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Research paper

The largest calamite and its growth architecture – *Arthropitys bistrata* from the Early Permian Petrified Forest of ChemnitzRonny Rößler^{a,*}, Zhuo Feng^{a,b}, Robert Noll^c^a *DAStietz, Museum für Naturkunde, Moritzstraße 20, D-09111 Chemnitz, Germany*^b *Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming 650091, PR China*^c *In den Birkengärten 30, D-67311 Tiefenthal, Germany*

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ABSTRACT

The largest petrified calamite is reported from the Early Permian fossil forest of Chemnitz, Germany. For the first time a sizable specimen of *Arthropitys bistrata* permits insights into both the internal anatomical structure and the spatial architecture of the complex branching system. The arboreal woody plant is characterized by a height of more than 10 m and at least three orders of axes which formed a large crown. Ontogenetic analyses of the main stem and the various branches of the plant demonstrate that most of the morphological and anatomical features that have been previously recognized as important inter-specific distinctions exhibit a considerable variability. Spheroid to elongate ovoid coprolites have been recognized in the pith cavity of one woody branch ranging from 1.4–2.8 × 2–5.8 mm in diameter. Semi- or undigested fragments of tracheids in the coprolites are identical with those of the parent plant and indicate their histologically pristine nature. According to the coprolite size and fossil records of detritivorous animals, we tentatively suggest that these coprolites were produced by specialized ancient myriapods. Growth rings are densely developed in the peripheral portion of the trunk in particular. As well as climatic cyclicality, they suggest that volcanism-induced environment turbulences become more serious and frequent, and finally buried the whole ecosystem *in situ*.

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1. Introduction

Arboreal sphenopsids were not only major constituents of Pennsylvanian and Permian wetland ecosystems, but during that time they also attained their maximum diversity. Along with various ferns, lycophytes and pteridosperms calamite remains dominate a large number of fossil plant assemblages in both sedimentary and volcanic environments (Barthel, 2004; Martín-Closas and Galtier, 2005; Wang et al., 2006; Kerp et al., 2007; DiMichele et al., 2009; Opluštil et al., 2009). They are typically characterized by underground rhizome systems and aerial upright stems. Vegetative axes include a central pith or cavity and can show considerable secondary growth especially during the Permian (Rößler and Noll, 2006). The upright axes produced whorls of leafy twigs at the nodes. However, several plants additionally possessed side branches diversifying their architecture (Hirmer, 1927; Boureau, 1964). As is already known from a number of historical accounts, their rhizomatous and upright axes exhibit a regular construction with distinct nodes and internodes and have similar cauline tissues (e.g. Williamson and Scott, 1884). However, developmental changes in calamitaleans were for many years underestimated, until Eggert (1962) provided a detailed investigation of the ontogeny of

Pennsylvanian arborescent Sphenopsida. Whereas studies on petrified calamitean trunks and their internal anatomy can be traced back nearly two centuries (Cotta, 1832), detailed examinations providing crucial knowledge of both anatomical and branching variation remained rare, like the post-Carboniferous record in general. Recently, based on finds from the Early Permian of Chemnitz sizable tree trunks have been investigated and resulted in much additional data (Rößler and Noll, 2006, 2007, 2010). Advances in the study of these younger forms demonstrated major peculiarities as compared to most other fossil calamites, and drew into question their detailed growth strategy, which remains unsatisfactorily understood.

With this contribution we continue the revision of Permian calamitaleans from their type locality Chemnitz. During excavations at this site, an increasing number of well-preserved specimens have been discovered (Rößler et al., accepted for publication). One of the most spectacular tree trunks recovered in 2008 was a more than 10 m long, richly branched calamite capable of providing more sophisticated information about the growth architecture of the genotype *Arthropitys bistrata*.

This species was established based on material originally described by Cotta (1832) as *Calamitea bistrata*. In the original description by Cotta (1832, p. 69), the type species was characterized as “showing alternating broad radial striations composed of a lot of fine striations and separated by narrow striations of different structures.” Because

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of major anatomical differences in comparison to *Calamitea striata*, Goeppert (1864) created *Arthropitys* to accommodate Cotta's species *bistriata*. On the basis of the analysis of new finds and a reassessment of existing collection material from the Permian of Chemnitz, Rößler and Noll (2010) emended *A. bistriata* and provided more detailed information about this plant including the variation in its internal anatomy. However, the multiple woody branch architecture from sizable calamitean trunks has never been documented in previous reports.

2. Materials and methods

The giant several times branched calamite tree was collected from the Early Permian volcanoclastics of the Zeisigwald tuff horizon, Petrified Forest of Chemnitz, Germany. It was found in parautochthonous position to its place of growth cut down and buried by deposits of a pyroclastic density current dated at 290.6 ± 1.8 million years ago (K.-P. Stanek, pers. comm., 2009). According to the palynostratigraphic results of Döring et al. (1999), the stratigraphic position of this fossil lagerstätte corresponds to the Upper Asselian/Lower Sakmarian boundary. Stratigraphic, geological and taphonomic details have been elucidated by Kretzschmar et al. (2008) and Rößler et al. (accepted for publication). It is worth mentioning that it is not only the different preservation types of fossil plants ranging from moulds or casts to anatomically preserved petrifications, but also fossil animals which are diverse and well preserved at this site (Rößler et al., accepted for publication). Thus, the Chemnitz fossil lagerstätte provides the most complete fossil forest ecosystem from the Permian known to date.

We discovered and collected more than 10 m of the main trunk (Fig. 1, Pl. I, 1) and its branches from the pyroclastics during field excavation. However, from the discovery situation we would predict

another 1–2 m distal and at least 2 m basal portions of the original plant, that have not been traced. Although in close proximity are several basal calamitean trunks of the same species still standing upright and rooting in the underlying palaeosol, we cannot provide final evidence which of them belongs to our large *A. bistriata* specimen.

In order to investigate the morphological and internal structure of the fossil tree in detail, we used a sand blaster to clear the stem's surface. The specimen was subsequently cut with a trimming saw to reveal both transverse and longitudinal (radial and tangential) sections. These surfaces were ground and polished and examined using reflected light microscopy.

Sections were photographed under reflected light using Nikon Eclipse ME 600 and Nikon SMZ 1500 microscopes attached to a Nikon DS-5M-L1 digital camera. Large overview photographs were made by using a Nikon D300 with the lens AF-S Micro Nikkor 105 mm 1:2.8 G, and Epson Perfection V330 scanner. Composite images were created using Adobe Photoshop CS v. 8.0, and corrected only for contrast and colour.

The trunk and its diverse branches are stored at the Museum für Naturkunde Chemnitz labelled KH0052, KH0054, KH0057, KH0058 and KH0072.

3. Systematic palaeontology

CLASS Sphenopsida
ORDER Equisetales
FAMILY Calamitaceae

GENUS *Arthropitys* Goeppert, 1864

Type species: *A. bistriata* (Goeppert, 1864) nov. emend.

Type locality: The city of Chemnitz, Germany.

Type stratum: The Early Permian Zeisigwald Tuff Horizon (Leukersdorf Formation).

SPECIES *Arthropitys bistriata* (Cotta, 1832) Goeppert, 1864, nov. emend. Rößler, Feng and Noll (Figs. 1–2; Plates I–VI)

Original diagnosis: in Cotta (1832, p. 69).

Emended diagnosis: Arborescent articulate woody plant characterized by at least three orders of woody axes, and whorls of leafy twigs regularly occurring at every 5th to 9th (rarely to 18th) node. Stems possess a circular central pith/cavity, primary and secondary vascular tissues. Parenchymatous pith is composed of circular to polygonal cells in perimedullary zone and diaphragms in nodal region. Internode length varies from 9.5 to 30 mm.

Primary xylem strands consist of circular carinal canals surrounded by metaxylem. Metaxylem elements are variable in diameter from 20 to 90 μm that centrifugally arranged in 2 to 5 layers, the smallest cells are directly connecting with the central carinal canals.

Secondary body is composed of fascicular wedges and interfascicular rays and gradually diminishes distally. Interfascicular rays are continuous between successive nodes, taper distally and are visible through the whole secondary tissue. Fascicular wedges gradually enlarge in width centrifugally, consist of radial files of thick-walled tracheids and narrow thin-walled fascicular rays. In transverse view, interfascicular rays are less than 1 mm wide and are made of 3–7 variable parenchymatous cells having a square to rectangular outline in transverse and radial views, irregular to polygonal outline in tangential view, and usually less high than wide in radial view. Secondary xylem has commonly scalariform secondary wall thickenings and horizontally elongated pits on radial walls. Thickenings are 2–4 μm apart (excluding the pit's width) and are sometimes forked, or very rarely reticulated. Tracheids are up to several millimeters in length. In transverse view, tracheid diameters average 20–100 μm radially and 35–70 μm tangentially. The outer surface is striate reflecting segmentation of the

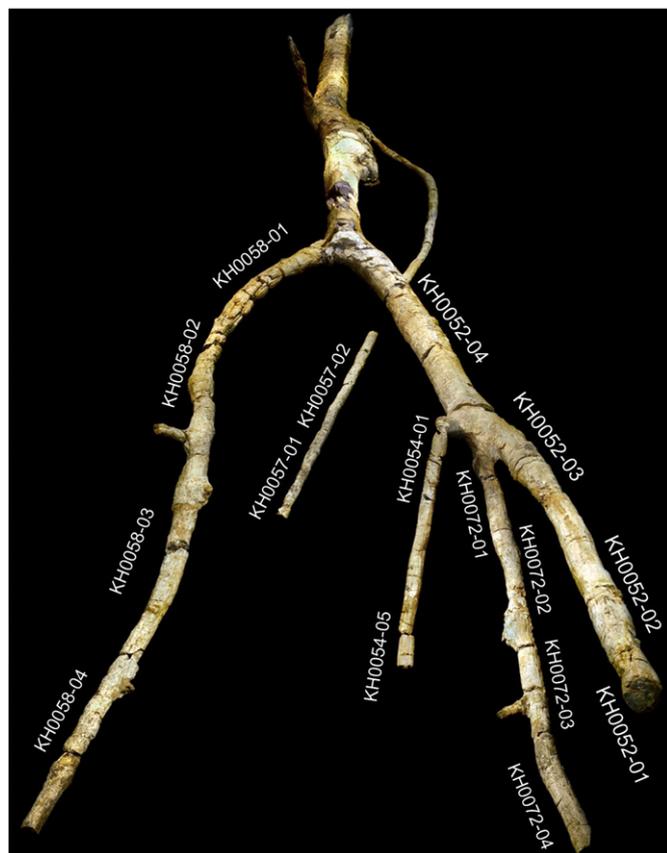


Fig. 1. Distal view of the *Arthropitys bistriata* trunk, showing the spatial architecture of the branches.



Fig. 2. Proposed reconstruction of *Arthropitys bistrata*, scale bar = 1 m, drawing: Frederik Spindler, Freiberg.

secondary body. Nodes are slightly incised with small, acute, millimeter-diameter, vertically enlarged leaf traces at every second or third fascicle.

Leafy twigs depart from whorls of usually 9–16 branches. Nodes between these whorls usually lack leafy twigs. Leafy twigs are 2–6 mm in diameter, lack secondary growth, are slightly enlarged centrifugally, and circular or elliptical in outline with an acute tip.

Several orders of woody branches form a complex branching system, either by successive unequal bifurcations of the main stem or occasionally from inside the wood as adventitious shoots.

Secondary roots of several millimeters to centimeters in diameter depart from the trunk base, show considerable secondary growth and lack carinal canals.

4. Description

4.1. Trunk architecture and branching

The frequently branched *Arthropitys bistrata* trunk is predicted to be not less than 15 m high with at least 3 orders of woody branches (Fig. 1, Plate I, 1). The spatial branching architecture is clearly resolvable in three dimensions (Plate II). In order to better define the branching pattern of the large calamite, we prepared and measured all pieces of the main stem and the branches of the plant.

According to the five prominent nodes of the main trunk, the whole plant can be divided into six portions, namely I, II, III, IV, V and VI in ascending order. Portion I is nearly 3 m long, representing the lowermost part of the find, but a lower middle portion of the original tree. This portion is compressed to an oblate outline with a diameter of 19.5–21 × 11.7–17.5 cm, and average girth of 57 cm. An obviously thin layer (Plate III, 1 and 2) on the surface of both lower and top regions of the stem is interpreted as cortex tissue, but detailed anatomical structure is lacking. Small six- to eight-sided holes of millimeter-size, are densely developed in the outermost tissues and are often filled with kaolinite (Plate IV, 8; Plate VI, 7). They cause a spongy structure at the stem periphery, and along with other evidence, such as fluid escape structures (Rößler et al., accepted for publication), they may have formed due to the influence of high temperature during the deposition of the embedding ignimbrite. The radial ribs and furrows are occasionally presented on the stem's surface of the lower region (Plate III, 3), the length of internodes varies from 1.8 to 3.0 cm. The internal anatomical structure is largely well preserved and shows thick secondary xylem surrounding the central pith.

Portion II is about 1 m in length, the average girth of this part is as the same as that of portion I, but most of the stem in this part is preserved as a cavity; therefore, the central pith and xylem in this portion are equivocal. Portion II is preserved as a severely compressed oblate outline with diameter of 18.5–21 × 13.5–14.5 cm. A narrow layer of cortex tissue is also preserved in portion II, nevertheless the alternating ribs and furrows on the surface of the stem are visible at the basal region.

Portion III is about 1.5 m long, the average girth of this part became smaller than those of the basal two portions reaching approximately 46 cm (diameter 14.5–18 × 12.5–14 cm), with a circular outline. The nodes are clearly presented on the stem's surface in the lower region (Plate III, 4), and the length of internodes varies from 1.7 to 3.0 cm.

Portion IV is nearly 2 m in length, forming a cylinder with an average girth of about 40 cm and a diameter of 11.5–14 × 11.5–12.5 cm. Portion IV is broken into many short pieces.

Portion V is about 2.2 m long, however, only 1.5 m are mounted to the specimen illustrated in Fig. 1 and Plate I, 1. It shows a circular outline and the girth is considerably smaller than in the lower portions, at 26 cm on average, with a diameter of 8.5–9.5 × 7.5–11.5 cm. Cortex

in portion V is not preserved, but the internal anatomical structure is well preserved.

Portion VI is about 0.5 m long, extending beyond the branching area illustrated in Plate I, 2 but does not represent the distal end of the tree. It shows a nearly circular outline and the maximum girth measures 20.5 cm, with a diameter of 6.1–6.7 cm. Cortex is not preserved, but the internal anatomical structure is well preserved (Plate I, 3–5).

The spatial organization of the frequent woody branches is clearly revealed in the distal view of the large calamite (Fig. 1). Between portions I and II, there is the first predominant branching region that occurs at about 2.9 m in height from the base of the preserved trunk. Here four woody branches departed within 0.6 m of the trunk, whereas three of them were not preserved, but left large scars on the trunk's surface (Plate III, 2, arrow indicates a branch scar). One slender branch originating from this region at an angle of 30–35° to the trunk, is preserved at more than 5.1 m in length (Plate I, 1, specimens KH0057-07 to 01). Its girth varies from 15.5 cm at the base up to 9.8 cm at the top, with diameters varying from 4.2×5.1 cm to 2.5×3.3 cm. The internode lengths of this branch vary from 9.5 to 21.5 mm (Plate III, 5, arrows indicate a whorl of leafy twig traces). In the upper portion of this 1st order branch one further lateral branch, a woody branch of 2nd order, departed. Whorled traces of leafy twigs are visible at several nodes (Plate III, 6 and 7), and exhibit oval to sub-circular shapes with variable diameters from 1.3 to 2.8 mm. The number of traces at each whorl is variable ranging from 10 to 14 in the median part (Plate III, 6) up to 16 in the upper part of the slender woody branch (Plate III, 7).

In the lower middle region of the same branch (specimen KH0057-05), large coprolites containing fragments of tracheids are well preserved in the central pith cavity (Plate IV, 1). Coprolites are of elliptical to sub-spherical shape, dimensions of the coprolites vary (1.4–2.8×2–5.8 mm, $n = 104$; Plate IV, 2). The small-sized tracheid fragments within the coprolites show simple scalariform thickenings (Plate IV, 3), indicating their histologically pristine nature and derivation from the parent wood.

The second prominent branching area of the main trunk occurs between portions II and III, at a height of 4.2 m, and is significantly enlarged compared to the internode segments of the trunk. It consists of three major scars of woody branches varying from 5.5 to 6.5 cm in width, although none of the branches themselves have been preserved (Plate IV, 4).

The third prominent branching area of the large trunk is appearing between portions III and IV at 5.7 m height. It is characterised by an apparent bifurcation of the trunk at an angle of 25–30°. The slightly smaller branch (KH0058-01 to 04) is preserved 3.22 m in length, and interpreted as a 1st order branch of the main trunk. The girth of this branch varies from 26 cm at the base to 17 cm at the top, with diameters varying from 6.5×9.5 cm to 5×5.7 cm. This woody branch bears further lateral shoots or 2nd order woody branches (Plate IV, 5). The width of branch scars measures from less than 1 cm (Plate IV, 6 and 7) up to 5 cm (Plate IV, 5).

The next prominent branching area of the trunk is located between portions IV and V, at a height of 7.5 m and is distinguished by a trifurcated branching pattern that results from two closely spaced bifurcations (Fig. 1, Plate II). Two relatively slender branches

are interpreted as 1st order woody branches, both of them departing from the main trunk at an angle of 30–35°. One of them (specimen KH0054-01 to 05) is preserved at 0.8 m in length, with a girth varying from 13.5 to 14.2 cm. There is no indication of further lateral branches recognizable on it. The other woody branch is preserved at 1.4 m in length (specimen KH0072-01 to 04), and possesses several 2nd order lateral branches departing 20, 60 and 90 cm distant from the base of the branch. The girth of the latter varies from 20.5 to 17 cm, with diameter varying from 6.7×6.2 cm to 5.5×5.0 cm. Cortex tissues of both woody branches are not preserved.

The uppermost prominent branching area of the trunk is recognized between portions V and VI, at a height of about 9.7 m and is characterized by a trifurcated branching pattern (Plate I, 2, 6) similar to those present at the height of 7.5 m. Two relatively slender branches result from two closely spaced successive bifurcations of the main axis (Plate I, 6) with angles of 35–40° and 80° and are preserved at length's of 17 cm and at least 13 cm. Their maximum girth's measure 15.5 cm and 16.5 cm. The most distal portion of the main trunk that was possible to excavate from the surrounding rock shows a girth of 20.5 cm. Even at this level woody branch traces indicate further ramification of the trunk (Plate I, 3–5).

4.2. Anatomy of primary and secondary tissues

We prepared 77 polished surfaces in both transverse (39) and longitudinal (38, radial and tangential) orientations to reconstruct the anatomical structure and internal vascular organization, i.e. parenchymatous pith and diaphragms, carinal canals, metaxylem elements, fascicular wedges with files of secondary xylem tracheids and fascicular rays, interfascicular rays, departure and course of branch traces, and finally growth rings recognized at the main trunk and at several of its different order woody branches.

4.2.1. Pith

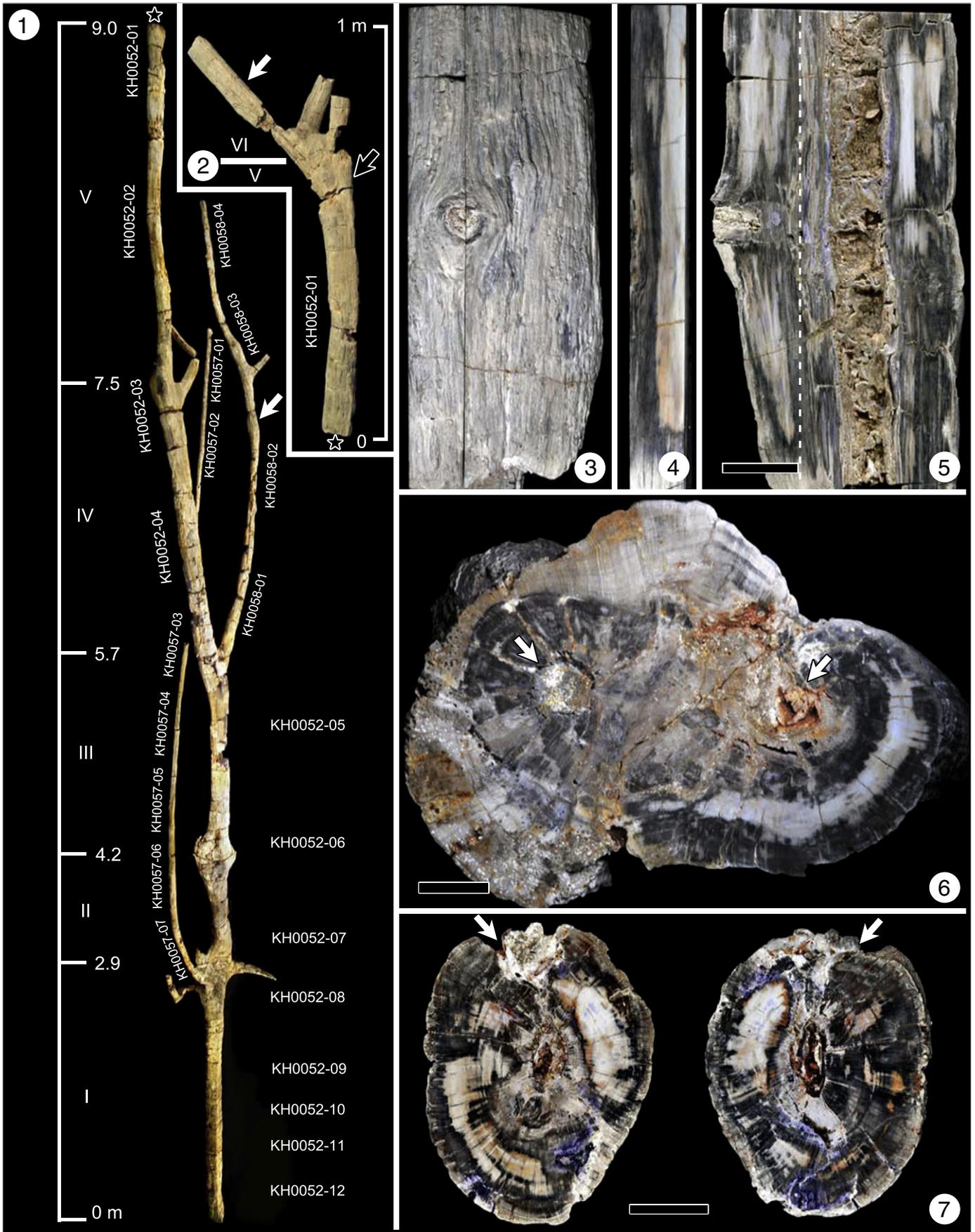
The pith of the main trunk shows an elongate elliptical shape in transverse view, recognizable at the lower (Plate IV, 8), middle and upper portions (Plate IV, 9), grading to a rather triangular shape at the top. The pith diameter varies from 4.4×0.9 cm to 2×0.2 cm, but certainly originally had a circular shape.

In the 1st order branches, the pith is rather circular in outline, and their portion of the branch diameter is much higher than in the main trunk (Plate IV, 10 and 11; Plate V, 1). However, those branches with a thicker xylem cylinder also tend towards an oval elongated pith (Plate V, 2). Pith diameters of the 1st order branches vary from 1.9×1.4 cm to 2.5×1.5 cm.

Parenchymatous diaphragms of the pith are well preserved in these branches, although they are commonly broken and packed into the pith cavity (Plate IV, 11, Plate V, 1 and 3). Diaphragms consist of parenchymatous cells that are crowded and of polygonal to brick-like shape (Plate V, 4), with cell diameters varying from 15 to 140 µm in height and 40 to 90 µm in width. The uppermost and lowermost two or three cell layers are horizontally elongated compared with the vertically elongate form of the middle ones. The distance between successive diaphragms varies, as with the nodes, from 9.5 to 27 mm. It shows the shortest distance close to the occurrence of

Plate I. *Arthropitys bistrata* from the Early Permian Petrified Forest of Chemnitz, Germany.

1. Gross morphology of the trunk. I, II, III, IV, V and VI (see Plate I, 2) indicate the portions of the tree divided by prominent branching nodes.
2. Most distal portion of the trunk continuing the part figured at Plate I, 1 (connection at the star).
3. Outer surface of the most distal stem segment (white arrow in Plate I, 2) showing the branch scar of a 2nd order woody branch, scale bar for Figs. 3–5 = 2 cm.
4. Tangential longitudinal section of the half specimen figured at Plate I, 5 (note the dash line) indicating that there is no visible trace between the pith periphery and the initial woody branch.
5. Radial longitudinal section of the most distal stem segment (white arrow in Plate I, 2) to illustrate a departing 2nd order woody branch.
6. Transverse section of a bifurcating trunk portion (black arrow in Plate I, 2), pith cavities indicated by white arrows, scale bar = 2 cm.
7. Transverse section of a woody branch (white arrow in Plate I, 1) to illustrate a departing 2nd order woody branch, scale bar = 2 cm.



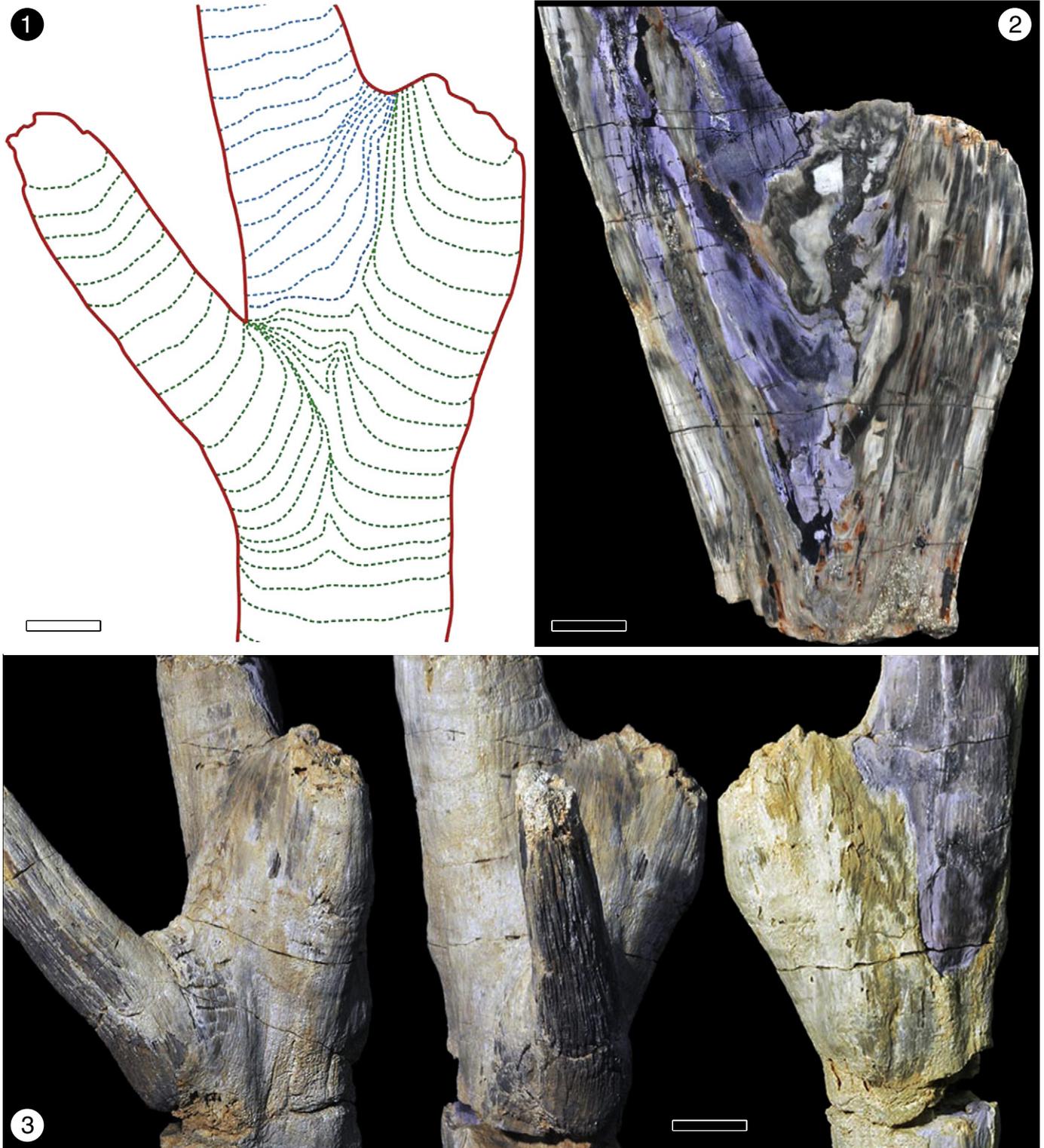


Plate II. *Arthropitys bistrata* from the Early Permian Petrified Forest of Chemnitz, Germany.

1. Reconstruction of the nodal lines in a multiple branched portion of the calamite, scale bar = 4 cm.
2. Radial longitudinal section of the trunk portion illustrated in Plate II, 1 and 3, scale bar = 4 cm.
3. Different aspects of the outer surface of a trunk portion showing successive closely spaced bifurcations, scale bar = 5 cm.

leaf whorls, and then gradually becomes longer reaching their maximum length somewhere in between the whorls.

At the pith periphery, there are several layers of parenchymatous cells in contact to the xylem cylinder (Plate V, 5). Compared with the

square-shaped parenchymatous cells of the inner pith parenchyma the outer pith parenchyma shows remarkable narrow and longitudinally elongated cells when close to the xylem cylinder (Plate V, 6). The cell diameter is 30–80 μm in width and 70–250 μm in height.

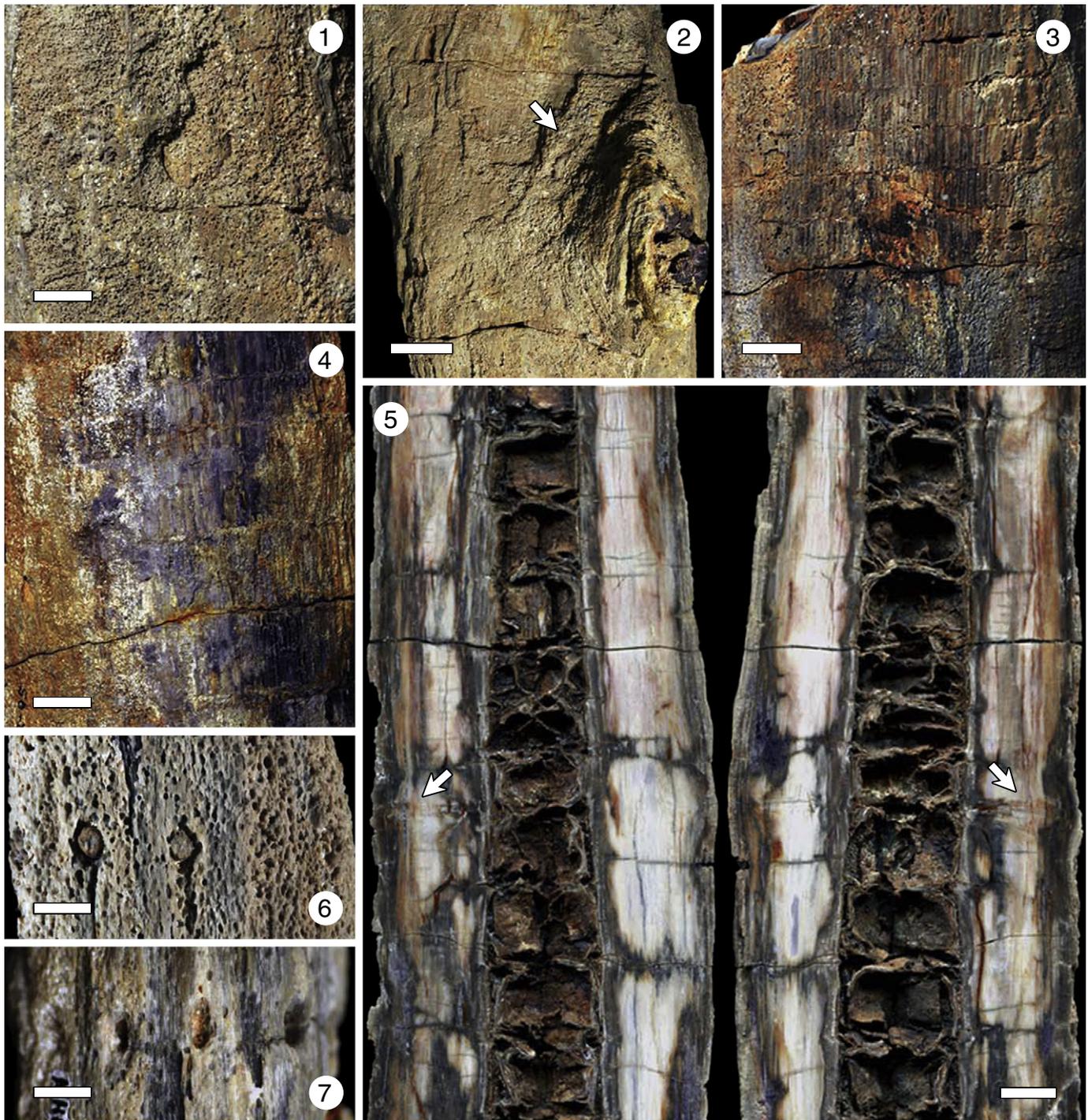


Plate III. *Arthropitys bistrata* from the Early Permian Petrified Forest of Chemnitz, Germany.

1. Cortical tissue in Portion I of the main trunk, note the frequency of pores, scale bar = 2 cm.
2. Cortical tissue becomes much thicker close to the branch (arrow), scale bar = 4 cm.
3. Ribs, furrows and nodal lines present on the surface of Portion I, scale bar = 2.5 cm.
4. Ribs, furrows and nodal lines present on the surface of Portion III, scale bar = 2 cm.
5. Well-preserved diaphragms and pith cavity of a woody branch (KH0057), arrows indicate a whorl with leafy twig traces visible through the whole secondary body, scale bar = 1 cm.
- 6, 7. Branch traces of leafy twigs arranged in whorls on the outer surface of woody branches, scale bars = 6 mm.

4.2.2. Carinal canals and metaxylem

Tissues of the primary vascularisation are situated between the pith parenchyma and the secondary xylem. The protoxylem is usually replaced by carinal canals, but commonly filled with delicate amorphous tyloses (Plate V, 7, arrow). In the examined specimens, carinal

canals are better presented in the main trunk than in the 1st order woody shoots. They show a sub-circular outline in transverse section (Plate V, 7), and diameters vary from 130 to 190 μm .

In transverse view, carinal canals are surrounded by 2 to 5 layers of sub-circular to polygonal shaped metaxylem elements reaching a

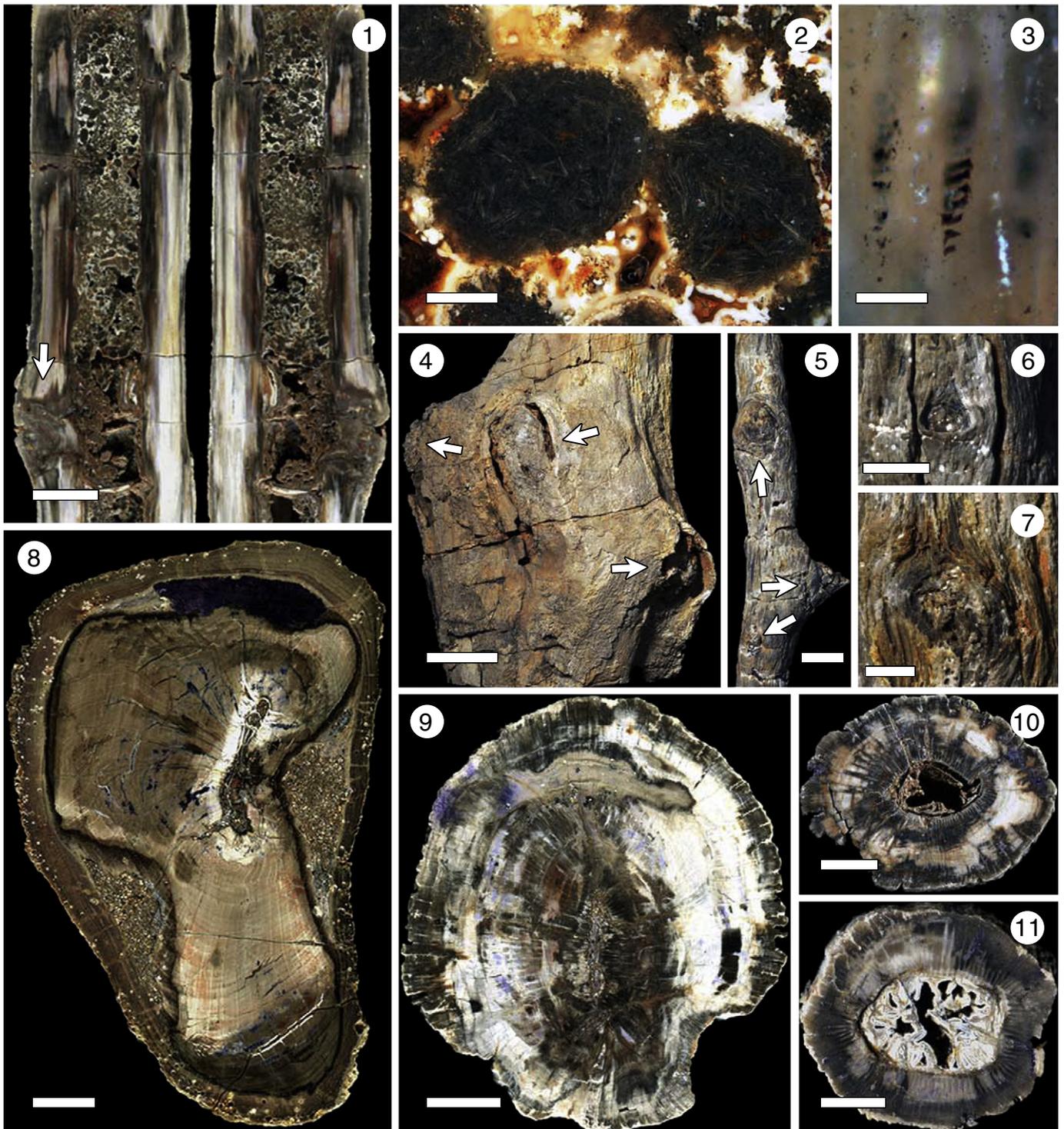


Plate IV. *Arthropitys bistriata* from the Early Permian Petrified Forest of Chemnitz, Germany.

1. Coprolites in the pith cavity of a woody branch (KH0057). Note the pathogenic reaction of the wood around a (?) boring hole probably caused by the coprolite producer (arrow), scale bar = 2 cm.
2. Close-up showing the spheroid coprolites, scale bar = 1 mm.
3. Scalariform thickenings of the tracheid fragments found in the coprolites, scale bar = 35 μ m.
4. Note three big scars (arrows) of woody branches on the lower portion of the main stem, scale bar = 7.5 cm.
5. Scars (arrows) of 2nd order woody branches on a 1st order woody branch, scale bar = 5 cm.
- 6, 7. Close-up to show the scars of 2nd order woody branches, scale bars = 1 cm.
8. Transverse section (TS) of Portion I of the trunk showing elliptical pith and extensive secondary growth, scale bar = 2 cm.
9. TS of Portion V, showing elliptical pith and surrounding wood, scale bar = 1.5 cm.
- 10, 11. TS of woody branches showing large pith cavities, scale bars = 1.5, 1 cm.

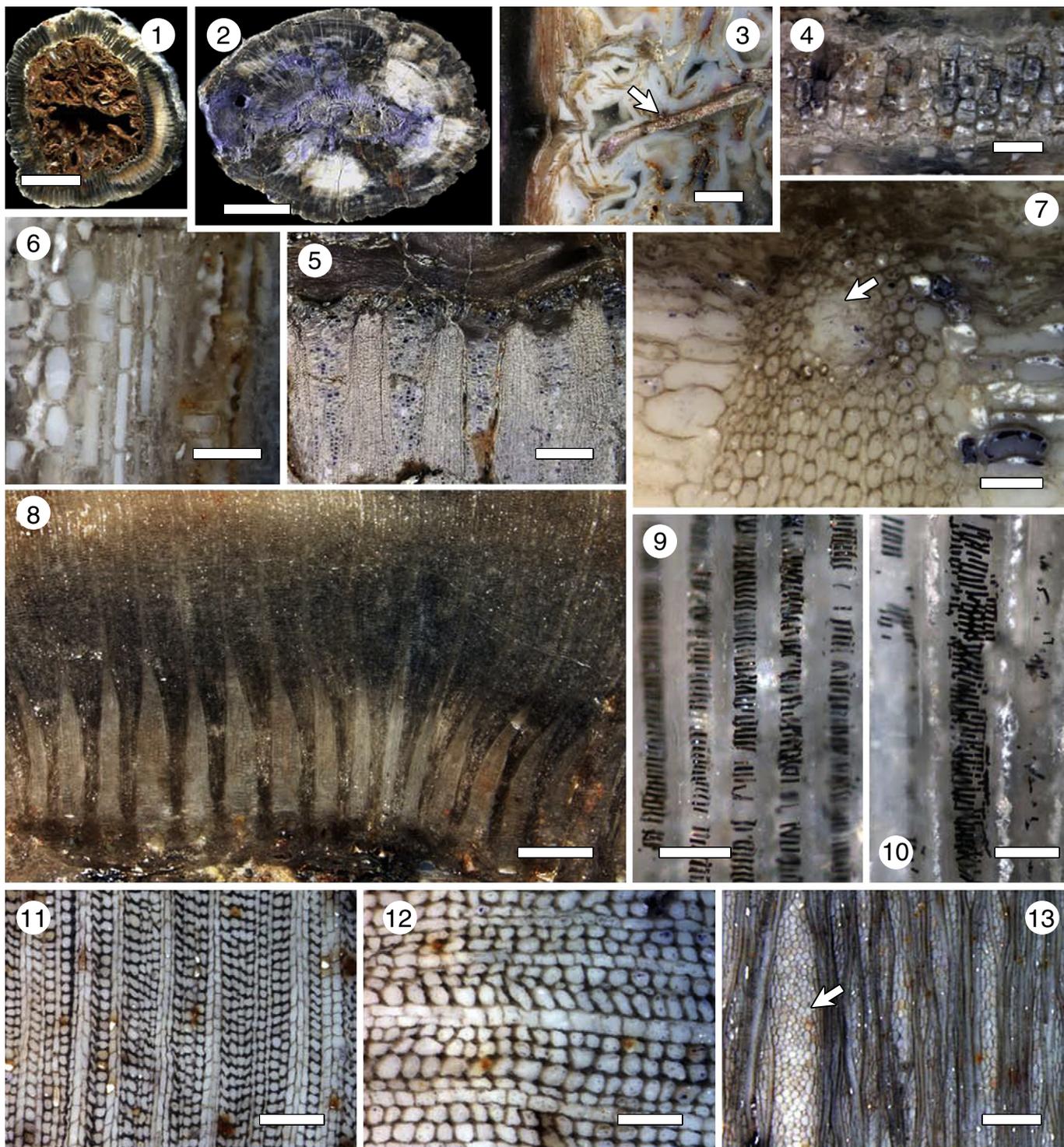


Plate V. *Arthropitys bistriata* from the Early Permian Petrified Forest of Chemnitz, Germany.

1. Transverse section (TS), showing a large pith cavity in the distal portion of a 1st order woody branch, scale bar = 1 cm.
2. TS of 1st order woody branch, note the elliptical pith surrounded by extensive wood, scale bar = 2 cm.
3. Radial longitudinal section (RLS) of pith cavity, note the pith diaphragm (arrow), scale bar = 2 mm.
4. RLS, showing parenchymatous cells of the pith diaphragm, scale bar = 200 μ m.
5. TS, showing pith periphery, fascicles and interfascicular rays, scale bar = 1 mm.
6. RLS, showing the peripheral parenchymatous cells of the pith that become vertically elongated close to the xylem (right side of the image), scale bar = 200 μ m.
7. Close-up to show carinal canal surrounded by several rows of metaxylem elements, note the tyloses (arrow) inside the carinal canal, scale bar = 150 μ m.
8. TS of a 1st order woody branch showing the acute shape of initial fascicular wedges, scale bar = 1.5 mm.
9. RLS, showing the common scalariform thickenings of the secondary xylem tracheids, scale bar = 75 μ m.
10. RLS showing occasionally forked to reticulated thickenings of the tracheid walls, scale bar = 75 μ m.
11. TS, showing tracheids square to sub-circular in shape, scale bar = 400 μ m.
12. TS, close-up showing rows of thick-walled tracheids and thin-walled parenchymatous ray cells, scale bar = 200 μ m.
13. Tangential longitudinal section, showing one multi-seriate interfascicular ray (arrow) and several fascicular rays, scale bar = 500 μ m.

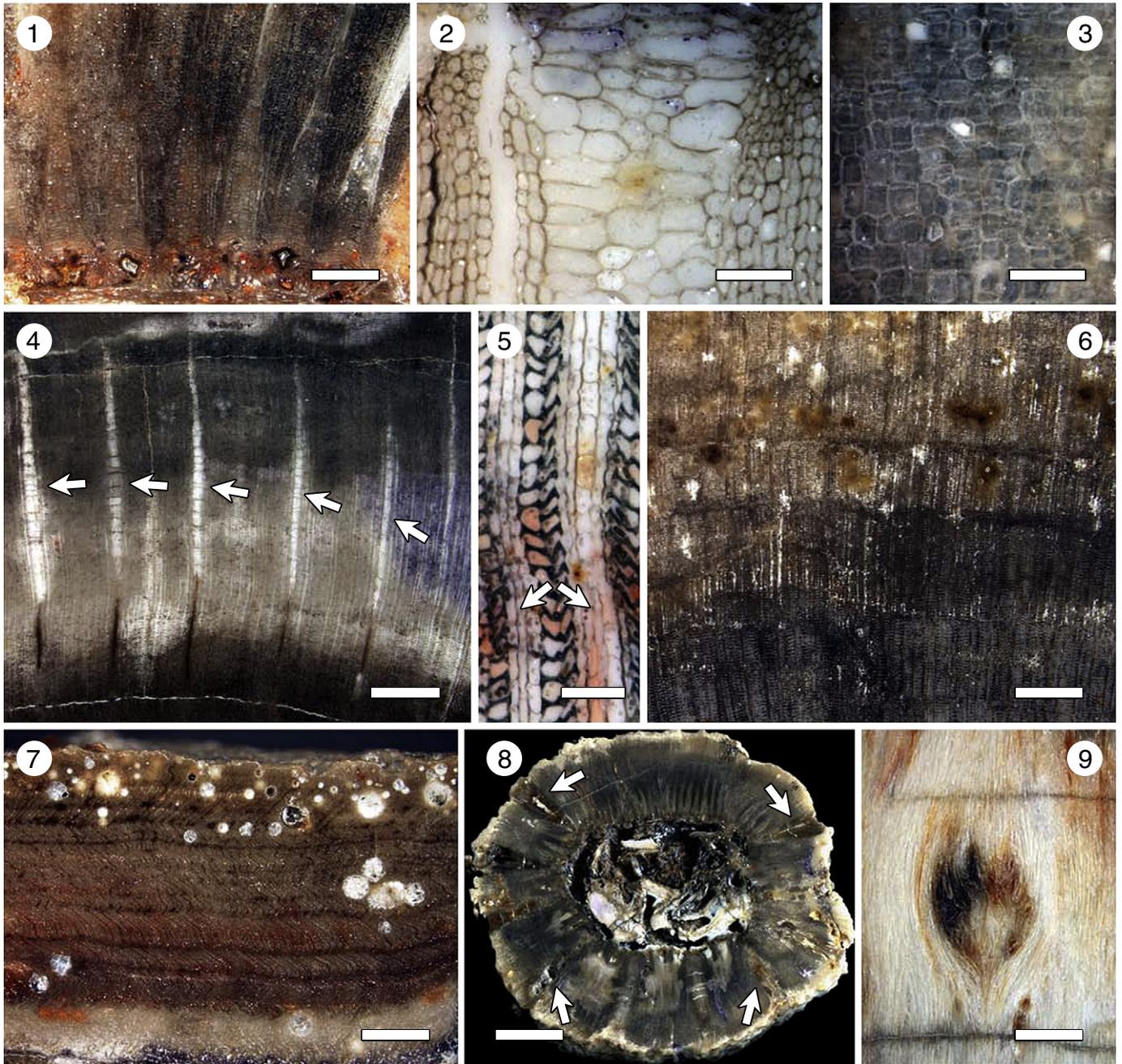


Plate VI. *Arthropitys bistrata* from the Early Permian Petrified Forest of Chemnitz, Germany.

1. Transverse section (TS), showing pith parenchyma (lower margin of the image) directly adjoining to interfascicular rays, scale bar = 1 mm.
2. TS, showing the tangentially elongated cells of an interfascicular ray close to the pith periphery, scale bar = 200 μm .
3. Radial longitudinal section, showing brick-shaped ray cells, scale bar = 200 μm .
4. TS, the interfascicular rays (arrows) become obviously wider in the early wood, scale bar = 2 mm.
5. TS, close-up showing the changes of ray cells in late wood (arrows) and early wood, scale bar = 200 μm .
6. TS, showing distinct growth rings in the outer wood, scale bar = 1.5 mm.
7. TS, growth rings are more densely developed in the wood periphery, scale bar = 2.5 mm.
8. TS, showing a whorl of the leafy twig traces, a few indicated by arrows, scale bar = 7 mm.
9. Tangential longitudinal section showing the vascular bundle of a leafy twig, scale bar = 2.5 mm.

diameter of 20–90 μm (mean = 38 μm , $n = 60$). They are centrifugally arranged, the smallest cells are directly attached to the carinal canal (Plate V, 7). In longitudinal view, they unfortunately did not show any detail of their thickenings.

4.2.3. Fascicular wedges

The secondary body of the calamite is composed of radially arranged fascicular wedges alternating with the parenchymatous interfascicular

rays (Plate V, 8). Fascicular wedges are commonly recognizable from the pith periphery to the trunk's outer surface. Each fascicular segment is composed of numerous radial files of thick-walled tracheids and intermediary fascicular rays.

The number of fascicular wedges surrounding the central pith is variable within the entire plant, both in the main trunk and its woody branches. In general, the number of fascicular segments is small close to the base of the stem or the departure point of the

parent shoot, but increases gradually upwards to reach and persist at a maximum complexity of the stelar construction and finally decreases again close to the top. In the main trunk fascicular strands vary in number from 95 to 102. In the woody branches, the number of fascicular strands changes from 74 to 115.

At the pith's periphery, wood wedges measure 200–300 µm in tangential width and widen rapidly to nearly 1 mm within the first 3 mm, then gradually enlarge towards the extraxylary tissues at the outermost trunk. Each wood wedge consists of less than 10 up to 25 tracheid rows and interspersed fascicular rays.

Secondary xylem tracheids usually show scalariform thickenings and horizontally elongated pits exclusively on their radial walls (Plate V, 9). The distance between adjacent pits vary from 2 to 4 µm (mean = 2.8, $n=50$). Thickenings are sometimes forked (Plate V, 10), very rarely they exhibit narrow reticulations. In transverse view, tracheids are square to sub-circular in shape, with diameters varying from 20–100 µm radially and 35–70 µm tangentially (Plate V, 11 and 12). Tracheids measure several millimeters in length.

Fascicular rays are evenly distributed among the tracheid files of the woody wedges, 15 to 85 µm wide, and consist of 1–2, rarely up to 3 rows of parenchymatous cells (Plate V, 11). The thin-walled parenchymatous cells are square to rectangular in transverse view (Plate V, 12), measuring 45–120 µm radially and 15–40 µm tangentially. In tangential view, parenchyma cells of uni- to tri-seriate rays show an irregular to polygonal outline, however, at the ray periphery, they are slightly elongated to rectangular (Plate V, 13).

4.2.4. Interfascicular rays

Interfascicular rays separate the woody wedges of the trunk and alternate at the nodes. They are directly connected with the pith parenchyma (Plate VI, 1). In transverse view, at the pith periphery, interfascicular rays are 225 to 475 µm wide tangentially, taper sharply in radial direction, but usually continue to the outermost wood. Cells in interfascicular rays are tangentially elongated at the pith periphery (Plate VI, 2) distinguishing them from the small-sized isodiametric pith parenchyma. Interfascicular rays consist of thin-walled parenchymatous cells that are square to rectangular in transverse view and measure 50–85 µm radially and 85–260 µm tangentially. In radial view, parenchymatous cells are brick-shaped, 30–90 µm high, but show considerable variability even within the same ray (Plate VI, 3). In tangential view, parenchymatous cells of tri- to multiseriate (up to 7 rows) rays show an irregular to polygonal outline, whereas, at the ray periphery, they are slightly elongated to rectangular. Width and number of parenchymatous cells in each interfascicular ray are sometimes variable corresponding to the growth rings (Plate VI, 4 and 5).

4.2.5. Growth rings

Growth rings are clearly visible throughout the secondary xylem cylinder of the main trunk (Plate VI, 6). They are also recognizable in the woody branches of the trunk (specimens KH0057, KH0058) and indicate that the latter exhibited continuous incremental growth after dormancies or growth interruptions. Growth rings are more densely developed and more frequently represented in the marginal, rather than in the central wood (Plate VI, 7), which lead to the interpretation that volcanic activity could have lasted over a longer period until it became more and more frequent close to the final eruption episodes responsible for entombing the whole forest. The comprehensive material of this calamite may enable comparison of the growth ring successions of the main axis and those of its woody branches in the future. This attempt aims to reveal the time of origin of the side branches, their chronological order and the duration of joint growth of the tree's woody organs.

4.2.6. Leafy twigs

Leafy twigs are arranged in whorls of both the main stem and its woody branches of different order. They originate from the margin

of the pith at every 5th to 9th node (Plate III, 5–7; Plate V, 8). Leafy twig traces are 2–6 mm in diameter, consist of a few sinuous tracheids and parenchymatous cells, but lack any secondary xylem (Plate VI, 9). Usually, the leafy twig traces are only recognized in small stems/branches or in the central region of the main trunk. Many places indicate that the leafy twigs may have been shed and successively overgrown. However, some of these, probably those especially exposed to light, may have re-grown and gradually increased their diameter as the traces indicate.

4.2.7. Woody branches

The growth of at least three orders of woody branches considerably contributed to the enlarged crown of the tree and caused a rather unusual appearance among calamitaleans (Fig. 1, Plate I, 1). The prominent branching areas of the main trunk at 5.7 m, 7.5 m and at 9.7 m indicate that 1st order woody branches were mainly formed in the course of successive trunk bifurcations (Plate I, 1). In several cases two closely spaced bifurcations can be recognized (e.g., Plate II, 1–3). However, these bifurcations are not equally formed, in all cases one of the resulting 1st order branches is more prominent compared to the other. As a result sylleptic branching pattern caused a pseudomonopodial or sympodial appearance. The longest 1st order woody branch (KH0057-07 to 01) departed at the first prominent branching region as a relatively slender shoot, but extends at least to 5.1 m length. The latter seem to have grown in a later growth phase of the tree and may be interpreted as a so-called water shoot.

Second and higher order woody branches were frequently recognized on the surface of 1st order branches, at least by their circular branch traces (Plate I, 3). Usually they originate from the parenchyma inside the secondary xylem cylinder with a diameter increasing dramatically within the first few millimeters (Plate I, 3–5, 7). They departed from nearly right to acute angles, possess thick secondary xylem increments and some kind of reaction wood. Regular growth rings reflect interrupted growth.

5. Discussion

5.1. The significance of Permian calamitaleans

From the fossil record, calamite trees were highly successful and flourished in tropical wetland environments throughout the world during late Palaeozoic times. They persisted for more than 60 million years from the early Pennsylvanian (Gerrienne et al., 1999) up to the Late Permian (Wang et al., 2003). The Pennsylvanian Coal Measures of Eurameria were formed in low-latitude humid environments largely covered by tropical rainforests (DiMichele et al., 2007). As the climate increasingly aridified through the late Palaeozoic geotectonic events, these rainforests collapsed, eventually being replaced by seasonally dry Permian biomes (Kerp, 1996; Montañez et al., 2007). Abrupt extinction of the dominant K-selected lycopsids and a switch to tree fern dominance took place (DiMichele and Phillips, 1996), followed by the demise of the *Psaronius-Medullosa* wetland ecosystem around the Pennsylvanian–Permian boundary in Eurameria (DiMichele et al., 2005). Although the causes of this aridification remain a matter of controversy, the consensus is that this climate shift led to the fragmentation of the Coal Forests into isolated rainforest islands surrounded by xerophytic scrub (Falcon-Lang, 2004; Roscher and Schneider, 2006; Falcon-Lang et al., 2009; Falcon-Lang and DiMichele, 2010; Sahney et al., 2010).

The Chemnitz fossil lagerstätte belongs to the Early Permian, but not only shows an outstanding record of fossil calamitaleans. The recently performed excavation at Chemnitz provided more than 1.800 plant remains and a comprehensive data-set of 3D coordinates obtained for every fossil find (Rößler et al., accepted for publication). This may not only offer a unique insight into a Lower Permian forest habitat with a dense hygrophilous vegetation of pteridophytes and

gymnosperms, but also provide information on its community structure and density. Fifty-three trunk bases, still standing upright in their place of growth may provide a crucial data set to estimate competitive situations between vegetation elements in more detail in the future. Large gymnospermous trunks up to 30 m in height, tree ferns up to 10 m in height and several types of medullosan seed ferns with different growth architectures and heights are commonly found at this site. Therefore, several floral elements living in the lower tier, and thus receiving less sunlight than those in the upper tier – had to develop different strategies to obtain essential amounts of light. Plants from the studied fossil forest were forced into some form of resource competition between each other. During that competition the calamites developed different ways to survive and even dominate within the laterally restricted habit. Evidently, during the early Permian, this plant group reached its evolutionary acme and developed different adaptations not known from any older occurrences. Calamitaleans from Chemnitz and from similar aged deposits in Tocantins/Brazil impart a different view of this plant group and their increasingly modified environments in the Early Permian (Rößler, 2006). The study of the largest calamite trunks ever found not only indicates much more variation in branching patterns than expected, but also a considerable amount of secondary growth combined with high portions (up to 50%) of non-lignified parenchymatous tissues in their wood. Therefore, it has been suggested that calamitaleans, although often placed among other hygrophilic elements in fluviolacustrine wetland environments, may have easily survived seasonal episodes of dryness during which they reduced water uptake and possibly shed their leafy twigs. This inference is supported by the large-diameter, long living trunks of closely related species, such as *Arthropitys ezonata*. The biomechanical behavior of the trunks, including the enormous weight and diverse types of lateral branches, need to be re-evaluated. Although they seem to have been well adapted to the gradual environmental changes that took place during the Late Palaeozoic, they became extinct at the end of the Permian.

5.2. Ontogenetic implication of the branching patterns

The almost complete and well-preserved calamite trunk described in this contribution has allowed us to obtain more detailed insights into the variation of the internal organization throughout the entire plant both from the main trunk and its lateral appendages. Since this new and more complete knowledge will considerably add to the existing view of calamitaleans exhibited in many textbooks, we would like to present a life reconstruction drawing for the Permian species *A. bistrata* (Fig. 2).

Two kinds of lateral branches have been recognized and recently confirmed in several Permian calamitaleans (Rößler and Noll, 2010). One is the leafy twig type, the other is the woody branch type. Leafy twigs were arranged in whorls, and in *A. bistrata* they usually grew at every 5th to 9th (rarely to 18th) node. Leafy twig traces are visible from the pith periphery throughout the whole woody cylinder up to the stem's outer surface. As recent investigation suggested they were free of any secondary growth and possibly abscised and re-grew seasonally (Rößler and Noll, 2010). The woody branches originated in at least two different ways. Most prominent is the repeated unequal bifurcation of the stem resulting in an unusual pseudomonopodial or sympodial branching type. Another mechanism to develop woody branches of higher order is recognized somewhere on the plant where they do not normally arise according to their phyllotaxy (Hartig, 1878). Although we cannot exclude the possibility that such woody branches originate directly from the pith periphery, and also probably from leafy twig traces, we got multiple evidence that they are frequently generated "elsewhere than normal" (Beentje, 2010). Consequently, this type of higher order woody branches is interpreted as adventitious shoot (Rößler and Noll, 2010). Adventitious shoots usually arose from the parenchyma inside

the secondary xylem cylinder (Plate I, 3–5, 7). They increased their diameter sharply with continuous increments of secondary xylem, closely matching the growth of the main trunk. As frequently seen in extant coniferous trees the woody branches in our calamite developed some kind of reaction wood, particularly pressure wood on the underside. Despite the high portion of interfascicular tissue recognized in this type of calamite it may represent a self-supporting tree habit. Both the large diameter and the crown architecture of this tree may underline our interpretation. This calamite conspicuously contrasts with vinelike or semi-self supporting habits reported from other calamitaleans, such as *A. deltooides* or *A. yunnanensis* (Cichan and Taylor, 1983; Wang et al., 2006).

For many decades research on fragmentary calamite remains had been confined to the taxonomic delimitation of species and genera. A fundamental basis for to understand general aspects of the morphology and the ontogenetic development of calamitalean sphenopsids was provided by Eggert (1962). A more complete perception arising from the latter study introduced a graphic model based on that in calamites whereby the number of fascicular strands increased by the addition of new strands at each node during the early growth and, after a stationary phase decreased later on respectively. Although we can confirm this established fact in general and recover the succession of epidogenetic, menetogenetic and apoxogenetic growth phases, the large calamite tree in the current study shows that the number of fascicular bundles seems to have been highly variable throughout the plant.

We traced the number of fascicular bundles and their development in several levels of the main trunk and in several woody branches. It appears that the number of fascicles surrounding the pith do not show much difference between the lower part (102, KH0052-09) and the top (95, KH0052-02) of the preserved trunk. We additionally analyzed the two better preserved woody branches using six transverse sections for KH0057-01 to 07 and four transverse sections for KH0058-01 to 04. We found essentially the same situation in the woody branches compared with the main trunk. The number of fascicular strands of branch KH0057 varies from 74 in the lower part (KH0057-06) to 91 in the middle part (KH0057-03), and to 88 close to the top (KH0057-02). In the branch KH0058, the number of fascicular strands varies from 89 in the lower part (KH0057-01) to 85 in the middle part (KH0057-03), up to 108 in the apical part (KH0057-04).

In both woody branches we observed that the number of fascicular strands increase dramatically close to the nodes that bear new shoots. Close to the section of 88 fascicles in KH0057-02, the number of fascicles reaches 115 because a whorl of leafy twigs is present in close proximity. The same situation was found in specimen KH0057-03, the number of fascicles increased from 91 up to 103 due to the occurrence of a new whorl of leafy twigs. These results indicate that the high variability of fascicle numbers is largely influenced by the occurrence of lateral shoots, both whorls of leafy twigs and/or woody branches.

It is worth mentioning that the presence of growth rings in the parent plant seems to have little ontogenetic meaning. In the intraxylary portion of the main woody cylinder, the growth rings are not so clearly presented, whereas, growth rings become more distinctly and densely obvious in the extraxylary portion close to the margin of the stem. This pattern may indicate that the fluctuation of environmental conditions became more influential and frequent before a series of volcanic eruptions buried the whole habitat. Nevertheless, from the sedimentological and palaeosol development we can suppose some sort of climatic cyclicity for the stratigraphic level from which our specimen was excavated.

5.3. Evolutionary dynamics of the branching system

The recent find provides the first opportunity to investigate the complex branching system of a large woody calamite. One of the

most significant and no less surprising features of this fossil plant is the spatial organization of its crown distinguishing it from the well known calamite reconstructions in textbooks (e.g., Taylor et al., 2009). Furthermore, the spatial organization of the branches plays an important role and meets fundamental demands in nutrient gathering, especially via the photosynthetic process. However, as yet, there has been very limited progress in the description and analysis of such branching patterns among late Palaeozoic calamitaleans at this level of detail.

Calamite trees (*sensu stricto*) have been previously estimated to have been up to 10 m tall with a more or less substantial layer of woody tissue around the central pith (Taylor et al., 2009). They were interpreted as having shown telescopic growth and, therefore they were often reconstructed in a rather uniform way with frequent branches at their nodes (Hirmer, 1927; Eggert, 1962; Leistikow, 1962; Boureau, 1964; Barthel, 2004; Rößler and Noll, 2007, 2010). They have also been proposed to show a homogenous architecture in a computer model attempt (Daviero and Lecoustre, 2000). As our investigation shows calamite trees of the *Arthropitys bistrata* type could attain a growth height of more than 15 m and are characterized by at least 3 orders of woody branches which doubtless formed a large crown for the plant. The spatial organization of its woody side branches is very similar to those of extant higher woody plants.

The new reconstruction of an *Arthropitys bistrata* calamite tree presented in this paper deviates substantially from those published before especially those by Hirmer (1927) which have been seen as the standard for a long time. However, a new reconstruction does not necessarily invalidate earlier ones but rather adds to the diversity of growth forms of equisetalean sphenopsids during the late Palaeozoic. This was the time when the sphenopsids achieved their highest diversity and there is no reason to assume that the group filled only a few niches with a restricted number of growth habits or tree architecture forms *sensu* Hallé et al. (1978). Actually, over the years several different growth forms of calamitaleans *s.l.* have been found. Free-standing forms without a rhizome were described much earlier by Grand'Eury (1877), Leistikow (1962), Barthel (1980), and Pfefferkorn and Fuchs (1991). A tuft tree reconstruction for a specific group of calamitaleans (*Calamitea*, *Calamites multiramis*) was presented by Remy and Remy (1978) and small, perhaps even herbaceous forms were found by Libertín et al. (2009). The reconstructions by Hirmer (1927) were major milestones in the understanding of the group and they were influenced by earlier works like those by Grand'Eury (1877). However, they were also inspired by too strict an adherence to the only growth form that survived the Permo-Triassic extinction, namely that of the *Equisetites-Equisetum* line. In this paper it can be demonstrated for the first time that equisetalean sphenopsids of the late Palaeozoic achieved growth forms with irregular branching and complex but irregular rooting structures (see Rößler et al., *accepted for publication*) that remind one much more of modern trees than those previously reconstructed for calamitaleans of the late Palaeozoic. Modern higher plants display a variety of architectures defined by the degree of branching, internodal elongation and shoot determinacy. Although plant architecture is believed to be determined by genetic programs (Wang and Li, 2006, 2008), plant architecture is crucially influenced by environmental factors such as light, temperature, humidity, nutrition, and habitat density. However, the formation of branching patterns in extant woody plants is a complex physiological process that remains inadequately understood (Wilson, 2000; Yang and Midmore, 2009). No other group of organisms is as dependent on optimization and adaptation as trees, whose alternation of generations is extremely slow in comparison to herbaceous or low plants and to animals. A tree can only survive by using the existent resources in the best way possible, by distributing its leaves in the air space and developing roots into the ground as efficiently as possible and at a minimum effort. Previous studies show that living plants respond to local heterogeneity in

abiotic and biotic conditions by changing module-level morphology, growth, and reproductive patterns (White, 1979; Kawamura, 2010). All plant shoots can be regarded as a series of developmental modules termed phytomers, which are produced from shoot apical meristems. The fate and activity adopted by these secondary, axillary shoot meristems is the major source of evolutionary and environmental diversity in shoot system architecture (McSteen and Leyser, 2005). Reliable data to model competitive situations in the Late Palaeozoic remain very rare. Early Permian calamitaleans probably responded to local variability in resource availability with changes in architecture to maximize their resource-gathering ability during competition with other plants, particularly medullosan seed ferns, *Psaronius* tree ferns and cordaitaleans—all of them in close proximity and frequently encountered from the same habitat at Chemnitz.

Since neighboring plants are an important factor of variability in resource availability, the architectural mechanisms by which plants can alter their resource-gathering ability indicate their potential for success in different competitive situations (Tremmel and Bazzaz, 1995; Kozovits et al., 2005; Grams and Andersen, 2007). Resource acquisition depends on the size and morphological adjustments of plant organs, the physiological activity levels of these parts, and how these change through time (Roloff, 2004; Grams and Andersen, 2007; Yang and Midmore, 2009). As a consequence, resource acquisition, allocation, and deployment abilities are important determinants of competitive success. Thus, plant architectural plasticity determines resource-gathering ability and therefore, in situations where resource availability is altered through neighboring plants, competitive success is the key to survive (Grime et al., 1986; Bazzaz, 1991; He et al., 2005).

6. Plant–animal interactions

Many fossil records of vascular plant and animal interactions from the Palaeozoic have been reported from across the world in recent years (Labandeira, 1998, 2006; Feng et al., 2010), including herbivorous damages on leaves and detritivorous borings with coprolites; whereby all major plant taxa acted as functional feeding resources (Labandeira, 2007). However, according to the fossil record, detritivory was likely to be the dominant mode of feeding on plants in Palaeozoic terrestrial ecosystems (Labandeira, 1998). According to published data and observations, terrestrial arthropods were the most frequently observed feeders on late Palaeozoic plants.

Compared with the multiple fossil records of small-sized coprolites (several tens of microns), which were principally assigned to oribatid mites (Labandeira et al., 1997; Rößler, 2000; Barthel et al., 2010; Feng et al., 2010), relatively large-sized coprolites remain sparsely documented throughout the Palaeozoic (e.g., Scott, 1977; Baxendale, 1979; Edwards, 1996). In a detailed study of coprolite assemblages from the middle Pennsylvanian coal balls of Lewis Creek, Kentucky, Scott and Taylor (1983) documented a much greater diversity of coprolites, and subdivided them into three size classes. Some of these coprolites, particularly the larger ones, contained abundant spores, and in some cases sporangia of ferns and lycophytes, or very rarely broken fragments of synangia or pollen organs.

In recent years the Permian Petrified Forest of Chemnitz was several times in the focus of plant–animal interactions. Rößler (2000) described small-sized coprolites recognized in boring galleries of the vascular tissue of climbing/epiphytic ferns or pteridosperms. In the current study, the central cavity of the longest woody branch (KH0057) of the calamite tree is filled with relatively large-sized coprolites (Plate IV, 1, 2). The coprolites contain tracheid fragments which indicate the detritivorous nature of the producer. Simple scalariform thickenings of the tracheid walls in the coprolites (Plate IV, 3) presumably represent non- or semi-digested plant tissues, which lead us to suggest that the animal fed on the living calamite plant.

Coprolites in woody plants are commonly associated with bored tunnels (Feng et al., 2010). However, there is only weak evidence of

animal borings in the studied specimen (Plate IV, 1). More interestingly, because calamite trunks commonly possess great richness in their parenchyma (Rößler and Noll, 2006, 2010), they may have served as a good functional feeding target plant for detritivores looking for a food resource.

As modern myriapods are dominantly detritivores, less often mycophagous and carnivorous, their Palaeozoic relatives may have lived in a comparable way (Rolfe, 1985). Therefore, we tentatively propose ancient myriapods as candidates for having produced the large-sized coprolites in our calamite. However, adult myriapods might not have lived in the central cavities of the calamite, rather only for certain phases during their life cycle, such as for egg deposition, during which they may have climbed up to the trunk and left fecal pellets in the pith cavity. Some of the recent relatives of such myriapods climb up on living trees to drink dew during the night. If the volcanic scenario of the Chemnitz fossil lagerstätte is taken into consideration we would also invoke certain escape reactions by the animals into available plant cavities during eruption. Our idea regarding the putative producer of the large-sized coprolites is additionally supported by several diplopod finds at the same excavation site (Rößler et al., accepted for publication).

7. Conclusions

- (1) The revision of Permian calamitaleans from Chemnitz, and particularly the study of the largest calamite trunk ever found, have shown, that this widely distributed plant group displayed more variation in both branching patterns and internal vascular organization than was previously reflected.
- (2) Both ontogenetic change and references to edaphic and ecological variation resulted in considerable anatomical variability, drawing into question the taxonomic practices applied during the long research history into this group.
- (3) The highly developed crown architecture of a *A. bistriata* tree caused by woody branches of different origin is interpreted as a result of competition with the neighboring plants in this spatially rather restricted environment. In such a habitat, living together with cordaitan gymnosperms, medullosan seed ferns and psaroniacean tree ferns, the calamite was probably well adapted to the environment.
- (4) Highly specialized functional features of the Permian calamitaleans could not alter their eventual fate during the gradual increasing aridity in the Permian, and their final disappearance as part of the Permo-Triassic mass extinction.
- (5) Ecophysiological response of the current calamite plant had sensitively recorded the environmental turbulences induced by the rising volcanic activities, which finally buried the habitat as prerequisite for this fossil forest.
- (6) For the first time large-sized coprolites have been discovered from the pith cavity of a living calamite. We suggest that ancient detritivorous myriapods may have targeted on this plant.

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