Sphenopsids of the Permian (I): The largest known anatomically preserved calamite, an exceptional find from the petrified forest of Chemnitz, Germany

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Abstract

The stem anatomy and internal organisation of a newly collected sphenophyte trunk is studied from the type locality of *Arthropitys*, the Lower Permian petrified forest of Chemnitz, Germany. The trunk was found nearly in situ, still standing upright, and embedded in coarse-grained pyroclastics of the Zeisigwald Tuff Horizon (Leukersdorf Formation, Erzgebirge Basin). This specimen – the basal portion of a huge woody tree measuring up to 60 cm in diameter – represents the largest anatomically preserved calamite trunk ever found. On the basis of current investigation the exceptional find has been attributed to *Arthropitys ezonata* Goeppert, which is more completely characterised and emended herein. This species is characterised by its rather homogeneous loose wood without clearly distinct interfascicular rays and fascicular wedges. For the first time we are able to show details of the primary body of this poorly understood species such as vascular strands and pith parenchyma. Comparisons are made with the generitype *Arthropitys bistriata* (Cotta) Goeppert and other species of the genus *Arthropitys*.
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1. Introduction

Arboreal giants dominated the Carboniferous and Permian low-latitude wetland forests (DiMichele and Phillips, 1994; Hilton et al., 2001). Among them were the calamite trees, unique hollow perennial trees, which are among the most interesting, but at the same time also the most puzzling, Late Palaeozoic plants (Leistikow, 1975). They include the largest sphenopsids known to date and combine a number of developmental and morphological peculiarities, such as arborescence and aerial growth linked to an underground system of rhizomes, hollow stems combined with extensive wood development and a nodal-branching architecture (Spatz et al., 1998).

Calamite trees sensu stricto were highly successful and flourished in different tropical wetland environments. They persisted for more than 60 million years from the Early Namurian (Gerrienne et al., 1999) up to the Late Permian (Wang et al., 2003). Although they were well adapted to the gradual environmental changes that happened during Late Palaeozoic times, they became extinct at the end of the Permian. The

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Calamitaceae occurred in several floral realms of both the Northern and Southern Hemispheres, and their fossil record from Euramerica, Cathaysia and Gondwana (Galtier, 1997; Rößler and Noll, 2002; Wang et al., 2003) is exceptionally rich and, additionally, diverse in terms of preservation.

Calamite trees may have been up to 10 m tall with frequent branches at their nodes and a more or less substantial layer of woody tissue around the central pith (Eggert, 1962). They are interpreted as having shown telescopic growth and, though they are often recon- structed in a rather uniform way, there is a growing awareness of the broad morphological diversity within this plant group (Hirmer, 1927; Leistikow, 1962; Boureau, 1964; Barthel, 2002, 2004). Daviero and Lecoustre (2000) proposed the first computer simulation of *Calamites multiramis* architecture.

Although calamites were easily able to reproduce vegetatively by their underground rhizomatous system, they also dispersed numerous spores. Calamite trees usually formed dense hygrophilous stands surrounding lakes, but they also grew in swamps and along river banks (Scott, 1979; Pfefferkorn et al., 2001). However, there is evidence that some members may have developed parenchyma-dominated water-storing succu- lent soft tissues and, therefore, may have tolerated periodic drier conditions (Barthel, 1989; Barthel and Rößler, 1994; Rößler and Noll, 2002).

The pith casts of hollow stems, coalified compres- sions of the leafy shoots and strobili are among the most common fossils found in Upper Carboniferous and Lower Permian strata, although instructive organ connections remain rather rare. Sometimes, in the case of coal balls or petrified forests, the stem tissues are also preserved; the latter often showing all cellular details.

In this contribution we describe a newly discovered silicified trunk that represents the largest anatomically preserved calamitean specimen known so far. Generally, it is characterised by a huge cylinder of homogeneous loose wood. Based on its anatomical characters it is attributable to the genus *Arthropitys* Goeppert. Al- though maximum stem diameters in calamite trees of about 1 m are frequently discussed in the literature (Grand'Eury, 1877; Hirmer, 1927; Mosbrugger, 1990; Spatz et al., 1998) until now the largest published stem actually evidenced by its permineralised tissues mea- sured only about 30 cm (Andrews and Agashe, 1965). Other examples are based on pith casts, up to 65 cm in diameter (Renault, 1893–1896; Langiaux, 1984, p. 35), unfortunately without any preserved parts of the secondary body, rendering highly speculative any estimate of the life sizes.

2. Geological and stratigraphical background

2.1. Locality and source strata

Although petrified forests are more widespread than commonly thought, only a few examples have become as famous as the Chemnitz Petrified Forest, where nearly an entire forest of Permian plants became fossilised (Sterzel, 1875, 1918). The origin of the Chemnitz Petrified Forest is closely related to rhyolithic explosive volcanism that happened almost 280 million years ago. One of the eruptions northeast of Chemnitz resulted in the formation of a pyroclastic sequence now referred to as the Zeisigwald Tuff Horizon. The latter is part of the Leukersdorf Formation that consists of approximately 800 m of sedimentary and volcanic deposits. The whole succession (Fig. 1) consists of three depositional cycles, which start at their erosive base with alluvial coarse clastics and develop fining upward into fine-grained palustrine or lacustrine cycle tops (Döring et al., 1999).

The stratigraphic position of the Leukersdorf For- mation corresponds to the Upper Asselian/Lower Sakmarian, which could be concluded from a rich microflora obtained from the palustrine Rottluff Coal situated within the lower part of the Leukersdorf Formation (Fig. 1). Palynostratigraphic investigation carried out by Döring et al. (1999) suggested close similarities of the lower Leukersdorf Formation to the late Asselian Slavjanskaja Svita of the Donezk Basin reference section. Further correlations based on eryopid and diadectid vertebrate remains delivered similar implications (Werneburg, 1993; Schneider et al., 1995). The Zeisigwald Tuff Horizon of the upper Leukersdorf Formation corresponds to an absolute age of about 278 million years as recently obtained by SHRIMP ion probe investigations (Nasdala et al., 1998).

Important fossil-bearing outcrops of this formation are situated within the whole city of Chemnitz (Erzgebirge Basin). Therefore, this set of localities is designated the Chemnitz Petrified Forest (Barthel, 1976; Rößler, 2001).

2.2. Taphonomic implications

The deposition of the Zeisigwald Tuff Horizon is the result of a multi-storey caldera eruption, i.e., a de- positional sequence of several devastating "glowing- cloud eruptions" and the repeated sedimentation of pyroclastic flow deposits (Eulenberger et al., 1995). Such hot, dense and unsorted flows are often connected with so-called surges, tremendous lateral blasts, whose
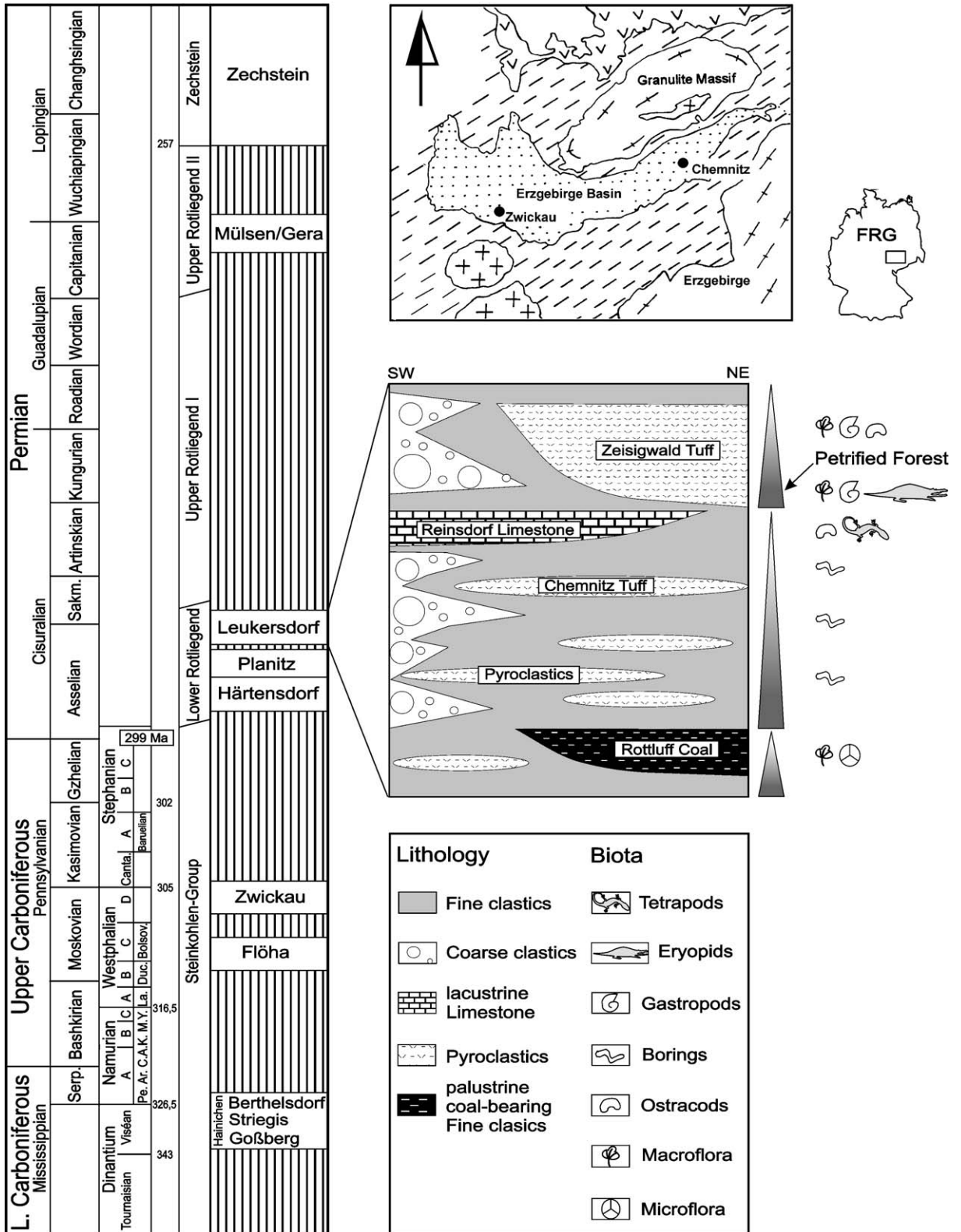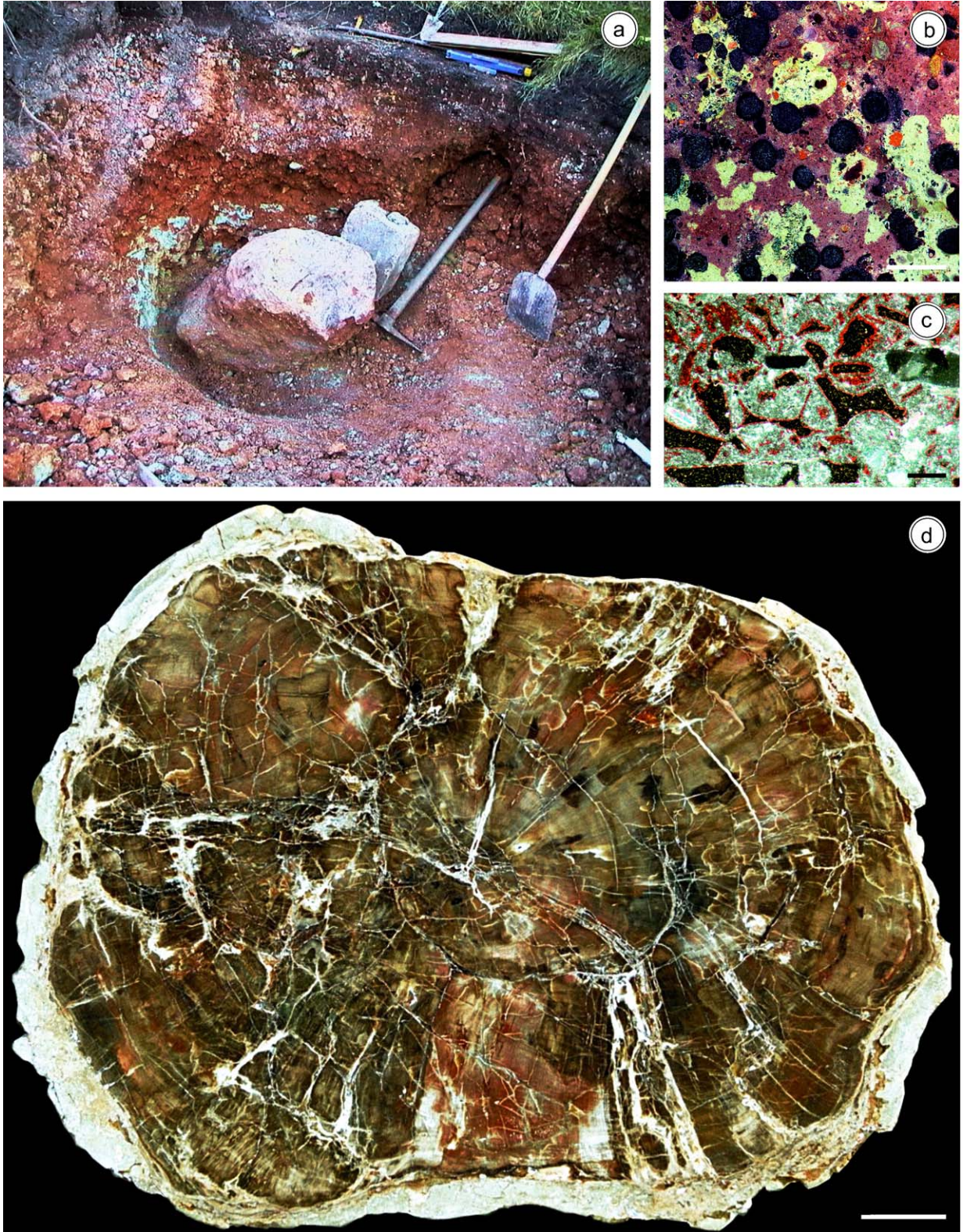
Fig. 1. Stratigraphic and geological frame of the Petrified Forest of Chemnitz.

force and direction are sometimes strikingly demonstrated by the parallel alignment of toppled large trees broken off at their bases (Hoblitt et al., 1981). Such a giant blast is interpreted as the key process for the origin of the Chemnitz Petrified Forest. At this time, the descending ashes buried and conserved the remnants of a unique ecosystem, thus creating conditions that led to the formation of a so-called petrified forest. The tops of the fossilised trees point towards the west, in the direction the annihilating blast was moving as it spread outwards from its epicenter during the first few seconds after the Zeisigwald volcano erupted. Enormous tree trunks were snapped like matchsticks and instantly stripped of their branches and bark, but they fell and remained lying for subsequent petrification near where they had stood only moments before.

The genesis of the Chemnitz Petrified Forest can be reconstructed based on comparison with the effects produced by the eruption of Mount St. Helens in the Cascade Range of Washington State, USA, in May 1980 (Hoblitt et al., 1981). Thorough study of the volcanic deposits (Wiatt, 1981; Burnham, 1994) and the appearance of the vegetation after this eruption has contributed greatly to our understanding of the events that occurred more than 280 million years earlier in Chemnitz.

In some cases (compare Fig. 2a) tree trunks even remained standing. The calamite tree described here was considerably affected by the eruption. The dense wood shows centimetre wide cracks filled with green-coloured tuff. Nevertheless, preservation by volcanic processes has clear advantages: plants were usually embedded very quickly, in or close to their original habitat (Behrensmeyer and Hook, 1992). Because of the rapidity and intensity of the processes related to volcanigenic fossilisation we have some of the most complete and perfectly preserved fossil plant assemblages known (Rößler and Barthel, 1998). For this reason, the Chemnitz locality provides favourable preconditions for the complex task of investigating both the well-preserved Permian floral elements and the permineralisation process itself (Nestler et al., 2003; Witke et al., 2004).

The major plant-bearing layer is situated at the base of the so-called base surge deposit of the Zeisigwald Tuff Horizon, a coarse-grained lapilli-containing ash tuff, which originated from the deposition of hyperconcentrated glowing clouds. The eruption caused the preser-

vation of a species-rich association of tree ferns, arboreal sphenophytes, different pteridosperms, conifers, cordaitaleans and climbing or epiphytic plants, and resulted in the formation of an exceptional fossil assemblage. Only here does such a large floristic diversity of Permian permineralised plants occur in situ. Everywhere, where the base of the Zeisigwald tuff crops out on the surface, we can still find the petrified trunks today.

The spectrum of preservational types is diverse, ranging from hollow impressions and imprints of plants in volcanic tuffs up to almost perfectly preserved specimens that reveal the fossilised remains of microscopic structures in the plants' internal anatomy. For a more detailed overview of the geological setting and the entire fossil record of the Chemnitz Petrified Forest refer to Rößler (2001).

3. Material, preservation, methods and storage

This study focuses on a recently collected *Arthropitys* trunk from the Permian of Chemnitz (Fig. 2a) that was found in situ incorporated in coarse-grained purple-red or pale-green coloured volcaniclastics (Fig. 2b, c) of the surge sequence of the Zeisigwald Tuff Horizon (Leukersdorf Formation, Erzgebirge Basin). Specimen is housed in the palaeontological collection (petrified wood collection) of the Museum für Naturkunde, Chemnitz, Germany, labelled MfNC K 5200.

The fossil plant studied here is three-dimensionally preserved as a siliceous cellular permineralisation. However, depending on the completeness of silicification, the material sometimes shows imperfect anatomical details. Since organic remains themselves have not been preserved in this kind of material, the low contrast makes it more difficult to recognise cell walls in particular, or characters below cell level in general.

Silica-rich fluids apparently penetrated the remaining wood, which subsequently led to several generations of dense quartz polymorphs (Witke et al., 2004). This may have happened when silicic acids, leached out of the volcanic deposits, filled up the cells, where they solidified and preserved the anatomical structure of the plant. Sometimes the surrounding tuffaceous matrix also is partly silicified.

The trunk was cut with a trimming saw to reveal both transverse and longitudinal sections of the stem. These

Fig. 2. *Arthropitys ezonata* Goeppert from the Permian Petrified Forest of Chemnitz. Surge sequence of the Zeisigwald Tuff Horizon. MfNC K 5200. (a) Base of a huge woody tree, still standing nearly upright, in situ and embedded in coarse-grained volcaniclastics, excavation 03.02.2002. (b) Accretionary lapilli containing ash tuff — the rock that incorporated the petrified forest of Chemnitz; surge sequence of the Zeisigwald tuff. Scale bar equals 30 mm. (c) Thin section from the Zeisigwald tuff surge sequence showing thick-walled vesicular shards. Scale bar equals 200 μm. (d) Transverse section about 120 cm above the base of the trunk. Scale bar equals 50 mm.

surfaces subsequently were ground and polished and examined using reflected light microscopy. All specimens, the newly found trunk and comparative material, were examined both from transverse and longitudinal (radial and tangential) finely ground and polished surfaces. Additional details were obtained from thin sections.

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. Overview photographs were made by using a NIKON F 70 camera combined with a SIGMA APO Macro 180 F 3.5 EX lens. The use of polarised light was helpful to increase cellular detail.

For comparative purposes additional material was investigated. One specimen (MfNC K 5249), formerly identified as *Dadoxylon*, proved to be an *Arthropitys ezonata* calamite and therefore is described herein. Several thin sections and one slice cut from Goeppert's type specimen of *A. ezonata* (MfNC K 3309) as well as a set of *Arthropitys bistriata* specimens from the Permian of Chemnitz were also available for comparison.

4. Systematics

Class: Sphenopsida
Order: Equisetales
Family: Calamitaceae

ARTHROPITYS Goeppert 1864
Type-species: *Arthropitys bistriata* (Cotta 1832) Goeppert, 1864
Further included species: *A. communis* (Binney) Renault, 1876, *A. medullata* Reault, 1876, *A. "lineata"* Renault, 1876, *A. bistriata* (Cotta) Goeppert var. *borgiensis* Renault 1888, *A. approximata* (Schlotheim) Renault 1890, *A. gigas* (Brongniart) Renault 1890, *A. bistriata* (Cotta) Goeppert var. *augustodunensis* Renault 1895, *A. bistriata* (Cotta) Goeppert var. *valdajolensis* Renault 1895, *A. gallica* Renault 1896, *A. major* (Weiss) Renault 1896, *A. porosa* Renault 1896, *A. rochei* Renault 1896, *A. communis* (Binney) var. *interlignea* Hirmer and Knoell 1935, *A. felixi* Hirmer and Knoell 1935, *A. bistriatoides* Hirmer and Knoell 1935, *A. hirmeri* Knoell 1935, *A. hirmeri* Knoell var. *intermedia* Knoell 1935, *A. jongmansi* Hirmer and Knoell 1935, *A. renaulti* Hirmer and Knoell 1935, *A. herbacea* Hirmer and Knoell 1935, *A. communis* (Binney) Hirmer and Knoell 1935 var. *septata* Andrews 1952, *A. kansana* Andrews 1952, *A. versifoveata* Anderson 1954, *A. illinoensis* Anderson 1954, *A. deltoides* Cichan and Taylor 1983, *A. yunnanensis*

(Tian and Gu 1995) ex Wang, Hilton, Galtier and Tian, 2003.
Remark: The quality and expressiveness of the material on which aforementioned 21 species of *Arthropitys* are based considerably differs from one another. Therefore, the reliability of some of the species listed above is doubtful. Several species are based only on small, isolated fragments. Others were derived from transverse sections only or did not show any characters of secondary growth, which is the main reason to make this generic assignment.

Arthropitys ezonata Goeppert 1864, nov. emend. Rößler and Noll (Figs. 2–7)
Holotype: The specimen mentioned by Goeppert (1864, 1865, p. 185, pl. LVIII, Fig. 1–6).
Type locality: Temporary excavation in the city of Chemnitz (Erzgebirge Basin), Germany.
Type stratum: The Lower Permian Zeisigwald Tuff Horizon of the Leukersdorf Formation (Fig. 1).
Synonymy and selected references:
1864–65 *Arthropitys ezonata* n. sp., Goeppert, p. 185, pl. 58, 1–6.
1877 *Arthropitys ezonata*, Grand'Eury, p. 289.
1896 *Arthropitys ezonata*, Renault, p. 10–11.
1918 *Arthropitys ezonata*, Sterzel, p. 261.
1952 *Arthropitys ezonata*, Andrews, p. 194.
1964 *Arthropitys ezonata*, Boureau, p. 309.
Emended diagnosis: Trunk consisting of central pith/cavity, primary and secondary vascular tissues. Pith narrow, of thin-walled hexagonal to polygonal parenchymatous cells, approximately two times longer than wide. More than 70 primary xylem strands, distance between adjacent strands less than 1 mm. Clearly developed carinal canals, surrounded by 2–3 rows of small, scalariform thickened metaxylem tracheids reaching 20–50 μm in diameter. Large secondary body of loose wood consisting of variable parenchymatous rays and radial files of 1–4 tracheids. Division into interfascicular rays and fascicular wedges recognisable up to several millimetres from the pith, but not visible over majority of secondary body. In transverse view interfascicular rays made of 2–5 parenchymatous cells, tangentially elongated at pith periphery, of polygonal to rectangular outline more centrifugally. In radial view ray cells are highly variable, normally of square to rectangular outline up to three times longer than high, but in some cases slightly higher than long. Fascicular wedges consist of tracheid files and fascicular rays initially with 10–18 tracheid rows, gradually enlarging and increasingly interrupted by secondary rays centrifugally. Rays of thin-walled parenchymatous cells showing nearly rectangular outline in
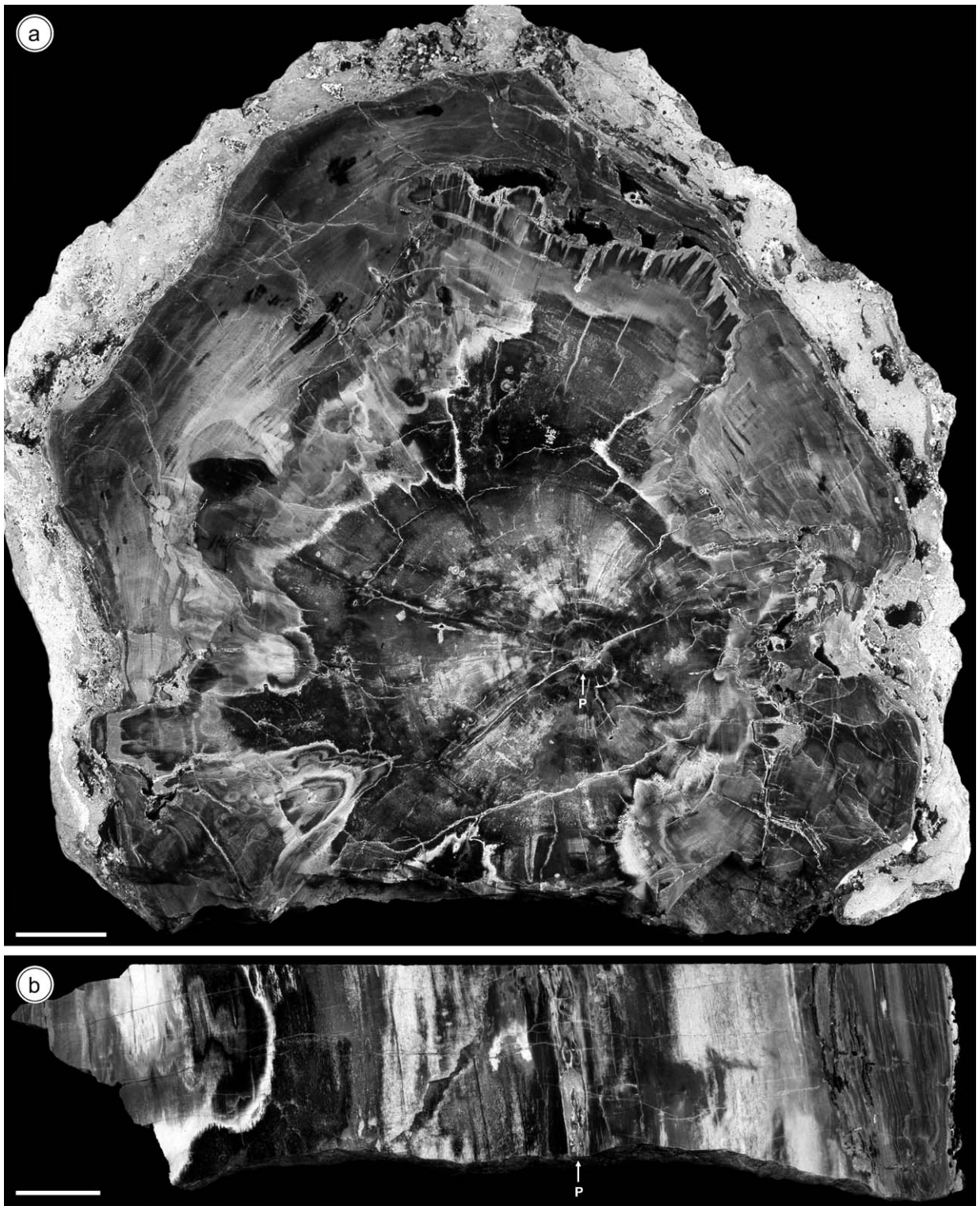
Fig. 3. *Arthropitys ezonata* Goeppert from the Permian Petrified Forest of Chemnitz. MfNC K 5200. (a) Transverse section obtained about 10 cm above the bottom of the trunk that is surrounded by a mantle of coarse-grained pyroclastics. Scale bar equals 50 mm. (b) Longitudinal section through the pith (p) from the bottom of the trunk. Scale bar equals 50 mm.

transverse and radial views; in tangential view parenchyma cells of irregular to polygonal outline. Rays up to 6 cells thick and 5–40 cells high rendering secondary body highly parenchymatous. Secondary xylem organized in radial files of 1–4 tracheids with scalariform secondary wall thickenings/pits on their radial walls. Thickenings 7 μm apart and sometimes forked. Tracheids up to 4 mm long, length continuously increasing from pith to stem periphery, in transverse view averaging around 50 μm tangentially and 60 μm radially in the inner wood, averaging around 60 μm tangentially and 70 μm radially in the outer wood.

Discussion: The species *Arthropitys ezonata* was erected by Goeppert based on a single specimen from Chemnitz that was subsequently cut into several pieces. One portion and several associated thin sections of the holotype are re-figured here (Fig. 6a–d). The latter is stored in the palaeontological collection (petrified wood collection) of the Museum für Naturkunde Chemnitz, Germany, labelled MfNC K 3309. From the literature, further occurrences of this species are known from such localities as St. Étienne and Autun, France (Jongmans, 1914).

5. Descriptions (Table 1)

5.1. Newly discovered specimen

The newly discovered specimen (MfNC K 5200) is 1.30 m long and varies from 470×600 mm in diameter near the bottom (Fig. 3a) up to 375×540 mm at the top (Fig. 2d), excluding extraxylary tissues, which are not preserved. The trunk is elliptical to circular in outline (Fig. 3a). The largest radius of the basal trunk measures 345 mm. Due to its silicified tuff cover we were not able to observe any branch traces or branches. However, there may have been no branches in this basal portion of the trunk.

The pith is small elliptical (Fig. 4a), 14–17 mm wide, slightly excentrically positioned and made of thin-walled hexagonal to polygonal parenchymatous cells that are elongated in transverse view, 70–190 μm wide and 80–270 μm high (Fig. 4c). The pith only slightly enlarges in vertical direction. Though completely crushed at a height of 120 cm above the base (Fig. 2d) the pith measures about 18 mm. As the largest longitudinal plane that we were able to obtain is shorter than 10 cm (Fig. 3b) and does not show any

nodal region, we can only conclude internodes may be longer than 10 cm. The outer periphery of the pith is surrounded by 74 primary xylem strands. The protoxylem is replaced by elliptically outlined carinal canals, 150 μm wide radially and 110 μm wide tangentially (Fig. 4d). Due to the mode of preservation the carinal canal is not clearly visible in every primary xylem strand. Carinal canals are surrounded by 2–3 layers of small, circular to oval metaxylem elements that reach 20–50 μm in diameter, but do not show further detail.

The secondary xylem preserved in our specimen consists of thick-walled tracheids and thin-walled parenchymatous cells forming a dense and quite enlarged cylinder of loose wood. The latter extends up to 330 mm in radial thickness, and in transverse view it seems to be very homogeneous beginning a few millimetres behind the protoxylem strands centrifugally. Small fascicular wood wedges measuring 0.45–0.6 mm in tangential width are distinct only at the pith periphery and consist of 10 to 18 rows of tracheids that are increasingly interrupted by small rays centrifugally. The space between the wood wedges, the so-called primary or interfascicular rays (0.2–0.45 mm), is filled with thin-walled parenchyma cells measuring to 50–210 μm tangentially and 40–100 μm radially. Primary rays taper considerably within a distance of approximately 1.5 to 2.5 mm from the pith periphery, but they continue to the stem periphery. However, within the large secondary body there is no recognisable differentiation of interfascicular zones and fascicular rays.

Rays are 1–6 cells thick and 5–40 cells high, providing a considerable parenchymatous portion to the secondary body reaching up to approximately 50% (Fig. 5e). The rays consist of thin-walled parenchymatous cells that are square to rectangular in radial and transverse view, measuring 50–130 μm (Fig. 5a). In radial view parenchymatous cells are of square to rectangular outline, but they show considerable variability even within the same ray. Normally they range from slightly-longer-than-high up to three-times-longer-than-high, but in some cases they are slightly higher than long. In tangential view parenchyma cells of uniseriate rays sometimes show slightly oblique end walls. Cells of bi- to multiseriate rays show an irregular to polygonal outline in tangential view and are 70–150 μm high and 30–100 μm wide.

Fig. 4. *Arthropitys ezonata* Goeppert from the Permian Petrified Forest of Chemnitz. MfNC K 5200. (a) Detail of Fig. 3a showing pith and surrounding vascular strands. Scale bar equals 5 mm. (b) Detail of Fig. 3b showing pith (arrows). Scale bar equals 10 mm. (c) Detail of panel a showing hexagonal thin-walled parenchyma cells of the pith. Scale bar equals 100 μm. (d) Detail of panel a showing several vascular strands at the pith periphery, carinal canals are indicated by arrows. Scale bar equals 250 μm.
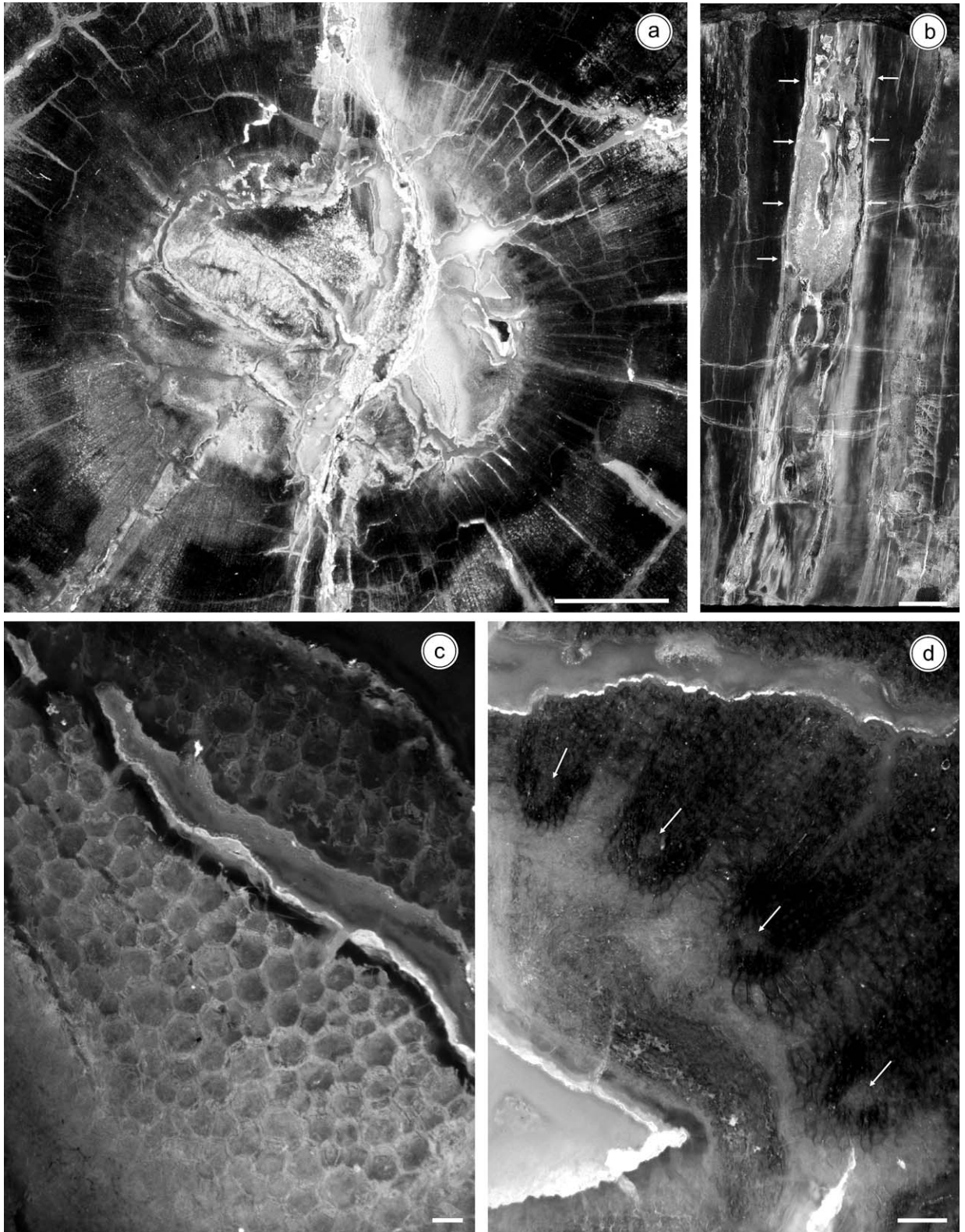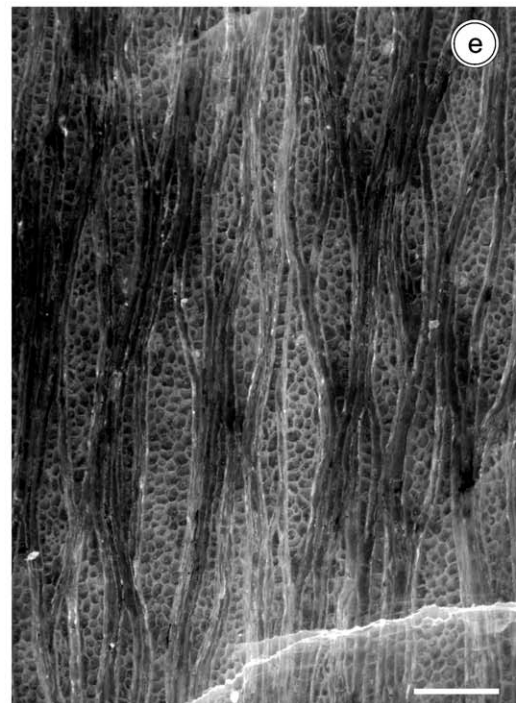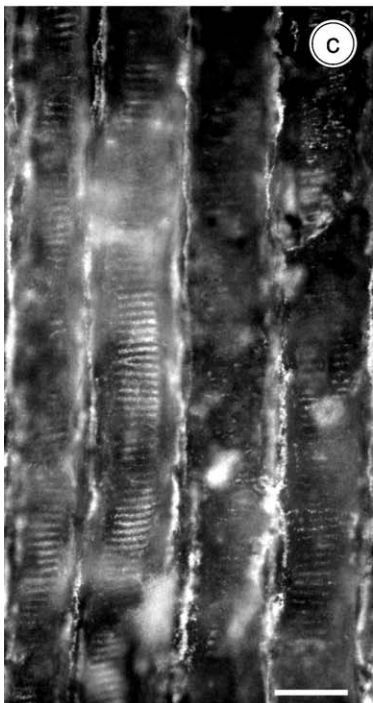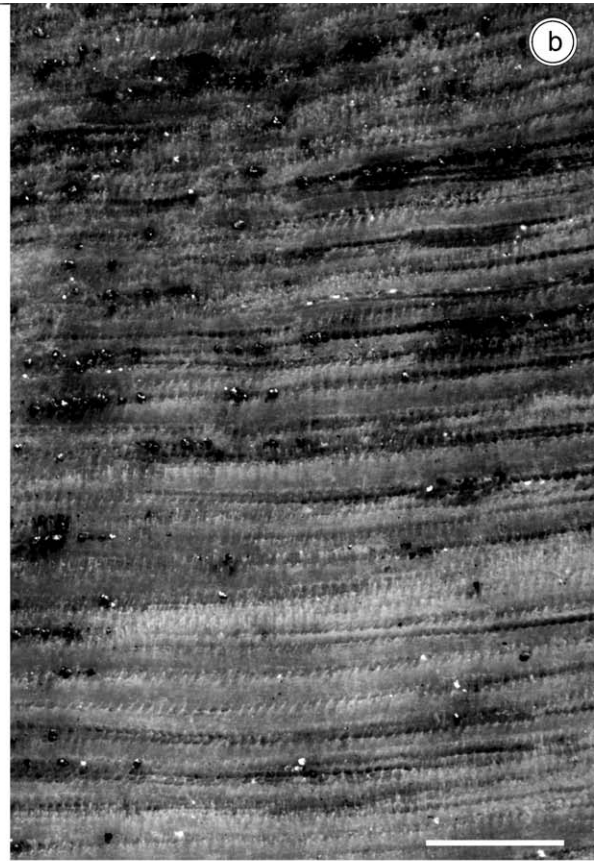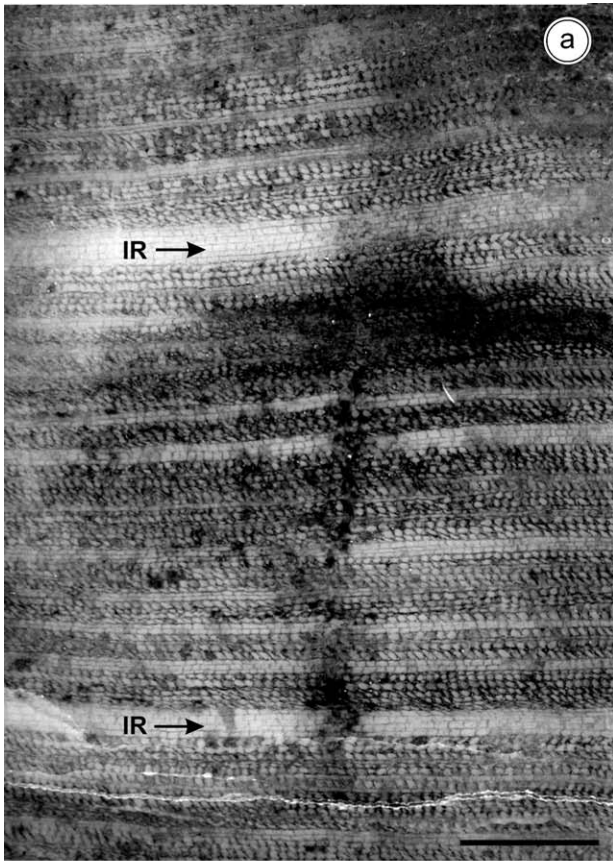
Secondary tracheids are organised in radial files of 1–4 tracheids and show scalariform secondary wall thickenings and/or pits on their radial walls with a vertical separation distance of approximately 7 µm (Fig. 5c, d). Thickenings sometimes fork. Tracheid diameters of the inner wood measure 48 µm (35–68) tangentially, 58 µm (45–70) radially. Near the margin of the trunk tracheid diameters are 63 µm (43–90) tangentially and 69 µm (60–95) radially. They are up to 4 mm in length.

Phloem, cortex tissues or periderm is not preserved in the studied specimen.

5.2. Holotype specimen

Specimen MfNC K 3309a, b with some thin section preparations is the only material that obviously remains from the single specimen on which Goeppert's type was erected. This sector of the secondary body measures 145 mm in radial extension (Fig. 6a–g) and a few centimetres in thickness. Characters of the primary body such as pith parenchyma, vascular strands, and primary xylem are not preserved. The secondary xylem exhibits a homogeneous loose type wood made of tracheid rows and parenchymatous rays. There is no clear distinction of interfascicular rays and fascicular wedges. Distinction of interfascicular (primary) and fascicular (secondary) rays is only visible within the innermost part of the secondary body (Fig. 6b). Although not easy to recognise the rays continuously dissect the secondary body. They are 1–5 cells broad and up to 30 cells high. Ray cells are parenchymatous, square to rectangular in radial and transverse view, rectangular with sometimes slightly oblique end walls observed in uniseriate rays in tangential view (Fig. 6e), but irregular to polygonal in bi- to multiseriate rays (Fig. 6d). Parenchyma cells are 50–150 µm (mean 74 µm) high and 30–100 µm wide in tangential view, they average 64 µm in radial dimension. Secondary tracheids are organised in radial files of 1–4 tracheids. They show scalariform secondary wall thickenings and/or pits on their radial walls (Fig. 6f, g). Near the pith tracheid diameters average 52 µm tangentially and 58 µm radially; near the periphery of the secondary body they average 64 µm tangentially and 63 µm radially. There are no extraxylary tissues visible.

5.3. Additional material

Recently more specimens have been recognised as calamite stems attributable to *Arthropitys ezonata* (Fig. 7a). Because of their overall appearance with a very small pith and conspicuously enlarged homogeneous wood, they were generally confused with conifers or cordaitaleans and in collections sometimes referred to as *Dadoxylon*. One of these specimens (MfNC K 5249) that partly shows surrounding fine-grained pyroclastics is figured in Fig. 7a–c. It measures 240 mm in diameter with a deformed pith of 21 × 9 mm in outline situated nearly centrally. Approximately 85 vascular strands surround the central pith, although there are no further details, like carinal canals, visible.

As in the other specimens described above there is no clear distinction of interfascicular zones and fascicular wedges except in the innermost zone of the secondary body (Fig. 7b, c). Sometimes one is led to recognise some kind of radial (fascicular/interfascicular) zonation, but otherwise this seems not to be justified for the complete radial extension of the woody cylinder. Nevertheless, rays continuously dissecting the secondary body are sometimes visible up to 60 mm long in transverse view, then they taper while other broaden. They vary considerably in size and are 1–5 (usually 3) cells broad and up to 25 cells high. The initiation of new fascicular rays in more external regions of the wood was recognised. Ray cells are parenchymatous, square to rectangular in radial and transverse view. In tangential view cells of the uniseriate rays show a rectangular shape, but an irregular to polygonal shape in bi- to multiseriate rays. Parenchyma cells are considerably variable and measure 40–130 µm (mean 72 µm) tangentially, 50–140 µm (mean 86 µm) radially.

Secondary tracheids are organised in radial files of 1–5 tracheids. Thickening/Pitting on radial tracheid walls is scalariform. There is no significant variability of the thickening/pitting pattern during ontogenetic development. Within the innermost wood tracheid diameter averages 50 µm tangentially and 59 µm radially; near the periphery of the secondary body tracheids average 60 µm tangentially and 72 µm radially. There are no

Fig. 5. *Arthropitys ezonata* Goeppert from the Permian Petrified Forest of Chemnitz. MfNC K 5200. Anatomical details obtained from oriented sections. (a) Transverse section from the innermost woody cylinder showing differentiation of interfascicular rays (IR) and fascicular wedges. Scale bar equals 1 mm. (b) Transverse section from the outermost woody cylinder showing homogeneous parenchymatous wood without any zonal differentiation. Distance from panel a measures about 230 mm. Scale bar equals 1 mm. (c) Longitudinal radial section that exhibits scalariform secondary wall thickening/pitting of the secondary xylem. Scale bar equals 50 µm. (d) Longitudinal radial section showing thickening/pitting pattern of cross field region. Scale bar equals 100 µm. (e) Longitudinal tangential section showing multiseriate rays. Note the high portion of parenchyma within the wood. Distance from the pith periphery measures about 240 mm. Scale bar equals 500 µm.
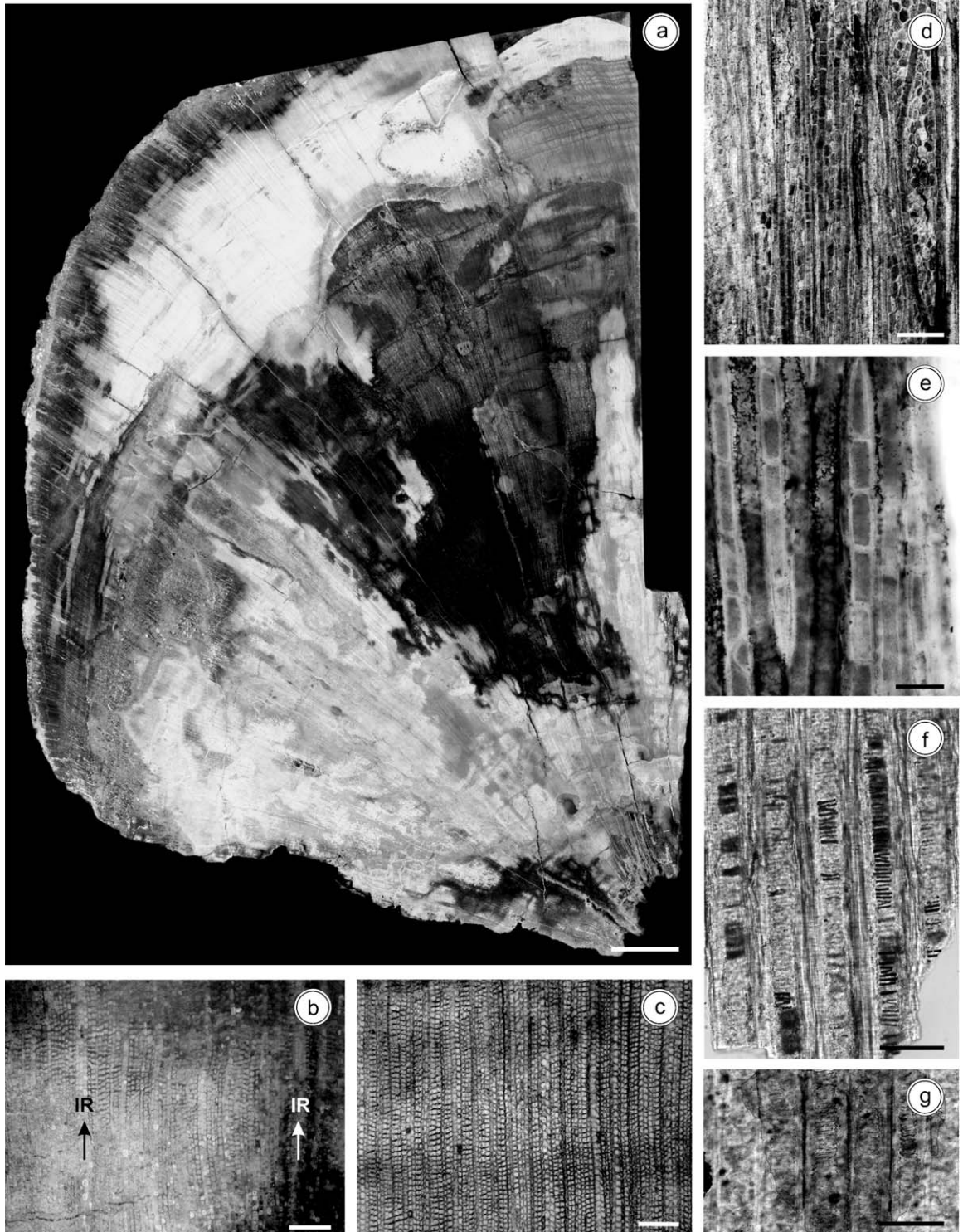
extraxylary tissues visible. The colour change in the outer part of the stem represents the outer xylem zone, where tracheids are considerably crushed.

6. Comparisons and affinities

We have no doubt that the new specimen described in this study clearly belongs to *Arthropitys*, the most common and widely distributed genus among permineralised Calamitaceae, introduced by Goeppert (1864) based on material from the Permian of Chemnitz. Based on anatomical details of the interfascicular rays three form genera of anatomically preserved Calamitaceae are recognised. *Arthropitys* is generally separated from *Calamodendron* Brongniart and *Arthroxylon* Reed by its interfascicular rays made of rather uniform, brick-shaped parenchymatous cells.

Although hundreds of specimens of varying size exist in different local collections, the last revision or detailed evaluation of the Chemnitz *Arthropitys* species were undertaken a long time ago (Goeppert, 1864). As a result, particularly the species from the type locality of this genus, like *Arthropitys bistriata* (Cotta) Goeppert and *Arthropitys ezonata* Goeppert, remain poorly characterised in comparison to later defined species. The growing knowledge and general awareness of high variability among both morphological and anatomical characters found in Calamitaceae additionally prevented further subdivision at the subgeneric level (Barthel, 1983).

The rich Carboniferous coal ball material enabled a considerable contribution to the understanding of the stem anatomy and internal organisation of sphenophytes (Williamson, 1871; Knoell, 1935; Hass, 1975). However, the question of correlating both branching features observed on large-sized pith casts (Weiss, 1884; Kidston and Jongmans, 1917) and anatomical structures obtained from rather small-sized coal balls remains largely unresolved.

Whereas roots may be sufficiently characterised by their internal anatomy (Leistikow, 1962; Agashe, 1964) the innumerable aerial axes, even in well defined species like *Arthropitys communis* (Binney) Renault, cannot provide conclusive evidence as to whether they represent main stems or lateral branches. Only a few species have been erected on such conspicuous characters as the dilating interfascicular rays in *Arthropitys deltoides* Cichan and Taylor, which were regarded as evidence of a liana-like growth form in this calamite (Cichan and Taylor, 1983).

The most recent comparison of different *Arthropitys* species with special emphasis on *Arthropitys junlianensis* from the Late Permian of China was provided by Wang et al. (2003). As the internal structure of *Arthropitys* axes is quite uniform, the characters used to differentiate the genus at a subgeneric level are rather limited. Characters such as the size of the pith, the number of primary vascular bundles, the size of carinal canals, length of internodes, the thickness of the secondary xylem wedges and the anatomy of the rays were used in a number of studies. However, as some previous authors stated (e.g., Andrews, 1952; Eggert, 1962) most of them represent features that change during the development of individuals and are therefore not applicable for classification.

Details of secondary growth, like the nature of tracheid wall thickening/pitting or the geometry of the interfascicular rays have been used more successfully for systematics (Renault, 1893–1896, 1895, 1896; Williamson and Scott, 1894). However, even in these cases evaluation of ontogenetic variation is helpful and recommended (Cichan and Taylor, 1983). Since extra-xylary tissues are known from only a few species (Agashe, 1964; Cichan and Taylor, 1983), their characters are not applicable to the majority of described species. Based on the unsolved problem of correlating both permineralised species and the various compression forms, which remains in discussion (Barthel, 2004), Rößler and Noll (2002) tried to evaluate both anatomical and morphological characters, such as branching patterns observed on larger permineralised specimens from the Permian of Brazil. However, since finds that show both aspects have unfortunately proved rare, attention is traditionally directed towards characters of the secondary body including its ontogenetic variation.

Fig. 6. *Arthropitys ezonata* Goeppert from the Permian Petrified Forest of Chemnitz. MfNC K 3309. Portion cut from the holotype. (a) Transverse section showing the only remaining specimen from Goeppert's type material. Scale bar equals 10 mm. (b) Thin section in transverse view showing innermost secondary xylem showing differentiation of interfascicular rays (IR) and fascicular wedges. Arrows indicate view to periphery, scale bar equals 500 μm. (c) Detail of panel a showing the homogeneous wood near the stem periphery. Distance from panel b measures about 100 mm. Scale bar equals 500 μm. (d) Thin section in longitudinal tangential view showing variation of the wood rays. Scale bar equals 500 μm. (e) Thin section in longitudinal tangential view showing detail of some uniseriate rays. Scale bar equals 100 μm. (f) Thin section in longitudinal radial view showing the scalariform secondary wall thickening pattern of the secondary xylem. Thickenings are preserved by lamellae of calcium fluoride within a silicified matrix. Scale bar equals 100 μm. (g) Thin section in longitudinal radial view showing the scalariform secondary wall thickening/pitting of the secondary xylem. Scale bar equals 100 μm.
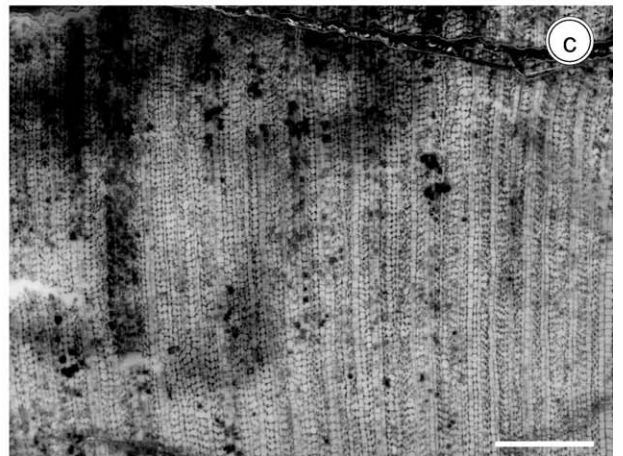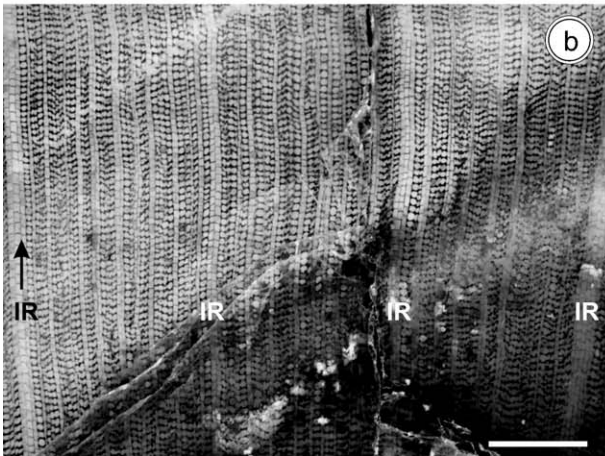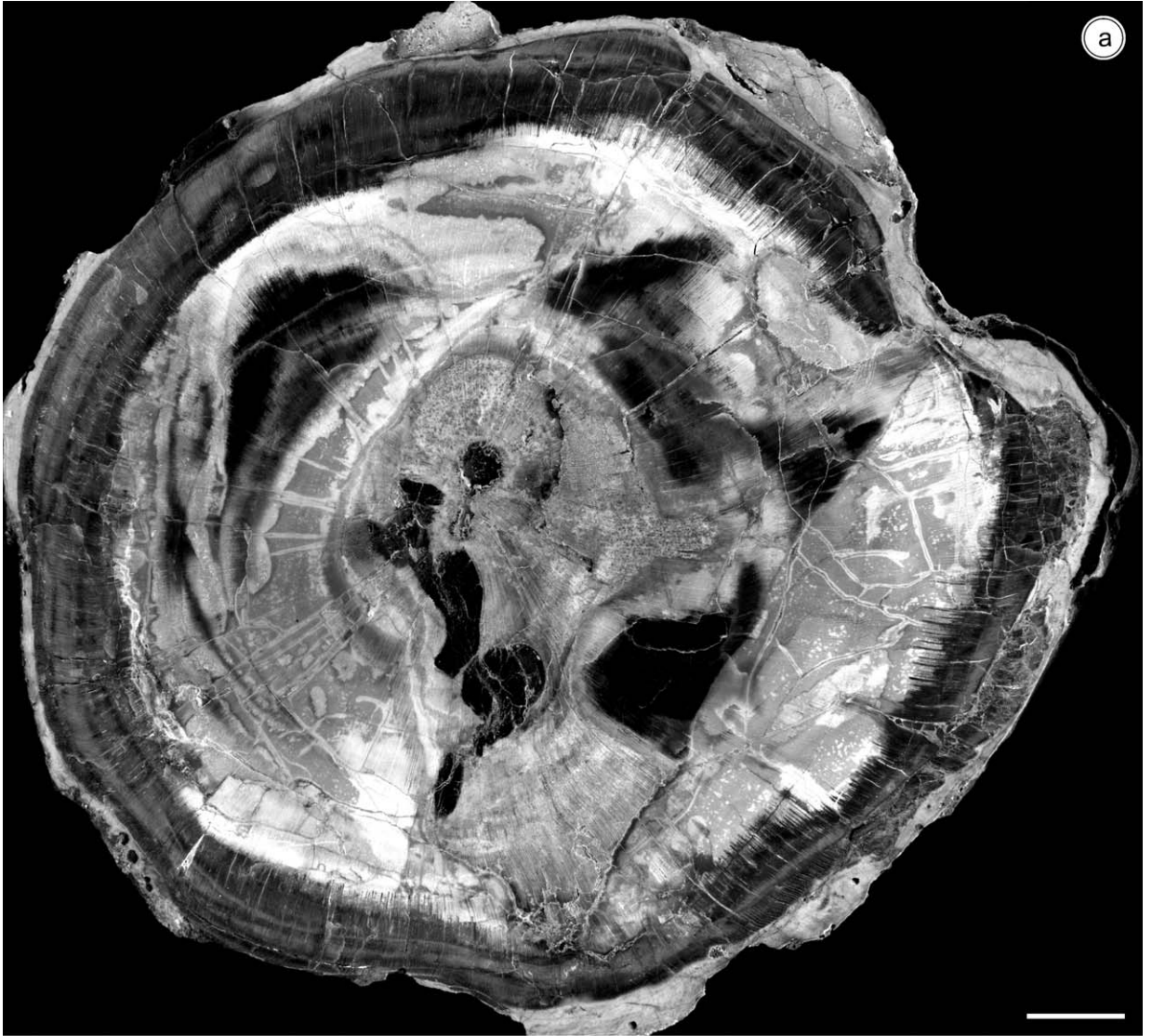
Table 1
Comparison of *Arthropitys ezonata* specimens

Characters	Holotype specimen MfNC K 3309	Newly discovered specimen MfNC K 5200	Additional material MfNC K 5249
Size (mm)	Sector of 145 mm radial width 43 mm high	470×600 bottom 375×540 top 1300 mm high	240 diameter 140 mm high
Pith diameter (mm)	Not preserved	14×17 bottom 18 top	21×9
Xylem strands	Not preserved	74 initially 450–600 μm wide	approximately 85 initially 450 μm wide
Carinal canal width (μm)	Not preserved	110 tangentially 150 radially	not preserved
Metaxylem	Not preserved	2–3 layers of small elements (20–50 μm)	not preserved
Secondary body Maximum width (mm)	145	330	130
Rays	Uniseriate to multiseriate 1–5 cells wide Up to 30 cells high	Uniseriate to multiseriate 1–6 cells wide 5–40 cells high	Uniseriate to multiseriate 1–5 cells wide Up to 25 cells high
Ray cells (μm]	Highly variable *transverse view:* square to rectangular, 35–90 tangentially, 40–120 radially	Highly variable *transverse view:* square to rectangular, 50–210 tangentially, 40–130 radially	Highly variable *transverse view:* square to rectangular, 40–130 tangentially, 50–140 radially
	Tangential view: irregular to polygonal (bi- to multiseriate) or rectangular (uniseriate) 50–150 high, 30–100 wide	*Radial view:* square to rectangular (usually longer than high)	*Tangential view:* irregular to polygonal (bi- to multiseriate) or rectangular (uniseriate) 80–220 high
		Tangential view: irregular to polygonal (bi- to multiseriate) or rectangular (uniseriate) 70–150 high, 30–100 wide	
Secondary xylem tracheids diameter (μm)	Internal: 52 tangentially, 58 radially External: 64 tangentially, 63 radially	Internal: 48 tangentially, 58 radially External: 63 tangentially, 69 radially	Internal: 50 tangentially, 59 radially External: 60 tangentially, 72 radially

In *Arthropitys*, the size and shape of the interfascicular rays is shown to vary considerably. The generitype, *Arthropitys bistriata*, and species, like *Arthropitys kansana* Andrews, *Arthropitys versifoveata* Anderson and some new forms currently treated under open nomenclature, like *Arthropitys* sp. A1 (Rößler and Noll, 2002), show very distinct interfascicular rays that consist of several rows of parenchyma cells and continuously dissect the secondary body. In other species, like *Arthropitys ezonata* Goeppert, *Arthropitys hirmeri* Knoell, *Arthropitys "lineata"* Renault, *Arthropitys junlianensis* Wang et al., and *Arthropitys* sp. A4 and B2 (Rößler and Noll, 2002), the characteristic radially banded appearance of the secondary xylem is lacking.

This is due to an abrupt tapering of the interfascicular rays centrifugally, providing the wood with a gymnosperm-like dense appearance in transverse section. If observed only in transverse view and from isolated fragments of the secondary body this appearance can easily be confused with other plants that exhibit a similar type of wood such as *Medullosa stellata* f. *lignosa* (compare Weber and Sterzel, 1896), or different species of *Pitus* (Galtier, 2002). However, we believe this not uncommon character, which was also recognised in anatomically preserved *Archaeocalamites* (Renault, 1893–1896, pl. XLIII, 1, Galtier, 1970, Smoot et al., 1982), is more conspicuous if observed on parts of the xylem periphery of larger secondary

Fig. 7. *Arthropitys ezonata* Goeppert from the Permian Petrified Forest of Chemnitz. MfNC K 5249. Additional recently discovered specimen. (a) Stem slice in transverse view. Scale bar equals 20 mm. (b) Detail of panel a showing innermost wood still separated in interfascicular rays (IR) and fascicular wedges. Arrows indicate view to periphery, scale bar equals 1 mm. (c) Detail of panel a showing outermost rather homogeneous wood. Distance from panel b measures about 70 mm. Scale bar equals 1 mm.

bodies, because in *Arthropitys* both the fascicular wedges and sometimes the interfascicular rays broaden during their secondary growth.

Although Cotta (1832) previously mentioned this type of rather homogeneous secondary body, his species *Calamitea lineata* (Cotta, 1832, p. 71, pl. XVI, 1) exhibiting a narrow alternation of parenchymatous and tracheid radial rows, has not been considered in subsequent studies. Renault (1876) even defined his own *lineata* species based on small-sized material from the Permian of Autun and Champ des Borgis, France, as he did for a considerable number of other newly defined species. Until now, neither Cotta's *C. lineata* nor the fact that Renault's *Arthropitys lineata* represents a synonym has been considered. A future re-investigation of Cotta's type material held in the British Museum (Natural History) since 1839 (Süß and Rangnow, 1884) and at the Museum für Naturkunde Berlin as well, may show whether or not his species *lineata* is justified.

Finally, we consider questions of both palaeobiology and taphonomy that arise from study of this specimen, e.g., the comparison of the classical pith cast preservation and permineralised specimens. Do we know any compression analogue to the *Arthropitys ezonata* specimens? Which kind of pith cast could represent the largest known calamites in the fossil record? The overwhelming number of calamite pith casts have diameters of 5 to 20 cm (Kidston and Jongmans, 1917). Therefore, one might not expect that a 15 mm diameter pith encircled by almost 30 cm wood, as observed in a mature *A. ezonata* stem, would be preserved. Instead, the majority of small pith casts usually are interpreted as coming from juvenile plants rather than from calamites of such enormous individual age as would have to be assumed for a huge woody calamite tree. Thus, most of the normal pith casts may have been taphonomically favoured during their formation, since the early ontogenetic stage of calamitean stems may have been characterised both by less axial stiffness and little secondary growth. The small amount of coal encircling most pith casts may underline the aforementioned assumption. However, this consideration seems to restrict the palaeobiological significance of compression material due to its limited ontogenetic spectrum.

7. Conclusions

Eruption and deposition of volcanic material is usually a dramatic and destructive process. Otherwise, volcanic events and their deposits provide us with exceptional conditions that favour preservation of floral elements. In some cases, as demonstrated at Chemnitz, the processes can capture and preserve an entire community. Although the preservational types they create are outstanding, the distribution of plants preserved is highly patchy. Most permineralised trunks from the Permian of Chemnitz have been found in one single layer, the surge sequence of the Zeisigwald Tuff Horizon. Both the rich fossil content of this deposit and the early scientific investigation (Cotta, 1832) are responsible for Chemnitz becoming the type locality of several well known, widely distributed Late Palaeozoic plants, like *Psaronius*, *Tubicaulis*, *Zygopteris*, *Medullosa*, *Calamitea* and *Arthropitys*.

Although the majority of studies dealing with anatomically preserved calamites are based on small or juvenile axes and branches frequently found in coal ball material, we took the opportunity to study a thick and adult woody specimen found in situ in its place of growth among *Psaronius* tree ferns, *Medullosa* pteridosperms and *Dadoxylon* type gymnosperms. Unexpected and obviously in contrary to both the conical base common in calamitean stems and the current interpretation of calamite ontogeny (Eggert, 1962), the pith diameter of the large *Arthropitys ezonata* specimen hardly enlarges on the 120 cm long distance from the base of the trunk (14×17 mm) up to the top (18 mm). Both the cylindrical, very narrow pith and the thick wood (Fig. 3a, b) may contrast with other specimens previously described, and underline the unique internal organisation of *A. ezonata* among anatomically preserved calamitean stems.

This contribution on *Arthropitys ezonata* Goeppert is the start of a revision of permineralised calamite taxa from the Permian of Chemnitz representing the first anatomically preserved Calamitaceae ever described. Species like *Calamitea striata* and *Arthropitys bistriata* date back to Cotta (1832) but are still poorly understood. Both new large-sized finds from the type locality and modern preparation techniques may help to re-evaluate anatomical and branching characters suitable for a more coherent systematics of permineralised calamite organs in the future.

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