



Anatomy and branching of *Arthropitys bistrata* (Cotta) Goepfert – New observations from the Permian petrified forest of Chemnitz, Germany

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ABSTRACT

Sizeable permineralized calamitean trunks from the Permian petrified forest of Chemnitz, Germany, enabled us to recognize two different branching patterns and wood anatomies for material currently classified as *Arthropitys bistrata*. This resulted in re-evaluation of the genericity of the widely distributed organ genus *Arthropitys* Goepfert 1864. As a result, a mosaic of anatomical and morphological characteristics has been recognized that permit *A. bistrata* to be characterized in much more detail than previously possible.

The first type of calamite previously included in *A. bistrata* is characterized by whorls of branches at every 5th to 9th node and simple scalariform thickenings in tracheid walls of the secondary xylem. Additionally it shows irregularly positioned woody adventitious shoots that also carried whorls of leafy branches. The second type shows reticulated thickenings and multiseriate pitting in secondary xylem tracheid walls and regular branching at every node. Branches alternate in successive nodes and, therefore, lie on the top of each other at every second node. Comparison with the type material suggests the two calamite forms need to be split taxonomically as follows. The first type of calamite is regarded as *A. bistrata* and emended herein, the second type is separated and introduced as *Arthropitys sterzelii* sp. nov.

The secondary tissues of both species are characterized by a high portion of parenchyma (around 45%). Sometimes irregular growth rings were recognized that may reflect some kind of seasonality and/or environmental influence. We suspect the leafy branches, which were free of any secondary growth in both species, were probably grown and absceded seasonally. Comparisons are made with both different calamitean species and other preservational forms.

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1. Introduction

Calamitalean sphenopsids belong to the most common and frequently found plant fossils in Late Carboniferous and Early Permian continental strata (Barthel, 2001; Frey et al., 2002; Martín-Closas and Galtier, 2005; Hilton et al., 2001; Kerp et al., 2007; Wagner and Mayoral, 2007). However, in comparison to the overwhelming amount of pith cast compressions, sizeable trunks that show detailed anatomical preservation of the plant tissues remained rather rare (Rößler, 2006).

Historically, the different calamitalean classification systems that developed were and continue to be based on the mode of fossil preservation. Classification of compression/impression is based mainly on branching features visible on the pith cast's surfaces. Classification of permineralized material is based on the anatomy of the calamite's primary and secondary tissues. The classical study by

Eggert (1962) significantly contributed to our knowledge of the morphology and growth of calamitaleans, but subgeneric classification continues to suffer from a lack of understanding of character ontogeny. This situation is complicated by the absence of distinctive characters with known variability ranges. Without knowledge of attached leaves or reproductive organs, neither classification reflects natural groups, so calamitalean classifications remain highly artificial. In this study, we complement the anatomically-based classification of the morpho-genus *Arthropitys* Goepfert with a better understanding of the plant's branching characteristics obtained from analysis of sizeable calamitalean permineralized trunks that provide a better understanding of the internal vascular organization of the stem as well as the position, frequency, anatomy and morphology of the branch traces.

Among anatomically preserved calamitaleans, usually three stem genera are distinguished (Boureau, 1964): the rare *Calamodendron* Brongniart 1849, recently revised and renamed as *Calamitea Cotta 1832* (Rößler and Noll, 2007); the rare *Arthroxylo* Reed 1952; and the quite common *Arthropitys* Goepfert 1864. The characters differentiating these taxa include the cellular organization of the interfascicular ray parenchyma (tapering end walls in *Arthroxylo* versus isodiametric brick-shaped cells in *Arthropitys* and *Calamitea*)

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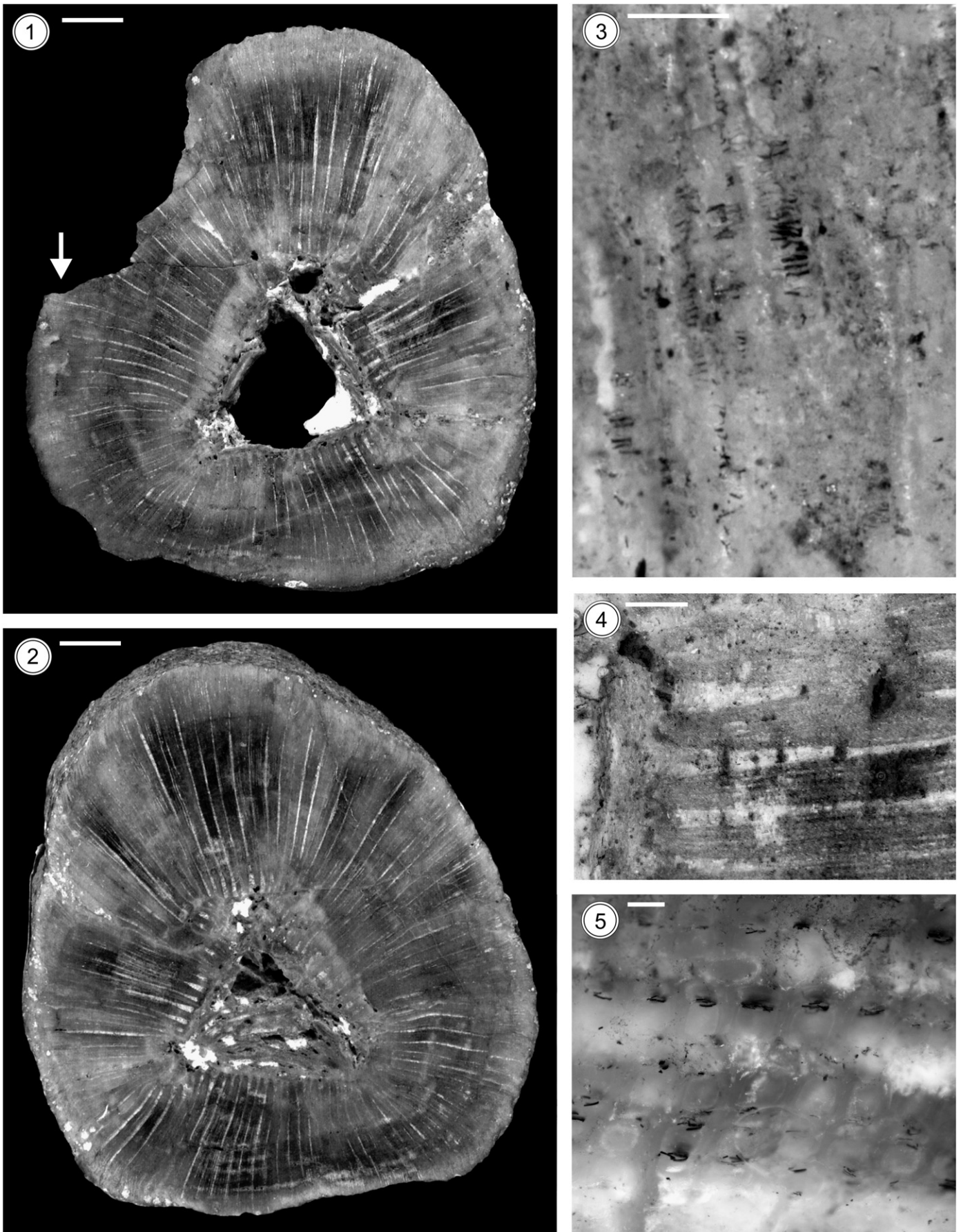


Plate I. *Arthropitys bistrata* (Cotta, 1832) Goeppert, 1864, lectotype. Fig. 1 Transverse slice, BMNH 13787, bar 5 mm. Fig. 2 Transverse slice, BMNH 13787a, bar 5 mm. Fig. 3 Radial longitudinal view obtained from broken edge (arrow in Fig. 1) showing scalariform wall thickenings of secondary xylem, bar=100 μ m. Fig. 4 Detail of Fig. 1 showing vascular wedges separated by interfascicular rays, bar=1 mm. Fig. 5 Detail of transverse view. Note black-coloured wall thickenings exclusively found on radial tracheid wall, bar=50 μ m.

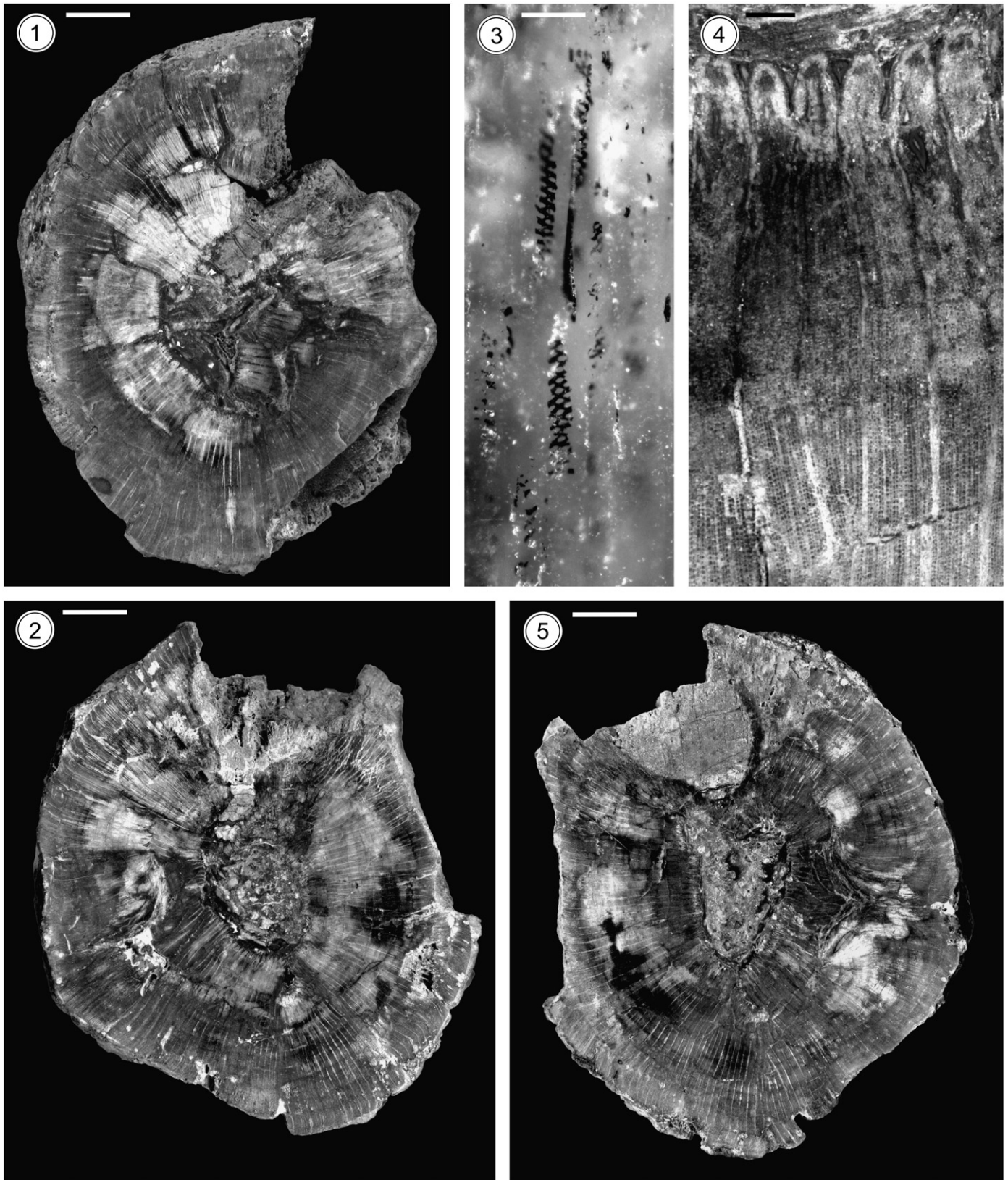


Plate II. *Arthropitys sterzelii* sp. nov. Fig. 1. Transverse slice, BMNH v.1779, figured in Cotta 1832, pl. XV, 4, bar = 5 mm. Fig. 2. Transverse slice, MfNC K 3173 (counterpart of BMNH v.1779), bar = 5 mm. Fig. 3. Detail from radial longitudinal section of MfNC K 3173 showing reticulated wall thickenings with narrow oval pits in secondary xylem, bar = 50 μ m. Fig. 4. Detail from transverse section of MfNC K 3173 showing vascular wedges separated by interfascicular rays, bar = 500 μ m. Fig. 5. Transverse slice, MfNC K 3173, 11 mm apart from transverse view shown in Fig. 2, bar = 5 mm.



Fig. 1. Proposed reconstruction of *Arthropitys bistriata*. Plant may have reached several metres in height, it shows whorls of leafy branches at every fifth or sixth node and irregular positioned adventitious shoots that also carried leafy branches. Additionally, narrow leaves were attached to main axes. Plant shows certain amount of secondary growth in both stems and secondary roots.

and the type of secondary xylem tracheids (two different types of tracheids are present in *Calamitea*, one type in *Arthropitys* and *Arthroxylo*).

Arthropitys is most frequently found and represents the majority among permineralized calamitaleans. It is known from the Mississippian (Namurian A, see Gerrienne et al., 1999) up to the Late Permian Lopingian (Wang et al., 2006). However, since the significance of individual anatomical and morphological wood characteristics has been overestimated, or the wood's ontogenetic variability not critically examined, subgeneric classification has been heterogeneous. While some morphospecies should be recognized as distinct entities, others probably are based on the study of different developmental stages. Although attempts have been made to define unique anatomical characters in the primary and secondary body, these typically have not been sufficiently diagnostic to classify the overwhelming majority of *Arthropitys* specimens. A better understanding of the characteristics of an individual taxon at different ontogenetic stages would allow for better clarification of taxonomically distinct plants.

Arthropitys is based on material originally described by Cotta (1832) as *Calamitea bistriata*. 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 there exist major anatomical differences in comparison to *Calamitea striata*, Goepfert (1864) erected the new genus *Arthropitys* to separate Cotta's species *bistriata*. Although both the type material of *Arthropitys bistriata* and rich collection material from the type locality have been available for a long time, an adequate study of the generitype had not been done until now. Several species of *Arthropitys*, like the classical *A. communis* Binney or the characteristic liana-like *A. deltoides* Cichan and Taylor, but also some recently studied forms, such as *A. junlianensis* (Wang et al., 2003), *Arthropitys yunnanensis* (Wang et al., 2006) or *Arthropitys ezonata* Goepfert, the largest anatomically preserved calamite ever described (Rößler and Noll, 2006), are all known in much more detail than the generitype itself. Consequently, the assignment of newly found calamitean specimens sometimes remained uncertain or was treated in open nomenclature (Rößler and Noll, 2002).

This study presents an analysis of newly collected material and a reassessment of existing material from the Petrified Forest of Chemnitz. The three-dimensionally preserved specimens show both the internal organization of the plant tissues and the type of branching allowing detailed investigation of the anatomy, internal organization and branching morphology of Permian calamitaleans currently classified as *A. bistriata*.

2. Material, storage and methods

The study material originates from the Lower Permian Petrified Forest of Chemnitz, Germany. This material was buried during episodes of explosive rhyolitic volcanism around 290 million years ago. The forest's stratigraphic position corresponds to the Upper Asselian/Lower Sakmarian boundary. Stratigraphic, geologic and taphonomic details are provided by Rößler (2006). The spectrum of preservational types ranges from moulds and casts of fossil plants in volcanic tuff to anatomically preserved permineralizations (Sterzel, 1918; Barthel, 1976; Rößler, 2001).

In 1839, a part of Heinrich Cotta's petrified wood collection was sold by his son Bernhard Cotta to the British Museum of Natural History (BMNH), London (Süß and Rangnow, 1984), where the specimens still remain available for study (Kidston, 1886, p. 4). This collection partly consists of several of Cotta's (1832) original specimens, including the type material of *A. bistriata*. (Plate I, 1–5, Plate II, 1). However, because the specimens published by Cotta (1832, pl. XV, 3–4) and re-figured in this contribution (Plate I, 1, Plate II, 1) are small, they fail to illustrate some key information. Both represent transverse slices of a few millimetres thickness. The nature of branching cannot be determined from these specimens. Also, the anatomical and morphological details preserved in the type material are limited, though we have re-evaluated as many of its anatomical characteristics as possible.

Plate III. *Arthropitys bistriata* (Cotta, 1832) Goepfert, 1864, MfNC K 1114. Fig. 1. Surface of stem with partial view into pith, AS=adventitious shoot, bar = 50 mm. Fig. 2. Transverse slice cut from upper portion of specimen showing departing branch traces of a whorl, original size. Fig. 3. Transverse slice cut from median portion of specimen, internode level showing 122 primary vascular strands, original size. Fig. 4. Views from position X in Fig. 1, radial longitudinal section (left) showing pith (enlarged in whorl position), tangential longitudinal section (central image) showing one whorl with branch traces (W) and surface of specimen showing one whorl and one single branch trace (BT) possibly representing initial stage of an adventitious shoot, bar = 10 mm. Fig. 5. Transverse slice cut from basal portion of specimen, internode level showing 90 primary vascular strands, original size. Fig. 6. Detail of Fig. 5 showing vascular wedges separated by interfascicular rays, bar = 500 µm. Fig. 7. Single branch trace on outer surface of trunk, bar = 2 mm. Fig. 8. Radial longitudinal section showing parenchyma cells of an interfascicular ray and one node diaphragm (N), bar = 500 µm. Fig. 9. Radial longitudinal section showing scalariform thickenings of secondary xylem, bar = 100 µm.

Plate IV. *Arthropitys bistriata* (Cotta, 1832) Goepfert, 1864, MfNC K 1114. Fig. 1. Two images showing outer surface of stem obtained from original tuff mould, note two whorls with branch traces (a), image from Sterzel (1918, fig. 69), bar = 10 mm. Fig. 2. Detail from Plate III, Fig. 4 (central image) showing one branch trace of whorl, bar = 2 mm. Fig. 3. Tangential longitudinal view showing nodal zone with two leaf traces, bar = 2 mm. Fig. 4. Tangential longitudinal view showing two nodes and associated internode, bar = 2 mm. Fig. 5. Radial longitudinal view showing an interfascicular ray and its brick-shaped parenchyma cells, bar = 200 µm. (see on page 108)

Plate V. *Arthropitys bistriata* (Cotta, 1832) Goepfert, 1864, additional material. Fig. 1. Tangential longitudinal view showing an adventitious shoot with secondary growth, MfNC K 675, bar = 10 mm. Fig. 2. Outer surface with large trace of a woody adventitious shoot, MfNC K 675, bar = 10 mm. Fig. 3. Slightly enlarged basal portion of a trunk with three massive woody root traces, MfNC K 5626, bar = 10 mm. Fig. 4. Transverse slice cut from top of specimen MfNC K 5626, bar = 10 mm. (see on page 109)

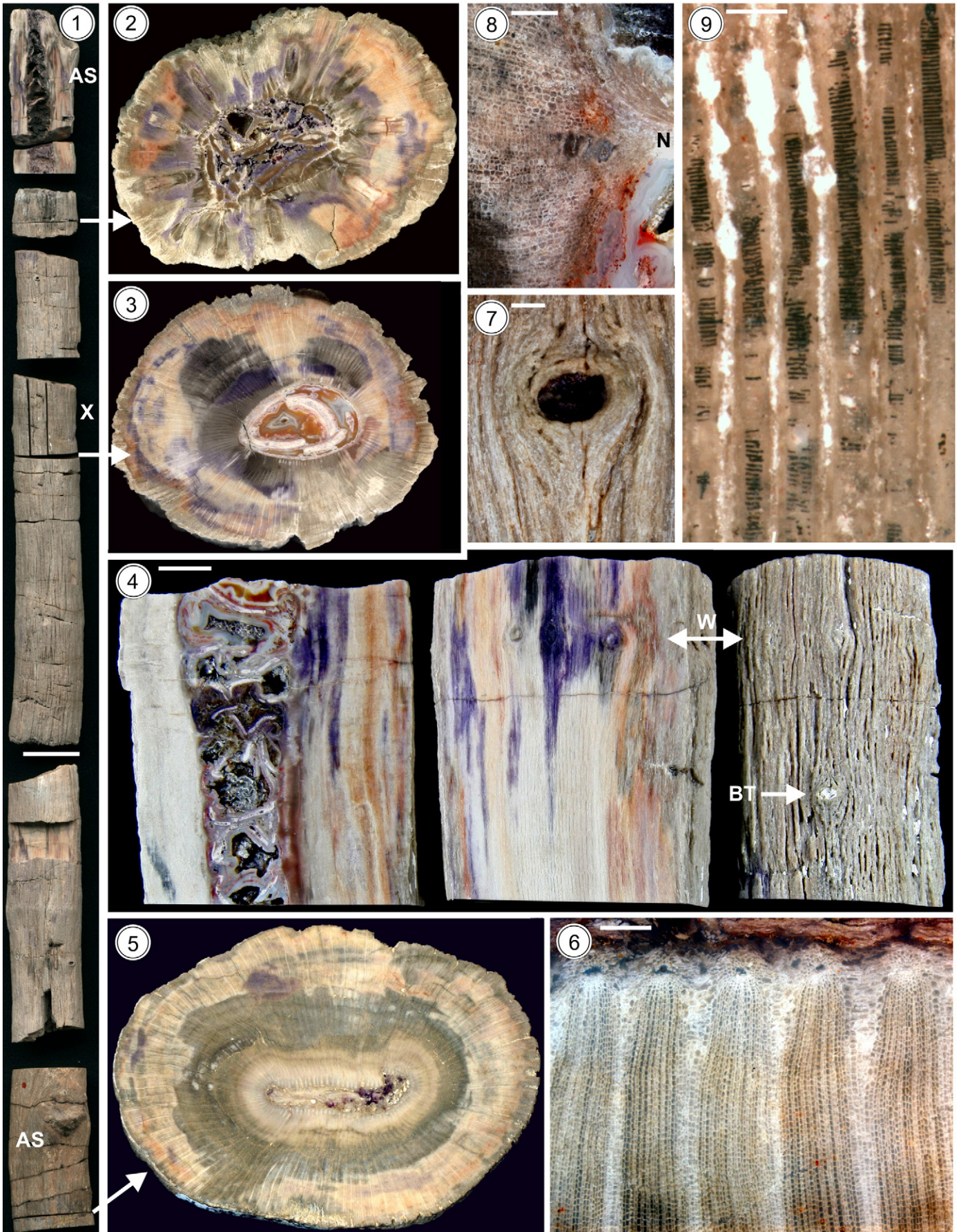


Plate III.

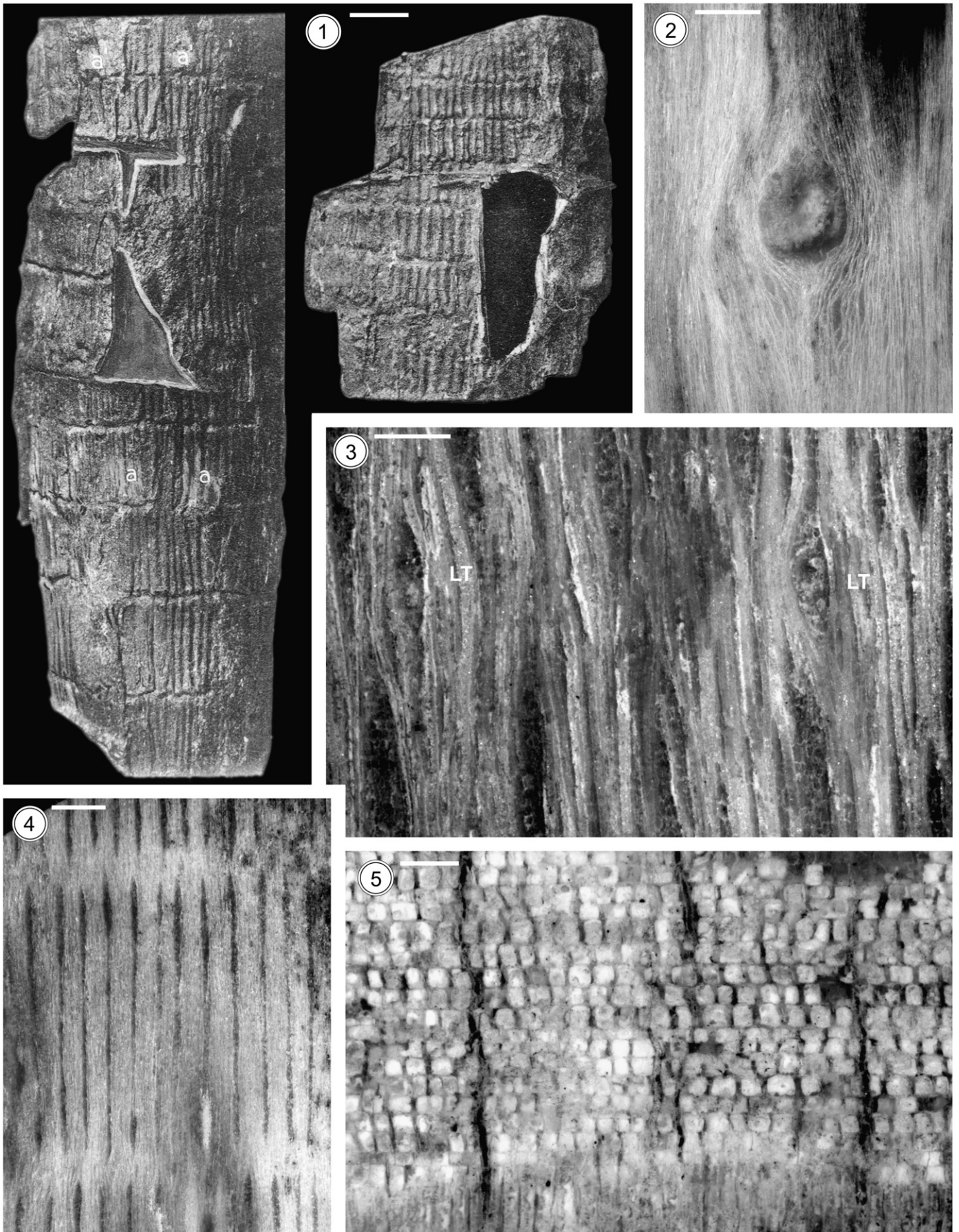


Plate IV (caption on page 106).

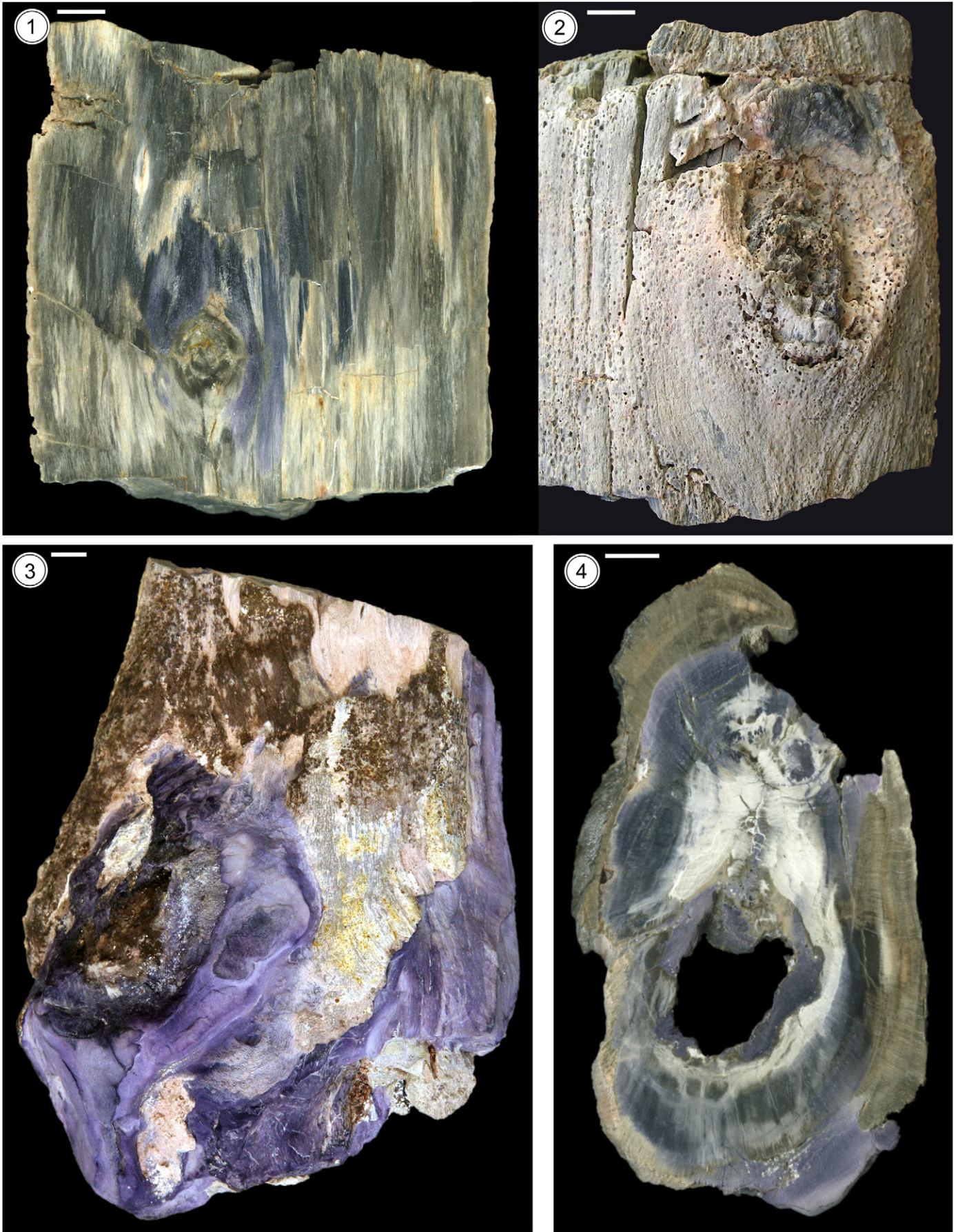


Plate V (caption on page 106).

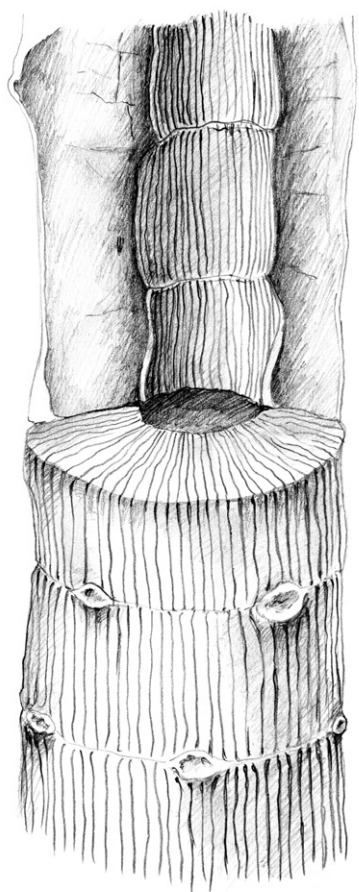


Fig. 2. Proposed reconstruction of *Arthropitys sterzelii* sp. nov. Plant may have reached several metres in height, and shows secondary growth. Regular branching occurs at every node, branches alternate in successive nodes and carry leaves.

Several significant specimens from the type locality do exist. Among them are counterparts of Cotta's originals and sizeable trunks collected decades ago as well as newly found trunks collected for this study. These specimens, K 1114, K 3271, K 675, K 5202, K 3213, K 3173, K 5251, K 3961, K 3257, K 4615, K 3285, K 3093 are stored at the Museum für Naturkunde Chemnitz. They show sufficient preservation to evaluate relevant diagnostic characters and are available for thorough investigation.

For comparative purposes, additional material was investigated from the Permian of Autun, France; Nová Paka and Pilsen, Czech Republic; Tocantins, Brazil; NW-Saxony Volcanite Complex and Freital (Döhlen-Basin), both in Germany, as well as the Pennsylvanian age *Arthropitys* coal ball material of the James Lomax thin section suite in the Chemnitz museum.

The material studied in this analysis is stored in the following institutions: British Museum (Natural History) London, U.K. (BMNH), Museum für Naturkunde, Chemnitz, Germany (MfNC), Museum für

Naturkunde of the Humboldt University, Berlin, Germany (MB), and the Geological Survey of Saxony, Freiberg, Germany (LfUG).

The trunks were cut with a trim saw to reveal both transverse and longitudinal (radial and tangential) sections. These surfaces were subsequently ground and polished and examined using reflected light microscopy. Additional details were obtained from a few thin section preparations.

Sections were photographed under reflected or transmitted 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 3D-scanner type C220ST-RD.

3. Systematics

Class: Sphenopsida

Order: Equisetales

Family: Calamitaceae

***Arthropitys* Goepfert, 1864**

Type species: *A. bistriata* (Cotta, 1832) Goepfert, 1864

***A. bistriata* (Cotta, 1832) Goepfert, 1864, nov. emend. Rößler and Noll (Fig. 1, Plates I, III–V, X, 1–2)**

Lectotype: The specimen figured by Cotta (1832, pl. XV, 3), re-figured here (Plate I, 1).

Additional material: Specimens MfNC K 1114 (Plates III, IV), MfNC K 3271 (Plate X), MfNC K 675, K 5626 (Plate V), MBPB 2000/964b.

Repository: The lectotype is stored at the British Museum (Natural History) London, U.K. under No. 13787; additional material is stored at the Museum für Naturkunde Chemnitz and the Museum für Naturkunde of the Humboldt University Berlin.

Type locality: The city of Chemnitz (Erzgebirge Basin), Germany.

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

Synonymy and selected references:

1832 *C. bistriata*, Cotta, p. 69, pl. XV, 3.

1864 *A. bistriata*, Goepfert, p. 183–185, pl. XXXII, 1, 7.

1881 *Calamites* sp., Stur, p. 49, text-fig. 12.

1887 *Calamites* sp., Stur, p. 35, text-fig. 14.

1918 *A. bistriata*, Sterzel, p. 258–261, pl. 4, 69ab, 70ab; pl. 5, 70 cd.

1976 *A. bistriata*, Barthel, p. 69, pl. 28, 18 and 20.

1983 *A. bistriata*, Barthel, p. 78.

1996 *Arthropitys* sp., Tunger and Eulenberger, p. 47, fig. 23.

2001 *A. bistriata*, Rößler, figs. 252, 254.

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

Emended diagnosis: Stem consists of a central pith/cavity and primary and secondary vascular tissues. Pith is circular, composed of thin-walled cells and is considerably enlarged at the nodes showing whorls. Parenchyma diaphragms occur in the nodal region. Primary xylem strands with carinal canals are surrounded by 2–4 rows of variable metaxylem cells that reach 20–100 μm (20–50 in the most complete specimen) in diameter. The smallest cells are directly attached to the carinal canal. The secondary body consists of interfascicular rays and fascicular wedges. Interfascicular rays taper distally and are visible through the whole secondary tissue. Fascicular wedges consist of radial

Plate VI. *Arthropitys sterzelii* sp. nov., MfNC K 3961, holotype. Fig. 1. Stem surface, bar = 50 mm. Fig. 2. Transverse slice cut from top of specimen, internode level showing 121 primary vascular strands, bar = 10 mm. Fig. 3. Detail of transverse section from base of specimen showing vascular wedges separated by interfascicular rays, preservation does not show primary tissues, carinal canals are laterally flattened, bar = 500 μm . Fig. 4. Outer surface of trunk's upper portion showing nodes with branch traces in alternating positions (BT), bar = 10 mm. Fig. 5. Tangential longitudinal view showing one node (N) and one branch trace (BT) without secondary growth, bar = 2 mm. Fig. 6. Tangential longitudinal view showing nodal zone with alternating interfascicular rays and one leaf trace (LT), bar = 500 μm . Fig. 7. Radial longitudinal view showing some variation of reticulated wall thickenings in secondary xylem, note horizontal elongated oval pits, bar = 50 μm . Fig. 8, 9. Radial longitudinal view showing reticulated wall thickenings and oval pits in secondary xylem, each bar = 50 μm . Fig. 10. Outer surface of specimen in nodal position showing vascular wedges and one branch trace, bar = 10 mm.

Plate VII. *Arthropitys sterzelii* sp. nov., MfNC K 5251, paratype. Fig. 1. Trunk surface, bar = 50 mm. Fig. 2. Transverse slice cut from top of specimen (see arrow), internode level showing 127 primary vascular strands, bar = 10 mm. Fig. 3. Tangential longitudinal view showing two nodes with branch traces in alternating positions (BT), bar = 10 mm. Fig. 4. Detail of Fig. 2 showing growth rings, note different distance between neighbouring rings, bar = 1 mm. Fig. 5. Detail of Fig. 4, growth ring made of tracheids with thickened cell walls, bar = 200 μm . Fig. 6. Detail of Fig. 2 showing three vascular wedges separated by interfascicular rays, bar = 200 μm . Fig. 7. Tangential longitudinal view showing one branch trace (BT) in nodal position, bar = 1 mm. Fig. 8. Tangential longitudinal view showing node with alternating interfascicular rays and two leaf traces (LT), bar = 500 μm . Fig. 9. Radial longitudinal view showing pith with several nodes, bar = 10 mm. (see on page 112)

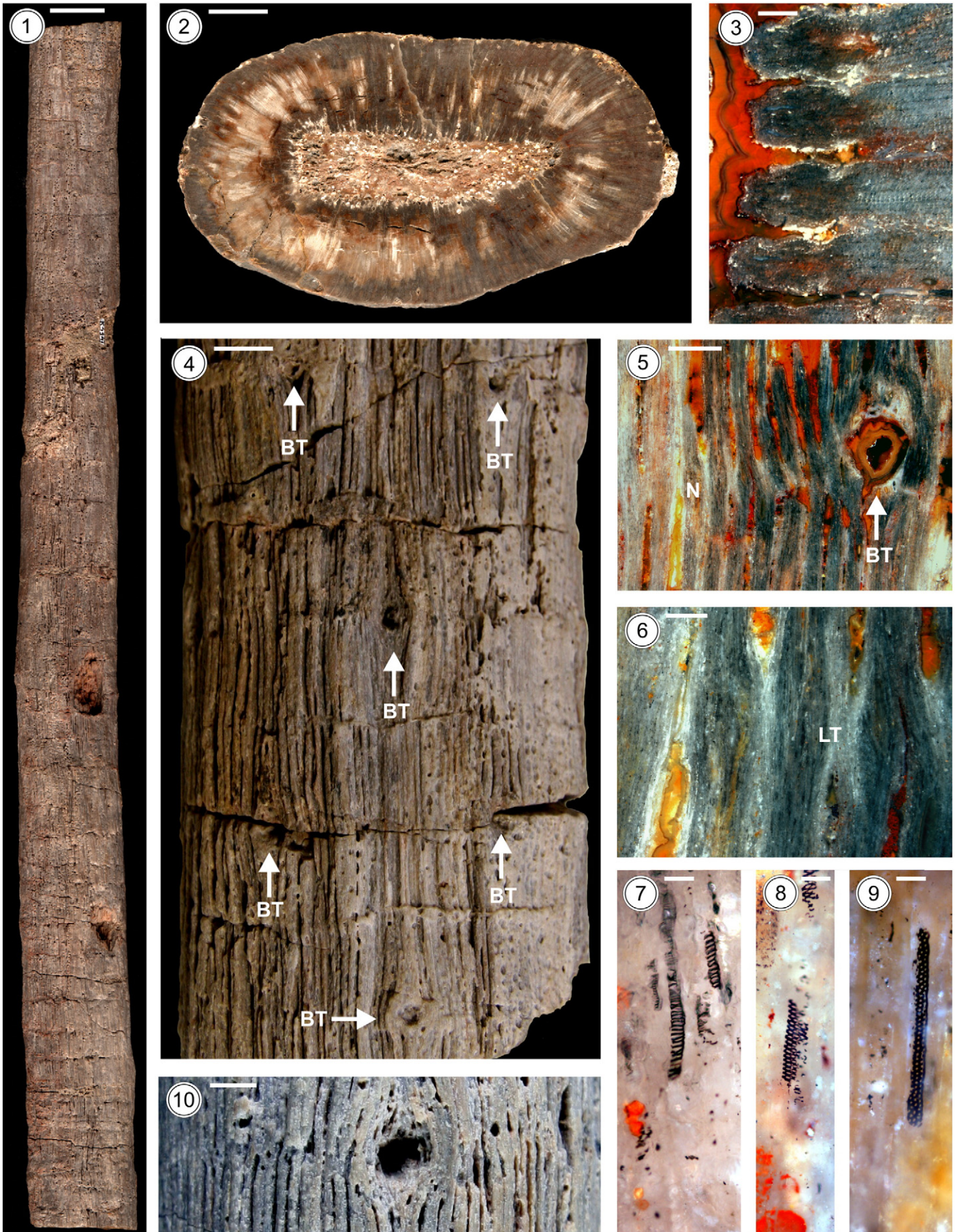


Plate VI.

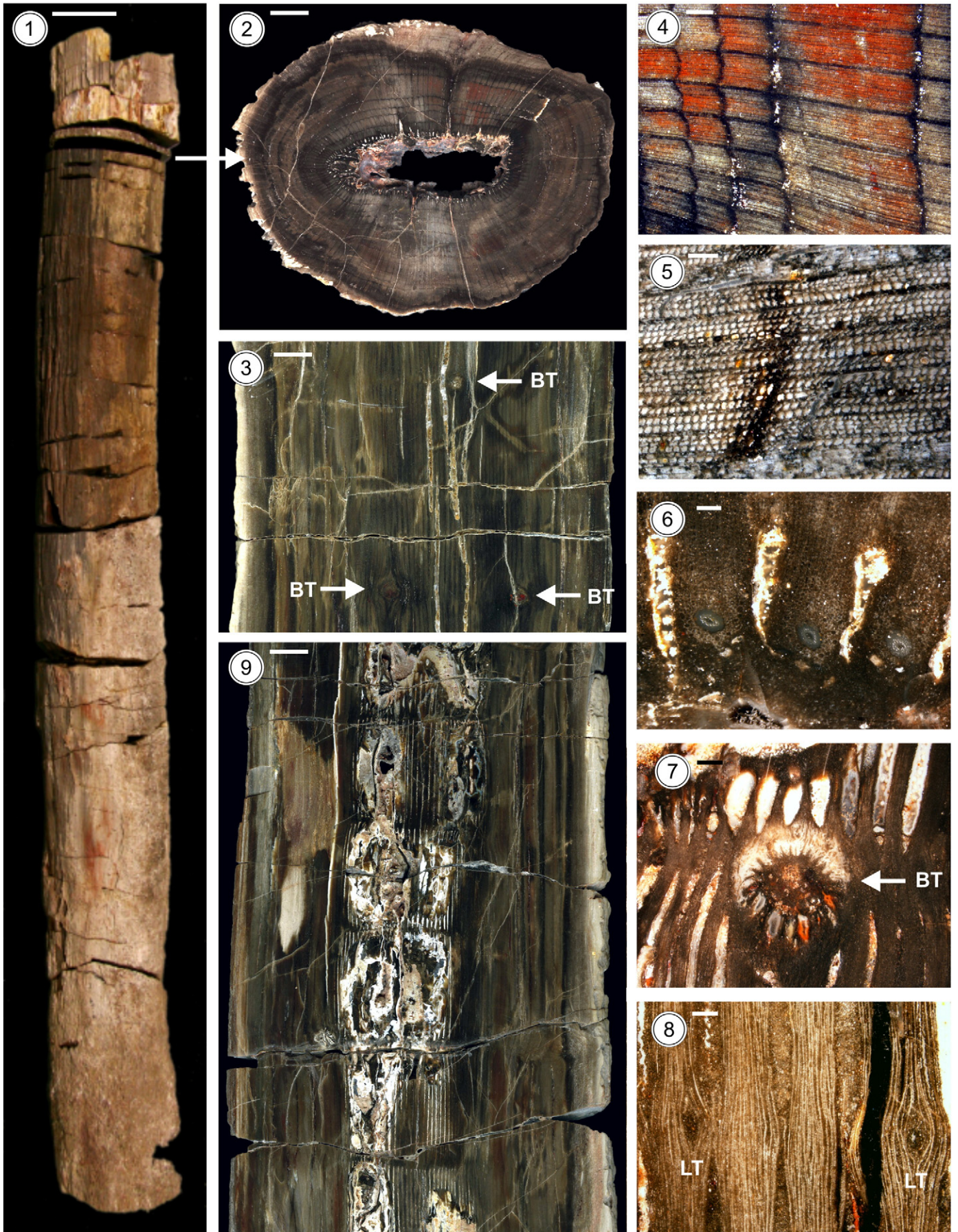


Plate VII (caption on page 110).

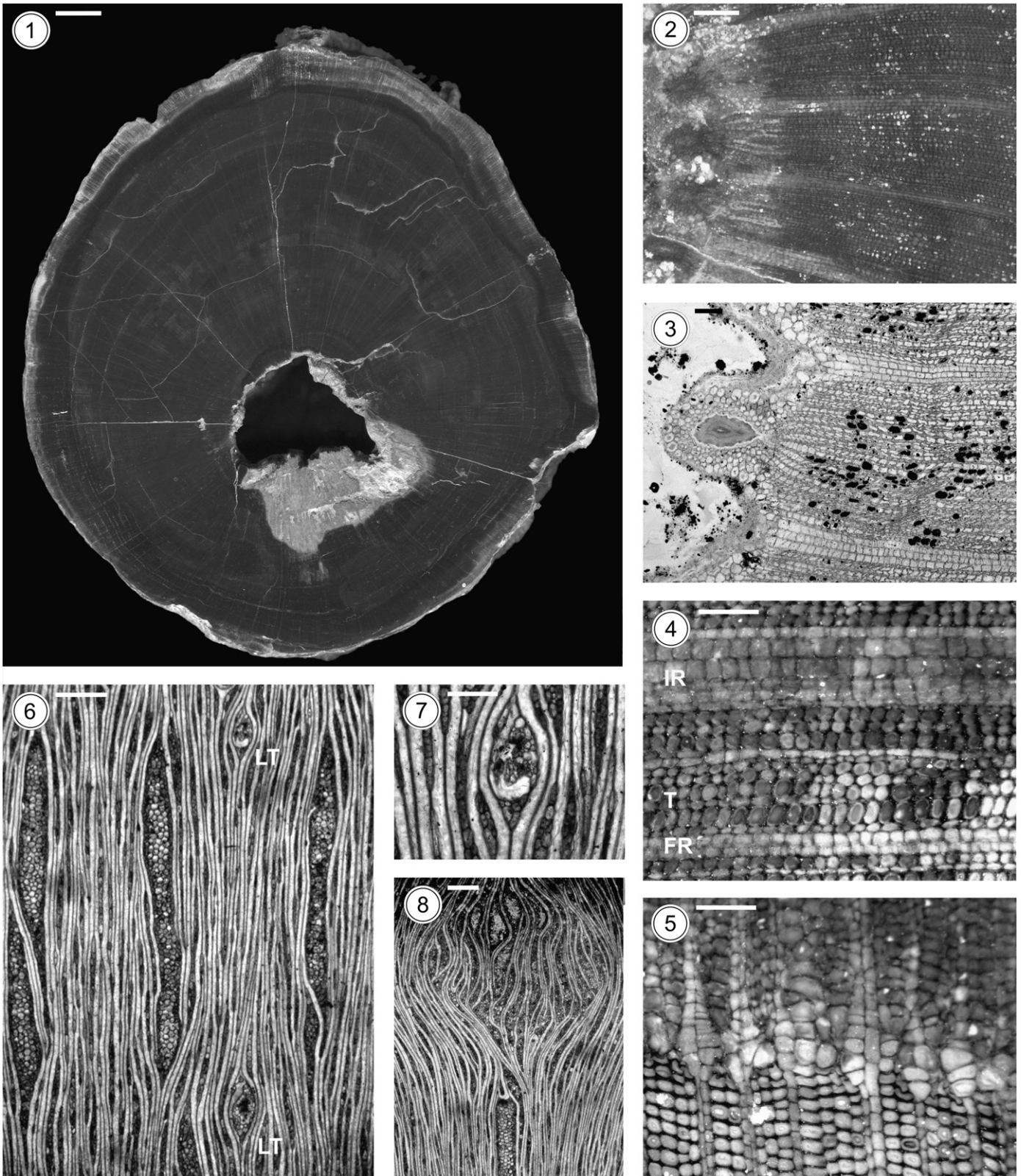


Plate VIII. *Arthropitys sterzelii* sp. nov., additional material. Fig. 1 Transverse section of a trunk showing extended secondary growth, MfNC K 3257, bar = 10 mm. Fig. 2 Detail of Fig. 1 showing vascular wedges separated by interfascicular rays, bar = 500 μm. Fig. 3 Detail of Fig. 2 showing primary tissues at pith margin and initial secondary tissues, thin section, bar = 200 μm. Fig. 4 Detail of Fig. 1 showing secondary tissues with interfascicular ray (IR), radial tracheid files (T) and fascicular rays (FR), bar = 200 μm. Fig. 5 Detail of Fig. 1 showing secondary tissue with concentric growth anomaly (widening of parenchyma after narrowing of tracheids), bar = 200 μm. Fig. 6 Tangential longitudinal section showing two nodal zones, associated internode and two leaf traces (LT), thin section, MfNC K 5628, bar = 500 μm. Fig. 7 Detail of Fig. 6, leaf trace, bar = 200 μm. Fig. 8 Tangential longitudinal section showing anatomical detail of branch trace, thin section, MfNC K 5628, bar = 500 μm.

files of 1–4 tracheids and narrow fascicular rays. In transverse view, interfascicular rays are less than 1 mm wide and are made of 3–7 variable parenchymatous cells having 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. Interfascicular rays are continuous between successive nodes. Fascicular wedges gradually enlarge in width centrifugally. Secondary xylem has scalariform secondary wall thickenings and horizontally elongated pits on radial walls. Thickenings are 8 µm apart and are sometimes forked. Tracheids are up to several millimetres in length. In transverse view, tracheid diameters average 58 µm radially and 48 µm tangentially in the inner wood, and 83 µm radially and 65 µm tangentially in the outer wood.

The outer surface is striate reflecting segmentation of the secondary body. Nodes are incised with small, acute, millimetre-diameter, vertically enlarged leaf traces at every second or third fascicle. Leafy twigs depart from whorls of usually 10–15 branches at every 5th to 9th node. Nodes between whorls usually lack branches. Branch traces are 2–6 mm in diameter, lack secondary growth, are slightly enlarged centrifugally, and circular in outline with an acute tip. At irregular distances, additional traces of circular to oval-shaped branches start inside the wood, rapidly enlarging by secondary growth, depart at acute-angles to the stem, and generate adventitious shoots. Sub-circular woody root traces of several centimetres in diameter are present at the stem base.

Arthropitys sterzelii Rößler and Noll, sp. nov. (Fig. 2, Plates VI–IX)

Holotype: Specimen MfNC K 3961 (Plate VI)

Paratype: Specimen MfNC K 5251 (Plate VII)

Additional material: Specimens MfNC K 3257, K 5628 (Plate VIII), MfNC K 4615, K 3247, K 3285, K 3093 (Plate IX), LFUG 160/RS 1986.

Repository: The holotype, the paratype, and additional material are stored in the palaeontological collection of the Museum für Naturkunde Chemnitz; one additional specimen is stored in the collection of the Geological Survey of Saxony at Freiberg, Germany.

Type locality: The city of Chemnitz (Erzgebirge Basin), Germany.

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

Etymology: This species is named in honour of Johann Traugott Sterzel (1841–1914), famous palaeobotanist and first director of the former Natural Scientific Collections of Chemnitz, today's Museum für Naturkunde of Chemnitz, Germany.

Synonymy and selected references:

1832 *C. bistrinata*, Cotta, p. 69, pl. XV, 4.

1864 *A. bistrinata*, Goeppert, p. 183–185, pl. XXXII, 4.

1881 *Calamites bistrinatus*, Stur, p. 31–35, text-figs. 4–7.

1887 *C. bistrinatus*, Stur, p. 27–31, text-figs. 6–9.

1888 *A. bistrinata*, Schenk, p. 108–109, text-fig. 51.

2002 *A. bistrinata*, Tunger and Eulenberger, p. 55, fig. 26, 27.

Diagnosis: Stem consists of central pith/cavity with primary and secondary vascular tissues. Pith is circular and surrounded by primary xylem strands with clearly developed carinal canals surrounded by 2–4 rows of small metaxylem elements. Secondary body shows division into interfascicular rays and fascicular wedges. In transverse view, interfascicular rays are slightly tapered centrifugally, and are made of 2–6 thin-walled rectangular-shaped parenchymatous cells. In radial view, ray cells are highly variable, usually of rectangular outline,

brick-shaped, and higher than long; in tangential view, they are irregular to polygonal in outline. Fascicular wedges consist of radial tracheid files and narrow fascicular rays, which gradually widen centrifugally. Secondary xylem tracheids show reticulate secondary wall thickenings and multiseriate pits on their radial walls. The reticulations are 8–10 µm high and 7–20 µm wide. Tracheids are several millimetres long. In transverse view, their diameters average 48–63 µm radially and 40–59 µm tangentially in the inner wood, and 45–83 µm radially and 45–62 µm tangentially in the outer wood.

Branching is regular, usually at every node, alternating in successive nodes, and lying on the top of each other at every second node. Usually 5 branch traces occur per node in juvenile axes, and irregularly between 2 and 5 traces in adult axes. Traces are broad-oval shaped, vertically acute, lack secondary growth, and range in size from 3 × 5 mm at the top of the axes to 13 × 18 mm at the base. Vertically elongated leaf traces occur at every node. Infrequently nodes without leaf traces may occur. The number of leaf traces around the stem is approximately one third of the number of fascicles.

4. Descriptions and results

4.1. Re-investigation of the type specimens (Cotta, 1832)

Two specimens figured by Cotta (1832, pl. XV, 3–4) and referred to as *C. bistrinata* are stored at the British Museum (Natural History) London. Both, BMNH 13787 and BMNH v.1779, have been re-studied here with the following conclusions: The specimens, formerly thought to be conspecific, actually differ in their anatomical characteristics. Cotta (1832, p. 69) identified one specimen (BMNH 13787) as most characteristic of the taxon. Therefore, BMNH 13787 figured by Cotta (1832, pl. XV, 3) is recognized to be the lectotype of *A. bistrinata* in the revised sense defined in this contribution. The importance of BMNH 13787 may also be emphasized by Göppert (1864), who introduced *Arthropitys* and prominently figured BMNH 13787 at pl. XXXII, 1.

The other specimen (BMNH v.1779, figured in Cotta, 1832, pl. XV, 4) differs in major characteristics at the sub-generic level and, therefore, needs to be re-classified. We therefore introduce *A. sterzelii* sp. nov. (see below).

The lectotype, BMNH 13787, is a polished transverse slice of 2–3 mm in thickness measuring 50 mm in maximum diameter (Plate I, 1, 3–5). The central pith is triangular, measures 13.5 mm in maximum width and is surrounded by 89 primary vascular strands. The pith margin shows remnants of parenchyma plates 0.6–1.0 mm wide and consists of poorly preserved compacted cells. The stem is clearly divided into interfascicular rays and fascicular wedges. This character is recognizable from the pith to the trunk margin. Vascular wedges initially measure 0.40–0.73 mm in thickness and consist of 6–8 tracheid files and small uniseriate fascicular rays. The distance between interfascicular rays initially measures 0.30–0.60 mm, but rapidly narrows to less than 0.2 mm within the innermost 1.5 millimetres. Radially, the fascicular woody wedges gradually enlarge to 1.75 mm maximum thickness. Carinal canals are nearly circular and measure 0.1–0.15 mm in diameter. Preservation is not adequate to recognize metaxylem. The xylem ranges in width from 10 to 21 mm. Secondary xylem tracheids are square to rectangular in transverse view and average 73 µm radially and 65 µm

Plate IX. *Arthropitys sterzelii* sp. nov., additional material. Fig. 1 Radial longitudinal view of a trunk, note long internode, MfNC K 4615, bar = 10 mm. Fig. 2 Detail of Fig.1 showing reticulated wall thickening and multiseriate circular pits in secondary xylem, bar = 50 µm. Fig. 3 Trunk segment after sand blasting showing vascular wedges, note narrow nodes with alternating branch traces (BT), MfNC K 3247, bar = 10 mm. Fig. 4 Radial longitudinal view showing reticulated wall thickenings and multiseriate pits in secondary xylem, MfNC K 3285, bar = 50 µm. Fig. 5 Radial longitudinal view showing variation of wall thickening reticulation and oval pits in secondary xylem, MfNC K 3093, bar = 50 µm. Fig. 6 Radial longitudinal view showing detail of wall thickening reticulation and multiseriate oval pits in secondary xylem, thin section, MfNC K 5628, bar = 20 µm.

Plate X. Fig. 1 Tuff mould showing outer surface preservation of *Arthropitys bistrinata*, note short distance between nodes, two nodes with whorls of large branch traces and Calamophyllites-like trunk leaves (see arrow and close-up), MfNC K 5487, bar = 50 mm. Fig. 2 *Arthropitys bistrinata* (Cotta, 1832) Goeppert, 1864, radial longitudinal and transverse sections of a small trunk, note pith enlargement in whorl position, MfNC K 3271. Fig. 3 Pith cast of a calamite suggesting small amount of secondary growth (see arrow), embedded in tuff rock from Chemnitz petrified forest, MfNC K 5629, original size. Fig. 4 Pith cast of a calamite suggesting large amount of secondary growth (see arrow), embedded in tuff rock from Chemnitz petrified forest, MfNC K 5627, bar = 10 mm. (see on page 116)

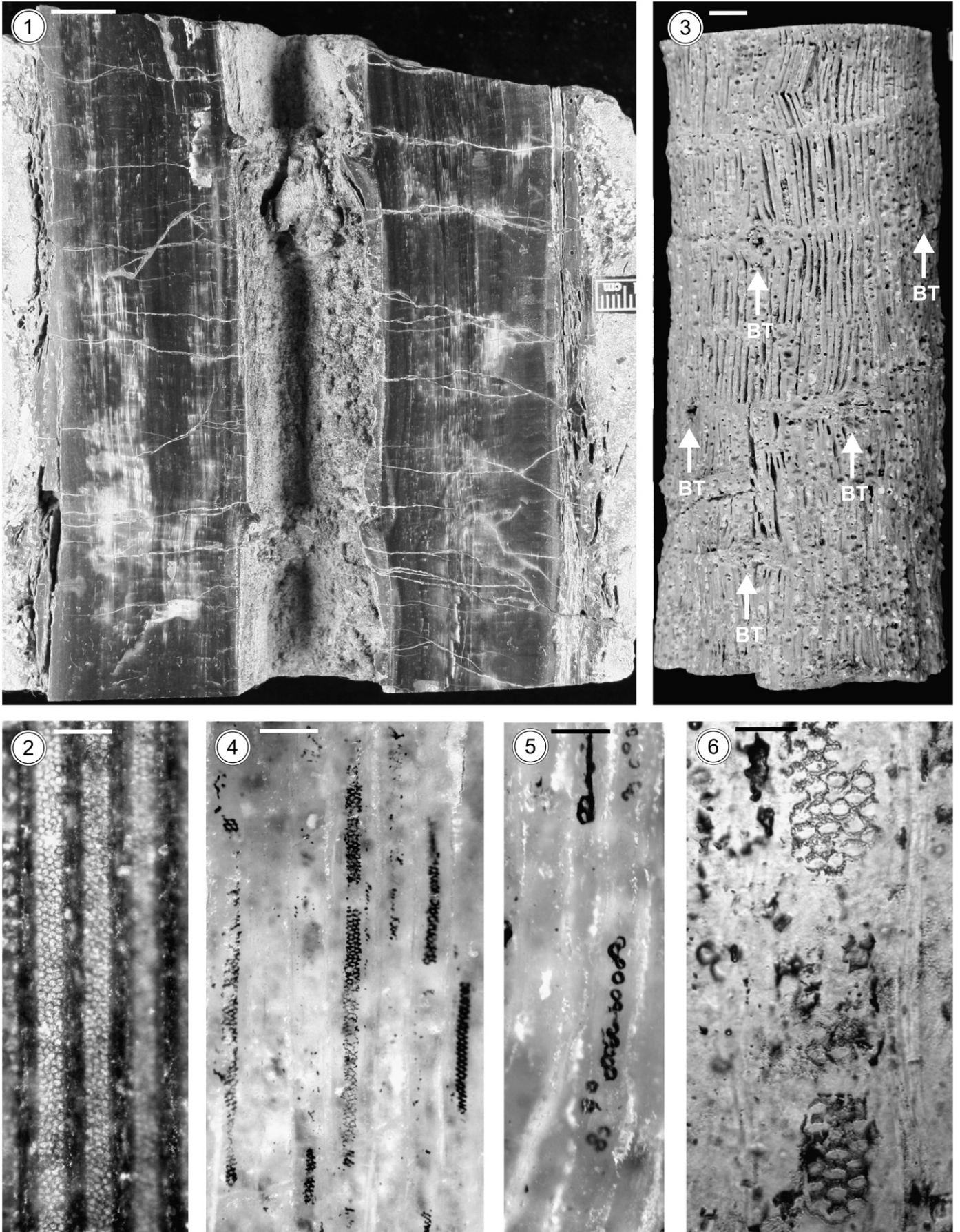


Plate IX.

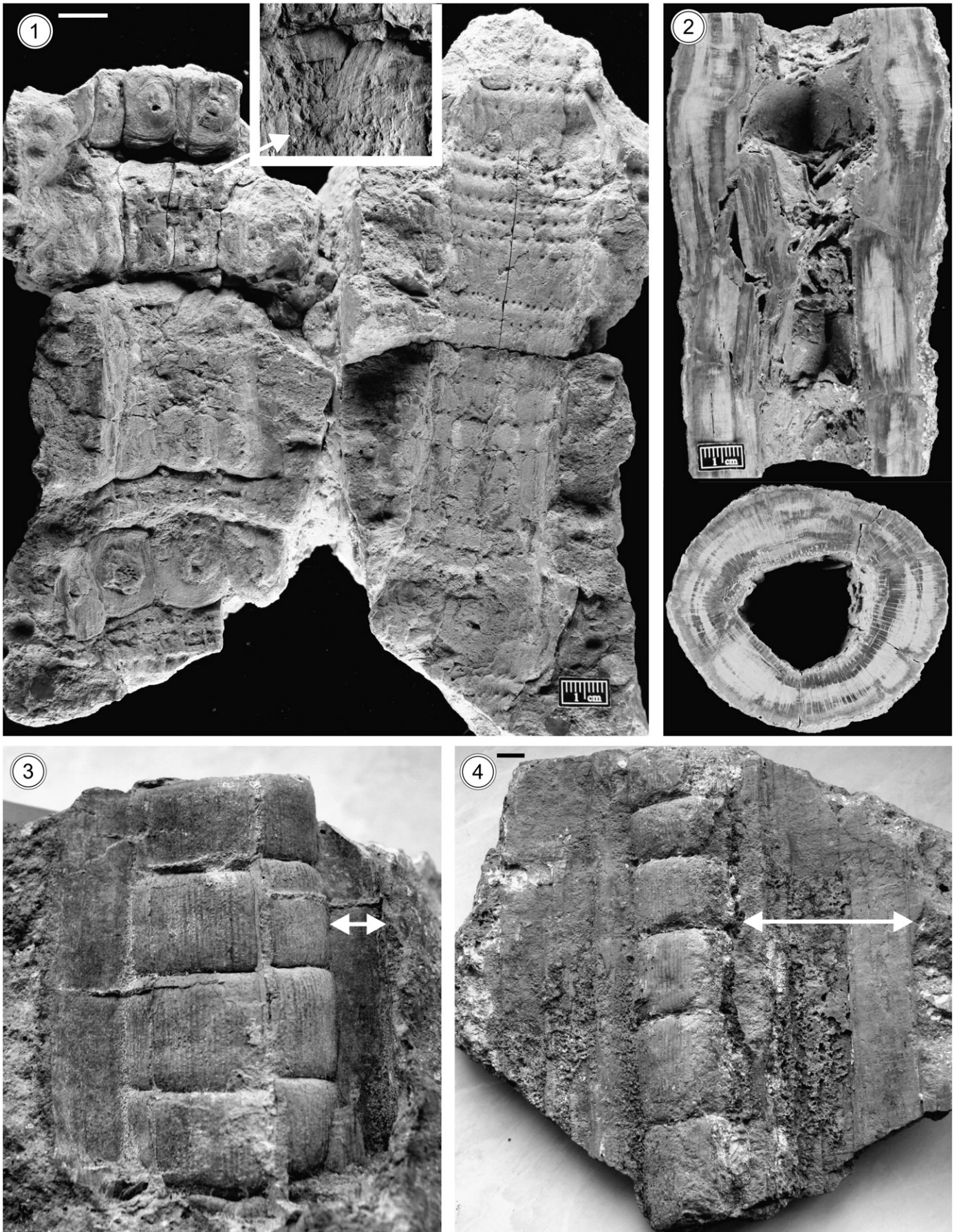


Plate X (caption on page 114).

tangentially. Even in transverse view, black-coloured lamellae indicate scalariform thickenings in radial tracheid walls (Plate I, 5). The margin of BMNH 13787 shows a small broken area making it possible to study the longitudinal surface of the secondary xylem. Although visible only in this small area, it was possible to recognize the simple scalariform type of secondary wall thickening (Plate I, 3). An additional slice cut from the same stem but not figured by Cotta is stored under the same collection number at BMNH (Plate I, 2).

BMNH v.1779 is another polished transverse slice 12–21 mm in thickness, and 55–74 mm in diameter (Plate II, 1). The specimen is slightly compacted and several vascular segments are squeezed into the pith. Additionally, we traced the counterpart of the BMNH v.1779 specimen to the Chemnitz collection (labelled MfNC K 3173; Plate II, 2–5). From the Chemnitz specimen, it was possible to study stem anatomy from both transverse and longitudinal surfaces. The counterpart specimen measures 74 × 58 mm in diameter. The central pith is oval shaped, 12 × 16 mm in maximum width and surrounded by 118 primary vascular strands. The transverse section of the stem shows clear division into interfascicular rays and fascicular woody wedges from the pith to the margin. Vascular wedges measure 0.42–0.74 mm in thickness and consist initially of 6–8 tracheid files and small uniseriate fascicular rays. Interfascicular rays average 0.15 mm in initial width thinning rapidly to 0.07–0.1 mm, but they continue to be clearly visible to the margin. The secondary xylem is 20 to 30 mm wide. Carinal canals are poorly preserved, but nearly circular in outline and measure 0.11–0.25 mm in diameter. Preservation is not adequate to recognize metaxylem. Secondary xylem tracheids are square to rectangular in transverse view and average 42 µm radially and 38 µm tangentially. The tracheid's secondary wall thickening shows a reticulate pattern forming multi-seriate oval to circular pits (Plate II, 3). Because of their small size, none of the Cotta specimens show branching.

4.2. Description of newly discovered specimens

A number of well preserved specimens, which have been found at the type locality enable us to get a more detailed understanding of both the generitype *A. bistrata* (see Table 1) and the newly described species *A. sterzelii* sp. nov. (see Table 2).

4.2.1. *A. bistrata*

4.2.1.1. General remarks. The taxon *A. bistrata* is best characterized from specimen MfNC K 1114 (Plates III, IV). The following description is mainly based on this specimen, with some details augmented by the study of other specimens. K 1114 was found in 1888 by Otto Weber in the city of Chemnitz, at the corner of Terrassen and Flora Streets. He traced this 1.5 m long specimen during construction of a fountain. It occurred 18 m below the street surface, and was found still upright (in growth position) standing and shrouded in the pyroclastics of the Zeisigwald tuff horizon. Thirty years later it was introduced and figured by Sterzel (1918). Unfortunately, he didn't provide any anatomical detail in his description of this specimen. The specimen occurs in several pieces (Plate III, 1), which are all parts of one individual and undoubtedly belong together. The exact position of a few pieces within the stem is not definitely established, since some pieces are cut-bounded and additional pieces are apparently missing. Still, the majority of this sizable calamite stem (99 cm length) remains in the collection of the Museum für Naturkunde Chemnitz (Plate III, 1).

4.2.1.2. Morphology/branching. The permineralized stem was obtained from a mould that recorded the outer surface of the calamite. The preserved surface pattern shows alternating furrows 2 mm wide interrupted by slightly constricted nodes (Sterzel 1918, fig. 69a,b, re-figured at Plate IV, 1). Internodes average 10.86 mm in length (min. 6.5 mm, max. 18 mm). In other specimens (K 3213, K 3271) internode lengths from 4 to 40 mm have been measured. Along

the stem, seven whorls can be seen, each containing 10 oval to circular branch traces (Plate III, 4, Plate IV, 2). Branch traces measure 2.1 to 5.8 mm in diameter and are composed of parenchyma and aquiline tracheids, but don't show any secondary growth. The distance between two successive whorls averages 94.7 mm (min. 58 mm, max. 130 mm). In other specimens (K 3213 and K 5202), the distance between successive whorls ranges from 33–335 mm.

In addition, isolated circular to oval-shaped traces 3–7 mm initial width are sometimes found on the stem's surface (Plate III, 4, 7). In contrast to the whorled branch traces that mark the departure of leafy twigs that originated in the pith, the isolated traces start about 10 mm radial distance from the pith from somewhere inside the wood. The traces depart the wood at an acute angle (approximately 35°), and enlarge rapidly by secondary growth from a few millimetres up to 30 mm over a radial distance of about 20 mm. The K 1114 stem has two such massive woody traces approximately one metre apart (Sterzel, 1918), and are interpreted as adventitious shoots departing from the stem's surface (Plate III, 1). The same structure can be seen in the tangential view of K 675 (Plate V, 1, 2), which is one of the largest known stems of this taxon (diameter 105 × 135 mm).

Recently we obtained the slightly enlarged basal portion of an *A. bistrata* stem (K 5626, Plate V, 3, 4). However, this specimen is mainly preserved by fluorite and, therefore, shows little anatomical detail. Nevertheless, one can recognize three massive woody traces (diameters in mm: 40 × 50, 60 × 70, 60 × 80) that show the positions from which adventitious roots departed.

4.2.1.3. Anatomy of primary/secondary tissues. At the base, the oval-shaped stem measures 52 × 75 mm in diameter (K 1114, Plate III, 5). The pith is compressed and may have had an original diameter of approximately 17 mm. It is surrounded by 90 primary vascular strands. Parenchymatous pith diaphragms occur at the nodes (Plate III, 4, 8), though sometimes they are broken and packed into the pith cavity. About 700 mm higher, the stem diameter is 43 × 55 mm (Plate III, 3), and the pith diameter is 13 × 21 mm. In whorl-providing zones, the pith is enlarged to 22–24 mm (Plate III, 4). At this level, 122 primary vascular strands surround the central cavity. The stem section studied may reflect the epidogenetic phase of development, i.e. the point where the stem apex was attaining its maximum dimensions and producing stem architecture having the greatest vascular complexity.

The protoxylem is replaced by elliptically outlined carinal canals, 50–150 µm wide radially and 60–100 µm wide tangentially (Plate III, 6). Some carinal canals are filled with delicate tyloses, and are surrounded by 2–4 layers of small, circular to oval metaxylem elements that reach 20–50 µm (mean 25 µm) in diameter, but do not show additional detail. The smallest elements are directly attached to the carinal canals.

The radial thickness of the secondary xylem ranges from 10 to 50 mm (15–29 mm in K 1114). The secondary xylem consists of thick-walled tracheids and thin-walled parenchymatous cells that form a cylinder composed of fascicular wood wedges and distinct interfascicular rays. At the pith's periphery, wood wedges measure 0.23–0.35 mm in tangential width and widen radially to 1.7 mm. Each consists of 6 to 32 tracheid rows. Interfascicular rays are 0.16 to 0.24 mm wide and consist of thin-walled parenchyma cells that are square to rectangular in transverse view. They measure 30–84 µm radially and 30–60 µm tangentially. Interfascicular rays taper gradually in radial direction, but continue to the stem's periphery. They are 3–8 cells thick and continue vertically between successive nodes (Plate IV, 4). As much as 45% of the wood consists of parenchyma. In radial view, parenchymatous cells are brick-shaped, 60–110 µm high, but show variability even within the same ray (Plate IV, 5). Usually they range from square to higher than long. In tangential view, parenchyma cells of bi- to multiseriate rays show an irregular to polygonal outline, but, at the ray periphery, they are slightly elongated to rectangular. Secondary xylem is organized in radial files of 1–4 tracheids. Tracheids show scalariform secondary wall

Table 1
Comparison of systematic significant characters in the lectotype and additional material of *Arthropitys bistrata*.

Specimen/characters	BMNH 13787 (lectotype)	K 1114	K 3271	K 675/K 781
Diameter (mm)	Max. 50	40–73	55 × 65	105 × 135
Distance between whorls (mm)	Absent	58 (up to 130) 10 whorls (7 at MfNC-pieces)	Absent	Absent
Internode length (mm)	Absent	11.9 6 8.6	40	20–28
Pith diameter (mm)	13.5	13–21 22–24 at node	25 33 at node	33
Xylem strands width (mm)	0.4–0.73	0.23–0.35 initially after 2 mm: 0.56 after 10 mm: 1.23 after 20 mm: 1.60	0.32–0.47 initially, after 10 mm: 1.25	0.57–0.79 initially after 20 mm: 1.67
Distance (mm) between carinal canals	0.69–1.1	Average 0.42 (0.21–0.91)	0.67–1.45	0.61–1.49
Carinal canal width (µm)	100–150	Small, with tyloses, 70 radial 100 tangential	Absent	50 radial 60–80 tangential
Metaxylem cell diameter (µm)	Absent	2 up to 4 rows 20–50	Absent	30–100
Secondary xylem maximum width (mm)	10–21	15–29	12–18	50
Interfascicular ray width (mm)	Initially 0.3–0.6 distally <0.2	0.16–0.24 initially, 0.09–0.24 distally, in tangential view from node to node, 3–7 cells per ray	0.46–1.0 initially, 0.07–0.19 distally	0.24–0.70 initially, 0.17–0.19 distally
Fascicular rays width (µm)	Absent	Transverse view: 1–3 rows, 20–100	<60	1–3 rows 30–120
Ray cells (µm)	Absent	Initially: 30–71 (56) radial 30–60 (38) tangential, distally: 70–84 radial 45–60 (50) tangential radial view: 60–110 (80) high, cells often higher than long, brick-shaped; tangential view: central cells polygonal, marginal cells rectangular	50–80 rad 40–50 tan	53–70 rad 43–70 tan
Secondary xylem tracheids diameter (µm)	65 tangential 73 radial	Initially: 56–80 (58) radial 40–65 (48) tangential, distally: 65–95 (83) radial 37–85 (65) tangential, 1–4 tracheid rows	Initially: 50–90 (73) radial 34–45 (40) tangential, distally: 56–61 (60) radial 35–57 (40) tangential,	Initially: 55–60 radial 35–55 tangential, medially: 75 radial 56 tangential, distally: 68 radial 50–80 tangential, Absent
Branch traces in whorls diameter (mm)	Absent	Oval to circular, without secondary growth 2.1–4.3 × 3.6–5.8	Absent	Absent
Adventitious shoots diameter (mm)	Absent	Release under 35° 30 at stem surface	Absent	40 at stem surface (15 up to 40 during 20 mm wood thickness)
Leaf traces diameter (mm)	Absent	0.16–0.2 × 0.87–1.0 at every second/third fascicle	Absent	Absent

thickenings and horizontally elongated pits exclusively on their radial walls. The pits have a vertical separation of 7–8 µm (Plate III, 9). Thickenings sometimes fork. Tracheid diameters of the innermost wood average 60 µm (56–80) radially and 48 µm (40–65) tangentially. Near the margin of the trunk, tracheid diameters average 83 µm (65–95) radially and 65 µm (37–85) tangentially. Tracheids measure up to 6 mm in length. Fascicular rays are evenly distributed among the vascular wedges and consist of 1–3 rows of parenchymatous cells.

Phloem, cortical tissues or periderm are not preserved in the studied specimens.

4.2.2. *A. sterzelii* sp. nov.

4.2.2.1. General remarks. Permineralized calamitalean trunk remains are frequently found; however, regardless of their apparent similarity, several major distinctions among calamitalean stems have been recognized. Among the Chemnitz *Arthropitys* permineralizations, which were previously thought to be monospecific *A. bistrata*, there are several sizable trunk specimens that differ markedly in both their anatomical characteristics and branching type from those specimens described above. In view of these observed differences several stems will be assigned to a new species as discussed in the following paragraphs. Five of the most significant specimens were selected and designated as holotype (MfNC K 3961), as paratype (MfNC K 5251) or as

additional material (K 3257, K 4615, K 3285, K 3247, K 3093, K 5628) to characterize the new species *A. sterzelii* sp. nov. The most famous historical specimen that will also be referred to *A. sterzelii* sp. nov., was figured several times (Stur, 1881, 1887; Schenk, 1888) and was recently relocated in the collections at the Geological Survey of Saxony in Freiberg. The specimen (LfUG 160, RS 1986) shows two successive nodes, each with several alternating branch traces. The following description subsumes major characteristics of all investigated specimens, and notes some ontogenetic variation within this species.

4.2.2.2. Morphology/branching. The holotype (K 3961) is 126 cm long and shows a maximum diameter of 78 × 100 mm. Two additional portions, which do not fit directly but unquestionably belong to this trunk specimen, indicate a total specimen length of approximately 180 cm. The paratype (K 5251) is a stem about 120 cm length and 75 × 100 mm maximum diameter. Internode lengths of all available trunk portions vary from 12 to 70 mm (average 27 mm). Branch morphology of *A. sterzelii* sp. nov. suggests considerable affinity to the *Calamites cruciatus* group. During early ontogenetic stages, every node may have shown up to 5 broad-oval-shaped branch traces 3–6.5 mm in thickness that tapered vertically (Plate VI, 5, 10, Plate VII, 3, 7; Plate VIII, 8). They alternate in successive nodes, and usually are aligned vertically at every second node (Plate VI, 4, Plate VII, 3). Although during later ontogenetic stages branch traces reached diameters up to 25 mm

Table 2

Comparison of systematic significant characters in the holotype and additional material of *Arthropitys sterzelii* sp. nov.

Specimen/characters	K 3961 (holotype)	K 3173	K 5251 (paratype)	K 3257	K 4615	K 3285	K 3093
Internode length (mm)	15–38	Absent	24–30 (27.5)	23	70	27	Absent
Pith diameter(mm)	Top: 12 × 46 (29) Base: 20 × 38 (29)	11 × 21 Parenchyma cells circular to polygonal 40–90 µm in diameter	14 × 38	25–30	20–25	21 × 37	ca. 10 × 35
Xylem strand swidth (mm)	0.51–0.87	0.42–0.74	0.59–0.66	0.54–0.58	0.56–0.93	0.49–0.71	Absent
Carinal canal width (µm)	Laterally collapsed 350–400 radial 50–120 tangential	Badly preserved 110–200 radial 150–250 tangential	180–190 radial 220–260 tangential	Oval 180–220 radial 70–120 tangential	Oval elongated 220–280 radial 70–230 tangential	Absent	Absent
Metaxylem cell diameter (µm)	Absent	Absent	3 rows 20–50	3–4 rows 20–110 (smallest inside)	2–4 rows, badly preserved	Absent	Absent
Secondary xylem maximum width (mm)	Top: 14–20 Base: 25–33	20–30	24–31	45–75	34–42	25–30	35–50
Interfascicular ray width (mm)	Initially 0.13–0.19 5 cells per row externally 0.1–0.12	Initially 0.15 medially to distally 0.07–0.1	Initially 0.19–0.29 medially 0.11–0.25 distally 0.23 2–5 cells per ray, narrow in growth zones	Initially 0.14–0.21, up to 6 rows per ray medially 0.11–0.14 in radial course dividing in single/double rows	Initially 0.39 3–6 rows per ray distally 0.1–0.26	Initially 0.25 6 rows per ray	Absent
Fascicular rays width (mm)	0.04	Badly preserved	Not preserved	<i>Transverse view:</i> square to rectangular, 50–80 (59) radial 20–50 (30) tangential <i>radial view:</i> square to rectangular, brick-shaped, close to tracheids usually higher than long 30–230 (115) high 40–100 (72) long <i>tangential view:</i> elongated at ray periphery, internal polygonal (IR) or rectangular elongated (FR)30–230 (90) high 28–50 wide	<i>Transverse view:</i> rectangular, 60–130 (88) radial 30–50 (44) tangential <i>radial view:</i> brick-shaped 70–150 (92) high, 70–100 (82) long <i>tangential view:</i> irregular to polygonal (IR), rectangular (FR), 40–90 (68) high	<i>Transverse view:</i> rectangular 60–100 (70) radial 30–50 tangential	<i>Radial view:</i> 60–150 (99) high 75 long
Ray cells(µm)	<i>Transverse view:</i> square to rectangular 50–160 (69) radial 20–40 tangential <i>radial view:</i> square to rectangular 20–160 (60) high 30–60 (35) long						
Secondary xylem tracheids diameter (µm)	Initially: 40–80 (63) radial, 40–90 (59) tangential distally: 40–90 (63) radial, 40–60 (53) tangential	31–50 radial 25–45 tangential	Initially: 41–50 radial 30–40 tangential distally:40–80 (67) radial 40–70 (56) tangential in growth rings double cell wall thickness but the same cell size	Initially:50–55 radial, 30–45 tangential, after 50 mm (distally):40–60 (53) radial, 40–80 (49) tangential	Initially: 55–60 radial 35–50 tangential after 25 mm (distally): 30–53 (45) radial 57–70 (62) tangential	Initially: 33–90 (55) rad 43–46 tan after 15 mm (distally): 60–90 (83) rad 40–60 (45) tan	Initially: 40–70(48) rad 40–45 tan after 25 mm(distally): 40–60(46) rad 45–60(50) tan
Branch traces diameter (mm)	Without secondary growth, at juvenile axes 5, at adult axes irregular 2–5 per node, top of specimen 3 × 5, base of specimen 13 × 18	Absent	Broad to narrow oval, vertically acute 4.5–6.5 horizontally 6.0–9.5 vertically	Broad-oval, vertically acute 2.0 horizontally, 3.2 vertically	Broad-oval, vertically acute 5.3–6.3 horizontally 4.2–5.0 vertically	Broad-oval, vertically acute 4(8) horizont. 5(10) vertically	
Leaf traces diameter (mm)	Initially: acute-oval 0.1–0.2 horizontally, 0.3–0.6 vertically distally: 8 mm distance between 2 LT, 1.78 × 0.32	Absent	Usually at every second IR, elliptical-elongated, upper end acute, 0.2–0.4 horizontally, 0.7–1.4 vertically	Absent	Elliptical-elongated, upper end acute 0.19 horizontally 0.65 vertically	Absent	Absent

thickness, they lack secondary growth. In tangential view, branch traces consist of a parenchymatous center encircled by undulating tracheids (Plate VIII, 8). Branch traces are recognizable in radial direction throughout the whole secondary xylem, unless they have become overgrown during the plant's growth and successive expansion of the wood. Their diameter increases rapidly within the first few millimetres of secondary tissue, but after this initial expansion, there is insignificant further diameter expansion.

In tangential view, one recognizes small, vertically elongated leaf traces, 0.1–0.6 mm wide and 0.7–1.4 mm high (Plate VI, 6, Plate VII, 8, Plate VIII, 6, 7). They usually occur at every node, but infrequently, individual nodes may lack leaf traces. The number of leaf traces around the stem is approximately one third of the number of fascicles. Leaf traces enlarge slightly as they depart from the pith. The pith diameter varies from 11 to 46 mm.

4.2.2.3. Anatomy of primary/secondary tissues. The pith is circular to oval shaped and is usually preserved as a cavity. In places the pith parenchyma is preserved and recognizable as circular to polygonal cells 40 to 90 μm wide. In the holotype specimen, the number of primary vascular strands surrounding the pith increases from 111 at the base of the stem to 123 at 125 cm above the base.

The protoxylem is replaced by circular to oval-shaped carinal canals (Plate VII, 6; Plate VIII, 3), 70 to 250 μm wide tangentially and 110 to 280 μm wide radially. They are surrounded by 2–4 rows of metaxylem elements, which are 20–50 (110) μm in diameter (Plate VIII, 2–3). Smaller elements are surrounded by larger ones, but don't show additional detail.

The radial extension of the secondary growth reached 10 to 33 mm in the holotype specimen (Plate VI), 24 to 31 mm in the paratype specimen (Plate VII) and up to 75 mm in specimen K 3257 (Plate VIII, 1). Secondary xylem tracheids are thick-walled and organized in radial files of 1–4 tracheids, laterally interrupted by parenchymatous rays. A cylinder of vascular wood wedges and radially continuing interfascicular rays result. Initial fascicular wedges at the pith's periphery measure 0.42 to 0.93 mm in tangential width. In radial course, they gradually widen up to 2.8 mm at about 30 mm distance from the pith and up to 6.1 mm at a distance of 75 mm from the pith. Fascicles enlarge considerably in their radial course and consist of 12 (internally) to 78 (externally) tracheid rows. Several uniseriate to triseriate fascicular rays occur between the fascicles. Interfascicular rays taper gradually but persist in their radial course. They are 0.1 to 0.39 mm wide and consist of 3 to 6 rows of thin-walled parenchyma cells. Occasionally they split. Parenchyma cells are square to rectangular in transverse view averaging 70 (50–160) μm radially and 30 (20–50) μm tangentially. In radial view, they are square to rectangular, brick-shaped, 115 (20–230) μm high and 82 (30–100) μm long. Close to tracheids they are rather higher than long. In tangential view, interfascicular rays are multiseriate and continue throughout the internodes. Fascicular rays are uniseriate to triseriate. Parenchyma cells are slightly elongated at the margin of the ray and polygonal in shape inside the ray. Secondary xylem tracheids are up to several millimetres long. In transverse view, they average 48 (31–80) μm radially and 46 (25–90) μm tangentially in the inner wood and 64 (40–90) μm radially and 55 (30–60) μm tangentially in the outer wood. Specimen K 5251 shows several growth rings formed from tracheids of the same size as the other tracheids making the wood of the stem, but the ring tracheids show a doubling of the cell wall thickness (Plate VII, 4, 5). Radial tracheid walls show equally spaced reticulated wall thickenings (Plate VI, 8–9, Plate IX, 2, 4, 6) vertically separated by 6.8–10 μm . The horizontal separation varies between 7 and 20 μm opening narrow oval pits in a multiseriate pattern. In a few places, where reticulations are horizontally elongated, one might recognize biseriate scalariform thickenings (Plate VI, 7). Sometimes inadequate preservation complicates the recognition of the reticulated pattern (Plate IX, 5).

Phloem, cortical tissues and periderm are not preserved in the studied specimens.

5. Discussion

5.1. Comparison and affinities with other anatomically preserved species

During this study we took the opportunity to compare our material with other anatomically preserved calamitaleans, especially those from the Permian of Chemnitz. One of them, until now thought to be rare, became known as *A. ezonata* (Goepfert, 1864). This species is characterized by its rather homogeneous loose wood without clearly distinct interfascicular rays and fascicular wedges. Recent revision by Rößler and Noll (2006) was based on a few exceptional specimens, one of them – the basal portion of a huge woody tree measuring up to 60 cm in diameter – represents the largest anatomically preserved calamite trunk ever found. Additional collection material has shown that both *A. ezonata* and *A. bistriata* have several characters in common, such as the type of branching and the scalariform wall thickenings in the secondary xylem tracheids. In both species leafy branches are arranged in whorls; between the whorls are nodes without branches. Nevertheless, the species differ in their secondary body. Unlike *A. ezonata*, which has a nearly homogeneous wood cylinder, the generitype *A. bistriata* shows distinct and continuous interfascicular rays and fascicular wedges throughout the whole secondary body. In one of the *A. bistriata* specimens (K 675), clearly separated woody wedges can be traced about 45 mm. A recently found undescribed specimen (KH 0052) shows continuous interfascicular rays throughout the 90 mm secondary body. However, because only large stems have been studied, the relevance of this character needs to be assessed for all of the plant's ontogenetic developmental stages.

One of the most famous specimens usually referred to as *A. bistriata*, is, after this revision, considered to belong to *A. ezonata* (Plate XI, 1–2). Labelled as MfNC K 1 and first illustrated by Sterzel (1918, pl. 5, fig. 71), it has been figured in several textbooks. A recently found specimen (K 5849) also belongs to *A. ezonata* (Plate XI, 3–5).

It remains difficult to assign compression specimens such as calamitalean pith casts to one of these species. Two examples (Plate X, 3–4) have different proportions between their pith and their secondary body. One of these suitably corresponds to the aspect shown by the anatomically preserved specimen K 1 (Plate XI, 1) that was recognized as *A. ezonata*. Nevertheless, without any anatomy, we cannot exclude the possibility that these specimens belong either to *A. ezonata* or to *A. bistriata*.

The anatomical characters that are of systematic significance in the genus *Arthropitys* remain under discussion in the literature. Many characters show considerable degree of variability and, therefore, are of uncertain systematic use. Several anatomical characters remain to be evaluated to determine their systematic utility. Wang et al. (2006) mentioned pitting in ray cells in the wood. This could be an interesting feature, though it seems to be unique to *A. yunnanensis*. Noll et al. (2004) noted similar pitting in the ray cells of a probable *Sphenophyllum* axis from Tocantins, Brazil.

Sometimes the size of secondary xylem tracheids is suggested to be of systematic significance (Cichan and Taylor, 1983). Whereas both *A. deltooides* (Cichan and Taylor, 1983) and *A. yunnanensis* (Wang et al., 2006) show relatively large average cell diameters (around 70 μm), other species such as *A. communis* and the related *A. junlianensis* possess smaller secondary tracheids (around 35 μm to 50 μm). As shown in *A. ezonata*, which can contain up to 330 mm extended secondary xylem, there is some variation in both tracheid size and shape between internal (close to pith) and external (close to stem periphery) wood (Rößler and Noll, 2006). The generitype for *A. bistriata* also exhibits notable variation in tracheid size between internal and external wood. In contrast, a species like *A. sterzelii* sp.



Plate XI. *Arthropitys ezonata* (Goepfert, 1864) Roessler and Noll, 2006. Fig. 1 Longitudinal section of a trunk showing pith, primary and secondary tissues, narrow node distances near a whorl of branches (arrow), MfNC K 1. Fig. 2 Specimen of Fig. 1, tangential section showing whorl of branch traces (arrow), bar = 10 mm. Fig. 3 Trunk portion showing one adventitious shoot, MfNC K 5849. Fig. 4 Transverse section of specimen shown in Fig. 3. Fig. 5 Transverse section of adventitious shoot shown in Fig. 3, bar = 5 mm.

nov. has large amounts of secondary growth, but rarely shows variation in tracheid size/shape between internal and external wood.

The number of currently published anatomically-based *Arthropitys* morpho-species is perhaps excessive. As suggested by other workers (e.g. Wang et al., 2003), some of these different taxa may represent different ontogenetic stages. We believe we have defined more consistent morpho-species among the species referred to as *A. bistriata*, *A. ezonata* and *A. sterzelii* in this contribution, because they have been defined by the use of both anatomical and branching characteristics.

Though of no taxonomic use, it is interesting to note the presence of growth rings in *A. sterzelii*. With several exceptions (e.g. Andrews and Agashe, 1965; Scott et al., 1986), growth rings are absent in most calamitaleans of Carboniferous age. However, this character was recently reported several times among Permian age calamitaleans from Brazil and China (Rößler, 2006; Wang et al., 2006). During this study we recognized growth rings in calamitaleans from the classical Chemnitz locality. Although the distances between successive rings vary considerably, we were able to match the succession of growth rings in the secondary xylem of several stems from the same site. Such growth rings are continuous through the entire circumference of the stem, although the size difference between the whole tracheids is not as prominent as the width of their cell walls. During the Early Permian, the Chemnitz region was strongly affected by volcanism, which could have caused repeated growth interruptions and temporary environmental changes. Traumatic events possibly caused by volcanism, wildfires etc. are indicated in a few cases (Plate VIII, 5). Alternatively, we cannot exclude the possibility of seasonality, as suggested by climatic models (Roscher and Schneider, 2006) of the Early Permian of Europe and Brazil.

5.2. Comparison with compression material

The majority of described calamitalean remains are preserved as compressions. Both sediment casts and moulds of the pith surface are common. Compressions of the stem's outer surface are less common. Since these aspects do not show the plant's tissues, comparisons with permineralized material remain highly problematic. As the early history of calamitalean palaeobotany shows, sometimes different preservational forms hide the true identity of fossil plants (Rößler and Noll, 2007). Nevertheless, compression material usually reflects the former plant's branching type, which contributes to our knowledge of a plant's growth strategies and, therefore, helps to reconstruct the plant. Only a few cases are known that enable direct comparison of both compression and anatomical preservation at the same site. One of these is the Permian petrified forest of Chemnitz. The specimen K 5487 (Plate X, 1) preserved as a tuff compression shows the surface aspect of *A. bistriata* with leaf remains still attached to the trunk and whorls of branch traces. The leaves may represent the *Calamariophyllum zaeiforme* type stem leaves as evidenced by Weiss (1884) from Wettin (Saale Basin) and recently by Noll (2001) from the Donnersberg region (Saar-Nahe Basin). Specimen K 5487 may be the remains of a small stem. The whorls of branch traces are still clearly visible and have not been overgrown during secondary growth.

Generally, the permineralized *A. bistriata* is comparable to the compression species *Calamites undulatus* (Sternberg) emend. Kidston and Jongmans (Barthel, 2002) or *Calamites alternans* (Germar) Stur which represent pith cast preservations, or *Calamites varians* var. *in-signis* Weiss or *Calamites goeppertii* Ettingshausen which are compressions of the outer surface of the trunk and show the large circular branch traces. Branching, usually known as *Calamitina* Hirmer, seems to be more variable than illustrated in popular reconstructions. Leafy branches are distichous, show *Asterophyllites equisetiformis* leaves and *Palaeostachya thuringiaca* strobili (Barthel, 2001). Other growth characteristics are recognizable in permineralized specimens. In *A. ezonata* (Plate XI, 1) the smallest nodal distances usually occur close to the following whorl of branches. Generally, both the number of branchless nodes between whorls and internode lengths are highly

variable depending on environmental factors such as nutrient or water availability. Unfortunately, the systematic importance of these "characters" has been overestimated in former times (e.g. Stur, 1887).

The branches of *A. bistriata* correspond to *Calamites schützei* (Stur, 1887, text-fig. 34–38), which also shows whorls of leafy branches separated by 5 to 13 branchless nodes. Another example is *Calamites approximatus* Brongniart from the Late Pennsylvanian of St. Étienne (France), which was put into synonymy with *C. schützei* by Stur (1887, text-fig. 16–17) and confirmed by Renault (1890, pl. LII, fig. 6; pl. LIII, fig. 1). The same type of branching is recognizable in *A. stephanense* from St. Étienne (Renault, 1890, pl. LIV, fig. 1).

As frequently seen in *A. bistriata*, solitary branch traces sometimes develop on nodes not containing whorls. These are interpreted as adventitious shoots. One of the compression species showing this aspect is *Calamites sachsei* figured in Stur (1887, Taf. V, fig. 1).

Branching morphology in *A. sterzelii* suggests close relations to the *C. cruciatus* group, which was erected exclusively based on branching. This quincunx type branching shows several branches at every node. These alternate in successive nodes and are aligned at every second node. This broad-based morpho-taxon includes a set of calamitalean preservational forms, among them the pith cast compression *Calamites multiramis* Weiss or the permineralized *Calamitea* Cotta, which was re-studied and revised recently (Rößler and Noll, 2007). These studies suggest that branching type alone has limited taxonomic relevance and that additional anatomical characteristics are required to differentiate taxa.

Stur (1887, p. 31, text-fig. 6–9) illustrated a specimen as *C. bistriatus* and stated this might be conspecific with *Calamites infractus*. Each taxon was interpreted to represent different preservational forms of the same plant. This specimen was traced to the collection in the Geological Survey of Saxony at Freiberg, re-studied and herein re-classified as *A. sterzelii*.

6. Conclusion

Calamitaleans were dominant plants within low-latitude wetland forests of the early Palaeozoic. However, the taxonomic richness making them very abundant in floral lists is rather a result of both their decomposition into single organs or organ fragments and their separate naming as morpho-taxa. There is a significant difference between the quick recognition of a calamitalean axis and its determination at the species level, especially for compression stem morphology and branching traditionally used for systematics. Now, using sizable specimens from the type locality, we apply morphological features to characterize permineralizations. This contribution has resulted in two completely different branching types being recognized among *Arthropitys* calamitaleans from the Early Permian Rotliegend of Chemnitz (Figs. 1–2).

With regard to their habitats, morphology and anatomy, calamitaleans have been understood as a rather uniform group – unique perennial plants combining a number of developmental and morphological peculiarities such as arborescence and aerial growth linked to an underground system of rhizomes and hollow stems combined with extensive wood development and a nodal-branching architecture (Spatz et al., 1998). Recently, this interpretation has started changing considerably. Newly collected calamitaleans from fluvio-lacustrine deposits in Tocantins/Brazil and from the volcanoclastics in Chemnitz Germany impart a different view of calamite trees and their increasingly modified environment in the Early Permian. Study of the largest calamite trunks ever found indicates that calamites had several different branching forms and more variation in branching patterns than previously thought. Findings confirm that only a few branches (adventitious shoots) seem to have been permanent. This characteristic would have a definite impact on calamitalean biomechanics (Plate III, 1; Plate V, 1–2). The plants show considerable secondary growth that starts, as expected, external to the stele, but sometimes without leaving

any indication of its existence on the pith surface. Therefore, major branches that may have influenced plant biomechanics are currently not illustrated in most reconstructions. Other branches that were herbaceous and probably grew and abscised seasonally are seen on the pith cast. Reconstructions based on this information alone do not adequately reflect the growth architecture of the calamite as a whole.

Some kind of climatic cyclicality is suggested by the growth rings found on several *Arthropitys* stems and roots. The large *A. ezonata* from Chemnitz is characterized by its rather homogeneous, loose wood that shows high portions (approximately 50%) of parenchyma in the secondary xylem. Therefore, it has been suggested that some, if not all, of the Permian calamitaleans, may have survived short seasonal episodes of dryness during which they reduced water uptake and shed their herbaceous branches (Rößler and Noll, 2006). This inference is supported by the large-diameter, long living trunks. An *Arthropitys* type calamite from Tocantins measures up to 40 cm in diameter and exhibits two primary bodies (i.e. a possible branching basal stem) and woody adventitious roots of variable size measuring 1 to 8 cm across (Rößler, 2006). This specimen points to calamite trees that may have become more and more independent from the underground rhizome during their ontogeny, a growth form that has already been suggested for some Late Carboniferous and Early Permian calamite species (Grand'Eury, 1877, pl. III, fig. 1; Leistikow, 1962, pl. XV, fig. 85; Barthel, 2002). Future research will investigate whether single calamite trees could have lived without their rhizome, at least from a later growth stage onwards, when the plant was supported and strengthened by the stem's secondary xylem and adventitious roots. The woody roots of different sizes may have anchored the upright stems in the sediment. The biomechanical properties of the axes, including the enormous weight and diverse types of side branches, need to be evaluated to see if such a growth form is feasible.

In addition to those interesting ecological aspects, all characters used for calamite systematics need to be re-evaluated with regard to their taxonomic significance. As stated several times by previous authors, many characters, such as frequently used measurement ratios or parenchyma and xylem anatomical features show considerable variability, which seems to be due to both ontogenetic change and references to edaphic and ecological variation. Large-diameter woody trunks also point to an extended longevity for individual Permian calamite plants. The high percentage of parenchyma may represent "succulence" to a certain degree. Both characters could be interpreted as adaptations to ensure adequate reproductive capabilities and survival in a more dynamic or disturbed environment, compared with the more stable climax vegetation of the Carboniferous coastal tropics. With regard to future plant reconstructions, one should take care to avoid over-interpreting the value of single preservation states such as pith cast compressions. Only the consideration of all aspects of the primary and secondary body, branching, and the ontogenetic development, will reveal the plant's growth habit as a whole, and will lead to more consistent knowledge of the extinct calamitaleans.

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