Calamitea Cotta, the correct name for calamitean sphenopsids currently classified as *Calamodendron* Brongniart

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Abstract

Recent investigation of calamite trunks from the Permian petrified forest of Chemnitz, Germany, show that the rare calamite form genus *Calamodendron* Brongniart 1849 can no longer be sustained. The oldest form genus representing this set of characteristics is *Calamitea* Cotta 1832. Collection material from the type locality, including sizeable trunks, enabled re-evaluation of diagnostic characters of both the stem anatomy and branching patterns of *Calamitea striata* Cotta, 1832. As a result, a mosaic of anatomical and morphological characteristics has been recognised, that permit *C. striata* to be characterised in much more detail than previously attempted. The genus is emended herein. The secondary body consists of two types of tracheids that are mainly differentiated by their size. The so-called "fibrous bands", which were formerly thought diagnostic for *Calamodendron*, are actually files of small tracheids. The ratio of large-diameter versus small-diameter tracheid files is proved to be highly variable, bringing into question the ontogenetic stage of the plant. A gradual transition from clearly segmented wood (innermost wood cylinder) to wood almost exclusively consisting of large-diameter tracheids (outer wood cylinder) was observed in both radial and vertical directions. Furthermore, tracheid wall thickening/pitting, which has usually been used for species separation, proved to be highly variable questioning the justification and significance of further described species. Tracheid wall thickening/pitting reaches from scalariform thickenings with simple elongated pits to reticulated thickenings with oval to circular pits. *Calamitea* differs from *Arthropitys* Goeppert and *Arthroxylon* Reed in having different tracheid types composing the secondary xylem and the smallest parenchyma proportion of the wood among calamitean plants. A reconstruction of the growth habit of *C. striata* is proposed, and comparisons are made with other calamitean species and other preservational forms.
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1. Introduction

The remains of calamite trees are among the most common and frequently found plant fossils of the Upper Carboniferous and Lower Permian (Weiss, 1876; Kidston and Jongmans, 1917; Cleal and Thomas, 1994; Barthel, 2001). They are best known from pith casts of their hollow stems and from coalified compressions of their leafy shoots and strobili. Most of them are fragmentary remains, preserving only a portion of the plant body, often without any connection between different organs. However, the fossil record of calamite plants is exceptionally rich and additionally diverse in

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terms of preservation. Besides the compressions there are three-dimensionally preserved remains, such as plant parts preserved in coal balls or permineralised trunks, which give insights into anatomy and internal organisation of the plant tissues.

One of the first permineralised calamite taxa described in detail was introduced in the literature by Cotta (1832, p. 67, Plate XIV, 1–4), and became known as *Calamitea striata*. Specimens that show both anatomical characters of the primary/secondary body and branching patterns on the surface of relatively large specimens have been observed only from a few localities. Among them is the type locality of *C. striata*, the Permian petrified forest of Chemnitz that provided sizable trunks of several metres in length and additional material appropriate for study of different growth aspects of this plant. For about 200 years this site has provided both the majority of *C. striata* specimens and the most complete finds of silicified axes. However, even the type species was poorly understood.

The purpose of this contribution is to communicate new observations regarding both the variability of internal anatomy and branching patterns shown by branch traces on the surface of several trunks, from which the tuffitic cover has been removed. Based on historical collection material from Chemnitz a number of isolated trunk segments have been proved to fit to each other, which lead to the restoration of a trunk of more than 4 m in length representing the largest known *Calamitea striata* specimen. Among other finds this exceptional fossil trunk, found in 1911, enables recognition of considerable variability in anatomical characteristics used in species separation. Therefore, this study can provide a completely new image of *C. striata* than that reflected in the broad palaeobotanical literature.

2. Research history outline

Cotta (1832) introduced the new genus *Calamitea* to store his two new species *Calamitea striata* and *Calamitea bistriata*. He correctly diagnosed that the prominent radial colour striation of the secondary body represents alternating zones of "dense and less dense tissues". However, his interpretation that the dark-coloured zones represent exclusively rays, which he concluded from the study of broken radial surfaces that also showed the narrow interfascicular rays, was wrong. Nevertheless, his publication was appreciated by several workers and caused a long-lasting dispute on the nature of calamitean plants.

Petzholdt (1841, p. 3) compared calamite remains preserved in Lower Permian tuffs of the Döhlen Basin, Germany with *Calamitea striata* and concluded that

these fossils may represent different preservational states of the same species and unquestionably have to be assigned to calamite plants, which in the middle of the 19th century were particularly known from pith cast compressions (Sternberg, 1825; Brongniart, 1828). The first detailed anatomical investigations were provided by Unger (1840); the figured material from Unger's study was presented in Petzholdt (1841).

Brongniart (1849) described *Calamodendron* as new genus and included both existing species of *Calamitea* Cotta, *Calamitea striata* and *Calamitea bistriata.* This decision reflects his incorrect idea that the "true *Calamites*", known from pith casts and thought to be similar and close to Equisetaceae, should be taxonomically distinct from those calamites with secondary growth ("Gymnosperms Dicotyledons"), for which he did not use the existing *Calamitea*, but proposed the new generic name. His explanatory statement favoured *Calamodendron* to prevent confusion with *Calamites:* «Ce sont des tiges de celle nature qui ont offer tune structure interligneuse, toute particulière, et que M. Cotta a désignées par le nom de *Calamitea*. Mais les *Calamitea striata* et *bistriata* seules rentrent dans ce genre»; «… la trop grande analogie des mots *Calamites* et *Calamitea* m'ont engagé à modifier un peu ce dernier nom» (Brongniart, 1849, p. 50). But this procedure was clearly unjustified. It was a step backwards in comparison to the views of Cotta (1832, p. 67), Unger (1840, p. 654), Petzold (1841, p. 3) and later Williamson (1869, 1871, 1887, p. 270), who correctly understood *Calamitea* and related forms as trunk portions of calamite trees belonging to Equisetaceae and simply distinguished from the pith cast compressions by showing internal structure: «Die Calamiten, darin wird mir jetzt wohl Jedermann beistimmen, waren demnach nichts Anderes als urweltliche Equiseten; denn wenn diese Ansicht, früher schon ausgesprochen, sich nur auf die äußere Aehnlichkeit zwischen beiden stützte, so ist die Wahrheit derselben doch jetzt erst durch den gleichen inneren Bau als entschieden zu betrachten» (Petzholdt, 1841, p. 8). A second mistake relates to the generic diagnosis of *Calamodendron* itself. The inappropriate characteristic of dubious "lignous fibers" was understood to be diagnostic at generic level and has been used unjustifiably to support *Calamodendron* for more than 150 years. During that time *C. striatum* had been thought to be characterised by radially elongated "fibrous bands" separating the fascicular wood from the interfascicular ray (Schenk, 1884; Solms-Laubach, 1887; Renault, 1898). *Calamodendron*, with its erroneous diagnosis, has been reproduced in many palaeobotanical textbooks (Potonié, 1899; Scott, 1900; Zimmermann, 1930; Ogura,

1972; Gothan and Weyland, 1973; Taylor and Taylor, 1993).

Göppert (1864/65) accepted *Calamodendron* Brongniart, because he also believed *Calamitea* to be an intermediate between *Calamites* and conifers. He recognised two different cell types, one designated "prosenchymatic" cells, which were elongated and thick-walled, the other designated "Treppengefäße", which were twice the diameters of the first. He compared these cells with the secondary xylem of conifers and stated that the cells of *Calamodendron* lack both the striation patterns and pits known from conifers and, therefore, concluded that *Calamodendron* was justified. However, he recognised substantial differences between *C. striatum* and *C. bistriatum* and, therefore, introduced the form genus *Arthropitys* to separate the latter species from *Calamodendron*.

Williamson (1869) described an unusually preserved calamite showing both the pith cast and the surrounding woody zone from a Coal Measures sandstone quarry in Oldham. A detailed anatomical investigation showed this specimen to be comparable to Cotta's *Calamitea*. Like some earlier workers, Williamson described of two different cell types each arranged in a linear series, and referred to as the vascular and the prosenchymatous tracts. However, in contrary to *Calamitea* he designated the cells of smaller diameter "vessels" and those of larger diameter "prosenchymatous cells". In some of the smaller cells, having the "shape of elongated tubes", he believed he could recognise cell wall strengthening by woody reticulations. However, the appearance of cell wall thickening in both cell types was mainly attributed to the infilling of mineral matter. Williamson (1869, 1887) interpreted the differences among these calamite remains as characteristic at generic level and introduced *Calamopitus*, later changed to *Arthrodendron* by Scott in Seward (1898) and finally re-named *Arthroxylon* by Reed (1952). The radial files of "prosenchymatous" elements in *Calamodendron* were eventually interpreted by Williamson as a primary medullary ray, similar to Cotta's earlier erroneous interpretation. Although Williamson recognised the conspecifity of *Calamitea* Cotta and *Calamodendron* Brongniart, thus recognising the mistake of Brongniart and others (Göppert, 1864/65; Grand'Eury, 1877; Schenk, 1883) differentiating between true calamites and "calamodendrées", he did not take the necessary nomenclatural steps. Williamson (1887) used in parallel (1) "ordinary *Calamites*" (instead of *Arthropitys* Göppert), (2) his new *Calamopitus* (later replaced by *Arthroxylon*) and (3) *Calamodendron* (instead of *Calamitea* Cotta) for characterising permineralised material. Finally, Williamson and Scott (1894) and Seward (1898) returned to the exclusive use of the old name *Calamites*. *Calamodendron* and *Arthropitys* were understood either as synonyms of *Calamites* or as subgenera.

Nevertheless, later researchers unconvincingly retained *Calamodendron* in Göppert's restricted sense. During the following decades a lot of new species of *Calamodendron* were described from several Late Carboniferous and Early Permian localities, but all of them were based on small woody fragments without the opportunity to evaluate the variability of any anatomical features adequately (Andrews, 1952; Renault, 1896, 1898). Although, several large trunks had been found at the type locality of Chemnitz, the type species, *Calamitea striata*, has not been revised until now.

This contribution will show that several anatomical characteristics used for the definition of *Calamodendron* species in the past are simply variations on the same characteristic. Features of the secondary body such as different width ratios of small-diameter versus large-diameter tracheid files and the type of tracheid wall thickening/pitting are shown to be highly variable and were recognised on several individuals, among them a trunk of more than 4 m in length (Plate III, 1). Sterzel (1893) already stated that the width of the black or white "striations" is highly variable (Plate I, 3) or largely depends on the preservation state, and he cited examples from Chemnitz and Nová Paka, the latter provided by Stur (1881). Finally, the diversity and high variability of tracheid wall structures have been shown for *Calamitea striata* by Schenk (1883, 1888) based on thin sections obtained from a specimen from the Döhlen Formation (Early Permian, Germany). For that reason Sterzel (1893) previously concluded that *Calamodendron congenium* Renault and *Calamodendron punctatum* Renault are synonyms of *C. striata*. The detailed anatomical study of *C. punctatum* by Marguerier (1972) considerably improved the knowledge about the variability of several tissue elements, however, she didn't recognise that there are no fibers close to the interfascicular rays but, rather small-sized tracheids. Other calamite species such as *Archaeocalamites esnostensis* (Smoot et al., 1982) and *Arthroxylon werdensis* (Hass, 1975) underline the variability of the thickening/pitting patterns among calamitean plants and imply that one should be cautious about using such features for taxonomic separation.

3. Material and methods

The material investigated during this study originates from the Lower Permian Petrified Forest of Chemnitz, Germany, the origin of which is closely related to rhyolithic explosive volcanism around 280 million years ago. The stratigraphic position of this Petrified Forest

corresponds to the Upper Asselian/Lower Sakmarian boundary. Stratigraphical and geological details are provided by Döring et al. (1999) and Rößler (in press).

The spectrum of preservational types is diverse, ranging from imprints of plants in volcanic tuff to anatomically preserved specimens (Sterzel, 1918; Barthel, 1976;

Plate I. *Calamitea striata* Cotta from the Permian Petrified Forest of Chemnitz. PP—pith parenchyma, PPc—pith parenchyma crushed, IR—interfascicular ray, FR—fascicular ray, CC—carinal canal, Mx—metaxylem, SX1—large-diameter tracheids, SX2—small-diameter tracheids.

1. Transverse section showing one sector of small-diameter tracheids flanked by sectors of large-diameter tracheids. Note the increasing homogenisation of the wood in a radial direction caused by a gradual increasing of the proportion of large-diameter tracheids. MfNC K 18, scale bar equals 500 μm.
2. Transverse section showing replacement of small-diameter tracheid files by large-diameter tracheid files. MfNC K 3366, scale bar equals 200 μm.
3. Transverse section showing variation in tangential SX1/SX2 thicknesses. MfNC K 18, scale bar 500 μm.
4. Relatively thick-walled cells of the pith parenchyma in transverse section. MfNC K 5204, scale bar 500 μm.
5. A few rows of SX2 separating the central IR from the dominating SX1 part. MfNC K 5204, scale bar 200 μm.
6. Transverse section of SX1/SX2 sectors showing inverse colour pattern in comparison to 1–3. MfNC K 5204, scale bar 1 mm.
7. Pith periphery in transverse section showing a plate of well-preserved parenchyma cells (PP), towards the centre of the pith parenchyma cells become increasingly crushed (PPc) and badly preserved. MfNC K 5204, scale bar 1 mm.
8. Pith periphery in transverse section showing radially enlarged, relatively thick-walled parenchyma cells (PP), carinal canals (CC) surrounded by two rows of small metaxylem elements (Mx) and inner part of secondary xylem represented by alternating SX1/SX2 sectors. MfNC K 3348, scale bar equals 1 mm.
9. Detail of 8. Scale bar equals 200 μm.

Plate II. *Calamitea striata* Cotta from the Permian Petrified Forest of Chemnitz. BT—branch trace, LT—leaf trace. (see plate on page 162)

1. Tangential section showing closely spaced nodes (indicated by white bars). Note the regular arrangement of branch traces alternating in successive nodes and lying on top of each other at every second node, MfNC K 5204, scale bar 10 mm.
2. Tangential section showing one node flanked by rather extended internodes; on the nodal line two branch traces without secondary growth, MfNC K 159, scale bar equals 10 mm.
3. Detail of 1 showing fascicular wood alternating at the nodal line and two leaf traces. Scale bar equals 1 mm.
4. Outer surface of a trunk showing prominent fascicular wood and one branch trace. Scale bar equals 5 mm.
5. Detail of 1 showing branch trace without any secondary growth. Scale bar equals 2 mm.

Plate III. *Calamitea striata* Cotta from the Permian Petrified Forest of Chemnitz, largest known trunk, from which cuts have been obtained in different levels. The sequence of fragments starts at the bottom of the left column and ends at the top of the right column. MfNC K 5204; IR—interfascicular ray, SX1—large-diameter tracheids, SX2—small-diameter tracheids. (see plate on page 163)

1. Surface of the trunk, scale bar equals 50 mm.
2. Transverse section showing crushed pith cavity and clear radial segmentation, 178 primary vascular strands, scale bar equals 10 mm, arrow indicating figured surface.
3. Transverse section showing clear radial segmentation, the woody cylinder is broken and partially squeezed into the pith, 183 primary vascular strands, scale bar equals 10 mm, arrow indicating figured surface.
4. Detail of 3, inner part of secondary xylem close to pith, but carinal canals not preserved. Note the equal width of the SX1 and SX2 sectors, scale bar equals 500 μm.
5. Transverse section showing relatively small pith and rather indistinct radial segmentation, 217 primary vascular strands, scale bar equals 10 mm, arrow indicating figured surface.
6. Transverse section showing relatively large pith and thin woody cylinder, radial segmentation not prominent, 216 primary vascular strands scale bar equals 10 mm, arrow indicating figured surface.
7. Detail of 6, initial fascicular wood at the pith periphery, scale bar equals 500 μm.
8. Transverse section showing relatively large pith and thin woody cylinder, radial segmentation not prominent, 240 primary vascular strands, scale bar equals 10 mm, arrow indicating figured surface.
9. Detail of 8, initial fascicular wood at the pith periphery. Note the small proportion of small-diameter tracheids, scale bar equals 500 μm.
10. Transverse section showing clear radial segmentation, but crushed wood cylinder, those parts are sometimes squeezed into the pith, 221 primary vascular strands, scale bar equals 10 mm, arrow indicating figured surface.
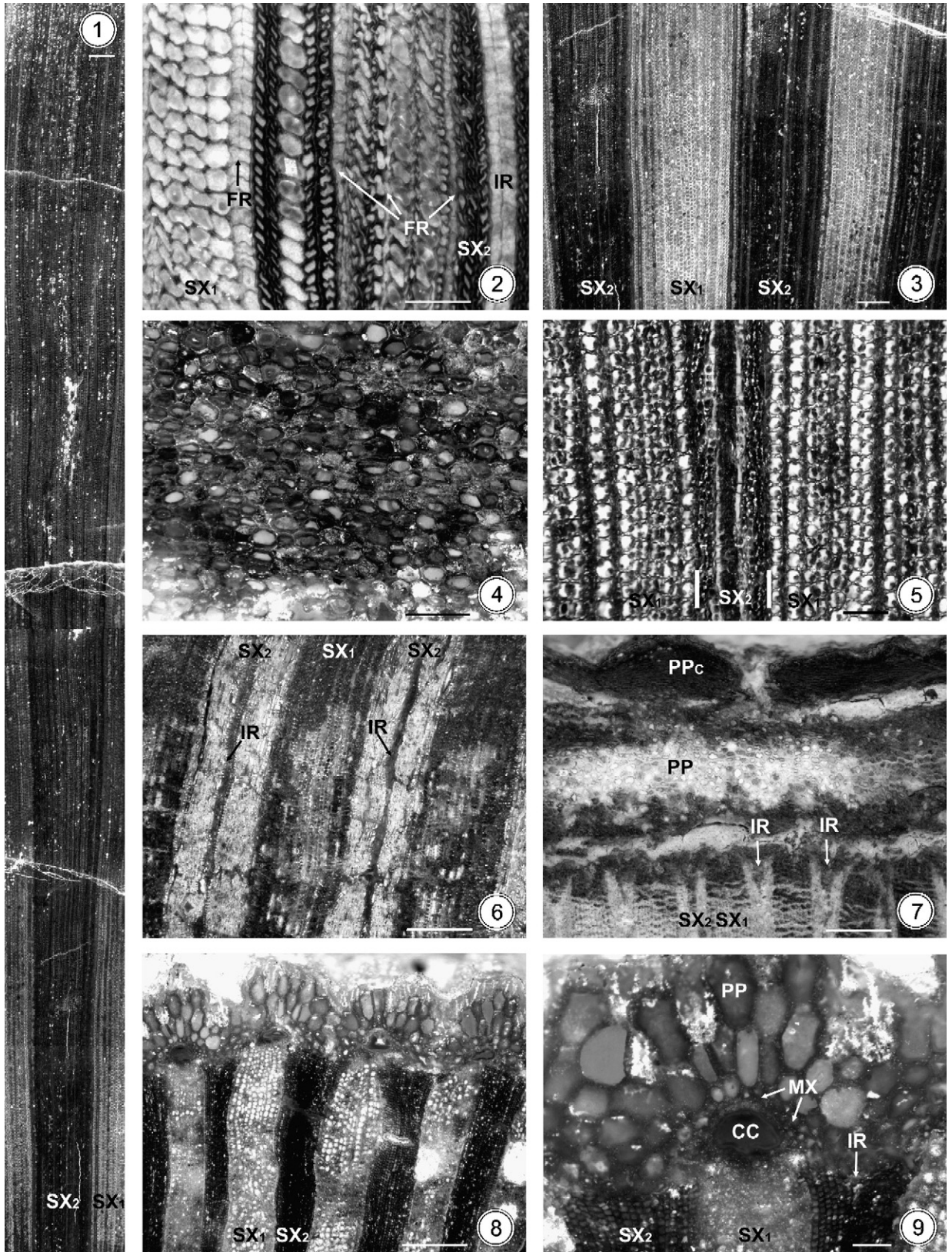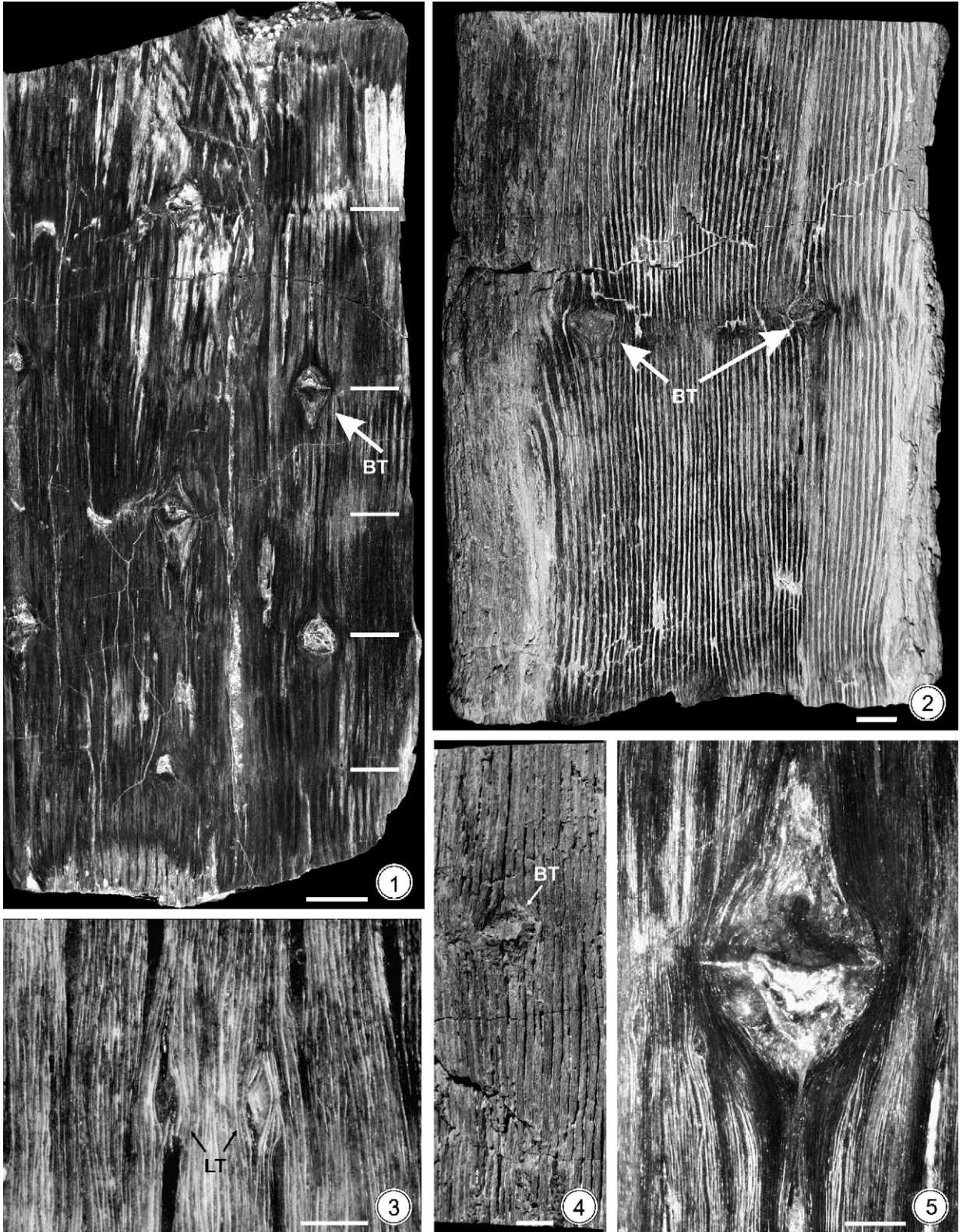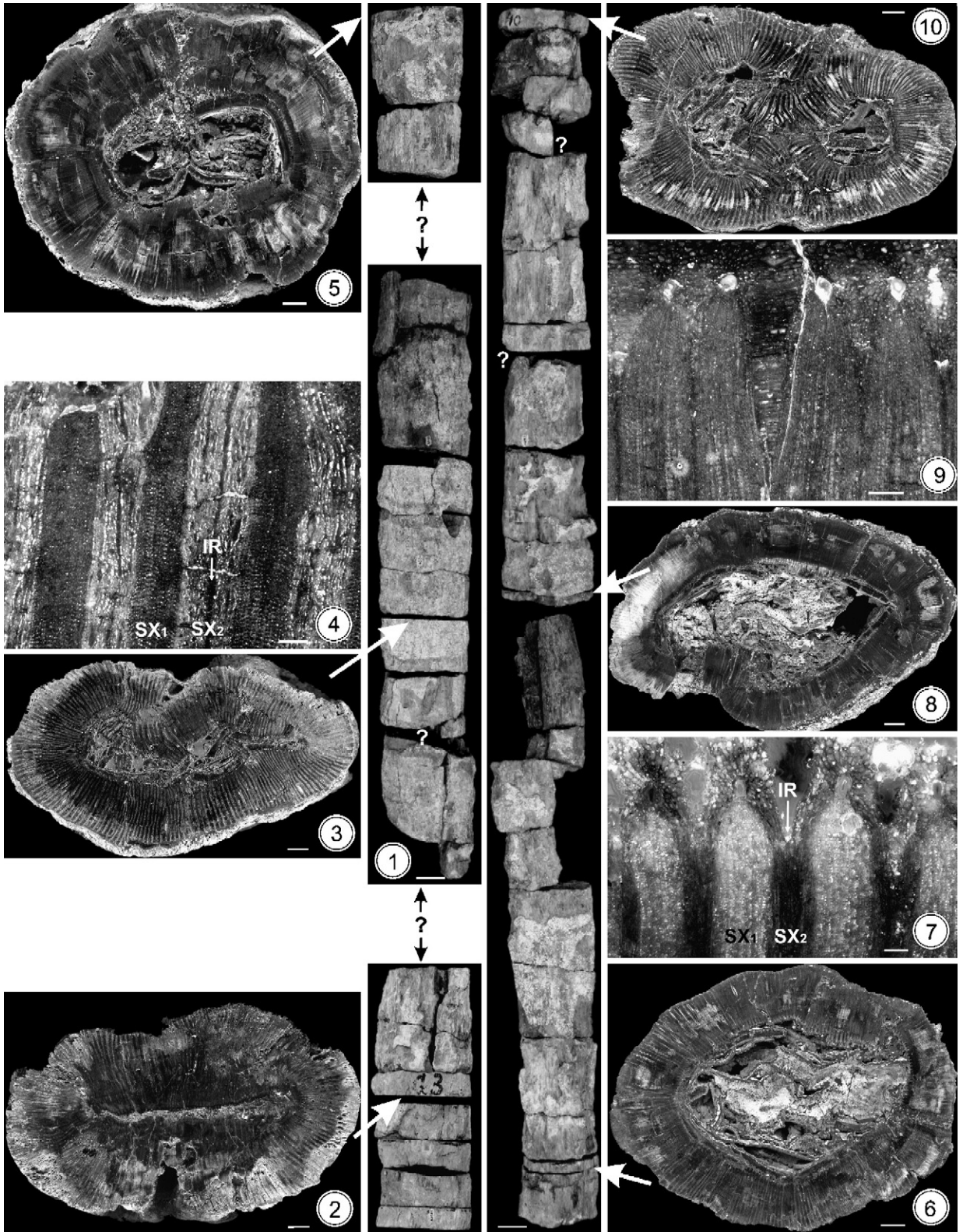
Plate I.

Plate II (*caption on page 160*).

Plate III (*caption on page 160*).

Rößler, 2001). Most of them are preserved as siliceous cellular permineralisations, but depending on the completeness of silicification, the quality and fidelity of preservation can differ considerably. Sometimes small organic remains, which have been transformed to vitrain during fossilisation (Nestler et al., 2003), are useful for recognising cell wall features (Plate IV, 3,4).

Fossils of *Calamitea striata* were found still partly embedded in coarse-grained pyroclastics of the Zeisigwald Tuff Horizon (Leukersdorf Formation, Erzgebirge Basin). Recent preparations (sand blasting and cutting thus) provided the opportunity for new observations, which had never been obtained from this species. The tuffaceous matrix was removed from the specimens, exposing surface features, such as branch traces. Both transverse and longitudinal sections of the trunks were prepared. Oriented surfaces were subsequently ground and polished and examined using reflected and transmitted light microscopy. Some details were obtained from thin section preparations.

Sections were photographed under reflected or transmitted light using a NIKON Eclipse ME 600 microscope

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Plate IV. *Calamitea striata* Cotta from the Permian Petrified Forest of Chemnitz.

1. Radial section showing secondary body and pith with densely spaced nodes (indicated by white bars). Arrow (BT) indicates one branch trace crossing the wood cylinder. Note the C-shaped parenchyma plates (arrows PP) that detach from the pith periphery. MfNC K 5204, scale bar equals 10 mm.
2. Radial section showing brick-shaped ray parenchyma cells, MfNC K 18, scale bar equals 200 μm.
3. Secondary xylem (SX1) in radial section showing thickening/pitting pattern; note some variation with dominating reticulated type, MfNC K 5204, scale bar equals 50 μm.
4. Secondary xylem (SX1) in radial section showing thickening/pitting pattern; note some variation with dominating scalariform type, MfNC K 5204, scale bar equals 50 μm.
5. Secondary xylem (SX2) in radial section showing circular to oval pits, MfNC K 18, scale bar equals 50 μm.

Plate V. *Calamitea striata* Cotta from the Permian Petrified Forest of Chemnitz. (see plate on page 166)

1. Transverse section showing the interfascicular ray attached to secondary xylem tracheids, MfNC K 3379, scale bar equals 200 μm.
2. Transverse section showing badly preserved interfascicular ray attached to a few files of small-diameter tracheids and surrounded by large-diameter tracheids; note the enlarging of tracheids in radial direction (arrow), MfNC K 3379, scale bar equals 200 μm.
3. Tangential section showing secondary xylem (SX1 right, SX2 left), interfascicular ray (IR) and fascicular rays (FR), MfNC K 18, scale bar equals 500 μm.
4. Tangential section showing detail of the interfascicular ray separating small-diameter tracheids of the secondary xylem (SX1), MfNC K 3379, scale bar equals 500 μm.

Plate VI. *Calamitea striata* Cotta from the Permian Petrified Forest of Chemnitz. (see plate on page 167)

1. Slightly thickened basal portion of a trunk, MfNC K 242, scale bar equals 50 mm.
2. Transverse section showing transition between SX1 and SX2, scale bar equals 200 μm.
3. Transverse section showing interfascicular rays (IR) and SX1/SX2 tracheid files, scale bar equals 500 μm.
4. Remaining slice from the type material figured in Cotta (1832, pl. 14, 1., BMNH 13775, scale bar equals 10 mm.
5. Transverse section of the smallest specimen, MfNC K 2066, scale bar equals 5 mm.
6. Transverse section of specimen MfNC K 3366 showing the maximum wood thickness (about 80 mm) ever observed in *C. striata*. Scale bar equals 10 mm.
7. Climbing fern axis (arrow) and diarch aerial adventitious roots of *Ankyropteris brongniartii* closely attached to a *Calamitea striata* trunk, scale bar equals 10 mm.

Plate VII. Specimens from the Permian Döhlen Formation (Döhlen Basin, Germany). (see plate on page 168)

1. *Calamitea striata* Cotta in transverse section, combined carbonised and permineralised preservation, Original of Sterzel (1893, Plate XI, 27), Mf NC F 10536, scale bar equals 10 mm.
2. Detail of 1 showing pith parenchyma, scale bar equals 200 μm.
3. Detail of 1 showing secondary body with crushed large-diameter tracheid files (SX1) and small-diameter tracheid files (SX2), scale bar equals 500 μm.
4. Detail of 3, scale bar equals 500 μm.
5. *Calamites multiramis* (Weiss) Kidston and Jongmans showing densely spaced nodal lines with regularly alternating branch scars, MMG PB SaP 3851, scale bar equals 20 μm.
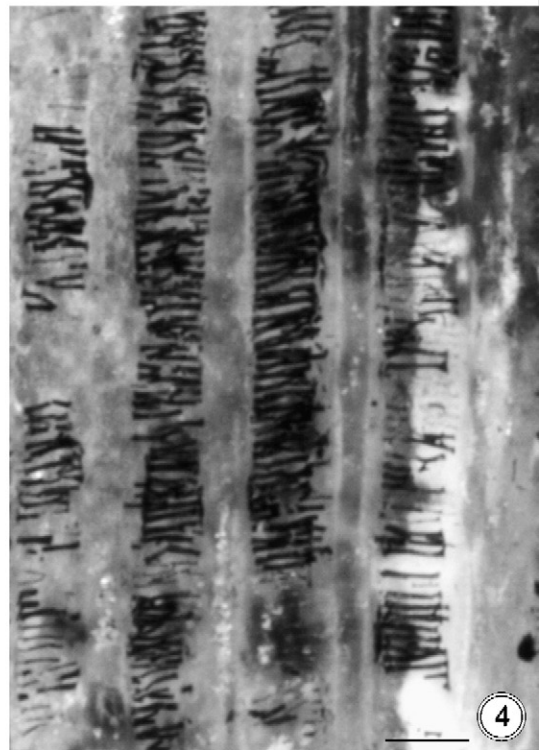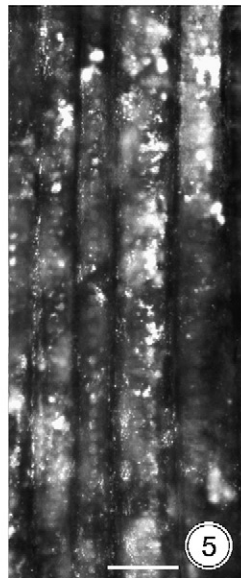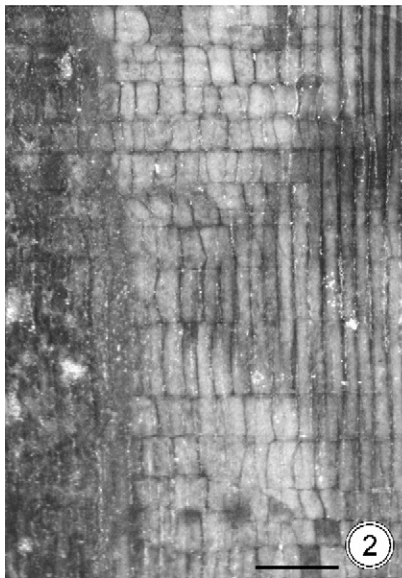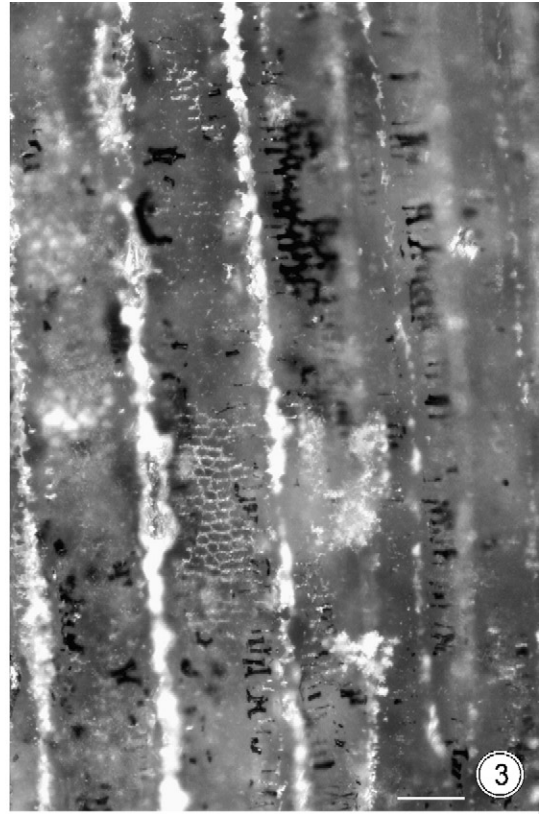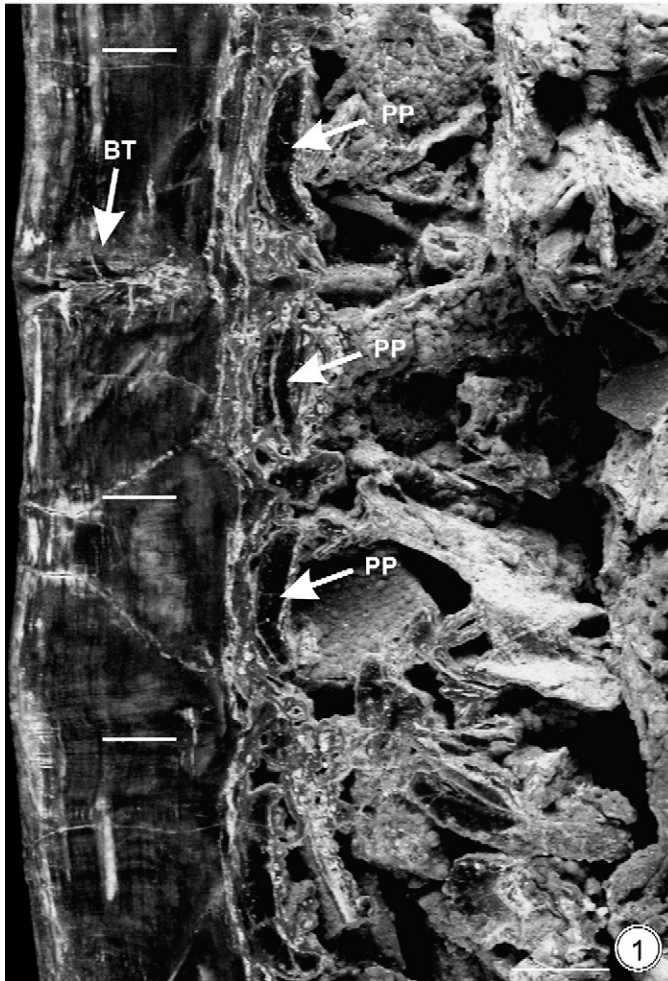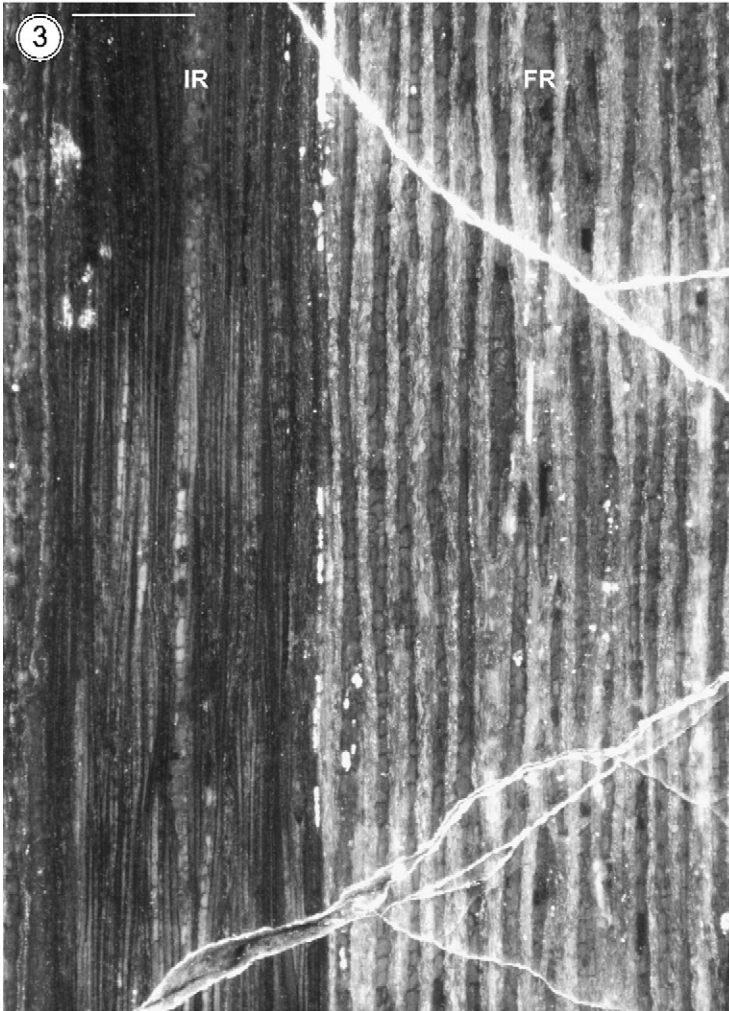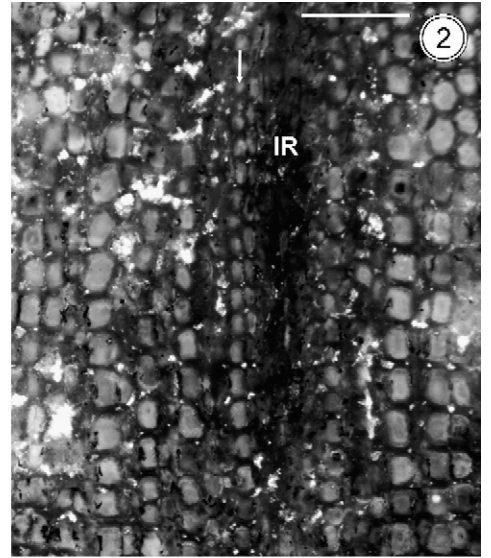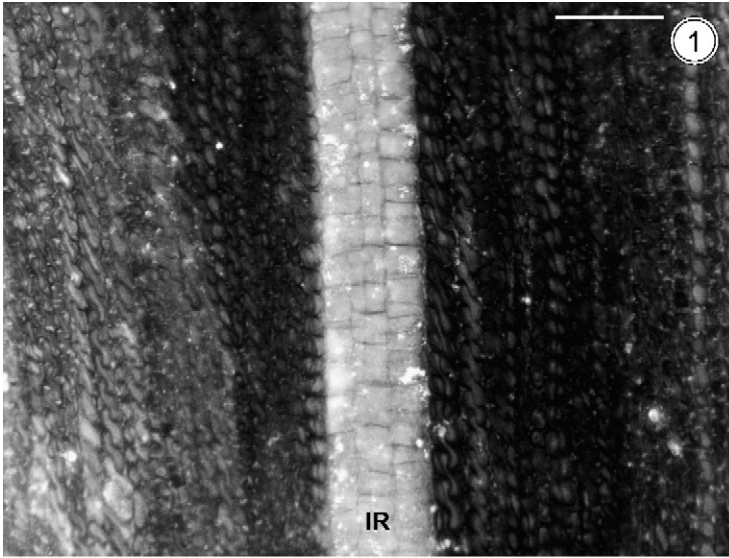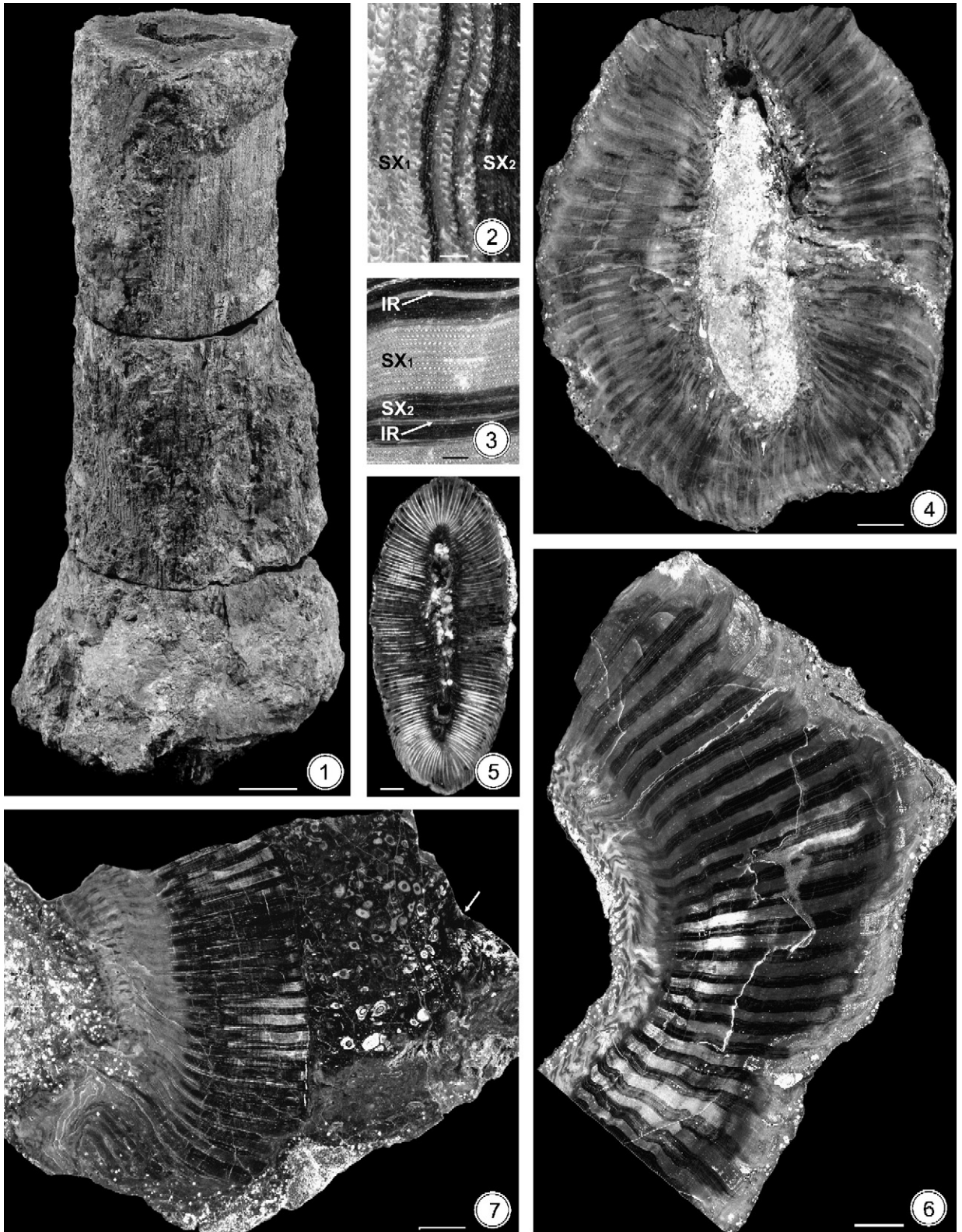
Plate IV.

Plate V (*caption on page 164*).
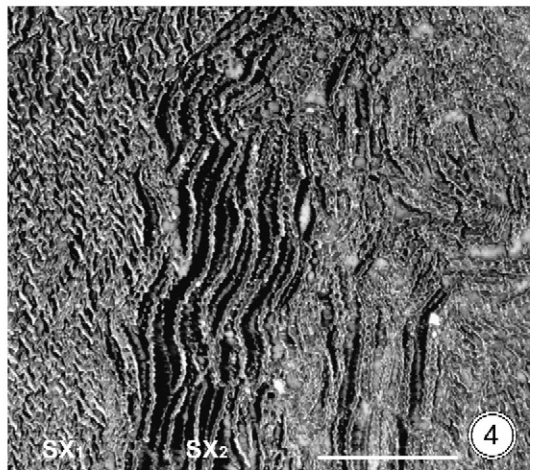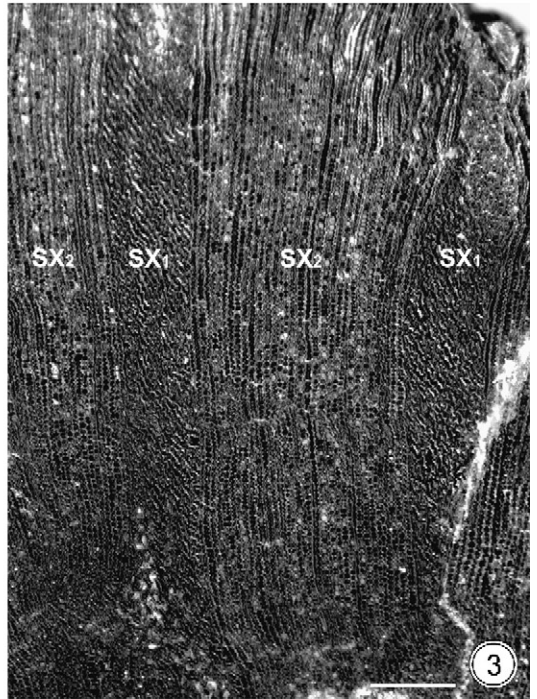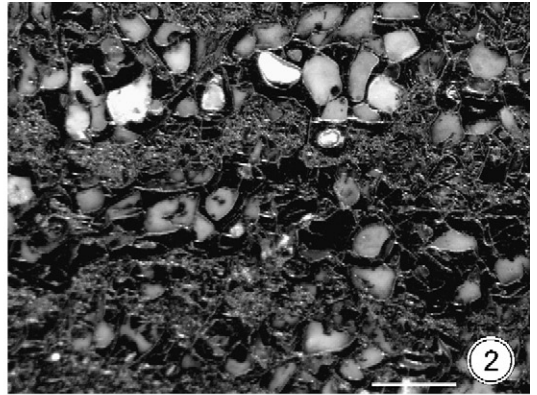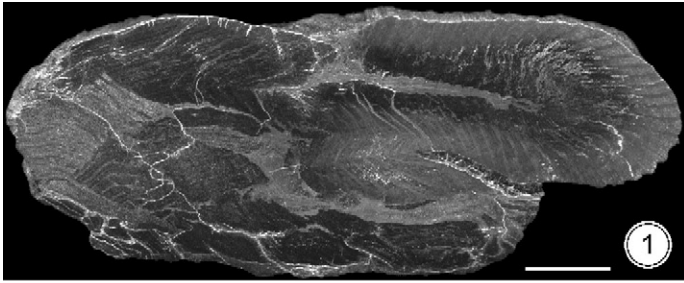
Plate VI (*caption on page 164*).

Plate VII (*caption on page 164*).

and a NIKON SMZ 1500 binocular microscope, both in connection with a NIKON DS-5M-L1 digital camera. Overview photographs were made by using a FUJIFILM S1 pro camera combined with a SIGMA APO Macro 180 F 3.5 EX lens or an Epson Perfection 4870 scanner.

For comparative purposes, additional material from the following regions was investigated: Autun, France; Nová Paka, Czech Republic; Döhlen Basin, NW-Saxony Volcanite Complex, Thuringian Forest Basin, Saar-Nahe Basin and Schwarzwald, Germany. Material, which the presented study is based on, is stored in following institutions: Palaeontological collection of the Museum für Naturkunde, Chemnitz/Germany (MfNC), Naturhistorisches Museum Schloss Bertholdsburg Schleusingen (NHMS), Staatliches Museum für Naturkunde Stuttgart (SMNS), Paläontologisches Institut am Museum für Naturkunde der Humboldt-Universität Berlin (MB), Staatliche Naturhistorische Sammlungen, Museum für Mineralogie und Geologie Dresden (MMG), Geological Institute of the Freiberg University of Mining and Technology (BAF), Palaeontological Museum Nierstein (PMN). Few remaining portions from the material published by Cotta (1832) are kept in the British Museum (Natural History), London, UK (BMNH) (Kidston, 1886). Unfortunately, the holotype of *Calamitea striata*, published by Cotta (1832, Plate XIV, 1) and re-figured in this contribution (Plate VI, 4) is badly preserved and lacks key information. It only represents one transverse section of a few millimetres thickness. This slice is insufficiently ground/polished and doesn't offer the possibility to elaborate diagnostic characteristics. Since radial and tangential surfaces are lacking, the remaining type material doesn't provide any evidence regarding the nature of small tracheids/fibers. However, there exist some historical large specimens from the type locality. These specimens, K 5204, K 18, K 159, K 632, K 2066, K 3348, K 3351, K 3366, K 3379, K 3387, K 3730 stored at the Museum für Naturkunde Chemnitz, show sufficient preservation and, are available for thorough investigation.

4. Systematics

Class: Sphenopsida
Order: Equisetales
Family: Calamitaceae
Calamitea (Cotta, 1832) nov. emend. Rößler and Noll
Type: *Calamitea striata* Cotta 1832

Synonymy and selected references:

1832 *Calamitea*, Cotta, p. 68.
1841 *Calamitea,* Unger in Petzholdt, p. 58.
1847 *Calamitea,* Unger, p. 31.

1849 *Calamodendron*, Brongniart, p. 50.
1864–1965 *Calamodendron*, Göppert, p. 180.
1875 *Calamitea,* Sterzel, p. 186.
1896 *Calamodendron,* Renault, p. 119–122.
1898 *Calamodendron,* Renault, p. 1.
1900 *Calamodendron,* Scott, p. 33, Fig. 10.
1930 *Calamodendron*, Zimmermann, p. 171, Fig. 103.
1964 *Calamodendron*, Boureau, p. 323.
1973 *Calamodendron,* Gothan and Weyland, p. 195.
1995 *Calamodendron,* Doubinger et al., p. 98.

Original diagnosis: in Cotta (1832, p. 67).
Emended diagnosis: Calamitean sphenopsid with secondary xylem consisting of two different types of tracheids, one showing approximately twice as large diameters as the other. Large-diameter tracheid files in front of the carinal canals, small-diameter tracheid files marginally.
Calamitea striata (Cotta, 1832) nov. emend. Rößler and Noll (Plates I–VI)
Holotype: Specimen BMNH 13775 (Plate VI, 4)
Repository: British Museum (Natural History), London, UK

Additional material: Specimens MfNC K 5204, K 18, K 159, K 632, K 2066, K 3348, K 3351, K 3366, K 3379, K 3387, K 3730
Type locality: The city of Chemnitz (Erzgebirge Basin), Germany
Type stratum: The Permian Zeisigwald Tuff Horizon of the Leukersdorf Formation
Further occurrences: Vosges (Val d'Ajol) and Massif Central (Autun, Grand'Croix, St. Étienne, Commentry, St. Éloy), France; Nová Paka, Czech Republic; Kansas, USA; Döhlen-Basin, Germany; Iano, Italy
Remark: The remaining specimens figured in Cotta (1832, Plate XIV, 1–4; Plate XV, 1–2) are thin transverse slices cut from few different trunks. However, it is not possible to show all necessary anatomical characteristics only from this material. To characterise the species adequately the use of additional material is recommended. The present contribution appoints and describes such material from the type locality (Plates I–VI).

Synonymy and selected references:

1832 *Calamitea striata*, Cotta, p. 67, Plate XIV, 1–4; Plate XV, 1–2.
1841 *Calamitea striata,* Unger in Petzholdt, p. 47, Plate VII, 8.
1947 *Calamitea striata,* Unger, p. 31.
1849 *Calamodendron striatum*, Brongniart, p. 50.
1852 *Calamodendron striatum*, Mougeot, p. 32, Plate V, 1–4.
1864–1965 *Calamodendron striatum*, Göppert, p. 180, Plates XXX, XXXI.
1876 *Calamodendron striatum,* Renault, p. 548.
1877 *Calamodendron striatum,* Grand'Eury, p. 291.
1881 *Calamites striatus,* Stur, p. 24, Figs. 1–3, Plate I, 3.
1886 *Calamites striatus,* Kidston, p. 4.

1893   *Calamites (cruciatus) striatus,* Sterzel, p. 82–87, Plate IX, 4; Plate XI, 28–34.

1893/96   *Calamodendron striatum,* Renault, p. 122, Plate LVIII, 1–5.

1898   *Calamodendron striatum,* Renault, p. 5, Plate I, 1–5.

1900   *Calamodendron striatum,* Zeiller, p. 155, Fig. 109.

1918   *Calamodendron striatum,* Sterzel, p. 258.

1952   *Calamodendron striatum,* Andrews, p. 201.

1964   *Calamodendron striatum,* Boureau, p. 323.

1976   *Calamodendron,* Barthel, p. 65, Plate XXIX, 10.

1982   *Calamodendron striatum,* Barthel, p. 76.

1998   *Calamodendron striatum,* Rößler and Barthel, p. 73, Plate III, 3.

2001   *Calamodendron striatum,* Rößler, p. 104, Figs. 243–245, 248, 261.

Emended diagnosis: Articulate trunks characterised by central pith/cavity, primary and secondary vascular tissues. Internode length variable. Branching regular at every node, usually 5–6 branches per node and alternating in successive nodes. Pith made of circular to polygonal parenchymatous cells, perimedullary zone and nodal region with parenchyma plates. Primary xylem bundles with carinal canals, radially and internally surrounded by a few rows of small metaxylem elements. Secondary body up to several centimetres thick, gradually diminishing to the top, showing radial segmentation of the fascicular wood separated by small interfascicular rays, both becoming tangentially slightly enlarged in radial direction. Fascicular wood highly variable, consisting of large-diameter tracheids (averaging 77 μm radially and 62 μm tangentially; up to 4.5 mm long) and small-diameter tracheids (averaging 39 μm radially and 38 μm tangentially; up to 3 mm long), both positioned in radial files, large tracheids in front of the carinal canals, small tracheids marginally, with interspersed small fascicular rays. Tangential width ratio of both tracheid type files variable. Proportion of large-diameter tracheids occasionally increasing in both radial and vertical direction; files of small-diameter tracheids dominate at the base of the trunk, and can be lacking at the top. Small-diameter tracheids with scalariform thickenings on radial walls elongate to circular pits. Large-diameter tracheids with scalariform, bifurcated to reticulated wall thickenings with elongated to rounded pits. Interfascicular rays continuously dissecting the wood, made of isodiametric to rectangular-shaped (higher than wide), thin-walled parenchymatous cells, usually triseriate, not more than 6 cells wide, sometimes dividing into several uniseriate parts vertically. Fascicular rays parenchymatous

Plate VIII. *Calamitea striata* transverse sections preserved in fine to medium-grained pyroclastics of the Döhlen Formation (Döhlen Basin, Germany) also known as *Calamites petzholdtii*. Note the different aspects depending on different preservational forms from 1 to 3.

1.   Complete stem showing flattened pith and carbonised secondary tissues. Found at Freital, below the 5th coal seam, MB.Pb. 2006/56, scale bar equals 10 mm.

2.   Almost complete stem showing numerous radial ruptures and carbonised remnants of secondary tissues. MMG PB SaP 3850, scale bar equals 10 mm.

3.   Stem showing less complete preservational form with few carbonised remnants of the secondary tissues. Found at Gittersee, BAF 1378/2004, scale bar equals 10 mm.

4.   Detail of the secondary body showing transition between compressed (carbonised) and three-dimensional (permineralised) preservation, MfNC F 10643, scale bar equals 2 mm.

5.   Detail of 4, MfNC F 10643, scale bar equals 500 μm.

6.   Detail of 4 showing pith cavity (PC), remaining carinal canals (CC) and innermost part of the secondary body. MfNC F 10643, scale bar equals 2 mm.

Plate IX. Different aspects of Permian compression preservational forms of the *Calamites cruciatus* group. (see plate on page 172)

1.   *Calamites multiramis* (Weiss) Kidston and Jongmans from the Early Permian Manebach Formation, Thuringian Forest Basin, Germany showing some internodes and branch scars close to the outer surface. NHMS WP 870, scale bar equals 10 mm.

2.   *Calamites multiramis* (Weiss) Kidston and Jongmans from the Early Permian Manebach Formation, Thuringian Forest Basin, Germany showing some internodes and branch scars as usually seen on the pith cast. NHMS WP 874, scale bar equals 10 mm.

3.   *Calamites multiramis* (Weiss) Kidston and Jongmans from the Early Permian Manebach Formation, Thuringian Forest Basin, Germany showing a pith cast with densely arranged nodes and vertical ruptures, which seem to result from breakage of the woody cylinder. NHMS WP 890, scale bar equals 50 mm.

4.   *Calamites* sp. from the Permian of Bad Sobernheim, Nahe Subgroup N4, Saar-Nahe Basin, Germany showing both vertical transition between enlarged internodes and densely spaced nodes and radial transition from the typical smooth pith cast up to a layer close to the outer surface showing alternating circular branch scars at every second node. F 12059, scale bar equals 10 mm.

5.   Detail of 4, scale bar equals 10 mm.

6.   *Calamites* sp. from the Permian of Bad Sobernheim (Saar-Nahe Basin), showing outer surface with alternating circular to oval branch scars at every second node. PMN coll. Stapf, scale bar equals 10 mm.
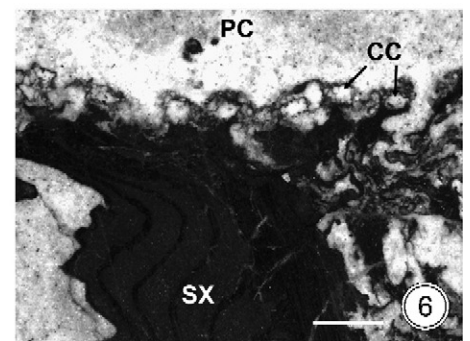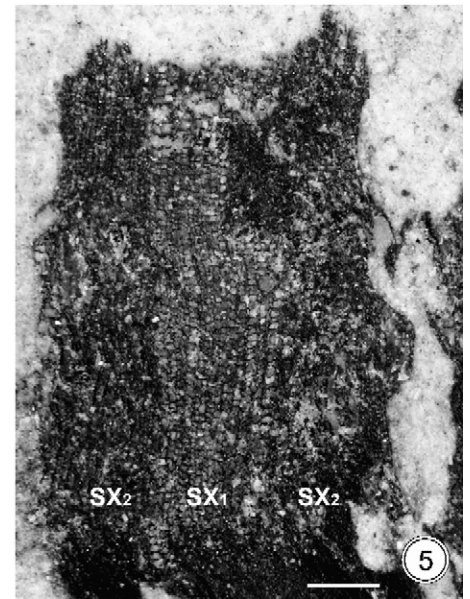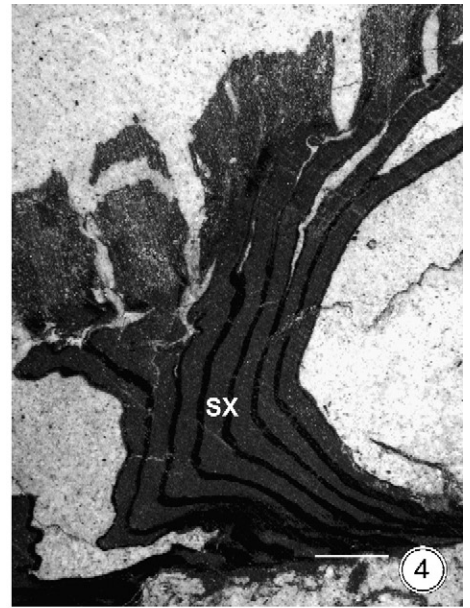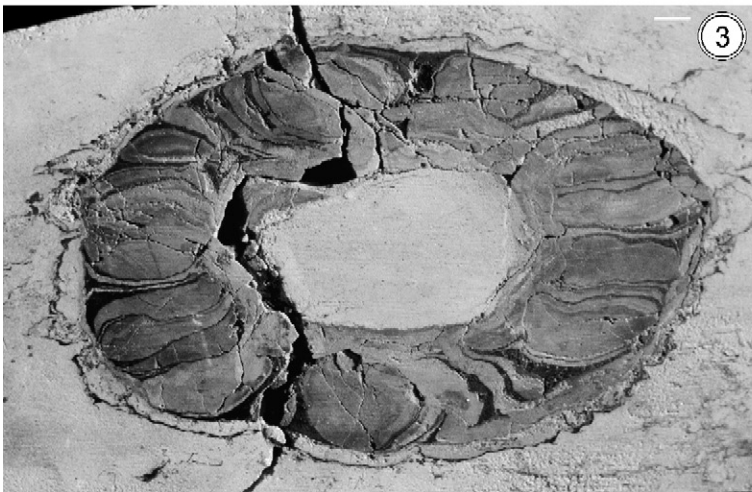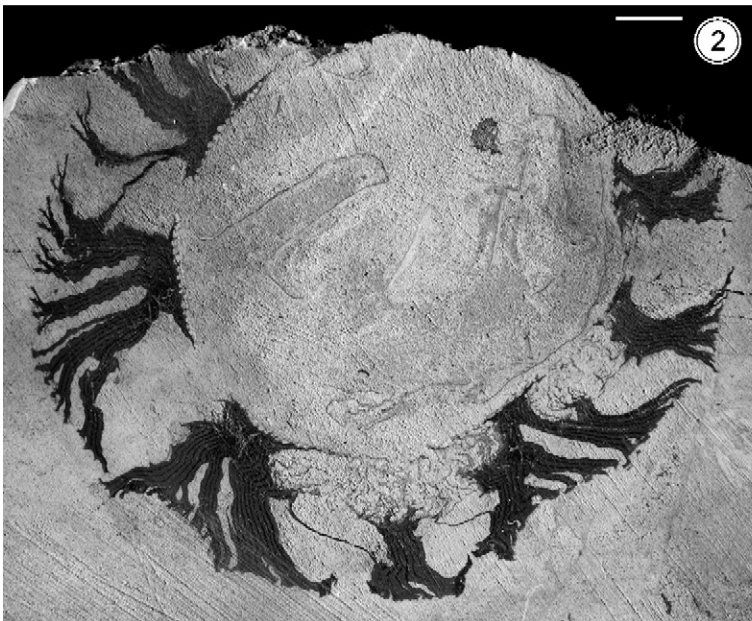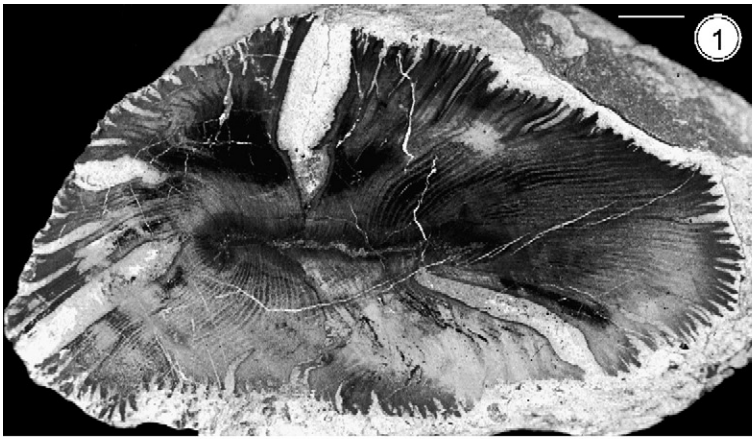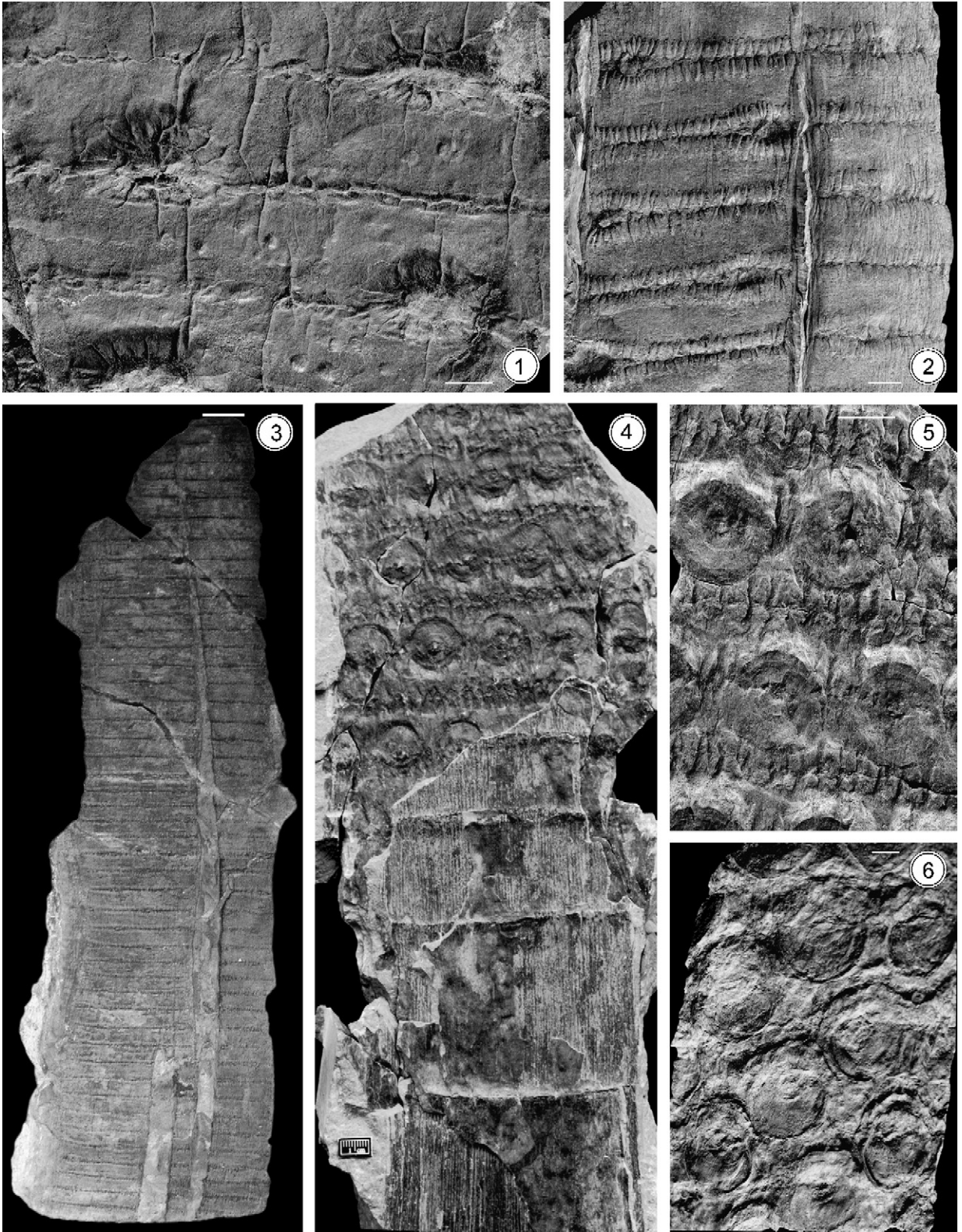
Plate VIII.

Plate IX (*caption on page 170*).

and narrow, usually uniseriate, sometimes biseriate and a few up to several tens of cells high, made of thin-walled, rectangular-shaped parenchymatous cells.

Further included species: It is likely that there are further species of this rather rare genus restricted to the Late Carboniferous and Early Permian. However, considering the high variability of the anatomical characteristics shown by *Calamitea striata* it is questionable if other species can be recognised. At least a critical revision of formerly used "diagnostic characteristics" is needed. Nevertheless, because the re-investigation of the type material of further species was beyond the scope of this contribution, we have refrained from putting further species among the synonymy of *C. striata*. Unfortunately the detailed evaluation of several French species carried out by Marguerier (1972) lacked comparison with the holotype or more informative material from the type locality of *C. striata*.

Description:

New information mainly comes from two sizeable trunks and several trunk portions. Specimen K 5204 is more than 405 cm long, up to 20 cm in diameter and composed of several pieces (Plate III). These are part of one exceptional find and undoubtedly belong together, but the exact position of a few portions within the trunk is not definitely established, since some pieces are cut-bounded or additional pieces could be missing. The number of primary vascular strands increases from about 178 close to the base of the specimen (not representing the trunk base) up to 240 at least 300 cm higher up, but decreases down to 220 counted at the top of the specimen, 405 cm above the base.

Specimen K 242 is a trunk base that shows a thickened lowermost part (Plate VI, 1) and internode lengths around 250 mm. This basal portion does not exhibit any branch traces. The number of primary vascular strands grades from about 105 at the base of the trunk up to 130 at least 50 cm higher up.

There are further specimens (Chemnitz: K 18, K 159, K 632, K 2066, K 3348, K 3351, K 3366, K 3379, K 3387, K 3730; Döhlen Basin: F 10643, F 10536), which provide numerous single aspects of anatomical structures and are reflected in the following description.

4.1. Morphology/Branching

The trunks of *Calamitea striata* reach a thickness of 50–200 mm with a clearly enlarged base. Connection to a rhizome has not been demonstrated. The largest available specimen is at least 405 cm long (Plate III). Extraxylary tissues have not been recognised, thus, the outer surface of the trunks is relatively smooth with a conspicuous vertical striation reflecting the radial segmentation of the wood.

The general outline in transverse view is elliptical to circular. The trunks are often taphonomically flattened or crushed. In these cases groups of wood wedges appear to be squeezed into the pith cavity (Plate III, 10), reflecting reduced stiffness of the woody cylinder in comparison to most calamite trunks of the *Arthropitys* type. Near the base of the trunks internodes are up to 250 mm long and without any branch traces. Internode lengths of the median to upper, branch-bearing trunk vary from 20 to 180 mm. Every node shows 5–6 rhombic to square branch traces of 10–15 mm thickness, which alternate in successive nodes, and lie on top of each other at every second node (Plate II, 1,2,4). Trunk portions that show enlarged internodes have 5 branch traces, those of shortened internodes have 6 branch traces at their nodes. In tangential view, branch traces consist of a parenchymatous centre encircled by undulating tracheids. Although they don't show any secondary growth (Plate II), branch traces are recognisable in radial direction throughout the whole secondary xylem (Plate IV, 1). Their diameter increases rapidly during the first few millimetres of the secondary tissue, later on only insignificantly.

4.2. Primary tissues

The pith cavity diameters of *Calamitea* are some of the largest known among permineralised calamitaleans. In our specimens they reach from 28 to 85 mm. The ratio of xylem cylinder diameter versus pith cavity diameter averages 1.65:1, grading from 2.5:1 at the trunk base up to 1.5:1 higher up in the trunk. Unfortunately we have no indication of what uppermost trunk portions look like. At the nodes the wood slightly extends into the pith, narrowing the central cavity (Plate IV, 1). Pith parenchyma is usually badly preserved. In transverse view one often recognises bar-shaped tissue fragments of some centimetres in length, which lie parallel to the pith periphery or protrude into the pith at the nodes (Plates I, 7 and III, 5, 8, 10). In radial view these tissue fragments appear as C-shaped plates (Plate IV, 1) that detach from the pith periphery starting at the nodes. Outside of these parenchyma plates, more centrally into the pith, parenchymatic cells appear to be radially crushed and less well preserved (Plate I, 7). In both transverse and radial views pith parenchyma cells are arranged in irregular rows. Cells are densely packed, usually of isodiametric outline, 90–230 µm in diameter (Plate I, 4). In front of the carinal canals parenchymatous cells are radially enlarged reaching 100–440 µm width and 70–240 µm in tangential direction (Plate I, 9). Cell walls are slightly thickened, up to 10–15 µm wide.

Details of the primary tissues with the carinal canals are rarely preserved (Plate I, 7). The ends of the narrow, wedge-shaped fascicle average 3.6 mm in length and 150–250 μm in width. Owing to poor preservation the metaxylem frequently is not recognisable. It is normally represented by one or two rows of small circular elements, which surround the radial and internal sides of the carinal canals, and are 30–40 (max. 60) μm in diameter (Plate I, 9). On the internal periphery of the carinal canals radially enlarged parenchyma cells adhere to the metaxylem elements. Carinal canals are of oval shape, averaging 330 (180–430) μm tangentially and 220 (180–370) μm radially. The number of primary xylem strands grades from 100 or slightly below 100 near the base of the trunk up to 240 in a distance of about 4–5 m, and may reflect epidogenetic and menetogenetic stages of growth. Then the size of the primary body grades down again (apoxogenesis).

4.3. Secondary tissues

The secondary body consists of heterogeneously constructed fascicular wood separated by small inter-fascicular rays. The maximum wood thickness observed in *Calamitea striata* is 80 mm (Plate VI, 6). Each wood fascicle consists of both large-diameter tracheid files (in front of primary xylem strands), small-diameter tracheid files (marginally) and small interspersed fascicular rays. The two types of tracheids are mainly differentiated by their diameter and are arranged in radial files (Plate I, 1–2). In transverse view a clear separation seems to be easily recognisable by the conspicuous bright/dark colour striation of the radial sectors (Plate I, 3). In detail, there is evidence of a considerable variability of this radial striation pattern (Plates I, 3 and III, 3, 7, 9). How-ever, this sketchy feature largely depends on preserva-tion and sometimes the colour of large-diameter and small-diameter tracheid files is inverted (Plate I, 6). The tangential width of both types of tracheid segments gradually increases in radial direction. However, their differentiation becomes less sharp during the few centi-metres of their radial course (Plate I, 1) and the portion of parenchyma increases, as more files of larger tracheids (type 1) displace the smaller ones (type 2) (Plate I, 2). This character could be interpreted as ontogenetic change. Plate V, 2 indicates that type 1 tracheids of the same file gradually enlarge in radial direction. Small (juvenile) trunks usually show that sectors of type 2 tracheids are wider than those of type 1 tracheids, whereas in large (adult) trunks this ratio is inverted. Median trunk positions show high variability of this character (Plate I, 3). Sometimes, in upper trunk portions the fascicular wood only shows a few radial files of

small-diameter tracheids or they seem to be lacking completely (Plate III, 9).

Type 1: This large-diameter tracheid type is rather non-uniform and often more or less deformed. Tracheid rows of conspicuously different diameters exist close together. In transverse view, tracheid diameters average 77 (50–90) μm radially and 62 (30–100) μm tangentially. Tracheids are up to 4.5 mm long. In radial and tangential sections cell walls show simple to bifurcate scalariform to reticulate thickenings with elongate oval pits (Plate IV, 3,4). There are 8–9 μm between successive thickenings. Between tracheid rows there are fascicular rays, which continue over a considerable radial distance, are 20–40 μm wide and are a few up to several tens of cells high. They vary from uniseriate to biseriate, made of rectangular outlined parenchyma cells, which are 40–130 μm (usually 60 μm) wide radially and 15–40 μm (usually 30 μm) wide tangentially in transverse section, rectangular to polygonal in tangential section and brick-shaped in radial section, with a typical height of 50–190 μm (Plate VI, 2).

Type 2: This small-sized tracheid type lies at the peri-phery of the fascicular wood and directly adjoins the inter-fascicular rays. Tracheids are up to 3 mm long and generally of uniform shape, in transverse section diameter averages 39 (20–67) μm radially and 38 (20–60) μm tangentially. In some specimens tracheid walls show sca-lariform thickenings. Distance between thickenings is 8–12 μm. In radial section tracheid walls show elongate oval to circular pits (Plate IV, 5).

The interfascicular rays continue from the pith up to the periphery of the woody cylinder, and reach a width up to 210 μm. They normally consists of three and up to six cell rows, but frequently splits in three to five uniseriate/biseriate rays in their radial/vertical course (Plate V, 4). In transverse view ray cells are rectangular shaped (Plate V, 1), 40–230 μm (usually 65 μm) wide radially and 20–60 μm (usually 45 μm) wide tangen-tially, polygonal-shaped and densely packed in tangen-tial section and brick-shaped to enlarged rectangular in radial section (Plate IV, 2), with a typical height of 60–180 μm. The ratio tracheids-parenchyma in the wood of *Calamitea striata* averages two thirds/one third.

Phloem, cortical tissues or periderm have not been discovered in the studied specimens.

5. Discussion

5.1. Comparison and affinities with other anatomically preserved species

Permineralised calamite specimens have traditionally not been assigned to the genus *Calamites* because it

has proven nearly impossible to demonstrate adequately which anatomically preserved trunks correspond to which specific *Calamites* pith cast or compression. As a result, anatomically preserved calamite trunks have been placed in three main form genera based on the structure of the secondary body, in particular the kind of the interfascicular rays (e.g. Andrews, 1952; Boureau, 1964; Wang et al., 2003). As established in this contribution we would like to retain *Calamitea* Cotta, the oldest generic name introduced for permineralised calamite material. The wood of *Calamitea* is characterised by a relatively small proportion of parenchyma and of two different types of tracheids. In contrast, *Arthropitys* Goeppert and *Arthroxylon* Reed exhibit both a considerably higher portion of parenchyma and uniform type of tracheids (Reed, 1952; Hass, 1975; Rößler and Noll, 2002, 2006). In *Arthropitys*, for example, the parenchyma reaches 50% of the secondary body, parenchymatous cells are rectangular to isodiametric in shape and show horizontal cell end walls. In the rare *Arthroxylon* the majority of the interfascicular rays consist of vertically elongated prosenchymatous cells with tapering end walls (Williamson, 1869; Reed, 1952). Although this generic level distinction remains a matter of discussion (Good, 1975), these characteristics distinguish groups of calamite stems until a more comprehensive knowledge of natural taxa can be established.

One of the conspicuous characteristics of *Calamitea* is the existence of two tracheid types, both arranged in radial files and composing more or less distinct sectors. The width of these sectors is highly variable (Plate I). Changes could have happened during the ontogeny of the plant (Plate III). Therefore, the use of any ratios based on the width of radial tracheid segments in taxonomic concepts as applied in former times (e.g. Renault, 1896, 1898), is shown to be questionable, especially if newly defined species were based only on small woody fragments. The evidence of variable width ratios between sectors of small-diameter tracheid files and sectors of large-diameter tracheid files has already been mentioned by Sterzel (1893), but he argued for preservational particularities rather than true anatomical variability. Regarding *Calamitea striata* from Chemnitz, he recognised that alternating files of the woody cylinder show prominent ribs at the trunk periphery (Plate II, 4), sometimes the large cells led to ribs, sometimes the small ones. Therefore, he questioned several species, such as *Calamodendron congenium* Gr.'Eury (see Renault, 1896, p. 124), *C. intermedium* Renault (1896, p. 125), and *C. aequale* Renault (1876, p. 575). The taxonomic significance of the type of tracheid wall thickening/pitting also has been a matter of discussion. Although *C. intermedium* was diagnosed as showing both elongate pits and multiseriate pits, this character was not interpreted with regard to

variability, but as a specific character (Renault, 1898). The type of tracheid wall thickening/pitting among calamites was recognised to be highly variable by several authors and has been found even in several species of *Calamodendron* (Marguerier, 1972). Our results (Plate IV, 3–5) help to underline this fact. Sterzel (1893) had already questioned the validity of *Calamodendron punctatum* Renault after investigation of several coalified/permineralised *C. striata* specimens from the Early Permian of the Döhlen Basin, in which he recognised tracheids with both scalariform and reticulate thickenings. Finds from the Döhlen Basin allowed comparisons between coalified, nearly uncompressed forms preserved in ash/crystal tuffs (Plate VIII) and permineralised material (Plate VII, 1–4).

A noteworthy characteristic of *Calamitea striata* is the reduced stiffness of the woody cylinder, which is frequently indicated by isolated wood wedges that have been squeezed into the pith cavity (Plate III, 3,10). This aspect has never been observed from the typical Euramerican *Arthropitys* species and additionally is helpful for comparison with different forms of compression preservation (see Section 5.2). The largest extension of the *C. striata* woody cylinder ever observed measures approximately 80 mm (Plate VI, 6), whereas the thickness of the largest secondary body of *Arthropitys* ever observed reaches 350 mm (Rößler and Noll, 2006).

A well-preserved primary body has been observed in only a few *Calamitea* specimens. Some species were only based on secondary xylem fragments, like *Calamodendron americanum* Andrews (1952, p. 201, Figs. 29, 30). This species, which lack the pith, primary body and extra stelar tissues, was described from the mid-Pennsylvanian of Kansas. Cell dimensions of 16 μm (for so-called fibrous/prosenchymatous tissue) and twice that size for tracheids are not known in any *Calamitea striata* specimen. This could suggest its validity.

5.2. Comparison with compression material

One of the most interesting aspects of calamitacean systematics is the correlation of compression and permineralised taxa. From the early days of palaeobotany onwards this topic has been a matter of debate. As proposed by Sterzel (1893), we can underline that *Calamitea striata* belongs to the sphenophyte group of *Calamites cruciatus* Sternberg as well as to the branching type of *Eucalamites* Weiss. This may be indicated by the typical quincunxial pattern of its branch scars (Plate II, 1). Nevertheless, Sterzel (1893, 1918) did not investigate the *C. striata* finds from Chemnitz in detail. Although there are several indications from other occurrences, an unequivocal assignment of any pith cast compression specimens to *Calamitea* must remain

conjectural. One of the most frequently found compression species that belong to the *C. cruciatus* group is *Calamites multiramis* (Weiss) Kidston and Jongmans. Although the general branching pattern between *C. striata* and *C. multiramis* is quite similar, showing 5–6 versus 6 branch scars per node, there seems to be a contradiction regarding the variability of internode lengths. In *C. striata* internode length ranges from 20 mm somewhere higher up to 250 mm at the trunk base. In contrast, internode length of *C. multiramis* usually does not extend beyond 70 mm (Barthel, 2004). However, there are a few specimens that exhibit longer internodes exceeding 90 mm (Jongmans, 1911, p. 152, Fig. 131). Moreover, the pith diameter of *C. multiramis* is usually twice as large as those of *C. striata.* But there are some characteristics that both species have in common. Both species commonly show preservational forms that exhibit a rip-open aspect in a vertical direction (Plates III, 2 and IX, 3). This feature seems to indicate reduced stiffness of the woody cylinder, as clearly observed in *C. striata*, and, therefore, supports the correlation of *C. multiramis* and *C. striata* as already mentioned by Barthel (1976, p. 66). In comparison to *Arthropitys* or *Arthroxylon*, *Calamitea* shows a significantly reduced parenchyma/xylem ratio in the wood, which seems to have led to rather brittle fracture behaviour of the *Calamitea*-trunks. This character also confirms the correlation of *C. striata* with tuffitic preservational forms sometimes designated "*Calamites petzholdtii*", which frequently exhibit rip-open in a radial direction (Plate VIII). This may be due to the shrinkage that may have happened during desiccation/carbonisation processes. The ratio of stem diameter to pith cavity diameter, which was recorded for 5 well preserved "*C. petzholdtii*" specimens, grades from 2.6 to 1.3:1. For typical *C. striata* from Chemnitz this ratio lies between 2.5:1 and 1.5:1. In places, where tissues were largely unaffected/uncompressed since early diagenetic stabilisation, "*C. petzholdtii*" specimens exhibit the typical *C. striata* behaviour (Plate VIII, 4) and confirm that these "species" simply are different preservational forms of the same taxonomic entity.

Calamites infractus Gutbier is another possible form of pith cast preservation synonymous with *Calamitea* permineralisations. It has been recorded from volcanics of the Early Permian of Zwickau, Erzgebirge Basin, and Rüdigsdorf, NW-Saxony Volcanite Complex (Sterzel, 1886, p. 57). The tufitic deposits of NW-Saxony additionally were the source of *Calamitea* permineralisations during recent years (Tunger, personal communication). Comparison with specimens from the Permian of Bad Sobernheim (Saar-Nahe Basin) suggests the existence of a group of calamitaleans of the *Calamites carinatus* type showing variable branching, sometimes with scars at every node, sometimes at every second node (Plate IX, 4–6; compare also Kerp and Fichter, 1985, p. 207, Plate III). The absence of any indication of the stem foliage at these specimens may be explained by the advanced ontogenetic stage of these types of stems. Before the stems have developed leafy branches the stem foliage should be abscised. *C. carinatus* from the Döhlen Basin tuffs shows coalified segments of pith parenchyma that compare well with parenchyma plates frequently recognised in the perimedullary zone at the pith margin of *C. striata* specimens from Chemnitz (Plates I, 7; III, 5, 6, 8 and IV, 1).

5.3. Growth form and ecological aspects of Calamitea striata

The reconstruction of the *Calamites cruciatus* type of arborescent sphenophytes is still under debate. The classic drawing published by Hirmer (1927) was first questioned and changed by Remy and Remy (1977) and, recently, Daviero and Lecoustre (2000) presented a computer-model of the growth architecture of *Calamites multiramis*, a well known Late Pennsylvanian/Early Permian *C. cruciatus*-group member (Barthel, 2004). But even this modern reconstruction can not resolve all questions. For example, the reconstruction model of Daviero and Lecoustre (2000) does not reflect the branch traces that penetrate the whole secondary xylem in a radial direction and slightly increase their diameter on this course without showing secondary growth. Although they were shown to be not overgrown and remain visible on the trunk surface, the reconstruction only shows leafy branches that form a trunk crown. However, the stem surface with branch scars points to a periodic abscission and repeated growth of leafy branches and is also indicated on some compressions (Plate IX, 4–6; Fig. 1). Although we have no indication of branches with secondary growth for *Calamitea striata* at the type locality, this seems not impossible. Renault (1898, Plate II, 4) figured a branch of *Calamodendron congenium* Gr. Eury showing secondary xylem from the Loire Basin, France. Nevertheless, all considerations in reconstructing these plants, which are confined to pith cast preservations, cannot characterise them adequately. It has sometimes been shown that pith cast impressions do not exhibit all branch traces (Kerp and Fichter, 1985).

Owing to the high proportion of lignified tissue elements in the secondary body of *Calamitea striata* and the general information regarding the biomechanical analysis of calamitalean plants provided by Spatz et al. (1998) we accept as true that this plant had a self-supporting habit.

Material from the Late Carboniferous of Commentry, France, provided evidence that leafy shoots of *Annularia*

spinulosa Sternberg and strobili of *Calamostachys tuberculata* (Sternberg) Weiss belong to pith casts of *Calamites multiramis* Weiss. However, there is multiple evidence that there exist several groups of calamitaleans having *A. spinulosa* leaves and *C. tuberculata* strobili (Remy and Remy, 1977). In this regard it seems necessary to separate the group of Late Pennsylvanian/Early Permian plants with *Calamites carinatus* branching from older groups known from the Middle Pennsylvanian Coal Measures (Barthel, 1980; Rößler and Thiele-Bourcier, 2000).
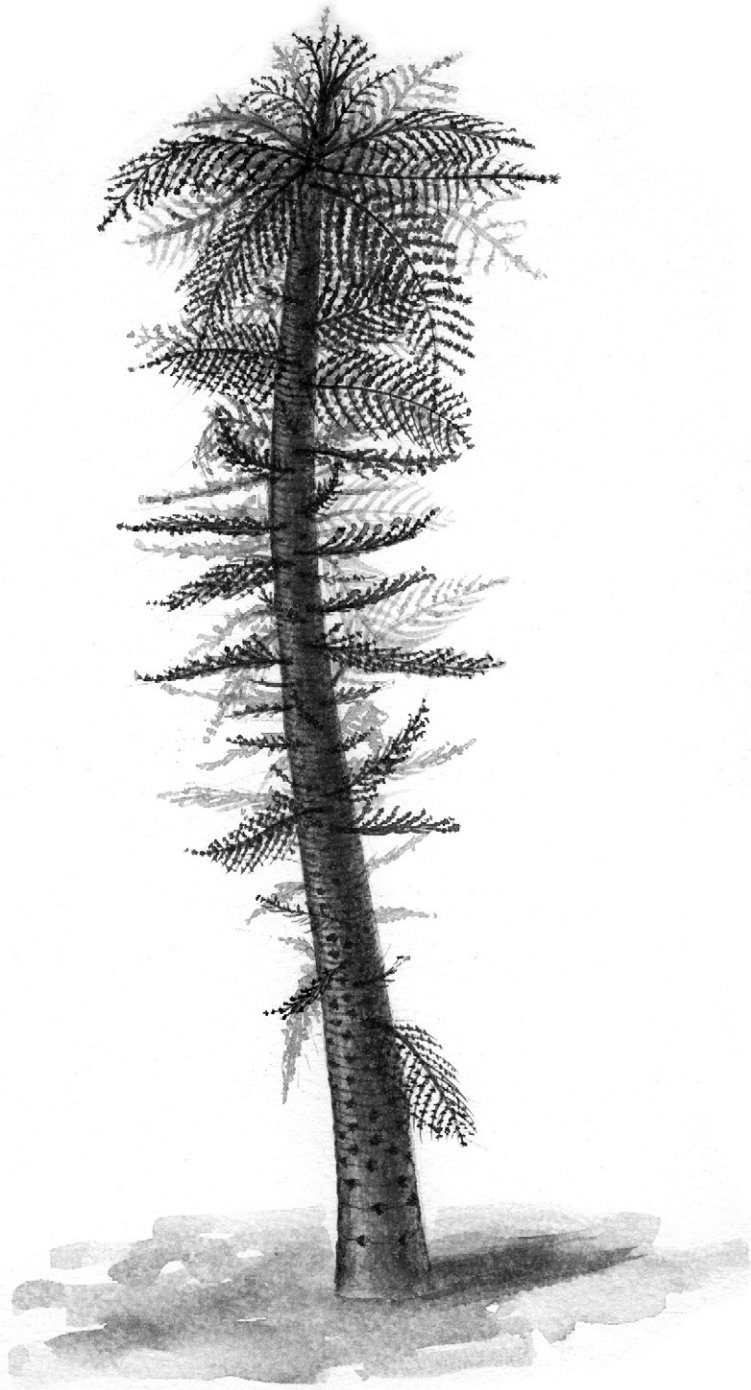
Fig. 1. Proposed reconstruction of *Calamitea striata*.

Contrary to what is known of other calamitaleans, such as *Calamites gigas*, *Calamitea striata* and related compression species are exclusively elements of hygrophile, peat-forming forested mires and, therefore, are frequently found within coal seams and in roof-shale floras usually associated with psaroneaceous tree ferns, sphenophylls, medullosan and callistophytalean pteridosperms, cordaitaleans, and rarely remains of *Sigillaria brardii* (Gothan and Gimm, 1952; Barthel, 2001; Rößler, in press). From Chemnitz we know of one specimen that shows an *Ankyropteris brongniartii* axis in growth position, embedded in a dense mass of its adventitious aerial roots on the periphery of a *C. striata* trunk (Plate VI, 7). Our interpretation that both plants exhibit their growth position rather than reflect only preservational proximity, indicates that at the outer surface of the trunk – at least in this ontogenetic stage – extraxylary tissues were very thin, because the *Ankyropteris* roots are directly attached to the woody trunk surface. In marked contrast to the late Palaeozoic arborescent lycopsids, which formed extensive amounts of periderm, the calamites appear to have produced little, if any, periderm, despite their tree-like stature. Although intact extraxylary tissues mainly have been shown for rather juvenile plants, a distinct phellogen never has been demonstrated (Agashe, 1964). The *Ankyropteris* specimen attached to *C. striata* additionally indicates that tree ferns were not the only hosts for climbers, scramblers and epiphytic plants, as summarised in Rößler (2000).

The present study may have shown that this group of fossil plants remains insufficiently understood. Subgeneric classification has been a source of confusion over time and, as former researchers tried to show (Cichan and Taylor, 1983) and the present study confirms, the aspect of ontogenetic variability remains poorly understood or at least largely underappreciated. Efforts to characterise calamite plants adequately must be continued to get a more detailed picture of them.

Acknowledgements

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