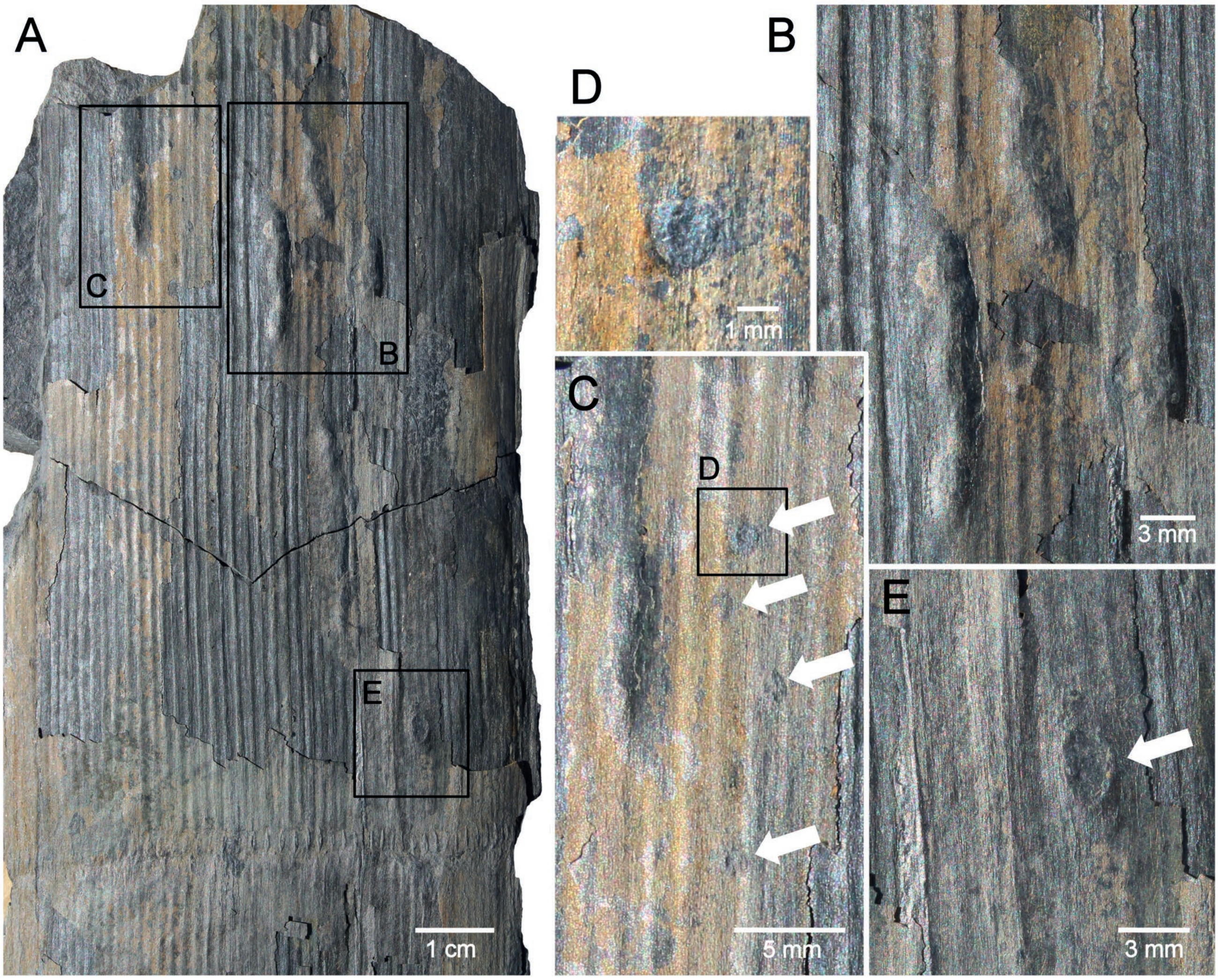

Fig. 4. Pith cast of a calamitalean stem (inventory number MAS Pal 1668) from the late Pennsylvanian (Asturian/Westphalian D) of the Piesberg quarry near Osnabrück, Germany. **A.** Pith cast that shows several borings of putative arthropods. **B.** Enlargement of the region with boring casts, which is marked in A by a box. **C.** Enlargement of the second area in A, with four Microconchida. They are attached to the outer cortex of the calamitalean stem and marked by arrows. **D.** Enlargement of the Microconchida specimen marked by a box in C. **E.** Enlargement of the third area, marked by a box in A. It shows a hole with a rim of reaction tissue, which is interpreted here as a boring from outside into the pith.

The Osnabrück Formation of Northern Germany was deposited in the Variscan Foreland Basin and is characterised by cyclic sedimentation probably controlled by both tectonics and climatically moderated base-level changes (Jones and Glover, 2005). Generally, three orders of cycles can be distinguished, whereby the more than 200 m thick sequence, which crops out in the Piesberg quarry, represents almost a complete second-order cycle comprising three third-order cycles (Jones and Glover, 2005). A typical third-order cycle is a fining upward sedimentation sequence starting with conglomerates, arenites, quartzitic and lithic sandstones at the base, followed by cross-bedded fluvial and alluvial sandstones (Jones and Glover, 2005; Leipner and Chellouche, 2019). The uppermost part of a third-order cycle consists of shale, typically with rooted palaeosols, followed by a coal seam, which is covered by a plant-rich roof shale.

According to Schultka (2000) and Haug *et al.* (2013), the section in the Piesberg quarry comprises seven coal seams named: “Zweibänke”, “Bänkchen”, “Dreibänke”, “Mittel”, “Johannisstein”, “Schmitzchen” and “Itterbeck”. Further small coal seams are known from boreholes. The most basal visible coal seam, “Zweibänke”, marks the base of the Westphalian D (Brauckmann and Herd, 2002; Jones and Glover, 2005). Recently, Leipner and Chellouche (2019) reported a newly discovered, ca. 1.5 m thick, lacustrine deposit situated approximately 7 m above the coal seam “Mittel”. The base of this deposit is sandstone. Accordingly, this lacustrine deposit consists of 5 beds of shale- to siltstone with varying grainsizes, and finely laminated stratification. The main lacustrine deposits with laminated facies are seen in beds 2 to 4. The two pith casts of calamitalean stems from the Piesberg quarry described in this paper (Figs 4, 5) derive from bed 2 of the lacustrine deposit.

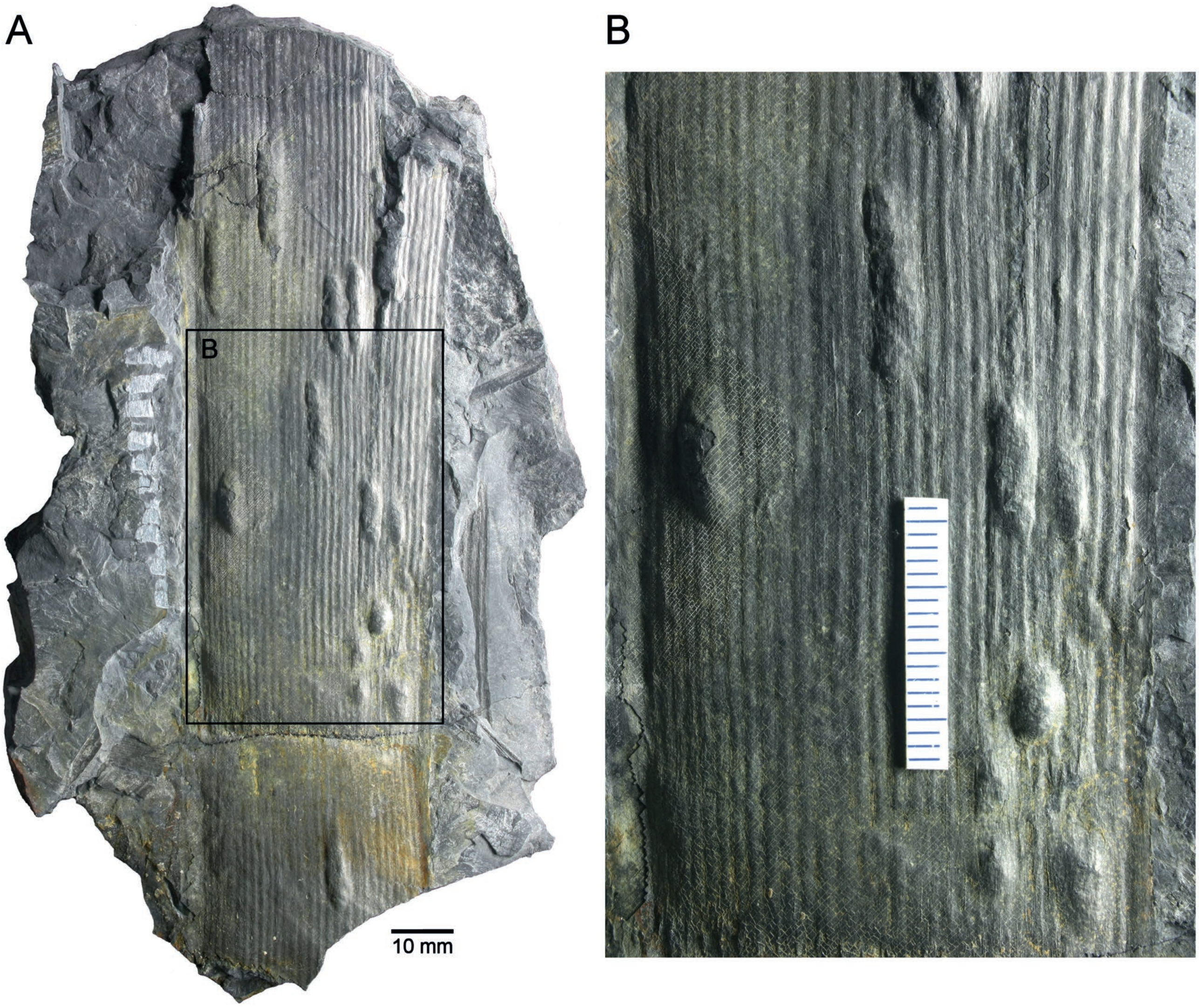

Fig. 5. Calamitalean pith cast (inventory number MAS Pal 1669) from the late Pennsylvanian (Asturian/Westphalian D) of the Piesberg quarry near Osnabrück, Germany. **A.** Overview. **B.** Detail photograph of the region marked in A by a box. Note the presence of several boring casts, which run parallel to the vascular bundles on the surface of the pith cast.

MATERIAL AND METHODS

Methods

The specimens were studied using a binocular (Euromex BMK) and a stereomicroscope (Carl Zeiss Jena). Photographs were taken using a Canon EOS 700D and a Canon EOS 450D digital camera. Additionally, a part of the boring cast of the specimen from Plötz, which is marked by the box "1" in Fig. 2A, was studied by means of Scanning Electron Microscopy (SEM). The SEM device was a Hitachi tabletop microscope TM4000Plus, which was used to take BSE and SE images (Fig. 3A, B). Additionally, some invertebrate coprolites, as well as the sedimentary infilling of the boring cast, were examined by energy-dispersive X-ray (EDX). The software Quantax75 was used to analyse the EDX spectra. Furthermore, scaled BSE and SE images were used for statistical analysis of the size distribution of the coprolites from the boring cast (see Fig. 3C).

Specimens examined

The first subject of this study is a pith cast of a calamitalean stem from the mine dumps of Plötz, near Halle (Saale). The second and third calamitalean pith casts came from the Piesberg quarry near Osnabrück. Specimens investigated here are stored in the collection of the Museum am Schölerberg in Osnabrück under the inventory numbers MAS Pal 1667, MAS Pal 1668 and MAS Pal 1669.

The specimen from Plötz (MAS Pal 1667, fig. 2) is a dark-grey coloured mudstone with reddish-brown staining resulting from weathered pyrite content. Some of the boring casts show pyrite decomposition, which points to higher pyrite content in boring casts compared to the pith cast. The contents of iron and sulphur in the matrix and the coprolites of the boring cast range between 15 to 35% and 3 to 32%, respectively.

Relicts of a thin layer of coaly substance were recognised on the surface of the pith cast. In summary, the specimen likely derives from the plant-rich roof shales of the coal seams.

The specimens from Osnabrück (MAS Pal 1668 and MAS Pal 1669, figs 4, 5) are also mudstones. The predominant colour is dark grey, which can be explained with the lower degree of weathering compared to the Plötz specimen. In the Piesberg specimens, a fine bedding structure was observed. Parts of the surface of the pith casts are covered by a thin coaly layer. Additionally, in some cases, a thin white to yellowish film on the endocast was recognised. This preservation is caused by a thin layer of gümbelite (Brauckmann and Herd, 2002).

Description

Specimen MAS Pal 1667 consisted of two almost complete, and a third incomplete, internode, which were separated by nodes from each other (Fig. 2). The pith cast was 12.5 cm long and 7.2 cm wide. The specimen was considerably compressed and only 0.3 to 0.5 cm thick. The internodes showed parallel longitudinal striations, which represent the impressions of the vascular bundles. The striations were narrow; about 10 striations over a width of 1 cm. Due to the absence of other diagnostic features, the specimen can only be assigned to *Calamites* sp.

Furthermore, numerous more or less isolated protruding cylindrical bulges were recognised on the surface of the pith cast. In total, there are at least 20 bulges on the "upper side" and 32 on the "underside" of the pith cast. The width of most bulges ranged between 3 and 5 mm. Only a few casts were narrower and only 1–2 mm wide. The length of the bulges varied considerably and ranged between 1.6 and 7.4 cm. In most cases (≈88% of total; n = 46), the bulges were restricted to only one internode. A few bulges (≈12% of the total; n = 6) crossed the nodes but became narrower at the nodal levels (Figs 2C, 6).

In almost all cases, the cylindrical bulges were longitudinally orientated and ran almost parallel to the impressions of the vascular bundles. One exception is the bulge, which ran at a small angle to the impressions of the vascular bundles (Fig. 2C). The sloping part of this bulge showed small

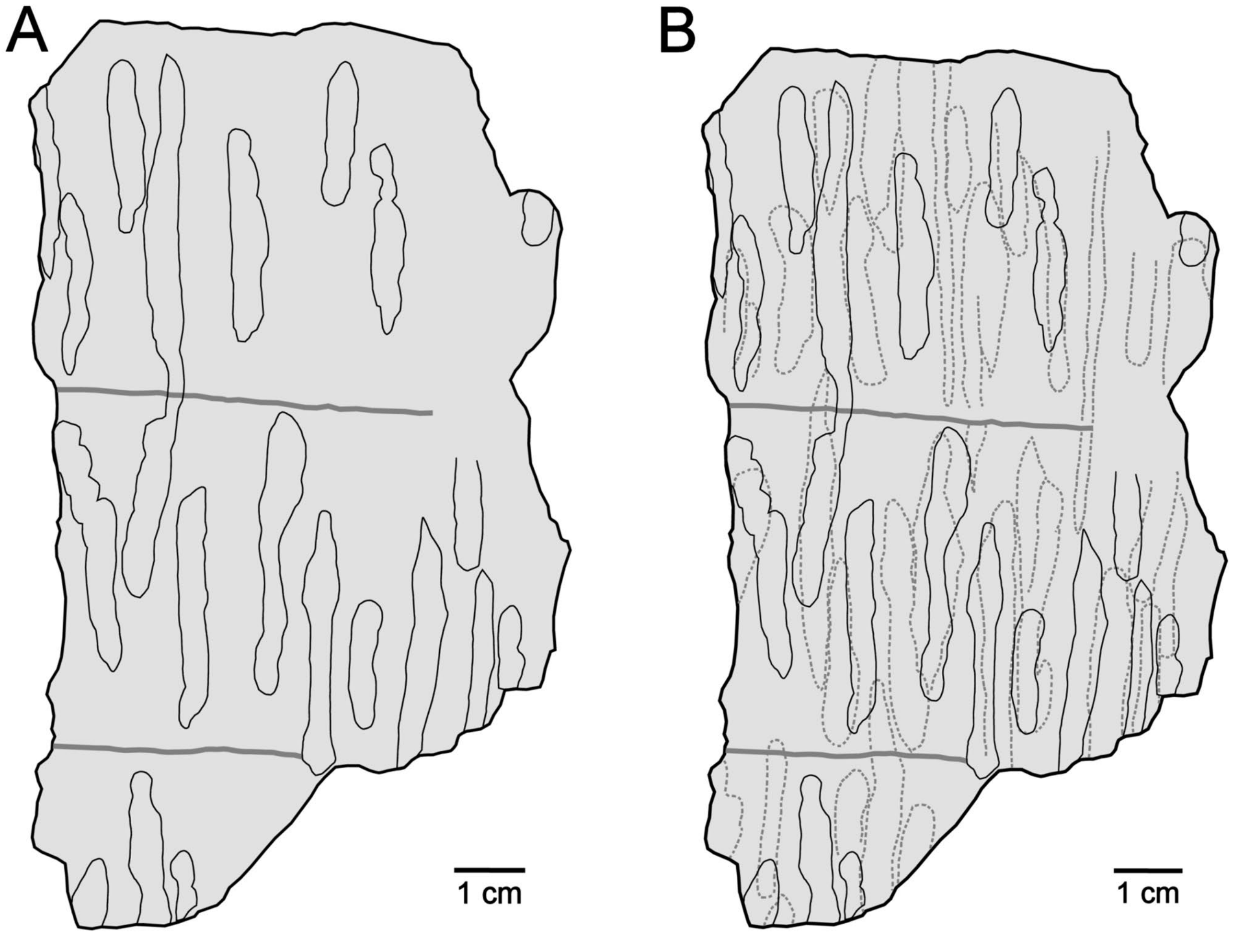

Fig. 6. Sketch of the specimen from the Plötz locality depicted in Figure 2. **A.** Sketch showing the borings on the upper side of the endocast of the pith cavity. **B.** Sketch showing both the boring casts from the upper side (black) and the underside (stippled) of the endocast of the pith cavity. Note that most boring casts are restricted to the internodes, and only a few boring casts lead over the nodes.

convexities. Similar structures with convexities were also described by Rößler and Fiedler (1996, fig. 7) as arthropod borings (“type 2”) on the outer margin of a gymnosperm wood from the early Permian of Germany.

As already mentioned, the protruding bulges were often covered by a thin layer of coaly substance, which represents the remains of the wood of the calamitalean stem. In such areas, the surface of the bulges was relatively smooth. Sometimes a fine longitudinal striation was visible, but not impressions of the vascular bundles. If this thin layer of organic matter was removed, the surface of the bulges was either smooth or wrinkled (Fig. 2C).

Both pith casts of calamitalean stems from the Piesberg quarry (Figs 4, 5) consisted of two incomplete internodes, which were separated by a node from each other. The first pith cast had a maximum length of 16.8 cm, a maximum width of 6.8 cm and was 0.7 cm thick. The dimensions of the second specimen were 16.1 x 4.7 x 0.1 cm, respectively.

Both pith casts showed well-preserved impressions of vascular bundles. The striation was slightly wider than in the specimen from Plötz; on both specimens, seven vascular bundles were counted over a width of 1 cm. Both specimens were also assigned to *Calamites* sp.

On the first specimen from Piesberg, five protruding bulges were visible, which resembled the structures of the specimen MAS Pal 1667. The width of the bulges was slightly narrower, and ranged between 2 and 3.5 mm. The length of the bulges was between 0.8 and 2.7 cm. All bulges were situated on the same internodal region. A further remarkable feature was a 3.5 x 2 mm hole in the vascular bundles, bordered by a slightly embossed rim (Fig. 4E).

On the surface of the internodes of the second specimen from Piesberg, 14 bulges were recognised that ranged between 2.5 and 4 mm in width and between 4 and 20 mm in length. All bulges ran almost parallel to the vascular bundles. The surface of the bulges was smooth. As in the specimen from Plötz, the pith casts, including the bulges, were covered by the remains of a thin layer of coaly substance, which also showed a fine longitudinal striation. Interestingly, on the surface of the coaly layer, in the specimen MAS Pal 1668, at least 4 Microconchida were attached (Fig. 4C, D). At the Piesberg, Microconchida are not rare and colonise plant remains and faunal elements, even insect wings (Wrede *et al.*, 2019).

Furthermore, the SEM investigation revealed the presence of small spherical bodies, concentrated in clusters in the bulges of specimen MAS Pal 1667 (Fig. 3). All spherical bodies were sub-spheroidal in shape. The size distribution of the spherical bodies (Fig. 3C) suggested the presence of two distinct classes: a smaller class between 37 to 74 x 37 to 63 μm in dimensions, and a larger class between 88 to 158 x 68 to 123 μm.

The spherical bodies were composed of small, unidentifiable potential plant remains that were arranged in a concentric internal structure (Fig. 3B). Energy dispersive X-ray (EDX) study revealed that the main components were carbon (mean content 44%), iron (mean content 24%), and sulphur (mean content 24%), which suggests that they consisted almost completely of carbon and pyrite. Furthermore, there were striking differences between the carbon contents of the spherical bodies and the matrix. While the content of carbon in the spherical bodies ranged between 34 to 54%, it was only between 6 to 17% in the matrix of the bulges. Because of their size, shape and composition, we interpret the spherical bodies as invertebrate coprolites. The presence of coprolites in the bulges strongly suggests that the bulges represent boring casts of animal origin.

DISCUSSION

Taphonomy and fossil diagenesis

The general anatomy of calamitalean stems is well-known from three-dimensionally preserved, permineralised specimens (e.g., Williamson, 1871; Seward, 1898; Wang *et al.*, 2006; Taylor *et al.*, 2009; DiMichele and Falcon-Lang, 2012; Rößler *et al.*, 2012a; Mencl *et al.*, 2013; Chen *et al.*, 2018). Accordingly, calamitalean stems consist of several concentric layers of tissue. In the centre is a pith that is either originally made of parenchyma in young calamitalean stems or hollow in older specimens. The margin of the pith cavity is encircled by parenchyma, which is followed by a ring of primary vascular bundles that contain the carinal canals for early water transport in the plant (Fig. 7A). From each vascular bundle, a wedge consisting of primary and secondary xylem is developed. In larger specimens, the wedges may form a thick, solid ring of wood. They are separated from each other by radial extensions of parenchymatous tissue, the interfascicular rays (Taylor *et al.*, 2009). Finally, the primary and secondary xylem is surrounded by a zone of thin extraxylary tissue (Fig. 7A).

Longitudinally, the stem is divided into nodes and internodes. In the pith cavity, the internodes are separated from each other by drumhead-like plates, the nodal diaphragms (e.g., Williamson 1871; Taylor *et al.*, 2009; DiMichele and Falcon-Lang, 2012, fig. 2A; Mencl *et al.*, 2013, pl. II, 1). The latter consist of parenchyma that becomes solid at the level of the nodes (DiMichele and Falcon-Lang, 2015), which is also indicated by the denser cell structure in contrast to the internodes (Williamson 1871, pl. XXIV, fig. 10).

The thin film of coaly substance on the boring casts likely represents the carbonised remains of the outer tissues, such as extraxylary tissue and xylem. Consequently, the borings were situated inside the stem: either in the pith, the marginal parenchyma or near the vascular bundles (Fig. 7A).

It is obvious that the stems were embedded into the sediment before less resistant tissues such as pith and parenchyma, which contained the borings, were decomposed. This is an indication of relatively rapid burial. On the other hand, the presence of Microconchida on the outer cortex of the Piesberg specimen (Figs 4C, D) suggests a certain period underwater before burial in the sediment, which enabled the Microconchida to colonise the stem. Associated findings of freshwater species such as syncarid crustaceans (A. Leipner, pers. obs., 2020) suggest a lacustrine environment, which supports the interpretation of these deposits as lacustrine (Leipner and Chellouche, 2019). A similar taphonomy and palaeoenvironment can also be hypothesised for the specimen from Plötz, which in all probability derived from the roof shales, which are also interpreted as lacustrine to palustrine sediments (J. W. Schneider, pers. comm., 2019; Laaß and Hauschke, 2019a).

In all specimens, and in contrast to the boring casts, the pith casts are very flat and only partially filled in with sediment. This suggests that the pith cavities were not entirely hollow and still contained a considerable amount of parenchymatous tissue during burial.

The presence of pyrite in the pith cast from Plötz indicates anoxic conditions during embedding and/or early diagenesis, which delayed decomposition of the soft tissue. Pyrite is obviously concentrated in the three-dimensionally preserved boring casts of the Plötz specimen (see also Fig. 3). The fact that pyrite is relatively incompressible might be an explanation why the boring casts were only little affected by diagenetic compression (Figs 2, 7C). In contrast, the rest of the pith cast was considerably compressed to a thickness of only a few millimetres, which might be a result of the lower content of pyrite and the high amount of compressible components such as mud and silt. This suggests that pyrite formation must had been already been finished before diagenetic compression began (Fig. 7B). This is also supported by the fact that the necessary sulphur for pyrite formation often derives from syngenetic or early diagenetic decomposition of organic matter.

Furthermore, diagenetic compression and heating contributed to coalification of the calamitalean wood. According to Schwab (1962), the coalification of organic matter in the Wettin Subformation was increased through the intrusion of the Petersberg porphyry, which is only 5 kilometres away from the Plötz locality. A common view is that

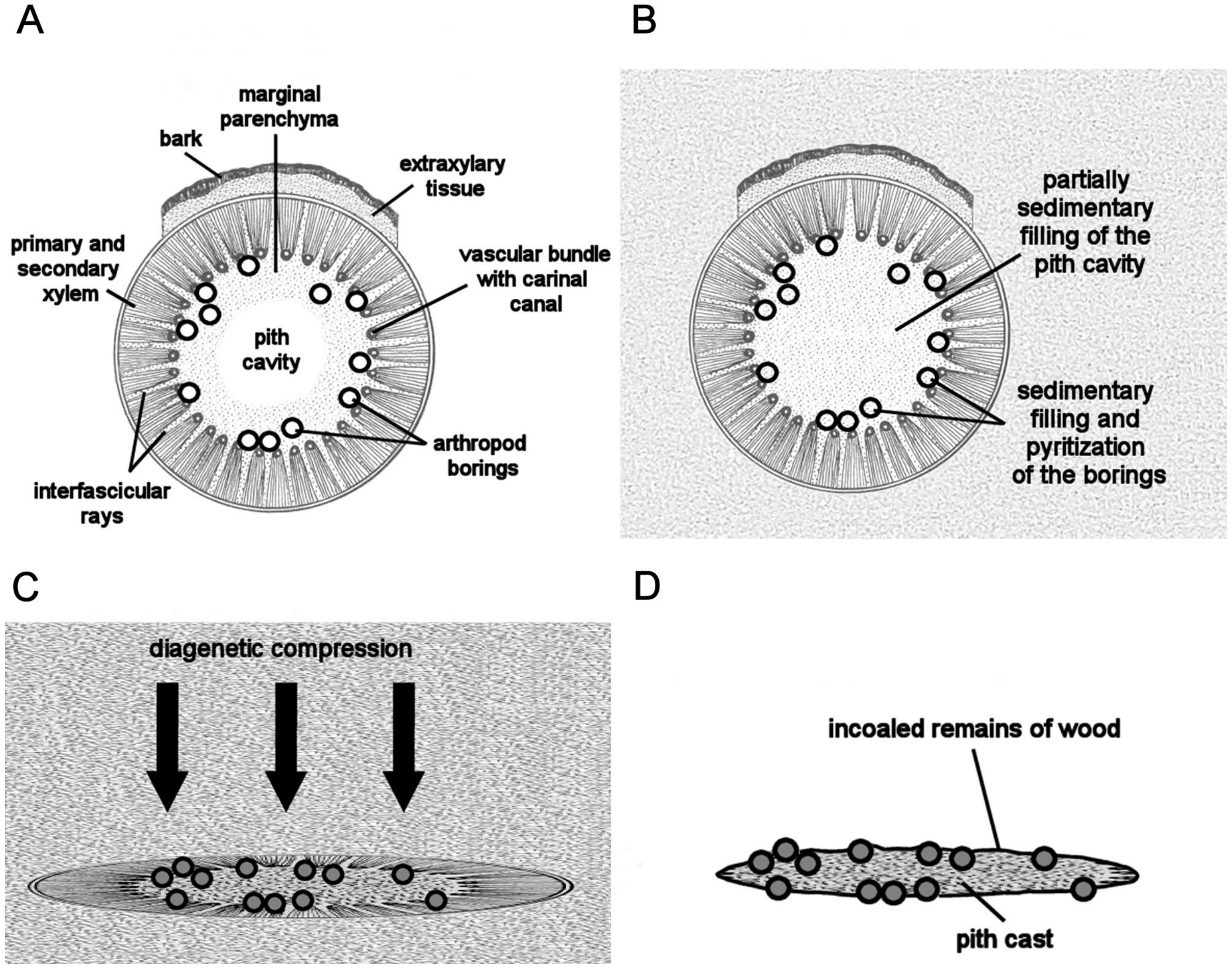

Fig. 7. Taphonomy and fossilization of the calamitalean pith cast with arthropod borings. **A.** Young calamitalean stem with arthropod borings in the marginal parenchyma of the pith cavity. **B.** Embedding of the calamitalean stem into the sediment. As the borings were hollow spaces, they were almost completely filled with sediment. As a result of decomposition of organic matter under low oxygen conditions, pyritization of the boring casts was possible. In contrast to the boring casts, the pith cavity was only partially filled with sediment due to the presence of the pith. **C.** Diagenetic compression of the sediment. Note that the pith cavity will be compressed, whereas the boring casts mainly resist diagenetic compression due to their higher content of incompressible pyrite. Furthermore, organic matter was carbonised. **D.** As a result of carbonisation, the plant material was transformed and compressed to a thin coal layer on the surface of the endocast. The boring casts near the surface of the endocast trace out on the endocast because of their three-dimensional preservation. Modified from Stewart (1983).

the anomalous high coalification rank of the sediments from the Osnabrück Formation was also caused by an igneous intrusion, the "Bramsche Massif" (e.g., Reich, 1948, 1949; Hahn and Kind, 1971). The presence of this hypothetical pluton is supported by the extremely high vitrinite reflectance of organic matter in Carboniferous rocks in the area around Bramsche (e.g., Teichmüller, 1951; Bartenstein *et al.*, 1971) as well as by magnetic anomalies (e.g., Reich, 1948, 1949; Hahn and Kind, 1971). Alternatively, the studies by Muñoz (2006) and Brink (2013) demonstrated that the high coalification rank could also be explained by deep subsidence of the sediments. However, this theory does not explain why the high coalification is only restricted to the area around Bramsche. More recently, as a further possible cause of the high coalification in the Piesberg quarry, circulating hydrothermal fluids along fault zones came into focus (Wüstefeld *et al.*, 2017).

In summary, this unique preservation of arthropod borings in compressed calamitalean pith casts was only possible under special taphonomic conditions, such as rapid embedding coupled with different sediment infilling of the borings and the pith cavity, as well as anoxic conditions preventing decomposition of the non-resistant tissues in the pith cavity that housed the borings.

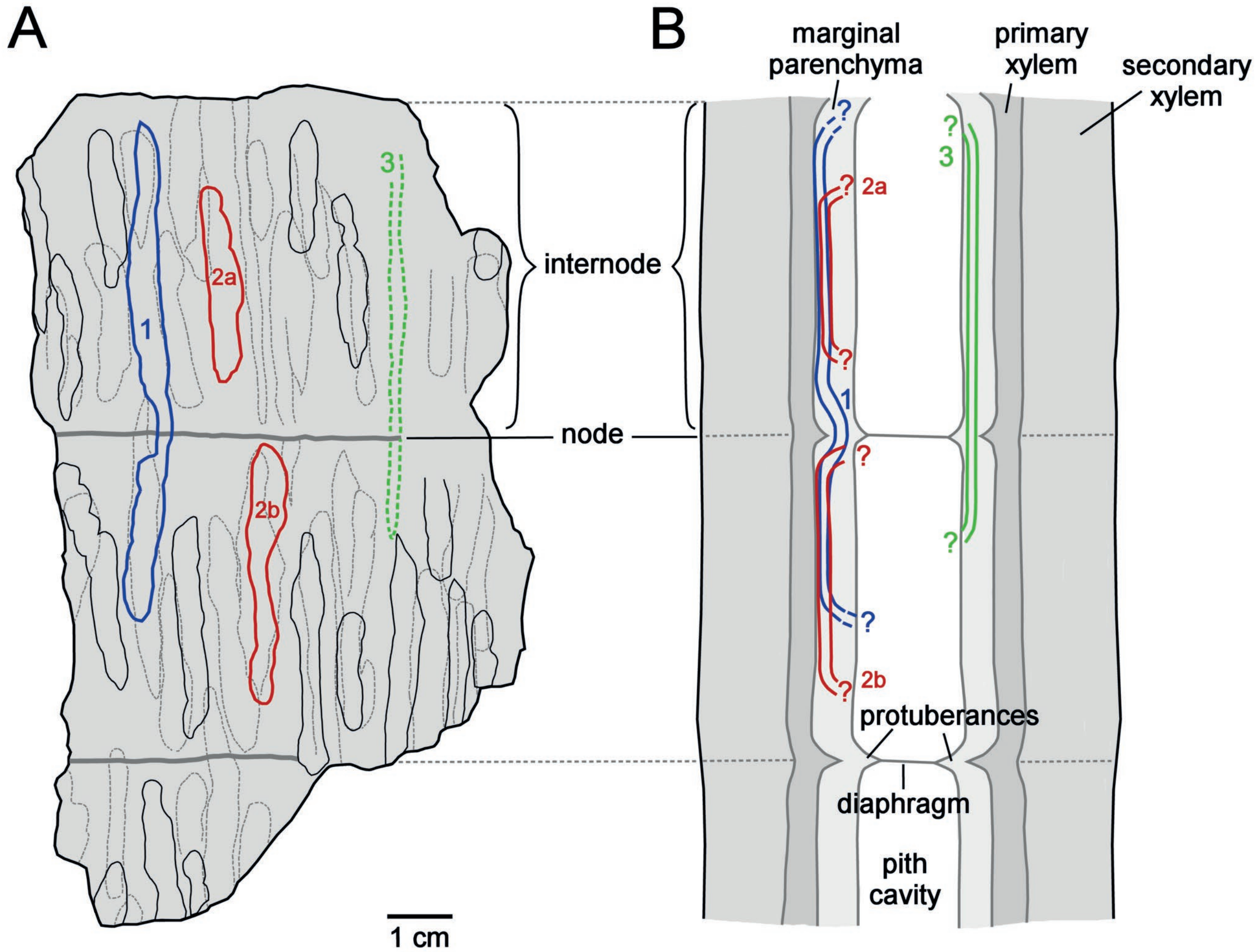

Fig. 8. Partial reconstruction of selected borings in the pith cavity of the calamitalean stem from the Plötz locality. **A.** Sketch from Figure 4B showing the boring casts on the upper side (solid lines) as well as the boring casts on the underside (stippled lines) on the pith cast. Furthermore, three representative boring casts (1, 2a, 2b and 3) are marked by different colours. Boring cast 1 (blue) runs over two internodes, whereby it crosses a node. Note that the boring cast becomes narrower near the node. Boring casts 2a and 2b (red) are restricted only to internodes. Boring cast 3 (green) also passes two internodes and crosses a node, but it is constantly narrow at the surface of the endocast. **B.** Reconstruction of the courses of the borings 1, 2a, 2b and 3 in the pith cavity. The variations of the diameters of the boring casts 1 to 3 in A. are interpreted here as resulting from their different distances from the outer border of the pith The presence of protuberances and diaphragms at the nodes might be the reason that the borings 1, 2a and 2b change their course to more central layers of the pith, which either resulted in a narrower diameter on the endocast (boring 1) or in the complete absence of the boring cast (2a, 2b) on the endocast in A.

Interpretation of the boring system

Most boring casts occurred in the internodes of the pith cast and appeared isolated from each other. In some cases, narrower tunnels could also be recognised near the nodes (Figs 2, 6, 8). Assuming that arthropods produced the structures in question, isolated cavities can be excluded, and connections between the tunnels must originally have been present. This suggests that only a part of the boring system is visible on the surface of the pith cast. Therefore, the question arises as to the original structure of the boring network and its location in the stem.

Possible interpretations are: 1) a system of large chambers existed, which were connected by smaller tunnels to each other, or 2) all borings originally had an almost constant diameter and possible connections between them are in most cases "invisible" due to the taphonomy and preservation of the fossil.

An argument for the first interpretation is the observation that in rare cases, large "chambers" are connected by narrower tunnels (Figs 2C, 8, boring 1). At first appearance this might be an indication for a complex network similar to that produced by polyphagan beetles in Permian gymnosperm wood. Such networks consist of cavities and tunnels of different diameters and shape such as a mother gallery, small larval tunnels and large lateral niches (Feng *et al.*, 2017, 2019). However, this interpretation seems unlikely here, because the large "chambers" in the pith cast differ considerably in their lengths. If they would represent specialised larval or pupation chambers, relatively continuous lengths and an arrangement in a regular pattern would be expected. Furthermore, interpretation 1 does not explain why most of the narrower tunnels are restricted to the nodes.

Therefore, it seems more likely that differences in boring diameter result from the anatomy of the calamite stem and the preservation. Observations on three-dimensionally preserved calamitalean stems revealed that the pith cavity at the nodes becomes narrower due to the presence of protuberances of the xylem and parenchyma (e.g., Williamson, 1871, pl. XXIV, fig. 10; DiMichele and Falcon-Lang, 2012, fig. 2A; Chen *et al.,* 2018, fig. 2b). Furthermore, the pith cavity is divided by nodal diaphragms into separate parts.

The vast majority of the boring casts is situated at the internodes, most likely in the outermost part of the pith, in the parenchyma close to the primary xylem (Figs 2, 4–6, 8). The reason might be that the internodal parenchyma was less resistant than the parenchyma at the nodes and, therefore, a potential attractive food resource. Representative examples are the boring casts "2a" and "2b" in Fig. 8. Only in rare cases did borings pass the nodes and extended over two internodal regions (e.g., boring cast "1" in Fig. 8). At the internodes, boring cast 1 protrudes substantially from the endocast by maintaining a relatively wide constant diameter of 3 to 4 mm. The narrower diameter of boring cast 1 near the node suggests that the borer probably evaded the solid nodal protuberance to reach the next internode. Consequently, the boring near the node runs more central within the pith, which later, after diagenetic compression, resulted in a less prominent appearance on the pith cast of the calamitalean stem (Fig. 8B).

Another example of a boring cast that passes a node, is boring cast "3" (Fig. 8). In contrast to boring cast 1, it does not show any striking variations in diameter on the surface of the pith endocast. Instead, it has a constantly, narrow diameter of 1 to 2 mm. In this case, it was probably not necessary for the borer to change its course to bypass the nodal protuberance, because this boring generally ran more distant from the external margin of the parenchyma. This would explain why it does not appear as prominent as other borings on the surface of the endocast after diagenetic compression.

These observations reveal a special feeding strategy according to which the culprits preferred non-resistant tissues of greater nutritional value, such as the parenchyma of the pith cavity, and avoided, if possible, penetrating solid wood.

Nevertheless, the boring hole that pierces the xylem in the Piesberg specimen, as well as the recognition that the borers in the Plötz specimen were able to overcome the hard nodal diaphragms, may be indications that the arthropods were equipped with mouthparts that were also strong enough to penetrate solid wood.

As known from three-dimensionally preserved specimens, the pith cavity of adult calamitalean stems is usually hollow in the centre and lined along its external margin by extensive parenchyma (Rößler and Noll, 2006, 2010; DiMichele and Falcon-Lang, 2012; Rößler *et al.*, 2012a). Consequently, the activity of the borers was likely restricted to the external margins of the pith cavity, which excludes associations between borings on opposite sides of the stem. This is supported by Figure 6, according to which the boring casts on the upper side of the endocast were not associated with borings on the underside.

Consequently, the most likely reconstruction of the boring system is that the animals mainly produced undifferentiated, longitudinally oriented tunnels with more-or-less constant diameter in the marginal parenchyma of the pith cavity. In doing so, they were obstructed by the solid protuberances and diaphragms in passing the nodes.

Herbivory or detritivory?

Another question is whether the borings were produced in living plants by herbivorous, or in dead plant tissue, by detritivorous, arthropods. Possible criteria for herbivory could be the presence of callus or other types of reaction tissue induced by arthropod damage to a living plant (Labandeira, 2006a). This is difficult to decide for the specimen from Plötz, because the original structure and details of the plant tissue are not well preserved. However, a single indication for a herbivore origin of the borings comes from the Piesberg specimen. As illustrated in Fig. 4E, the specimen MAS Pal 1668 shows a hole in the xylem, which is bordered by a slightly embossed rim that might represent wound response tissue of the living plant. Although a connection between the hole and the tunnel system of the internode-was was not substantiated, it seems very likely that both structures were produced by the same arthropods during the lifetime of the plant, because of the dimensions of the hole match the width of the boring casts.

Comparisons and possible producer

The borings described in this study differ from all previously reported borings in calamite stems. The borings in the calamite stem from the Latest Gzhelian of Texas described by Xu *et al.* (2018) were either located in the subcortex of the bark or in fungal-laden wood, but not in the pith. Further differences concern the diameter of the tunnels. While the specimen described by Xu *et al.* (2018) consists of a 2 mm long and 0.12 mm wide gallery and numerous 20 µm wide tunnels, the borings from the Plötz and Piesberg sites are considerably larger and between 3 and 5 mm in width.

In some features such as the feeding strategy, as well as the location in the stem, the borings from Plötz and Piesberg resemble the arthropod borings in *Arthropitys bistriata* from the early Permian Petrified Forest of Chemnitz, Germany (Rößler *et al.,* 2012a, b) and the borings in the pith and xylem of *Arthropitys*-type calamitalean stems from the Permian fossil forest of northern Tocantins, Brazil (Rößler, 2006, fig. 8b; Neregato *et al*., 2017, plate IX, figs 1, 2 Rößler *et al*., 2020). There is also evidence for wound-response tissue around the holes in the xylem of the specimens from Chemnitz and Brazil, which is a strong indication that the arthropods may have attacked the living plant (Rößler *et al.,* 2012a). The invertebrate coprolites in the pith cavities of *Arthropitys bistriata* and the *Arthropitys*-type calamitalean stems from Brazil are, however, considerably larger than the coprolites in the Plötz specimen and do not fit in length into the tunnels of the Plötz and Piesberg specimens. Furthermore, the boring cavities of the specimens from Chemnitz and Brazil are irregular and do not show the distinct pattern of longitudinally-oriented borings near the border and between pith and xylem as in the specimens described here.

The borings from Plötz and Piesberg can also be distinguished from a calamite stem from the Late Pennsylvanian (Moscovian) of the United Kingdom described by Seward (1898) and Stopes (1907) that showed evidence of arthropod activities in the pith cavity. Comparisons of the borings are impossible because the specimen described by Stopes (1907) is only known from a single thin section. According to Correia *et al.* (2020), the structures in question can likely be assigned to DT284 and were probably produced by oribatid mites. However, tunnel networks of oribatid mites are commonly less than few hundred µm wide (e.g., Goth and Wilde, 1992; Scott *et al.*, 1992; Labandeira *et al.,* 1997; Kellogg and Taylor, 2004; Feng *et al.*, 2010a, 2012, 2015a, 2017; Feng, 2012; Slater *et al.*, 2012; Wan *et al.*, 2016; Wei *et al.,* 2019; see also Appendix Table 1). As the borings in the pith casts from Plötz and the Piesberg are considerably larger in diameter than the tunnel networks of mites, oribatid mites as possible culprits seem very unlikely.

Further important information about the possible producer of the tunnels in the calamite stems can be deduced from the size, shape and composition of the invertebrate coprolites (e.g., Baxendale, 1979; Scott and Taylor, 1983). Small coprolites comparable to those in the borings of the Plötz specimen are known from oligochaete annelids, collembolans, insectan micro- and macroarthropods, oribatid mites, and myriapods (Labandeira *et al*., 1997).

Modern oligochaete annelids inhabit organic-rich soils or decomposing litter (Wallwork, 1976a, b), but are not known to bore into wood (O´Connor, 1967; Labandeira *et al*., 1997). Therefore, they can be excluded as possible producers.

Collembolans (springtails) are known since the earliest terrestrial ecosystems evolved (Edwards *et al*., 1995, 2012; Trewin and Kerp, 2017). They excrete coprolites that range between 30 and 150 µm in diameter (Scott and Taylor, 1983; Goth and Wilde, 1992) and are often irregularly shaped (Labandeira *et al*., 1997). Most modern springtails are detritivores and live in soil and litter. They prefer a diet that consists of softer tissues such as bacteria, algae, fungi, partly degraded parenchyma, pollen and spores, faecal pellets, and dead animals (Labandeira *et al.*, 1997 and references therein). However, some springtails are also able to switch between detritivore and herbivore, depending on the available food resources (Endlweber *et al*., 2009). Collembolans, however, do not possess strong mouthparts that enable them to create tunnels in wood (Goto, 1972; Labandeira *et al.*, 1997; Labandeira, 2019), which excludes them as possible producers of the coprolites in the calamite stems from Plötz and Piesberg.

The faecal pellets of most adult wood-boring insects are considerably larger than the coprolites in the specimen from Plötz (Labandeira *et al.*, 1997). If at all, only coprolites of their subadult stages are of comparable size. A group that produces such small coprolites are the wood-boring beetle larvae from the Late Carboniferous and Permian of China and Germany (Feng *et al.*, 2017, 2019). Of particular interest are also the small holometabolous insects described by Nel *et al.* (2013), which suggest that early radiation of small eumetabolan insects already began in the Moscovian. Among others, Nel *et al.* (2013) described the earliest-known holometabolous insect larvae (*Metabolarva bella*) from the Piesberg quarry (Fig. 9C), which, with respect to its body dimensions, would fit well into the borings described in this paper. However, coprolites of wood-boring holometabolous insect larvae can be clearly distinguished from all other wood-boring arthropods, including the sub-spheroidal coprolites described here, because they excrete cylindrical segments of an extruded bolus mass (Labandeira *et al*., 1997). The same is true for cockroach faecal pellets, which are also cylindrical and considerably larger than the coprolites in the calamite stem from Plötz (Scott and Taylor, 1983).

Insectan microarthropods such as diplurans, archaeognathans and thysanurans also produce small coprolites, but they are typically irregularly shaped and often show projecting fragments (Labandeira *et al.*, 1997). In contrast, the coprolites found within the tunnel system of specimen MAS Pal 1667 are rather smooth and do not show irregularities (Fig. 3).

As already stated, both size classes of coprolites observed in the specimen from Plötz also fall into the range of oribatid mites and resemble the coprolites of oribatid mites as they are smooth and nearly spherical. As pointed out by Labandeira *et al*. (1997), oribatid mites were already essential to the decomposition of plant tissues in Carboniferous coal-swamp forests. Like their modern relatives, most of

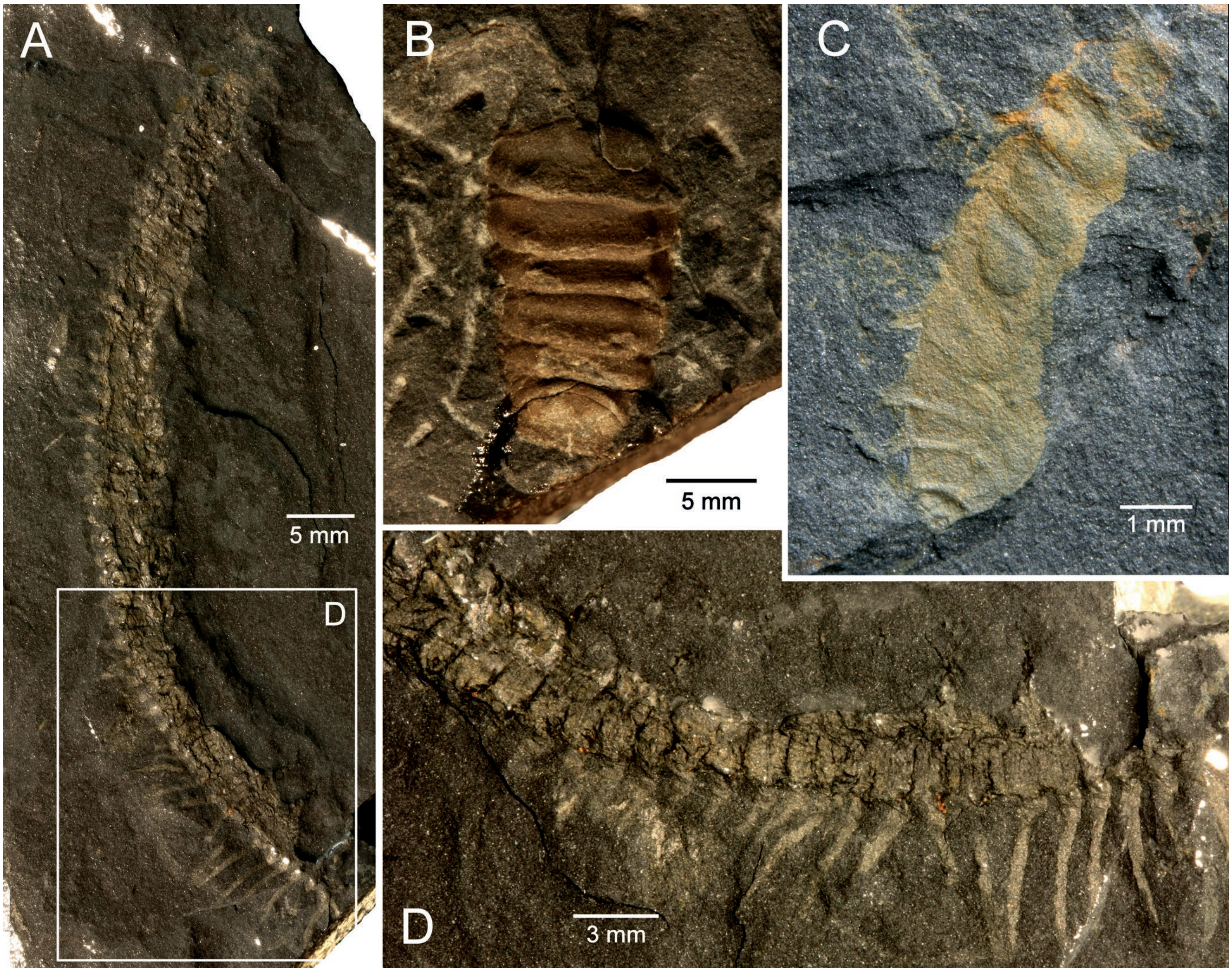

Fig. 9. Fossil record of arthropods from the Piesberg quarry discussed in the paper as possible producers of the borings in the calamitalean stems. **A.** *Acantherpestes* sp. (Diplopoda, Archipolypoda) from the roof shale above coal seam "Zweibänke" (inventory number MB.A.4315a). Photograph taken under immersion. **B.** Head and five tergites of *Amynilyspes* sp. (Diplopoda, Oniscomorpha) from the roof shale above coal seam "Dreibänke" (inventory number MB.A.4316). **C.** Holometabolous larva *Metabolarva bella* from the roof shale above coal seam "Zweibänke" (inventory number MAS Pal 588). **D.** *Acantherpestes* sp. (Diplopoda, Archipolypoda). Enlargement of the region marked by the box in A. Photograph taken under immersion. MB – Museum für Naturkunde Berlin.

them inhabited soil and litter, but some mites were also able to bore into wood (Labandeira *et al.*, 1997). Nevertheless, oribatid mites appear unlikely as possible producers of the boring systems in the Plötz and Piesberg specimens, because the tunnel systems of oribatid mites are considerably smaller in diameter than those described here.

It is possible that the borings were produced by another, larger, herbivorous arthropod and later revisited by oribatid mites. In fact, in the fossil record there is evidence for the co-occurrence of different arthropods in wood borings. Wei *et al.* (2019) also found two size classes of coprolites in the pith cavity of the Late Permian conifer *Ningxiaites shitanjingensis*. They came to the conclusion that herbivorous arthropods, likely ancient millipedes, produced the borings in the pith of the living plant; this was supported by the presence of wound-response tissue. Later, oribatid mites revisited the tunnel system and produced smaller coprolites, probably after the death of the plant.

An alternative interpretation might be that all coprolites were produced by the same culprit, and the distinct size classes of coprolites were produced by different ontogenetic stages of the arthropods. An example of this is the network of the beetle borings described by Feng *et al*. (2017), which contained four size classes of coprolites produced by different ontogenetic stages. This co-occurrence of different ontogenetic stages was also reflected in the morphology of the boring network, which comprises tunnels and chambers of different dimensions. However, the almost constant diameter of the borings in the Plötz and Piesberg specimens, as well as the absence of larval tunnels, rather suggests that all arthropods represented the same ontogenetic stage and were similar in body size.

Myriapods were also common arthropods in late Carboniferous ecosystems (e.g., Rolfe, 1985; Shear and Kukalova-Peck, 1990; Wilson and Anderson, 2004; Wilson *et al.*, 2005; Ross *et al*., 2018). They produced a wide range of coprolites between 80 μm and several millimetres in diameter (Scott and Taylor, 1983; Goth and Wilde, 1992), which were spherical to cylindrical in shape (Scott and Taylor, 1983). Consequently, they could be possible producers of the larger coprolites in the calamitalean stem from Plötz.

The vast majority of modern myriapods are detritivores, but herbivorous, mycophagous or carnivorous taxa also exist (Shelley, 1999; Kime and Golovatch, 2000; Rößler *et al*., 2012a). The ecology of Palaeozoic myriapods was likely to have been similar (Rolfe, 1985; Shear and Kukalová-Peck, 1990; Kime and Golovatch, 2000).

Kime and Golovatch (2000) recognise five main trends in the ecological evolution of millipedes, which already began in the late Palaeozoic. They distinguish between forms that 1) bore in soil (geobionts), 2) live in litter or the uppermost soil layers (stratobionts), 3) live in caves (troglobionts), 4) climb on trees (epiphytobionts), as well as 5) forms that bore in wood (Miller, 1974) and live under the bark (xylobionts or subcorticoles).

Xylobiont millipedes tend to be minute in body size and possess either flat-backed or particularly slender bodies of only a few millimeters in length. As a diet, they prefer less-resistant cortical tissues under the bark (Kime and Golovatch, 2000). Remarkably, wood-boring millipedes produce order-of-magnitude larger tunnel diameters than oribatid mites (Labandeira *et al.*, 1997; D´Rozario *et al.*, 2011; Wei *et al*., 2019), which would fit into the dimensions of the boring casts of the fossils described here. Moreover, the elliptical hole in the calamite wood of the Piesberg specimen (Fig. 4E) indicates that the producer possessed a flattened body shape, as known from modern xylobiont millipedes. At the same time, the dimensions of the hole are a proxy for the body size of the wood borer, which was smaller than 3.5 mm in width and 2 mm in height.

Small-sized millipedes were relatively common in the Carboniferous and have been reported from numerous localities (e.g., Hannibal and Feldmann, 1981, 1988; Hannibal, 1984; Racheboeuf *et al.*, 2004; Wilson and Anderson, 2004; Wilson *et al*., 2005; Ross *et al*., 2018) including the Piesberg (Schultka, 1988). According to Schultka (1988), at least two diplopod taxa occurred at the Piesberg: The first is a member of the Archipolypoda and belongs to the genus *Acantherpestes* (Fig. 9A, D). Characteristic features are the slender body, long legs and prominent tergal spines, which suggest that this diplopod lived above the ground and was probably capable of climbing trees (epiphytobiont). The second diplopod from the Piesberg was assigned to the genus *Amynilyspes* (Schultka, 1988). This diplopod also possessed tergal spines and was probably capable of volvation as a protection against predators (Hannibal, 1984; Racheboeuf *et al.*, 2004) (Fig. 9B). However, these diplopods from the Piesberg are slightly too large to have produced the borings in the calamite stems. Besides, the tergal spines would have prevented boring in wood. At best, it can be speculated that only the juvenile stages of these diplopods lacked spines and probably bored in wood.

Alternatively, unknown xylophagous millipedes might have already existed in the late Carboniferous, and probably evolved from above-ground taxa or epiphytobionts similar to the diplopods depicted in Figure 9. According to Kime and Golovatch (2000), only a few modifications in body- and leg anatomy, such as specialized legs for climbing, are necessary for stratobionts to become epiphytobionts or xylobionts.

Similar tunnels as described here from the localities Plötz and Piesberg have also been described in gymnosperms, pteridophyte and lycopsid stems (e.g., Geinitz, 1855; Linck, 1949; Häntzschel, 1975; Rößler and Fiedler, 1996; Naugolnykh and Ponomarenko, 2010; D'Rozario *et al*., 2011) and were attributed to insects, beetles or millipedes (see Appendix Table 2). Among them, the borings of type 2 depicted by Rößler and Fiedler (1996, figs 4, 5) most resemble with respect to their size, shape and longitudinal orientation the boring casts described here. In particular, the longitudinal orientation might reflect a specialised feeding behaviour, according to which the arthropods predominantly eroded tunnels parallel to the fibres of the tissue, which was likely to have been mechanically easier than in transverse direction. This is also consistent with the observations of Rößler and Fiedler (1996), who suggested that the borers preferred the non-resistant outer cortex of the stem and avoided entering the solid xylem. Similar feeding strategies to avoid structurally more resistant vascular tissue have also been observed from the possible diplopod borings in the pith cavity and the parenchyma of the tree fern *Psaronius* described by D'Rozario *et al*. (2011), Rothwell and Scott (1983) and Scott and Taylor (1983), and the possible millipede borings described by Wei *et al*. (2019). This suggests that Palaeozoic wood-boring millipedes probably also preferred less-resistant tissue such as pith, parenchyma, or the outer cortex of stems, but if necessary were also able to penetrate solid xylem.

By contrast, the putative beetle borings described by Linck (1949) pierced solid wood without discernible privileged direction. The beetle borings described by Naugolnykh and Ponomarenko (2010) also penetrated solid wood but predominantly run parallel to the longitudinal wood fibres. Other early beetle borings were remarkably complex and consisted of an entry tunnel, a mother gallery, lateral niches and larval tunnels and were built in several plant tissues of different hardness (Feng *et al.,* 2017, 2019). This suggests that early beetles did not show any preference for a special stem tissue and possessed sharp mouthparts that enabled them to bore in all stem tissues, including solid wood.

In summary, it can be concluded that the morphology of the tunnel system, as well as the feeding strategy of the borers in the stems from Plötz and Piesberg, indicate xylophagous millipedes as possible producers. We, therefore, tentatively attribute the borings described here to this clade. This is also supported by the large coprolites in the stem from Plötz, which fall into the size class of myriapod coprolites. In contrast, the smaller class of coprolites in the specimen MAS Pal 1667 were either produced by juveniles of the same species or, more likely, by oribatid mites that subsequently visited the borings.

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Appendix Table 1

Occurrence of small borings in stems from the Carboniferous to Triassic, mostly attributed to oribatid mites and, in some cases, filled with small-sized coprolites with diameters up to 120 µm; class 3 according to Scott and Taylor (1983), class 1 after Goth and Wilde (1992).

Stratigraphy	**Type of borings**	**Possible producer**	**Boring diameter in mm**	**Coprolite diameter in mm**	**Host plant**	**Tissue**	**Localities**	**References**
Early Carboniferous, Mississippian	Borings	Oribatid mites	Unknown	unknown	Pteridosperm	Wood	Esnost, near Autun, France	Rex (1986), Rex and Galtier (1986)
Early Carboniferous, Mississippian	Borings	Unknown	≈ 0.03	–	Gymnosperm	Wood	East Kirkton, Scotland	Chaloner *et al.* (1991)
Early Carboniferous, Mississippian	Coprolite-bearing borings	Probably oribatid mites	0.08 – 0.16	≈ 0.05	Lycopod axis	Unknown	Pettycur Limestone, Pettycur, Fife, Scotland	Chaloner *et al.* (1991)
Early Carboniferous, Upper Mississippian	Coprolite-bearing borings	Unknown insect	0.375	0.072–0.135 x 0.054–0.105	Lyginopterid seed fern *Trivena arkansana*	Pith, secondary xylem, phloem, and cortex	Fayetteville Formation of Arkansas, U.S.A.	Dunn *et al.* (2003)
Middle Pennsylvanian (late Bolsovian–early Asturian)	Coprolite-bearing tunnels and galleries	Oribatid mites	0.12–0.41	0.015–0.097	Marattialean tree ferns (*Psaronius*)	Rootlet lumens and adjacent tissues of Psaronius root mantle	Pennant Sandstone Formation near Bristol and Caerphilly, southern U.K.	Falcon-Lang *et al.* (2015)
Middle Pennsylvanian (late Bolsovian–early Asturian)	Coprolite-bearing tunnels and galleries	Oribatid mites	0.058–0.454	0.014–0.130	Cordaitalean trunks	Pith, xylem	Pennant Sandstone Formation near Bristol and Caerphilly, southern U.K.	Falcon-Lang *et al.* (2015)
Pennsylvanian	Borings	Oribatid mites	ca. 1	0.05–0.10	All plant groups	All tissues	several Midcontinent and Appalachian localities, U.S.A.	Labandeira *et al.* (1997)
Early–middle Pennsylvanian	Coprolite-bearing borings	Unknown arthropod	0.3–0.6	< 0.075	Cordaitalean stems (*Premnoxylon*)	xXlem	Hance Formation at the base of the Breathitt Group, Cranks Creek, southeastern Kentucky, U.S.A.	Cichan and Taylor (1982), Scott and Taylor (1983)
Middle Pennsylvanian (Westphalian D)	Coprolite-bearing borings	Oribatid mites	≈ 0.1	< 0.01	*Sphenophyllum* stem,	Between adaxial secondary xylem and abaxial outer cortical tissues	Illinois, U.S.A.	Labandeira and Beall (1990)
Middle Pennsylvanian (Westphalian D)	Coprolite-bearing borings	Unknown arthropod	0.3–0.4	≈ 0.01	Cordaitalean stems	Xylem	Illinois, U.S.A.	Labandeira and Beall (1990)

Late Pennsylvanian, (Moscovian)	Damage in the pith cavity, probably DT284	Oribatid mites	Unknown	–	Calamite stem	Pith cavity	United Kingdom	Seward (1898), Stopes (1907)
Late Pennsylvanian (Gzhelian)	Galleries and tunnels (DT284)	Beetles (Archostemata)	Galleries: 2 x 0.12 tunnels: 0.020	–	Calamite stem	Subcortex or fungal-laden wood	Texas, U.S.A.	Xu *et al.* (2018)
Late Pennsylvanian––early Permian	Coprolite-bearing borings	Probably oribatid mites	< 1	0.01–0.10	cordaitalean stems (*Cuyoxylon*)	Xylem, parenchym	San Ignazio Formation, Southern Anden, San Juan Province, Argentina	Césari *et al.* (2012)
Late Carboniferous––early Permian	Coprolite-bearing galleries	Oribatid mites	Irregular	< 0.1	Unidentified wood	Secondary xylem	San Ignacio Formation, Frontal Cordillera, Argentina	Méndez-Bedia *et al.* (2020)
Early Permian	Coprolite-bearing galleries	Unknown arthropods	Different sizes	0.054–0.073	*Psaronius* (pteridophyta) and associated epiphytes (*Callistophyton*, *Ankyropteris brongniartii*)	Bark, phloem and root mantles	„Petrified Forest" of Chemnitz, Germany	Rößler (2000, 2001)
Early Permian	Coprolite-bearing galleries	Unknown arthropods	Different sizes	0.030–0.042	*Psaronius* (pteridophyta) and associated epiphytes (*Callistophyton*, *Ankyropteris brongniartii*)	Bark, phloem and root mantles	„Petrified Forest" of Chemnitz, Germany	Rößler (2000, 2001)
Late Permian	Coprolite-bearing galleries	Oribatid mites	Variable	0.026–0.128	Gymnospermous wood	Pith and xylem	Tarlong valley, southern Bogda Mountains, Xinjiang Uygur Autonomous Region, northwestern China	Wan *et al.* (2016)
Early Permian	Tunnels	Oribatid mites	0.1	0.018–0.038	pteridosperm (*Myeloxylon*)	Vascular bundle of a petiole	Taiyuan Formation, China	Seyfullah *et al.* (2009)
Early Permian	Coprolites in and around glandular cavities	Unknown	–	0.028–0.035 x 0.017–0.024	Pteridosperm (*Callospermarion undulatum*)	Secretory cavities	Shanxi Province, northern China, and Taiyuan Formation, China	Hilton *et al.* (2002)
Early Permian	Coprolite-bearing borings	Oribatid mites	0.11–0.53	0.023–0.064 x 0.019–0.055	Gymnospermous wood	Secondary xylem	Crock village, Manebach Formation, Thuringia State, Germany	Rößler *et al.* (2014), Feng *et al.* (2015a)
Early Permian, Rotliegend Cisuralian	Coprolite-bearing borings	Oribatid mites or springtails	Unknown	0.020–0.030	Cordaitalean stems	Xylem	Wetterau, Germany	Goth and Wilde (1992)

Stratigraphy	Type of borings	Possible producer	Boring diameter in mm	Coprolite diameter in mm	Host plant	Tissue	Localities	References
Middle Permian, Guadalupian	Irregular cavities	Unknown arthropod	Irregular	0.020–0.050	Coniferous wood (*Plyophyllioxylon hulstaiense*)	Pith chamber	Lower Shihhotse Formation of the Hulstai coalfield, Inner Mongolia Autonomous Region of northern China	Feng *et al*. (2012)
Middle Permian	Galleries and chambers	Oribatid mites	< 1	Typ 1: 0.120 x 0.115 Typ 2: 0.150 x 0.125	Pteridosperms, *Vertebraria* roots, *Australoxylon wood*	Parenchyma of roots, secondary wood	Bainmedart Coal Measures, Prince Charles Mountains, Antarctica	Slater *et al*. (2012), Slater (2013)
Late Permian, Lopingian	Cavities in pith	Oribatid mites	Irregular	0.030–0.050	Gymnosperm wood (*Ningxiaites specialis*)	Pith and adjacent xylem	Sunjiagou Formation in the Shitanjing coalfield, Ningxia Hui Autonomous Region, China	Feng (2012)
Late Permian, Changhsingian––Arstinskian/ Kungurian	Coprolite-bearing borings	Oribatid mites	0.2–3.0	0.020–0.065	Coniferophyte and ginkgophyte stems	Secondary xylem	Northern Helan Mountains, inner Mongolia (Nei Mongol), Ningxia Huizu Autonomous Regions, China	Feng *et al*. (2010)
Late Permian, Arstinskian/ Kungurian	Coprolite-bearing borings	Oribatid mites	0.2–3.0	0.0375–0.070 × 0.055–0.145	Coniferophyte and ginkgophyte stems	Secondary xylem	Northern Helan Mountains, inner Mongolia (Nei Mongol), Ningxia Huizu Autonomous Regions, China	Feng *et al*. (2010b)
Late Permian	Coprolite bearing galleries	Probably beetles	Irregular	0.015–0.090	Glossopteridalean stem and root wood (*Australoxylon* sp.)	Xylem	Skaar Ridge, Antarctica	Harper *et al*. (2017)
Latest Permian	Coprolite-bearing borings	Oribatid mites	Variable	0.02–0.03	Conifer wood (*Ningxiaites shitanjingensis*)	Pith	Sunjiagou Formation of Northwest China	Wei *et al*. (2019)
Late Permian-Early Triassic	Coprolite-bearing borings	Oribatid mites	Highly variable between 0.35–1.0	0.060–0.115	Unidentified wood	Different tissues	Central Transantarctic Mountains, Antarctica	Kellog and Taylor (2004)
Late Triassic, Carnian	Coprolite-bearing borings	Oribatid mites	< 3	0.04–0.05 x 0.08–0.100	Pteridophyta (*Itopsidema vancleaveii)*	Parenchyma	Petrified Forest, Chinle Formation, Arizona, U.S.A.	Ash (2000)
Late Triassic, Carnian	Coprolite-bearing cavities in roots	Oribatid mites	< 0.6	0.008–0.080 x 0.008–0.205	Bennettitalean roots	Roots	De Geerdalen Formation on Hopen Island, Svalbard Archipelago, Arctic	Strullu-Derrien *et al*. (2012)

Appendix Table 2

Occurrence of medium-sized borings in stems from the Carboniferous to Triassic, sometimes filled with coprolites in the range between 120 μm – 1 mm; class 2 according to Scott and Taylor (1983) and Goth and Wilde (1992).

Stratigraphy	**Type of borings**	**Possible producer**	**Boring diameter in mm**	**Coprolite diameter in mm**	**Host plant**	**Tissue**	**Localities**	**References**
Middle Pennsylvanian (late Bolsovian–early Asturian)	Irregular structure	Herbivorous insects	Irregular cavity	0.3–0.7	Cordaitalean leafy branches	Cambium, secondary xylem	Pennant Sandstone Formation near Bristol and Caerphilly, southern U. K.	Falcon-Lang *et al.* (2015)
Late Pennsylvanian	Coprolite-bearing borings	Probably millipeds	Unknown	0.4	Tree fern (*Psaronius*)	Parenchyma	Appalachian Basin, U.S.A.	Rothwell and Scott (1983), Scott and Taylor (1983)
Late Carboniferous– –Late Permian	System consisting of entry tunnel, mother gallery, lateral niches and larval tunnels	Beetles (*Pectichnus multicylindricus* igen. et isp. nov.)	Tunnels and chambers of different sizes	Four classes: I: < 0.050 II: > 0.050 III: < 0.150 IV: < 0.542 × 0.958	Conifer wood	Bark, cambium, secondary xylem	Manebach and Winnweiler, Germany; Shitanjing Coalfield, Ningxia Huizu Autonomous Region, Northwest China; Paczkov-Pilce, Poland; Sestajovice, Czech Republic	Feng *et al.* (2017, 2019)
Late Permian	Boring in pith	Insects or diplopods	Irregular	0.944 × 1.190– –1.065 × 1.120	Tree fern (*Psaronius*)	Predominantly pith and adjacent xylem	Yunnan Province, southwest China	D'Rozario *et al.* (2011)
Late Permian	Borings	Beetles	≈ 0.2–0.3	≈ 0.05	*Australoxylon*	Wood	Bainmedart Coal Measures, northern Prince Charles Mountains, East Antarctica	Weaver *et al.* (1997)
Late Triassic	Borings	Beetles	1–1.5	Unknown	Conifer wood	Xylem	Keuper of Streufdorf, Thuringia, Germany	Linck (1949), Hantzschel (1975)

Appendix Table 3

Occurrence of large borings in stems from the Carboniferous to Triassic, sometimes filled with coprolites with diameters larger than 1 mm; class 1 according to Scott and Taylor (1983) and class 3 after Goth and Wilde (1992).

Stratigraphy	Type of borings	Possible producer	Boring diameter in mm	Coprolite diameter in mm	Host plant	Tissue	Localities	References
Early Carboniferous, Mississippian	?	Unknown arthropods	?	20–26	?	?	Loch Humphrey Burn in the Kilpatrick Hills, Strathclyde, U. K.	Scott (1977)
Early Carboniferous, Mississippian	?	Unknown arthropods	?	≈ 5	?	?	Glenarbuck in the Kilpatrick Hills, Strathclyde, U. K.	Scott (1977)
Carboniferous?	Damaged petiole	Unknown arthropod	ca. 5	–	Pteridosperm rhachis (*Myeloxylon*)	Petiole, vascular bundles	Moorside, Oldham, U. K.	Holden (1910)
Pennsylvanian	Coprolite-bearing borings	Unknown arthropod	Unknown	Unknown	Pteridosperm *(Johnhallia lacunosa)*	Parenchyma	Indiana, U.S.A.	Stidd and Phillips (1982)
Middle Pennsylvanian	Stem borings (*Pteridiscaphichnos*)	Possible cockroach	60–130 (galleries) 4–6 (tunnels)	1 x 3	Marattialean tree fern (*Psaronius*)	Parenchyma	Illinois, U.S.A.	Labandeira and Phillipps (2002)
Late Pennsylvanian	Stem borings	Unknown	≈5 x 10	–	Medullosan seed fern	Parenchyma (stem)	Illinois, U.S.A.	Labandeira *et al.* (1998)
Late Pennsylvanian	Root borings	Unknown	≈3 x 5	–	Marattialean tree fern (*Psaronius*)	Parenchyma (roots)	Illinois, U.S.A.	Labandeira *et al.* (1998), Labandeira (2013)
Late Pennsylvanian	Borings	Unknown arthropod	1–3	–	*Sigillaria*	Outer tissue	Saxony, Germany	Geinitz (1855)
Late Pennsylvanian	Coprolite-bearing borings	Unknown arthropod	1–1.3	1.0–2.7 x 1.8–4.0	Pteridosperm	Parenchyma	Calhoun and Friendsville coals of southeastern Illinois, U.S.A.	Lesnikowska (1990)
Late Pennsylvanian (Westphalian D)	Coprolite-bearing borings	Unknown arthropod	≈ 10	3 x 1	Pteridosperm (*Psaronius*)	Between ground tissue and sclerenchyma	Illinois, U.S.A.	Labandeira and Beall (1990)

Stratigraphy	Type of borings	Possible producer	Boring diameter in mm	Coprolite diameter in mm	Host plant	Tissue	Localities	References
Late Pennsylvanian (Westphalian B)	?	Unknown arthropods	?	< 3 x 1	?	?	Middle Coal Measures of Swillington, near Leeds, West Yorkshire, United Kingdom	Scott (1977)
Early Permian	Irregular system of borings (typ 1)	Unknown arthropod	4–13	–	Gymnosperm wood (*Agathoxylon* sp.)	Tissues under bark	„Petrified Forest" of Chemnitz, Germany	Rößler and Fiedler (1996)
Early Permian	Straight borings (typ 2)	Unknown arthropod	4–10	–	Gymnosperm wood (*Dadoxylon* sp.)	Tissues under bark	„Petrified Forest" of Chemnitz, Germany	Rößler and Fiedler (1996)
Early Permian	Coprolite-bearing pith cavity	Probably myriapod	ca. 20 (diameter of the pith cavity)	1.4–2.8 × 2.0–5.8	Calamite (*Arthropitys bistriata*)	Pith and xylem	„Petrified Forest" of Chemnitz, Germany	Rößler *et al.* (2012a, b)
Permian	Irregular cavities	Unknown arthropod	Irregular	Up to 3	Calamitalean stems (*Arthropitys*)	Pith and xylem	Filadélfia and Araguaína cities, State of Tocantins, Parnaíba Basin, central-north Brazil	Rößler (2006), Neregato *et al*. (2017), Rößler *et al*. (2020)
Permian	Circular holes	Unknown arthropod	13–20	?	Seed fern stem and roots	Pith	Fossil Forest of Northern Tocantins, Parnaíba Basin, central-north Brazil	Rößler *et al*. (2020)
Permian	Borings	Unknown	Unknown	Unknown	Conifer wood	Xylem	Lázně Bělohrad, Krkonoše Piedmont Basin, Czech Republic	Frič (1912), Mencl *et al.* (2013)
Middle Permian, Kazanian	Shafts and tunnels	Possible beetle larvae (Coleoptera, ?Permocupedidae)	2.8	–	Conifer wood	Xylem	Tikhie Gory, Tatarstan, right bank of the Kama River, Russia	Naugolnykh and Ponomarenko (2010)
Late Permian	Borings	Beetles, oribatid mites	–	–	*Dadoxylon*	Wood	Karroo, South Africa	Zavada and Mentis (1992)

Stratigraphy	Type of borings	Possible producer	Boring diameter in mm	Coprolite diameter in mm	Host plant	Tissue	Localities	References
Late Permian	Coprolite-bearing borings	Probably millipedes and mites	Variable	2 classes: 0.110–0.146 × 0.178–0.247 and 0.08–0.100 × 0.112–0.147	Conifer (*Ningxiaites shitanjingensis*)	Pith	Sunjiagou Formation of Northwest China	Wei *et al*. (2019)
Late Triassic	Borings	Beetles?	< 1	–	Conifer wood (*Araucarioxylon arizonicum*)	Bark and xylem	Petrified Forest, Chinle Formation, Arizona, U.S.A.	Ash and Savidge (2004)
Late Triassic, Carnian	Possible larval or pupation chambers of wood-boring beetles	Holometa-bolous insects, beetles?	8–2 x 20–6	–	Conifer wood (*Araucarioxylon arizonicum*)	Bark and xylem	Petrified Forest, Chinle Formation, Arizona, U.S.A.	Hasiotis *et al*. (1998), Lucas *et al*. (2010), Tapanila and Roberts (2012)
Late Triassic	Coprolite-bearing borings	Beetles?	2–10	Unknown	Conifer wood	Xylem	Petrified Forest, Chinle Formation, Arizona, U.S.A.	Walker (1938), Häntzschel (1975)