

CYCADODENDRON GALTIERI GEN. NOV. ET SP. NOV.: AN EARLY PERMIAN GYMNOSPERM STEM WITH CYCADALEAN AFFINITY

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Premise of research. In our modern flora, the Cycadales represent one of the oldest-known gymnosperm clades, with their evolutionary roots tracing back to the late Paleozoic. Their radiation and wide distribution in the Mesozoic are well documented by numerous fossils. In contrast, the fossil record of late Paleozoic forms is restricted to a few specimens, thus leaving open questions on the origin and early evolution of cycads. A petrified stem with cycadalean affinity has been found in Saxony (central-eastern Germany) in Holocene gravel deposits of the Zwickauer Mulde river as a result of fluvial transportation from its original lower Permian locality.

Methodology. The specimen was sectioned transversely, radially, and tangentially. Its provenance was clarified by comparing fossil woods of various localities in the upstream catchment area. Samples of these localities were exposed to ultraviolet light of different wavelengths, revealing distinctive fluorescence patterns related to specific geochemical conditions during the fossilization process. Plant anatomical studies were performed by macroscopic and microscopic documentation, including photo scanning, microscopic photography, and anatomical measurements.

Pivotal results. *Cycadodendron galtieri* gen. nov. et sp. nov. originates from the Chemnitz Fossil Lagerstätte, an autochthonous floral assemblage of early Permian age (291 Ma; Sakmarian–Artinskian) that has been buried and conserved by pyroclastics in a geological instant. Several anatomical characteristics provide evidence for its cycadalean affinity: (1) a wide pith with numerous scattered medullary bundles, (2) a pith-peripheral vascular system with endarch primary xylem bundles, (3) at least nine successive vascular segments with secondary xylem and phloem, (4) araucarioid-type pitting of secondary xylem tracheids, and (5) primary rays and medullary bundles traversing the vascular segments.

Conclusions. *Cycadodendron galtieri* gen. nov. et sp. nov. provides insights into stem anatomical characteristics of the oldest-known cycads, for example, revealing that polyxyly was an early-derived feature in cycad evolution. Its provenance reveals that the arborescent but generally small taxon was part of intramontane forested landscapes thriving on a well-drained mineral substrate in an alluvial plain setting and experiencing seasonally dry paleoclimate.

Keywords: late Paleozoic, Permian, paleobotany, gymnosperm evolution, cycads, wood anatomy.

Online enhancements: appendixes.

Introduction

Cycads represent one of the oldest lineages of extant seed plants, today represented by 10 genera and 371 species (Calonje

et al. 2022). The long evolutionary history of cycads starts in the late Paleozoic (Norstog and Nicholls 1997). Bayesian molecular dating sets the cycad clade divergence to the late Carboniferous–early Permian and the development of the crown group of extant cycads to the late Permian (274.5 Ma; Condamine et al. 2015). Their global radiation after the Permian–Triassic global mass extinction during the early Mesozoic is reflected by several stem and foliage fossils (Archangelsky and Brett 1963; Delevoryas and Hope 1971; Gould 1971; Lutz et al. 2003; Hermsen et al. 2007). The vast similarity of Mesozoic and Cenozoic cycad fossils to their living relatives suggests that the clade of Cycadales

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generally experienced only minor evolutionary changes of anatomical and morphological features over more than 200 Ma (e.g., Artabe et al. 1991, 2005; Taylor et al. 2009).

As cycad radiation in the Mesozoic is undoubtedly reflected by diverse fossil evidence, our knowledge of their early evolution in the late Paleozoic is still limited because of a sparse fossil record. Therefore, several critical questions on early cycad evolution patterns are still debated, including the exact timing of their first appearance, relations to potential parental or sister lineages, and patterns of early diversification and paleogeographic distribution. The oldest fossils of putative cycadalean affinity were described from lower–upper Pennsylvanian strata and share some characteristics with cycad megasporophylls (Cridland and Morris 1960; Leary 1990). Similar fossils, such as *Phasmatocycas* and *Spermopteris*, are also known from lower Permian strata (Mamay 1969, 1973; Gillespie and Pfefferkorn 1986), but their apparent affinity to modern cycad megasporophylls was debated (Axsmith et al. 2003). Nevertheless, several other cycad-like fossil taxa first appeared in the (lower) Permian, including megasporophylls and foliage, some of which provided clear evidence of their cycad affinity (Renault 1882; Mamay 1976; Zhu and Du 1981; Kerp 1983; Gao and Thomas 1989; Mei et al. 1992; Pott et al. 2010; Pott and Launis 2015; Feng et al. 2017). Therefore, the Permian may be regarded as the period of initial cycad diversification coinciding with a wide paleogeographic distribution (Spiekermann et al. 2021). In contrast to foliage and reproductive organs, the stem anatomy of late Paleozoic cycads is poorly documented, as the fossil record is restricted to a few questionable specimens of lowermost Permian strata, to date (Renault 1896; Bancroft 1914; Caldas et al. 1989) and a recently investigated specimen from the middle Permian of Brazil (Spiekermann et al. 2021). The lack of data on wood anatomical features depicts a significant bottleneck in understanding ancient cycad evolution, their overall appearance and growth architecture, and their paleoecology.

Here, we report on a new gymnosperm stem, *Cycadodendron galtieri* gen. nov. et sp. nov., of lower Permian strata from central-eastern Germany. The specimen exhibits distinctive characteristics of fossil and extant cycad stems, thus providing rare insights into the stem anatomy of this plant group in the late Paleozoic. We compare its features with those of fossil and extant relatives, discuss its evolutionary and adaptational significance, and shed light on the paleogeographic and ecological background of the cycad origin.

Material and Methods

Origin of the Specimen

The specimen K9883 originates from an abandoned gravel pit close to the settlement of Biesern near Rochlitz (Saxony, central-eastern Germany; lat. 51°29.08'N, long. 12°48'14.50'E). The Biesern gravel pit exposes Quaternary fluvial deposits of the Zwickauer Mulde river system implicating fluvial transportation and dislocation of the specimen from its original fossil locality. To adequately assess the evolutionary significance of the find, it is necessary to provide evidence concerning the provenance and primary site of formation, including its stratigraphic context.

In general, sediments of the Biesern gravel pit originate from the upstream catchment of the Zwickauer Mulde river system, providing a restricted area that covers the crystalline-metamorphic complex of the western Erzgebirge Mountains and its northern forelands near the German-Czech border (fig. 1). Within this drainage area, fossil-wood-bearing strata of primary origin that are subjected to erosion are known only from the Permian Chemnitz Basin, particularly the Chemnitz Fossil Lagerstätte in the Leukersdorf Formation (Rößler 2021), and a few other sites in the stratigraphically older Härtensdorf and Planitz Formations. In contrast, petrified woods from the neighboring Flöha Basin are transported by the Flöha and Zschopau rivers into the Freiburger Mulde river, which joins the Zwickauer Mulde river about 20 km north of Biesern at Sermuth. Thus, petrified woods from the Flöha Basin can be excluded. In proximity to the Biesern gravel pit but somewhat downstream of the Zwickauer Mulde river, pyroclastic and clastic fossil-wood-bearing strata of the lower Permian North Saxon Volcanic Complex are exposed (e.g., Hoffmann et al. 2013; Repstock et al. 2018; Hübner et al. 2021).

To indicate the provenance of fossil wood in recent years (Matyssová et al. 2008, 2010; Trümper et al. 2018), several efforts have been made to detect a site- or host-rock-specific mineralogical pattern. In particular, spectroscopic methods have been applied based on site-specific lattice perturbations and trace elements in the principal fossilization agent SiO₂. With different excitations, such as electrons or ultraviolet radiation, a pattern based on the silicification process can ideally be detected and documented by cathodoluminescence and, most recently, also by UV photoluminescence, a promising new method for detecting the provenance of silicified fossil wood (Rößler 2021). A site-specific “fingerprint” usually reflects diverse facets of the fossilization process and follows in content various applications of provenance analysis of quartz raw materials, which have been used with success for some time (Zinkernagel 1978; Götze et al. 2001; Götze and Hanchar 2018). The inventory of methods used in this context has recently been extended to silicified woods and fossiliferous cherts (Götze and Rößler 2000; Trümper et al. 2018, 2020) to assign fossil wood from secondary deposits to a primary site where the petrified wood was formed. UV photoluminescence proved to be particularly helpful because it does not require thin sections and thus provides rapid and nondestructive results (Trümper et al. 2020; Lócse et al. 2019). Therefore, we confined our investigation to reflected UV light with 254- and 365-nm wavelengths.

As several finds show, the Chemnitz photoluminescence pattern based on the silicification history is identical to the Biesern specimen and different from the other specimens examined (app. S1; apps. S1, S2 are available online). Like agates of the Chemnitz region (Götze et al. 2015), the quartz of the silicified woods shows a typical pattern under UV exposure at 254-nm wavelength that mainly consists of intense greenish photoluminescence, which is mostly centrally positioned in the wood and additionally occurs in SiO₂-filled cracks. The 500-nm emission band characterizes this green photoluminescence due to incorporated uranyl ions bound to the silica surface. Uranyl contents down to 1 ppm are proven sufficient to cause the characteristic photoluminescence, as Götze et al. (2015) demonstrated for volcanic agates from different localities in Europe and North and South America. The linkage between uranium mineralization

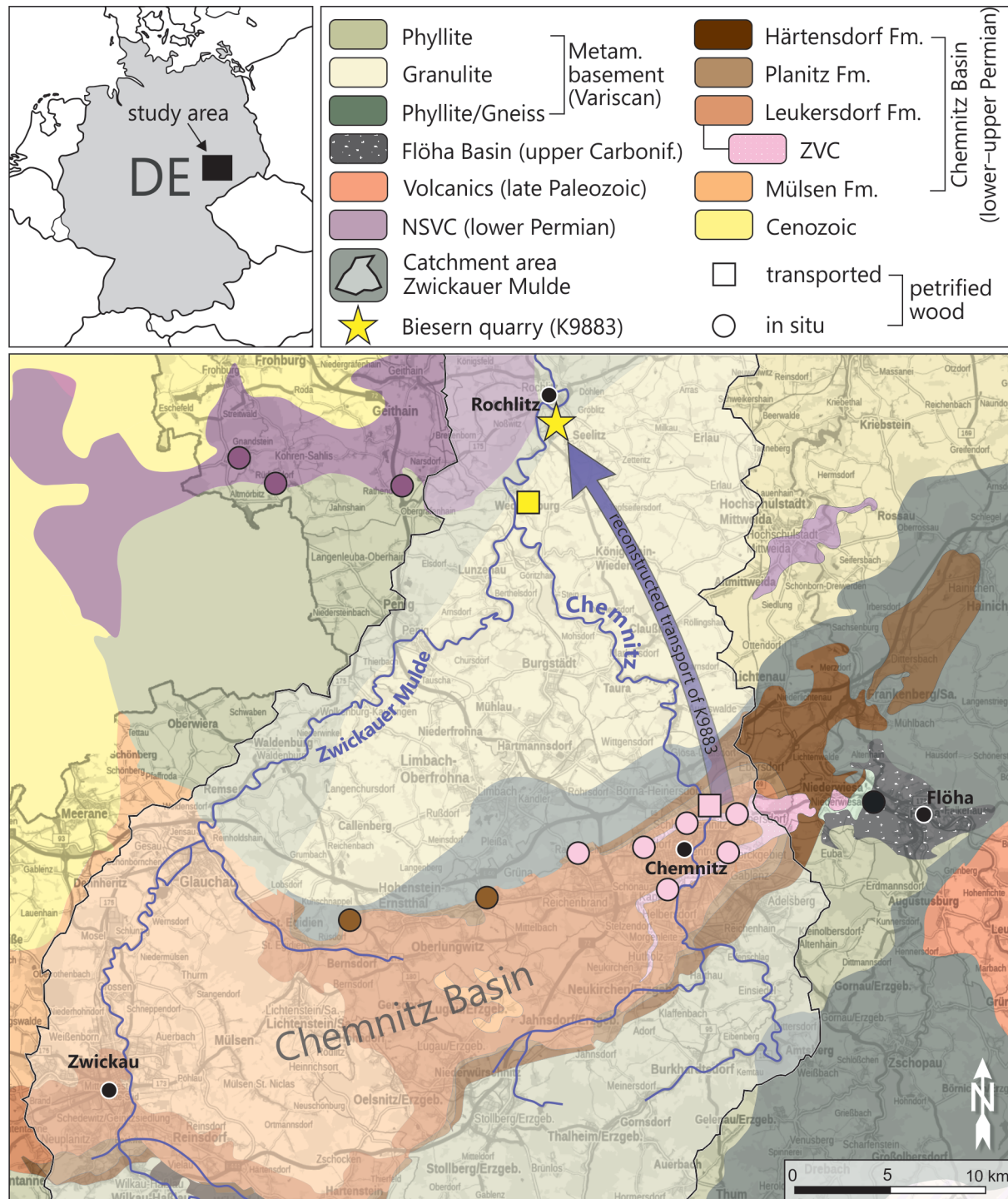


Fig. 1 Geography and geology of the source area of the fossil cycad stem, combining the catchment area of the Zwickauer Mulde River/Chemnitz River with the most important localities of mainly in situ found petrified wood and their stratigraphic affiliation. NSVC = North Saxony Volcanite Complex; ZVC = Zeisigwald Volcanic Complex.

and silicification was additionally substantiated based on uranium deposits in Australia and Canada (Pan et al. 2021). Orange-red to violet photoluminescence is frequently observed in the periphery of the green central regions. In addition, predominantly orange-red to

violet photoluminescence occurs under UV exposure of the 365-nm wavelength.

The photoluminescence pattern characterized here from the Chemnitz fossil site is identically recognizable in the new specimen

from Biesern and also occurs in other silicified woods from this locality (app. S1). In contrast, silicified woods from the Late Paleozoic North Saxon Volcanic Complex sites show different photoluminescence patterns or even lack any photoluminescence (app. S1). Several additional petrified wood sites of the Härtensdorf and Planitz Formations in the Chemnitz Basin also provide different photoluminescence patterns. In some localities, the photoluminescence of the quartz is absent. The latter also applies to younger silicified stems originating from Meso- to Cenozoic strata, as evidenced by finds of the Cretaceous fern trunk *Tempskya* (app. S1).

In conclusion, the evidence concerning the primary site of origin of the new specimen K9883 from Biesern is based on (1) the provenance of the Zwickauer Mulde river deposits and (2) the specific UV-photoluminescence of the silicified (petrified) specimen. Specific photoluminescence patterns in K9883 detected under UV at 254- and 365-nm wavelengths reflect the unique geochemical fingerprint of silicified woods of the Chemnitz Fossil Lagerstätte. In contrast, photoluminescence patterns in silicified woods from other potential sites differ from those of the Chemnitz finds and can be excluded. As a result, the Biesern find shows a clear affinity to the Chemnitz Fossil Lagerstätte from which it was dislocated by the Chemnitz river that erodes the Zeisigwald pyroclastics, carries numerous Permian silicified blocks of wood in a wide range of dimensions from millimeters to several decimeters, and drains the northeastern Chemnitz Basin into the Zwickauer Mulde river (fig. 1).

Geology and Fossil Record of the Source Area

Lower Permian terrestrial strata are restricted to local-scale intramontane depressions of the degrading Variscan mountain range in central Europe. Most of them experienced significant volcanic activity during the lower Permian (Benek et al. 1996), which is recorded by minor and major volcanic deposits that intercalate with red-colored clastic strata mainly of alluvial origin and characterized as “wet red beds” sensu Schneider et al. (2010). The Chemnitz Basin represents a 70 × 30-km large northeast-southwest extending sedimentary basin structure (fig. 1). Its predominant sedimentary environment is a low-energy alluvial plain setting encompassing fluvial, lacustrine, and palustrine formations and also basin-marginal alluvial fan deposits (Schneider et al. 2012). The sedimentary succession is subdivided into four stratigraphic formations, spanning a time interval of lower–upper Permian, with a significant depositional gap during the middle Permian (upper Cisuralian–upper Guadalupian; Schneider et al. 2012). Only the three lower formations (Härtensdorf-, Planitz-, Leukersdorf-) are fossiliferous, spanning over a restricted stratigraphic section from the Asselian to the Artinskian (fig. 2). The area was located within the paleotropical belt at a near-equator position. The lower Permian paleoclimate of the Chemnitz Basin is supposed to have been seasonally dry, with a trend of increasing aridity stratigraphically upward, in accordance with the overall aridization trend recorded in late Paleozoic continental strata (e.g., Roscher and Schneider 2006).

Among the fossil localities of petrified woods in the Chemnitz Basin, the Chemnitz Fossil Forest of the upper Leukersdorf Formation provides the most considerable quantities of silicified woods in various dimensions. These woods are frequently found in an area mainly covered by the urban settlements of Chemnitz but also

in the Chemnitz river, which erodes the outcropping fossil-bearing pyroclastics. The autochthonous fossil assemblage of the Chemnitz Fossil Forest was preserved in a geological instant by pyroclastic ejecta of a nearby Plinian-style eruption at 291 ± 2 Ma (e.g., Rößler et al. 2012b; Luthardt et al. 2016, 2018; Rößler 2021; see fig. 2 for excavation profile). The fossil ecosystem once represented a basin-central wet forest ecosystem growing in a clastic alluvial plain setting (Schneider et al. 2012; Luthardt et al. 2016) and predominantly consisted of hygrophilous–mesophilous plants, such as cordaitaleans, psaroniacean tree ferns, medullosan pteridosperms, and arborescent calamitaleans but also dry-adapted walchian conifers (e.g., Rößler 2000; Rößler et al. 2012a, 2012b; Luthardt et al. 2021). Even though growing under seasonally dry paleoclimate, the ecosystem benefited from a near-surface groundwater level that remained nearly constant throughout the year, as indicated by paleosols formed under moist to wet conditions (Luthardt et al. 2016, 2017).

Sample Preparation and Analysis

The only 3-cm-long stem segment of K9883 was first sectioned transversally and polished. One of the two resulting pieces was cut radially and tangentially, so two radial and one tangential section(s) were available for documentation and closer examination (see fig. 3). The sections were digitized by using a standard photo scanner (Epson Perfection V600) at a resolution of 1600 ppi. Polished sections of K9883 were investigated under reflected light using a Nikon SMZ1500 microscope mounted with a Nikon SD-5M-L1 digital camera and a Nikon Eclipse ME600 microscope mounted with a Nikon SD-5M-L1 digital camera. Microscopic measurements of stem anatomical elements were performed using NIS Elements software (ver. 3.2). Extracted data were treated by applying basic statistics, including minimum, maximum, and mean values. Primary data on anatomical measurements are summarized in appendix S2. Stem anatomical sketches and figure plates were rendered using the Corel DRAW (ver. 17.0) vector graphics software.

Results

Systematics

Order—Cycadales Bercht et J. Presl 1820

Family—Incertae Sedis

Genus—Cycadodendron Luthardt, R.Rößler
et D. Stevenson, gen. nov.

Type Species—Cycadodendron galtieri Luthardt,
R.Rößler et D. Stevenson, sp. nov.

Etymology. The name reflects the specimen’s cycadalean affinity in combination with the most conspicuous feature of abundant wood, which is typically associated with the tree growth habit (*-dendron*).

Plant Fossil Names Registry number. PFN003158 (for new genus).

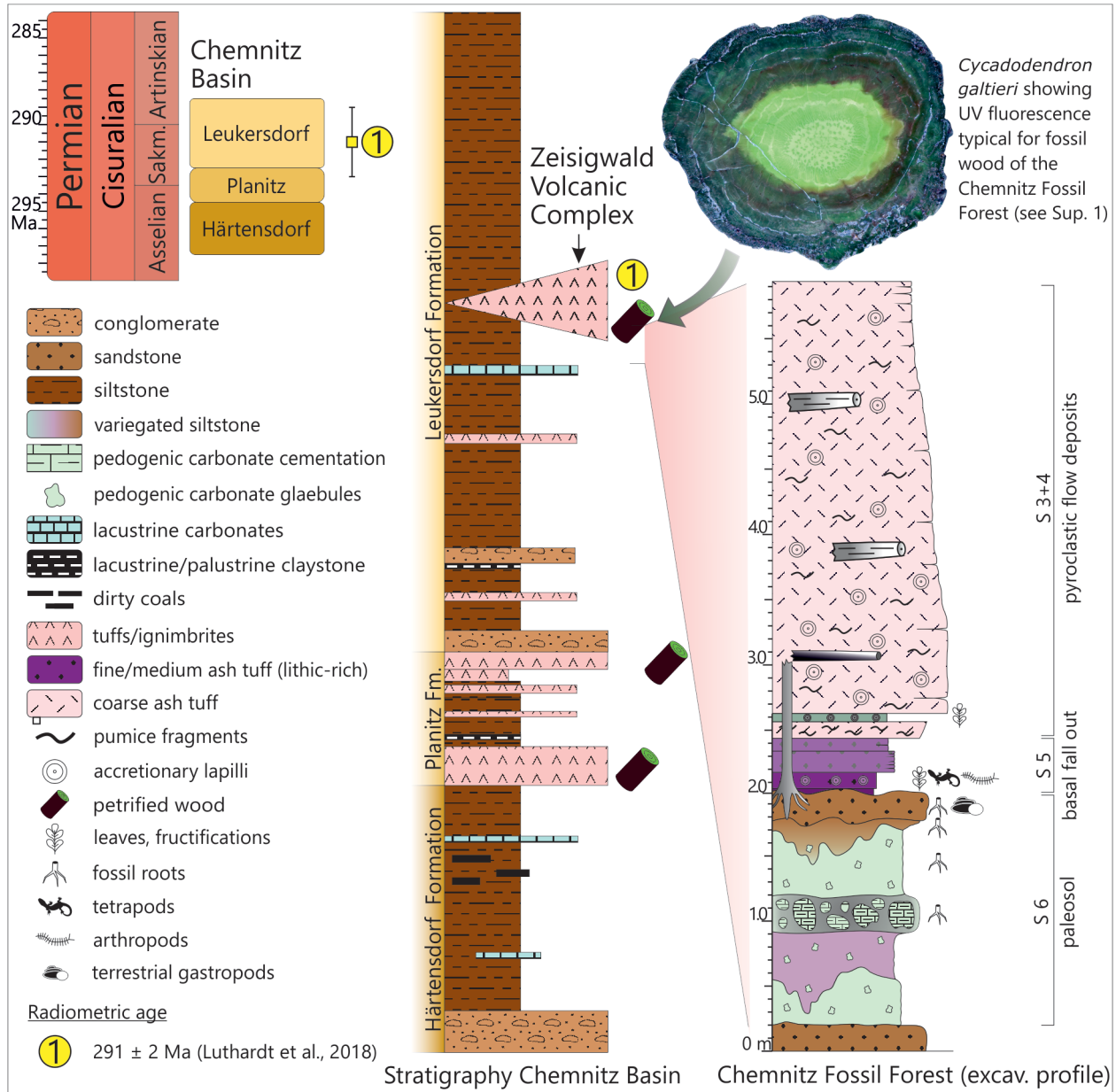


Fig. 2 Stratigraphy and age of the lower Permian formations in the Chemnitz Basin. *Left*, stratigraphic position in the International Chronostratigraphic Chart (ver. 2022/10). *Middle*, sedimentary succession of the corresponding formations with the stratigraphic position of *Cycadodendron galtieri* (K9883) at the basal pyroclastics of the Zeisigwald Volcanic Complex. *Right*, detailed lithological excavation profile of the Chemnitz Fossil Forest showing the paleosol in which in situ petrified plants are rooting and the embedding basal pyroclastics.

Generic diagnosis. Slender stem with wide parenchymatous pith; primary vascular system consisting of densely arranged interconnected medullary bundles scattered throughout the pith and circularly arranged bundles in the pith periphery; metaxylem tracheids of vascular bundles with multiserial-bordered pits; successive vascular segments with centripetal xylem and centrifugal phloem; innermost vascular segment with distinctly wider primary rays compared to the outer segments; wide-lumen secondary xylem tracheids with araucarioid-type pitting; medullary bundles obliquely traversing the vascular segment(s) through primary rays.

Type material. See type species below.

Species—*Cycadodendron galtieri* Luthardt, R.Rößler et D. Stevenson, *sp. nov.*

Etymology. In honor of our colleague and friend Jean Galtier, a renowned paleobotanist from Montpellier, France. We owe him significant contributions to the knowledge of the evolution and anatomy of Paleozoic fossil plants.

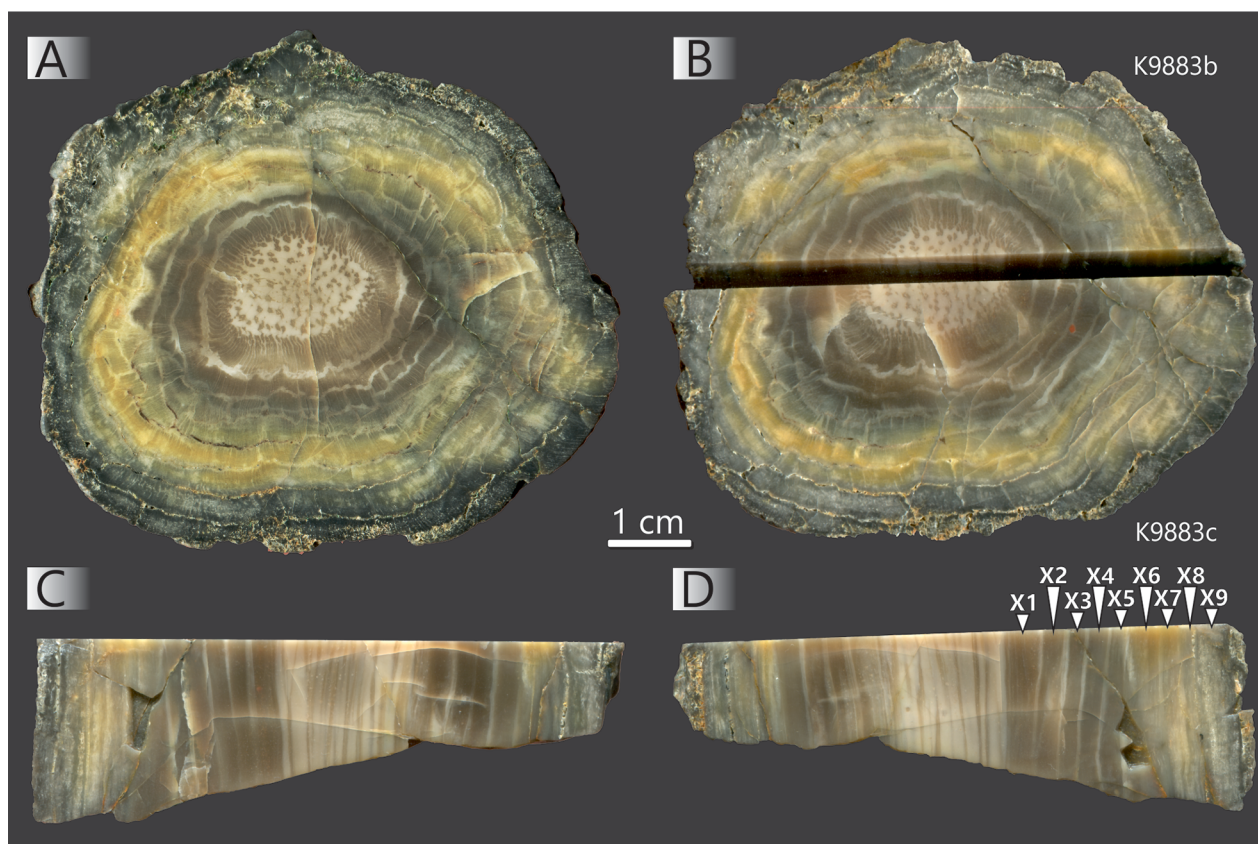


Fig. 3 Overview of polished sections of *Cycadodendron galtieri* gen. nov. et sp. nov. (K9883, holotype). A, General view of the specimen in transverse section. K9883a. B, Counterpart of the specimen, additionally cut in radial sections. K9883b, K9883c. C, D, Radial sections of the specimen; successive vascular cylinders are indicated by arrows and X1–X9 in D. K9883b, K9883c. All specimens are at the same scale.

Plant Fossil Names Registry number. PFN003159 (for new species).

Holotype. K9883a–d; transverse polished section (K9883a), radial polished sections (K9883b, K9883c), and a tangential polished section (K9883d), stored at the paleontological collection of the Natural History Museum of Chemnitz.

Stratigraphy and age. The specimen was found in Quaternary fluvial deposits near Biesern, Saxony, Germany (lat. 51°29.08'N, long. 12°48'14.50'E). Based on site-specific photoluminescence pattern under UV light, the specimen originates from terrestrial, volcanogenic strata hosting the Chemnitz Fossil Forest, Chemnitz Basin (291 ± 2 Ma, Leukersdorf Formation, Sakmarian–Artinskian, early Permian).

Specific diagnosis. See generic diagnosis above.

Remarks. We decided to provide a combined generic and specific diagnosis, following the general discussion on this issue provided by Bickner and Tomescu (2019). Our knowledge on cycad diversity and phylogenetic framework in the late Paleozoic is very poor to date. Thus, there is no reliable basis to decide which of the anatomical characters are crucial to define either the genus or the species. In addition, as extant cycads show, anatomical characters of the stem are not necessarily critical to differentiate natural taxa on generic level, except for *Dioon* being the only genus with pycnoxylic wood. For example, polyxyly occurs in the genera *Cycas* and *Bowenia* and in some species of *Macrozamia*,

Lepidozamia, and *Encephalartos*. Therefore, using a combined generic and specific diagnosis provides more flexibility for future assessments based on newly discovered specimens and whole-plant reconstructions.

Description. The stem has a diameter of 69 mm × 56 mm, but the original dimensions are supposed to have been larger, as the outer stem part, including the cortex and vestiges of cataphyll or leaf bases, is not preserved (fig. 3).

Pith. The slightly oval-shaped pith has a diameter of 18 mm × 12 mm, occupying nearly one-third of the preserved stem diameter (figs. 3, 4A). It mainly consists of parenchymatous ground tissue, showing mostly decomposed isodiametric cells (fig. 5C). What appear to be mucilage canals or cavities may be present in the pith, but these have not been unequivocally demonstrated (fig. 5D).

Primary vascular system. The primary vascular system consists of more than 100 collateral vascular strands scattered in the pith (figs. 4, 5A, 5B), here designated as medullary bundles, and circularly arranged pith-peripheral vascular strands. The medullary bundles in the pith are generally variable in shape, but many appear radially elongated. They measure 230–1120 μm ($n = 30$) in diameter and show a trend of increasing size from the pith center to the margin (fig. 5A). In longitudinal sections, the primary orientation of the medullary bundles is vertically straight upward without passing through primary rays or forming

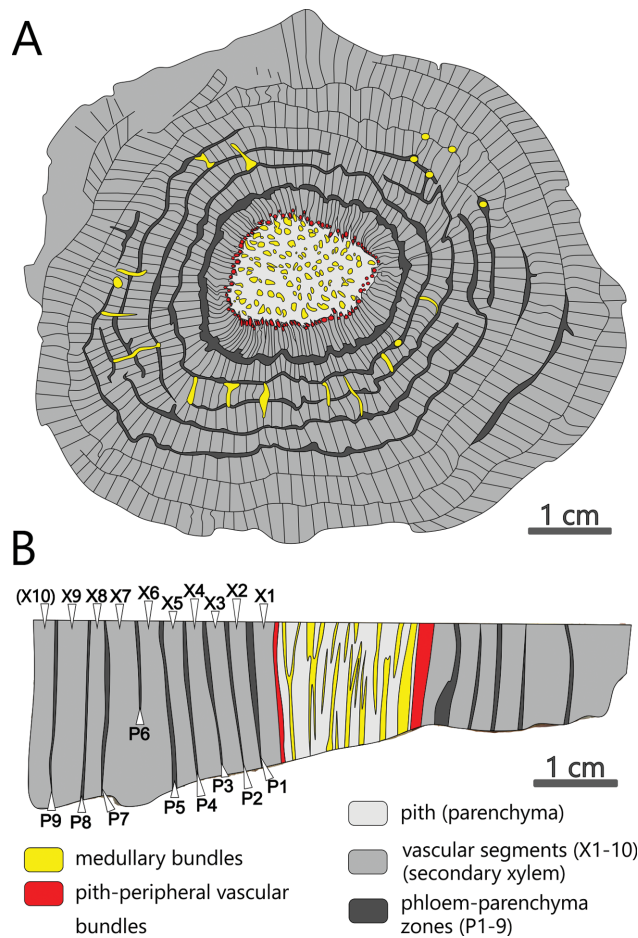


Fig. 4 Anatomical sketches of *Cycadodendron galtieri* gen. nov. et sp. nov. with the overall arrangement of stem tissues. A, Transverse section showing the pith with medullary bundles and pith-peripheral bundles, successive vascular segments, and traversing medullary bundles. K9883a. B, Radial section exhibiting vertical arrangement of stem tissues and indicating the number of successive vascular segments and phloem-parenchyma zones. K9883b.

leaf traces (figs. 4, 5B, 5D). The medullary bundles are dividing and anastomosing (fig. 5B), thus forming a loose network of interconnected strands (fig. 4B). Cell structural details are insufficiently preserved so that the arrangement of primary xylem with respect to primary phloem remains unclear. Some better-preserved metaxylem tracheids have diameters of 90–150 μm ($n = 5$; fig. 5C). Walls of metaxylem tracheids show circular, multiseriate, and densely packed bordered pits in radial section (fig. 5D, 5E). Circularly arranged along the pith periphery, around 90 endarch strands are located (fig. 4). These strands are composed of metaxylem tracheids and widely resemble the medullary bundles in shape and diameter (fig. 6A). The strands are closely associated with secondary xylem wedges of the innermost vascular segment.

Successive vascular segments. The specimen exhibits at least nine 1.6–4.5-mm-wide concentric segments of secondary xylem and phloem (X1–X10 in fig. 4), pointing to the development of successive bifacial cambia that contribute to secondary thickening of

the stem. The innermost vascular segment consists of 1.4–3.1-mm-long and 0.2–0.6-mm-wide wedges of secondary xylem and phloem (fig. 6A). The secondary vasculature is dissected by broad primary rays measuring 55–100 μm in width (fig. 6A). The secondary xylem is arranged in wedges consisting of one to four tracheid rows in between two adjacent rays (fig. 6A, 6B) and is dissected by thin secondary rays (17–56 μm in transverse section; $n = 44$). Tracheids are 34–74 μm wide in transverse section (mean: 52 μm ; $n = 82$) and exhibit tangentially oval-shaped lumina. Walls are comparably thick, measuring 14–41 μm (mean: 24 μm ; $n = 31$). They have araucarioid, multiseriate-bordered pits with thin, oval-shaped, and diagonally oriented apertures (fig. 6F). The secondary phloem occurs at the outer periphery of the secondary xylem, showing obliquely oriented cell rows, most likely due to compression (fig. 6D, 6E). Phloem zones have a radial extension of 0.5 mm, but cellular details are not preserved. The xylem of each of the polyxylic vascular segments exhibits distinctly narrower primary rays compared to the innermost segment (X1; fig. 6B, 6C). The vascular segments X2–X10 possess irregular outlines and are sometimes tangentially interrupted by thicker primary rays and/or medullary bundles (fig. 6C). The xylem segments are regularly alternating with phloem-parenchyma zones (C1–C9 of fig. 4; see also fig. 6C, 6E). The secondary phloem is poorly developed and sometimes completely absent, especially in the outer vascular segments (X6–X10). In these parenchymatous phloem zones, mucilage canals or cavities may be expected but were not unequivocally detected. The successive xylem cylinders increase in thickness from the stem center to its periphery, whereas the width of phloem-parenchyma zones slightly decreases (fig. 7).

Traversing horizontal bundles. In the successive vascular segments, several bundles were identified in transverse sections, based on their conducting tissues cut in longitudinal orientation, which implicates subhorizontal to oblique growth (figs. 6D, 8). In section K9883a, eight bundles occur in the third vascular segment (X3), where each of them follows a widened primary ray in between xylem wedges (figs. 4A, 6D). The bundles are 0.23–0.84 mm wide ($n = 8$). Three of them continue into the fourth vascular segment (fig. 4A). Some bundles immediately turn to the side after leaving the xylem cylinder and run horizontally to obliquely upward (fig. 8). In section K9883c, four bundles were identified in the first vascular segment (X1), continuing into the second (fig. 6A). They also pass through thickened primary rays in between xylem wedges. The origin of these bundles from either medullary bundles in the pith or from pith-peripheral vascular strands remains unclear. However, their overall appearance and growth orientation are identical to medullary bundles occurring in many extant cycads (fig. 10).

Discussion

Anatomical Comparison and Taxonomic Affiliation

Extant cycads have several autapomorphic anatomical characters that define them as a separate order within gymnosperms and several other characters that define groups, families, and genera within the order (Stevenson 1990, 1992). These are coralloid roots, a primary thickening meristem producing derivatives centrifugally, pith cell packets, girdling leaf traces, omega pattern of petiole vascular bundles, buffer cells surrounding the archegonium, and double integument vasculature. The mature anatomical

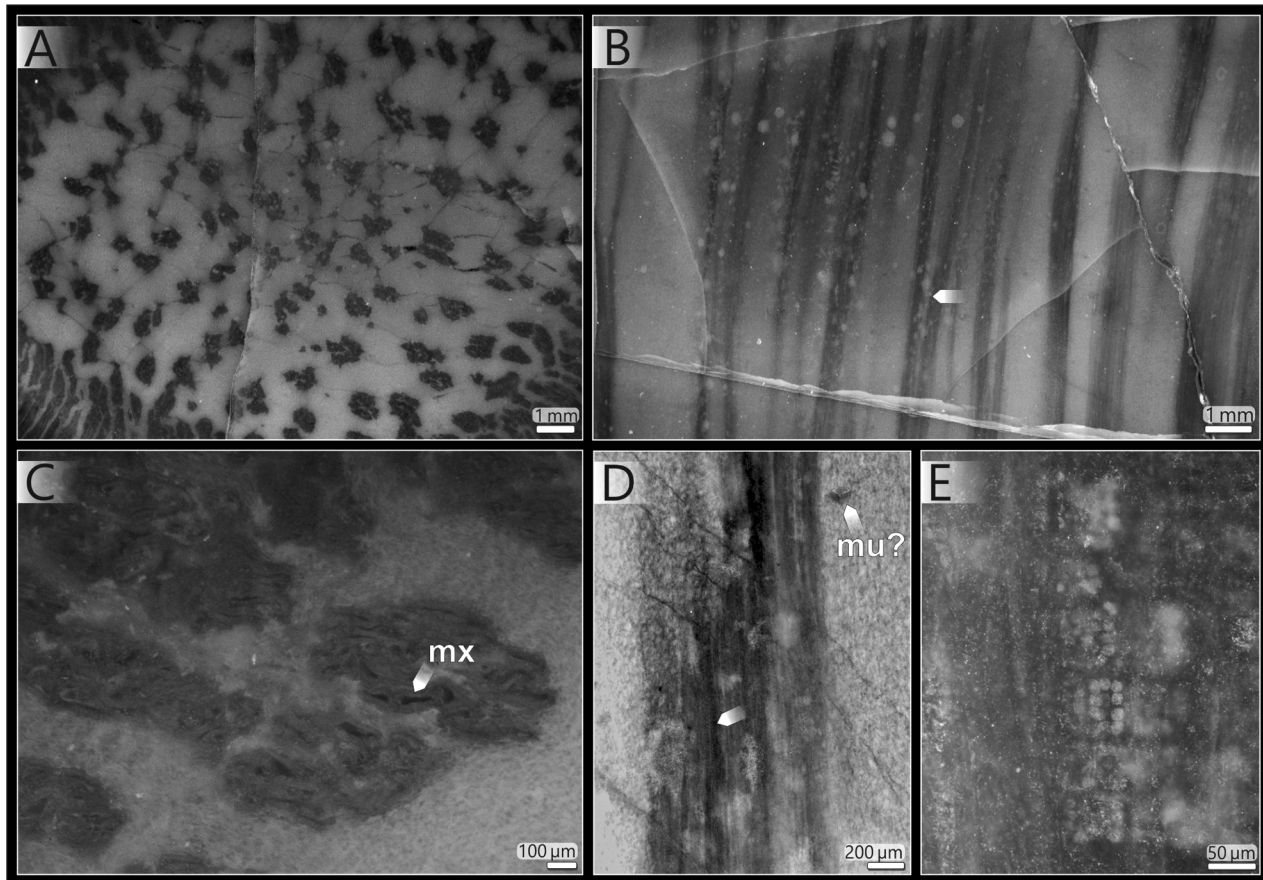


Fig. 5 *Cycadodendron galtieri* gen. nov. et sp. nov. Anatomical characters of the pith and scattered medullary bundles. A, Pith transverse section with dark-colored medullary bundles in bright parenchymatous tissue. B, Pith in radial sections with vertically elongated medullary bundles that sometimes divide (arrow) and anastomose. C, Medullary bundle with thick-walled, crumpled metaxylem tracheids (mx) in transverse section. D, Medullary bundle in radial section showing tracheids with multiseriate pitting (arrow) and a putative mucilage canal or cavity (mu). E, Close-up of tracheids with roundish, multiseriate-bordered pits in radial section.

stem structures found in extant relatives are also commonly found in fossils (Hermsen et al. 2007; Martínez et al. 2012, 2017; Spiekermann et al. 2021). All extant cycads have girdling leaf traces (figs. 9A–9D, 10H, 10I) and an omega pattern of the vascular bundles' arrangement in petioles. Additionally, the genus *Cycas* and the Encephalartea Miquel (comprised of *Encephalartos*, *Lepidozamia*, and *Macrozamia*) all have successive cambia that produce tracheids with araucarioid-type pitting (fig. 10E, 10F) and medullary bundles that traverse the rays, along with associated mucilage canals (fig. 10G, 10H, 10J). In addition, many cycads have cone domes in their pith, representing mostly dome-shaped relicts of vascular tissues resulting from cone formation at the stem apex (Stevenson 2020; fig. 9F, 9H–9J).

Stem anatomical characteristics of *Cycadodendron galtieri* strikingly differ from most fossil stems known from the late Paleozoic. The only group sharing some similarities is the medullosans (e.g., Delevoryas 1982; Stewart and Rothwell 1993; Luthardt et al. 2021). Both medullosans and *Cycadodendron* exhibit a wide pith with scattered and interconnected vascular strands (medullary bundles in *Cycadodendron* or central vascular strands in medullosans; referring to Luthardt et al. 2021) and circular vascular segments around the pith. By contrast to the pith

medullary bundles in cycads, central vascular strands of medullosans were producing secondary xylem and phloem. Some adult medullosan stems are supposed to exhibit successive vascular segments, similar to those of *Cycadodendron* (e.g., in *Medullosa stellata* var. *gigantea*; see Luthardt et al. 2021, pl. II, figs. 1–3). However, in contrast to *Cycadodendron*, medullosans generally have several independent and nonconcentric vascular segments in the stems (see fig. 2 in Luthardt et al. 2021). In addition, the secondary xylem of medullosans is characterized by distinctly wider tracheids and wide parenchymatous rays.

Cycadodendron galtieri shares several macroscopic and microscopic features with fossil and extant cycads, such as a wide pith with (proper) medullary bundles, a polyxylic vascular system with consecutive vascular segments each producing centripetal secondary xylem and centrifugal phloem, pith-peripheral endarch vascular strands separated by primary rays, and medullary bundles traversing the vascular segments, most likely continuing as girdling traces in the stem periphery. To our knowledge, only three cycad-like fossil stems are known from the late Paleozoic to date: *Cycadoxylon* sp. Renault 1879, *Ptychoxylon* sp. Renault 1889, both from Carboniferous–Permian transitional strata of France, and *Iratinia australis*

Spiekermann et al. 2021 from mid-Permian strata of Brazil. Whereas the latter shows a clear affinity to the cycad clade, the cycad affinity of the older taxa from France is doubtful due to missing key characters (Pant 2002). In comparison, *C. galtieri* differs in some essential anatomical characteristics of the conducting tissues from these three other fossil taxa, e.g., the presence of numerous medullary bundles in the pith, the circular shape of the vascular system, and successive vascular segments with wood growing exclusively towards the stem periphery, all only occurring in *Cycadodendron*.

Compared to Mesozoic–Cenozoic fossil cycads and extant relatives, *Cycadodendron* is distinctly smaller referring to its stem diameter. Similar anatomical features include the presence of medullary bundles in the pith, also occurring in several extant cycads and fossil relatives of the Meso- and Cenozoic (e.g., Artabe and Stevenson 1999; Artabe et al. 2005; Martínez et al. 2017). However, in comparison, the high bun-

dle density in the pith of *Cycadodendron* is quite conspicuous compared to most of the fossil taxa. In addition, the supposed absence of mucilage cavities or canals in the pith and cortex of *Cycadodendron* would be unique among cycads but is most likely a result of poor preservation of soft tissues in the specimen. The structure and arrangement of secondary tissues of the successive vascular segments of *C. galtieri* are very similar, if not identical, to those of many modern and some fossil cycads, with the initial vascular segment typically developing from endarch strands. The presence of both secondary xylem and phloem points to a bifacial cambium in each vascular cylinder, as it occurs in all known cycads. Moreover, broad medullary/primary and narrow secondary rays also occur in many cycads (Greguss 1968). In contrast to most extant cycads, the wood of *Cycadodendron* reveals a distinctly higher amount of secondary xylem and only minor portions of ray parenchyma. A similar xylem/parenchyma ratio is documented from the

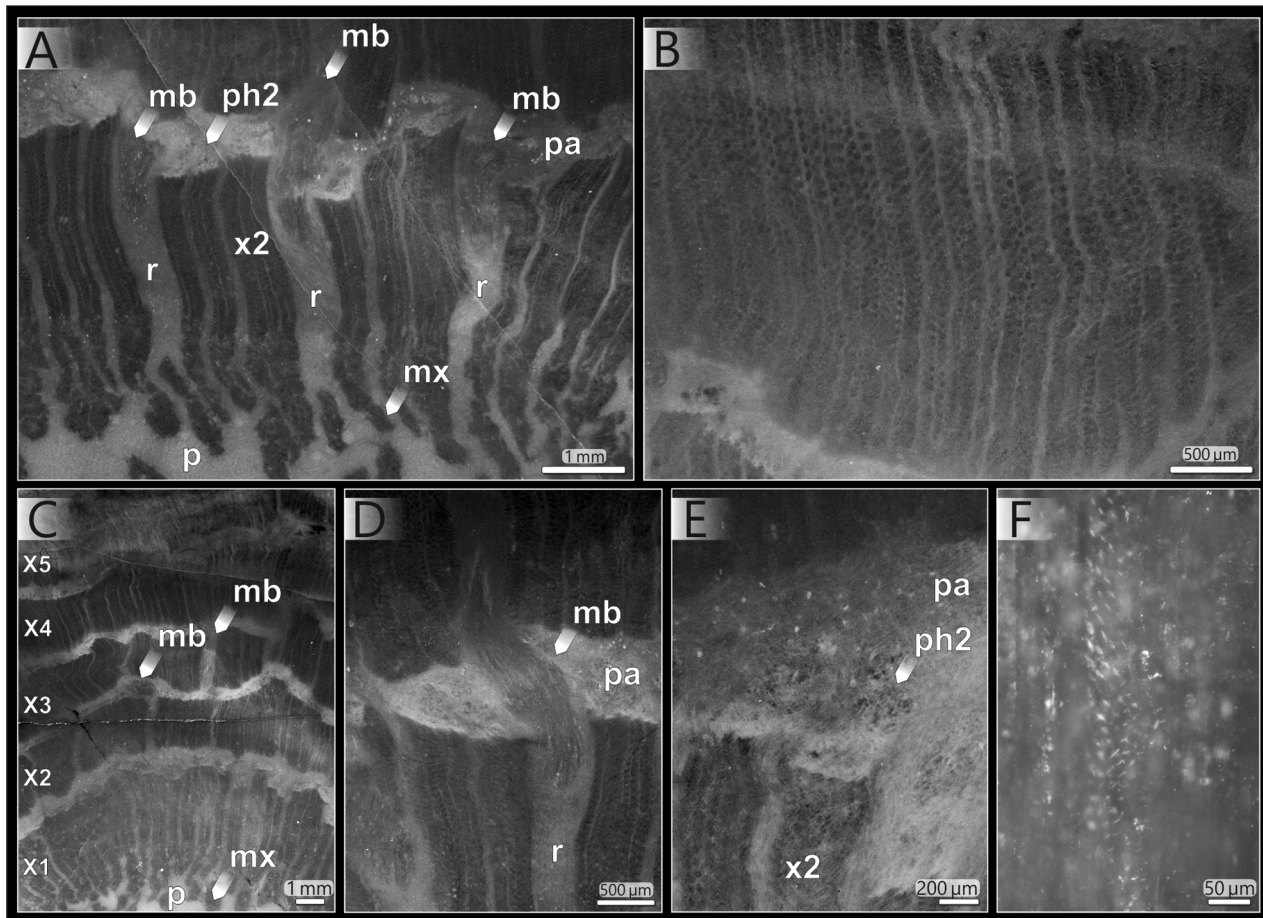


Fig. 6 *Cycadodendron galtieri* gen. et sp. nov. Anatomical details of the successive vascular cylinders. **A**, Tissues of the innermost vascular segment (X1) in transverse section. Note the wedge-shaped appearance of endarch strands consisting of pith-peripheral primary strands, as well as secondary xylem and phloem; exceptionally broad primary rays result from medullary bundles that pass obliquely upward. **B**, More homogeneous secondary xylem of one of the following vascular segments showing distinct primary rays, transverse section. **C**, Overview of five inner vascular segments (X1–X5), sometimes dissected by medullary bundles passing through the secondary xylem. **D**, Medullary bundle passing from one vascular segment to the next by passing the phloem-parenchyma zone. **E**, Details of poorly preserved secondary phloem in the transition of the marginal secondary xylem, embedded in the parenchyma. **F**, Detail of secondary xylem tracheids in radial section revealing araucarioid-type pitting. mb = medullary bundle; mx = metaxylem; p = pith; pa = parenchyma; ph2 = secondary phloem; r = primary ray; x2 = secondary xylem.

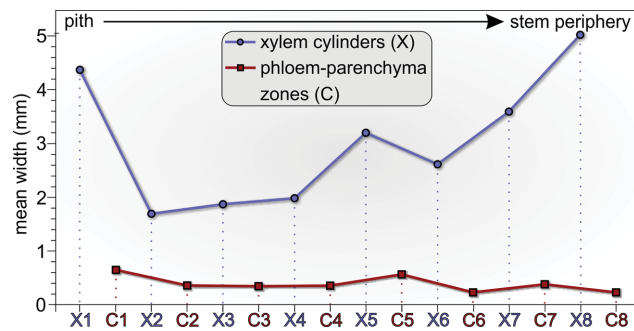


Fig. 7 Growth trend of the mean width of successive vascular cylinders versus mean width of phloem-parenchyma zones from the pith to the stem periphery (according to Terrazas 1991).

mid-Permian cycad stem *Iratinia australis* and is supposed to represent a plesiomorphic feature in the Cycadales (Spiekermann et al. 2021). Secondary xylem tracheids of *Cycadodendron* resemble most modern and fossil cycads in having multi-seriate, araucarioid-type pitting and similar overall dimensions (Sifton 1920; Greguss 1968). Tracheid diameters of fossil cycads generally vary within a range of 8–57 μm (table 1). In comparison, the tracheids of *Cycadodendron* are distinctly wider (34–74 μm ; average: 52 μm), nearly as wide as those of medullosans at the same locality (Luthardt et al. 2021). As wide and long tracheids enable increased water transport through the stem (Pittermann 2010), the huge tracheid diameters of *Cycadodendron* might reflect a particular adaptation toward more wet conditions and/or a shaded habitat in the forest understory. A potential future comparison with data of living *Cycas* species (currently unavailable in the literature) could test this hypothesis: in particular, *Cycas panzhuensis* growing in a xeric habitat compared with *Cycas multipinnata* growing in the understory of a semirainforest.

The presence of medullary bundles in the vascular system is another important feature that *C. galtieri* has in common with some fossil and extant cycads, including the extant genera of *Encephalartos*, *Macrozamia*, and *Lepidozamia* (Greguss 1968; Pant 2002) and the fossil genera *Michelilloa*, *Menucoa*, *Wintucycas*, and *Zamuneria* (Artabe and Stevenson 1999; Martínez et al. 2012, 2017). Wood-traversing bundles occur in the younger xylem cylinders of *C. galtieri* and pass through several of them. However, it remains enigmatic where these bundles are formed and how they pass through existing xylem cylinders. Worsdell (1896, 1906) described medullary bundles in a polyxylic stem of *Macrozamia*. In this and other extant and fossil taxa, medullary bundles run in the cortex and continue as girdling traces (fig. 10B, 10D, 10G, 10H, 10J). In *C. galtieri*, some of the bundles initially turn sideways after entering one of the phloem-parenchyma zones between the xylem cylinders, which we interpret as initial girdling traces in the outer cortex of an earlier ontogenetic stage.

In conclusion, anatomical features of *C. galtieri* indicate its affinity to the Cycadales, consequently representing the oldest-known anatomically preserved cycad stem to date. The wide anatomical similarities of *C. galtieri* compared with other fossil and extant cycads demonstrate the early development of various cycad-specific anatomical features in the early Permian, including

successive concentric cambia producing polyxylic stems. In the combination of anatomical features and some key distinctive

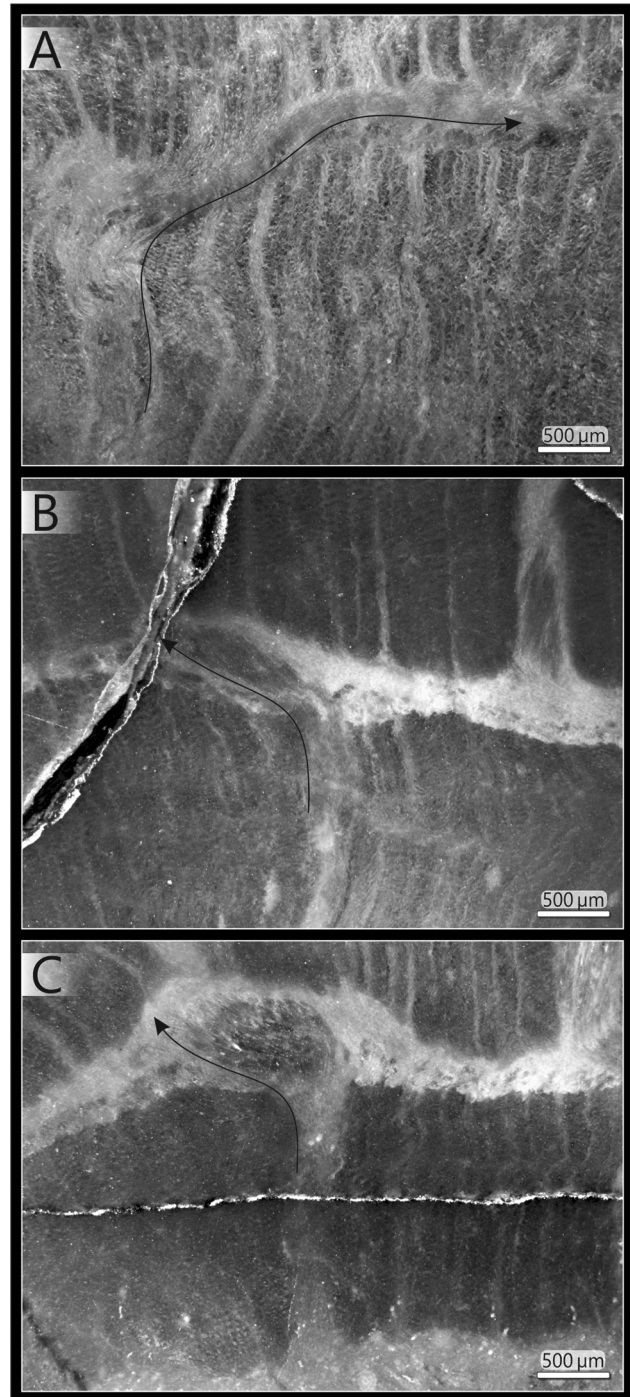


Fig. 8 *Cycadodendron galtieri* gen. et sp. nov. Orientation of medullary bundles passing through the successive xylem cylinders with an indication of their girdling nature in transverse sections. A, Bundle passing to the right in a phloem-parenchyma zone between two xylem cylinders. B, Bundle passing to the left in the phloem-parenchyma zone after emerging through a xylem cylinder. C, Subvertical bundle nearly cut in transverse section, migrating to the left in the phloem-parenchyma zone.

characters, such as supposed small dimensions referring to stem diameter, the dense arrangement of pith medullary strands, and wide secondary xylem tracheids, *C. galtieri* differs from all known fossil and extant taxa. The preservation bias of some important taxonomic features, such as the structure of cortex and leaf bases, impedes a closer comparison to younger fossil and extant taxa. As the here described specimen is unique in the combination of preserved anatomical characters in comparison with (fossil) taxa from literature, we propose establishing both a new genus and a new species.

Evolution and Function of Successive Cambia in Cycads

Among most gymnosperms, the ability to develop multiple successive cambia in adult stems is a distinctive character of cycads that occurs only in some of the extant species, mainly belonging to the genera of *Encephalartos*, *Macrozamia*, *Lepidozamia*, and *Cycas* (Worsdell 1896; Greguss 1968). In the fossil record, the oldest-known cycads are monoxyletic (e.g., Gould 1971; Smoot et al. 1985; Spiekermann et al. 2021). The oldest polyxylic fossil specimen previously known, *Sinocycadoxylon liianum* Zhang et al. Yang, is of Middle Jurassic age (Zhang et al. 2012), but it was not until the late Mesozoic that the feature became more common, as in the fossil genera *Bororoa*, *Brunoa*, *Menucoa*, and *Worsdellia* (e.g., Artabe and Stevenson 1999; Artabe et al. 2004; Martínez et al. 2012, 2017). Therefore, it has been assumed that polyxyly is a young evolutionary feature within cycads that has been derived from monoxyletic secondary vascular systems during the Mesozoic (Artabe et al. 2004). However, *C. galtieri* unequivocally demonstrates that polyxylic vascular systems already occurred in the earliest cycads of the late Paleozoic. Nevertheless, it remains an enigma which state, monoxyletic or polyxylic, is plesiomorphic in the cycads, as all phylogenetic analyses show the polyxylic *Cycas* as sister to all other living cycads.

An interesting aspect of the successive cambia in both fossil and extant cycads is that the phloem of each ring is intact, thus indicating that these cambia were not active for long after a new one was formed. If the cambia were simultaneously active, the secondary phloem of each segment would be crushed. There is some evidence of a minor amount of crushed phloem that appears as narrow lines in the illustrations of Terrazas (1991), but this is more an exception. According to the long evolutionary history of the ability to form successive cambia, this feature might represent more than just a genetic peculiarity. In extant plants, multiple successive cambia are not unique to cycads but have been also reported from some Gnetales and angiosperms, possessing either vine-like growth habits or growing in dry or salt-rich environments, like mangroves (Carlquist 2007; Robert et al. 2011). However, the successive cambia of cycads are unique within seed plants because the xylem produced by these successive cambia is composed of tracheids with scalariform to araucarioid pitting and there are no vessels, as in Angiosperms and Gnetales (Greguss 1968). If present, the medullary bundles traverse the secondary rays along with a mucilage canal, as in *Macrozamia* (Worsdell 1896; fig. 10G, 10J). Multiple successive cambia produce several zones of xylem and phloem, resulting in an increased phloem/xylem tissue ratio compared to arborescent plants with just one cambium, which possess a wide xylem cylinder and a narrow phloem zone (Robert et al. 2011). The primary function of the

phloem is the basipetal transport of assimilates produced by the leaves, and some water storage in the highly elastic ray parenchyma cells is also essential (Carlquist 2007; van Bel et al. 2014). The close connection of the xylem and phloem results in a circular conducting system with a regular fluid exchange in a diurnal rhythm, in which the phloem contributes to partially reduce water stress in the xylem and plays a role in embolism repair (Pfautsch et al. 2015). That the phloem of polyxylic cycads was active for life is indicated by the noncrushed phloem zones, as reported above. Therefore, the ability to form multiple phloem zones by successive cambial activity might represent an adaptive feature that allows plants to grow in rather stressed environments, as has been also proposed for *Corystospermales* (Artabe and Brea 2003). Given that successive cambia date back to more than 290 Ma, the resulting arrangement of conducting tissues is a successful evolutionary adaptation. This idea is further supported by the late Paleozoic fossil record, implicating that “modern” floral elements of this time, including the cycads, mainly evolved in dry habitats of uplands (e.g., Kerp 2000; Looy et al. 2014; see below). Therefore, the potential functional role of successive xylem/phloem zones might have improved drought resistance but might have also promoted tissue storage function and mechanical support (Carlquist 2007).

Growth Habit

The secondary xylem is the dominant tissue in the stem of *C. galtieri*, giving sufficient mechanical support to the plant. The fact that the majority of extant polyxylic cycads are arborescent (Whitelock 2002) suggests that *C. galtieri* was an arborescent, self-supported cycad with a slender, woody stem, perhaps similar to the extant *Zamia obliqua* (Stevenson 2004) or the fossil *Leptocycas gracilis* (Delevoryas and Hope 1976). The 10 successive vascular cylinders indicate that the specimen probably depicts the basal stem section of an adult individual (Artabe and Stevenson 1999). Considering its comparably small diameter (probably not much more than the preserved part), we suppose that this ancient cycad was generally small in overall dimensions. The growth pattern (fig. 7) shows that vascular cylinders became thicker with the increasing individual age of the plant. This pattern is consistent with the polyxylic growth trend in extant *Cycas* stems (Norstog and Nicholls 1997), although this aspect is poorly known in any other extant cycad with polyxylic growth.

Paleoecology and Habitat Inferences

Cycadodendron galtieri represents one of the few specimens of the upper Carboniferous–lower Permian fossil record that can be unequivocally assigned to Cycadales. In addition to several finds of foliage and reproductive organs of similar or slightly older stratigraphic age, *C. galtieri* is the oldest-known fossil that provides insights into the stem anatomy of early cycads and habitat preferences.

As the provenance analysis has clearly shown, *C. galtieri* originates from pyroclastic strata of the Zeisigwald Volcanic Complex that host the autochthonous fossil assemblage of the Chemnitz Fossil Forest (Luthardt et al. 2018). The specimen described here presents the first unequivocal proof of ancient cycads

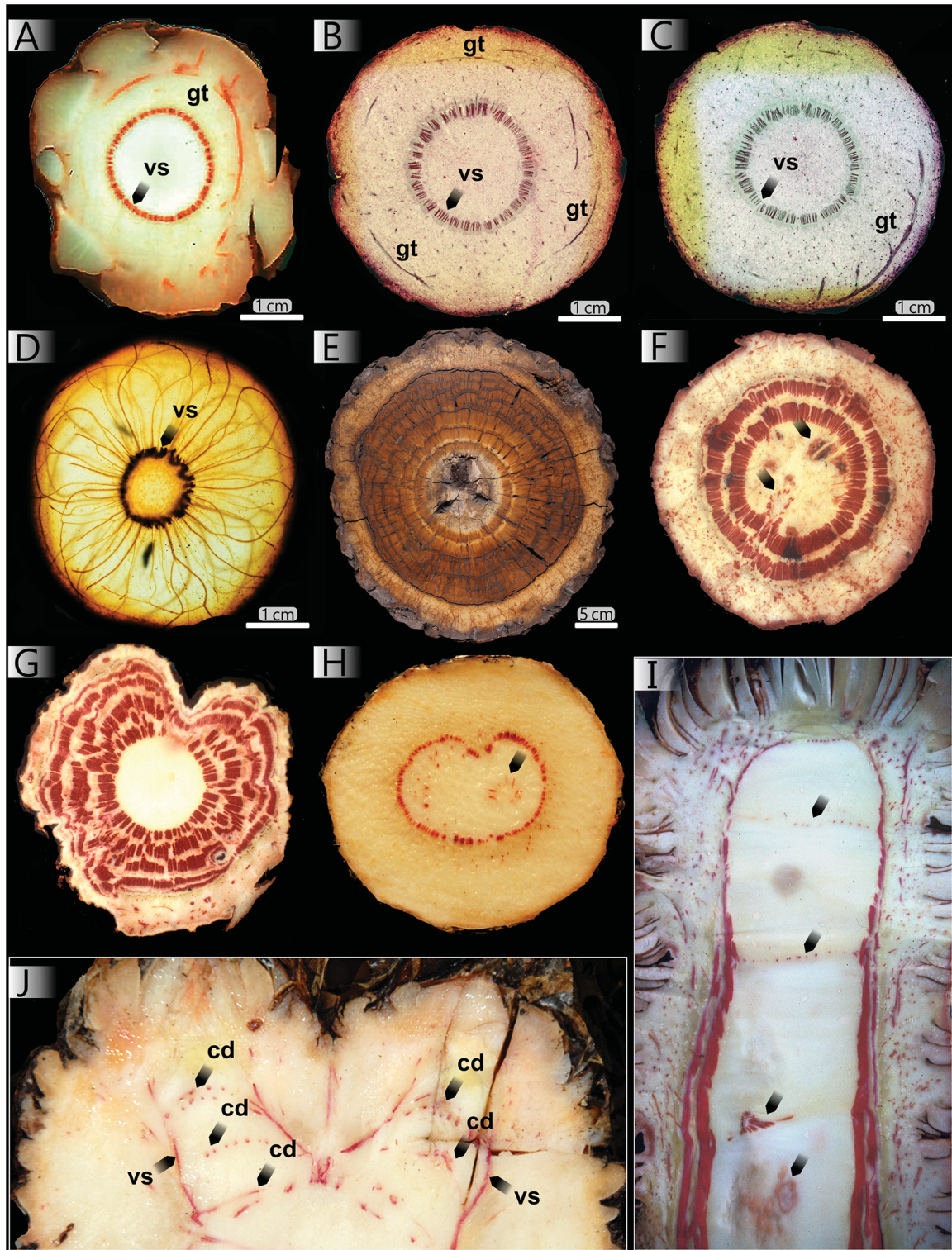


Fig. 9 Extant cycads and some of their clade-specific anatomical features. A, Transverse section of a young stem of *Cycas revoluta* with thin vascular segment (vs) and girdling traces (gt). B–D, *Zamia integrifolia*. B, Portions of several girdling leaf traces in the outer cortex. C, Girdling leaf trace with several of the bundles that formed it. D, Clearing of a stem showing the complicated vascular pattern of leaf traces. E, Polyxylic vascular system in an old *Cycas revoluta* stem of 37 cm diameter. F, G, Polyxylic vascular system of *Cycas rumphii* with cone domes (in F, arrows). H, *Zamia vazquezi*, showing initial “branching” of the stem by dividing vascular system and cone dome (arrow). I, Radial section of *Cycas rumphii* showing developing a polyxylic vascular system in the lower stem section (red), cone domes (arrows), and girdling traces (red) in the cortex. J, Radial section of a bifurcating *Zamia vazquezi* stem showing a thin vascular system and cone domes (cd).

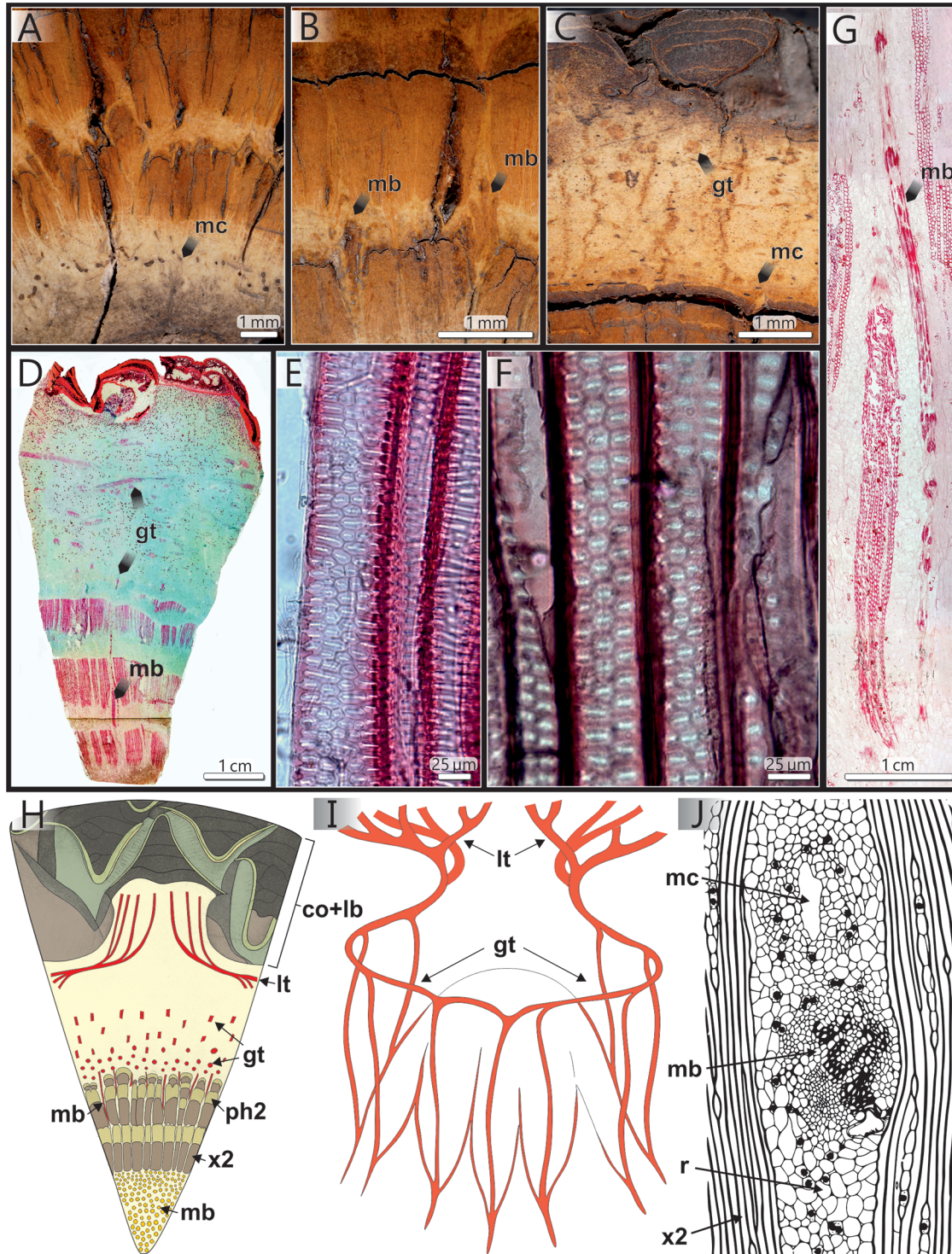


Fig. 10 Details of cycad-specific stem-anatomical features. A–C, *Cycas revoluta* (details of fig. 9E). A, Pith with mucilage canals (mc) and two of the vascular cylinders. B, Close-up of traversing medullary bundles (mb) through the vascular cylinders. C, Cortex with mucilage canals and leaf girdling traces (gt) in the cortex parenchyma. D, Microscopic, colored historical thin section of a *Macrozamia* stem showing a polyxylic vascular bundle, a medullary bundle that is traversing the vascular cylinders to end up as a girdling trace in the cortex. E, Radial section of *Bowenia serrulata* secondary xylem showing multiseriate bordered pits with araucarioid-type pitting. F, Secondary xylem tracheids of *Macrozamia corralipes* with multiseriate bordered pits and araucarioid-type pitting. G, Close-up of medullary bundle traversing the consecutive vascular cylinders in A at the position of the arrow. The bundle traverses the medullary ray parenchyma. H, Schematic sketch of a *Macrozamia* transverse section displaying the major anatomical details: medullary bundles both in the pith and traversing the vascular cylinders, secondary xylem (x2) and phloem (ph2) formed from multiple successive cambia, girdling traces in the cortex, and leaf traces (lt) passing to old leaf bases (lb) in the outer cortex (co); redrawn from Worsdell (1896). I, Schematic sketch of a 3D girdling trace system showing the development from girdling traces to leaf traces in *Dioon spinulosum*; redrawn from Langdon (1920). J, Microscopic tangential section showing a medullary bundle traversing the primary ray (r) of a vascular segment accompanied by a mucilage canal in *Dioon spinulosum*; redrawn from Langdon (1920).

Table 1

Comparison of Tracheid Diameters Documented from Various Fossil Cycad Stems

Taxon	Age	Tracheid diameter (μm)	Reference
<i>Cycadodendron galtieri</i>	Early Permian	34–74 (52)	This study
<i>Iratinia australis</i>	Middle Permian	22–35 (28)	Spiekermann et al. 2021
<i>Antarcticycas schopfii</i>	Early Triassic	28 $\times$ 16	Smoot et al. 1985
<i>Vladiloxylon troncosoi</i>	Upper Triassic	38 $\times$ 55	Lutz et al. 2003
<i>Lyssoxylon grigsbyi</i>	Upper Triassic	9–25	Gould 1971
<i>Sinocycadoxylon lianum</i>	Middle Jurassic	35–40 $\times$ 35–50	Zhang et al. 2012
<i>Lioxylon liaoningense</i>	Middle Jurassic	25–45	Zhang et al. 2006
<i>Brunoa santarosensis</i>	Cretaceous	10–51/10–41	Artabe et al. 2004
<i>Zamuneria amyla</i>	Lower Upper Cretaceous	14–35 (23)/13–29 (21)	Martínez et al. 2017
<i>Wintucycas stevensonii</i>	Upper Cretaceous	8–18 (12)	Martínez et al. 2012
<i>Centricycas antarcticus</i>	Upper Cretaceous	18–57	Cantrill 2000
<i>Borora anzulovichii</i>	Cenozoic (Paleogene?)	12–36 (26)	Petriella 1972

Note. Data taken from literature provide different styles of presentation and statistic treatment, given either in a range of radial diameter (x – y) or in radial versus tangential ($x \times y$). Values in parentheses for tracheid diameter reflect averages.

in this autochthonous fossil assemblage. Among the fossil foliage of several Chemnitz sites, *Pterophyllum cottaeanum* and *Noeggerathia zamitoides*, two putative cycad foliage types, were reported (Sterzel 1918). Paleoclimatic and site-specific conditions of the Chemnitz forest habitat have been well studied in the past decade (e.g., Rößler et al. 2012b; Luthardt et al. 2016, 2017; Rößler 2021). The well-constrained link between the new fossil and its place of origin provides the first glimpse of the in situ habitat of a late Paleozoic cycad. *Cycadodendron galtieri* was growing in a subhumid, seasonally dry paleoclimate (Luthardt et al. 2016, 2017). The forested landscape is best described as a low-energy, flat alluvial plain in the center of the spatially restricted intramontane Chemnitz Basin (Schneider et al. 2012). The local conditions of the forest site were characterized by sufficient water supply throughout the year by near-surface groundwater. Dispersed geological investigations revealed that local substrate conditions were variable in the forest habitat, ranging from well-drained sandy soils to waterlogged clayey substrate (Luthardt et al. 2016). Most fossil stems are derived from the Chemnitz-Hilbersdorf reference site, which also provides the highest diversity of fossil stem taxa among all fossil spots at the locality (Rößler 2021). Local conditions of the Chemnitz-Hilbersdorf site are characterized by a sandy and densely root-penetrated paleosol that shows oxidizing, well-drained, and slightly alkaline conditions indicated by the presence of carbonate nodules (Luthardt et al. 2016). Most likely, *Cycadodendron* was growing in this environment, thus exhibiting similar habitat preferences as most extant cycads (Norstog and Nichols 1997; Whitelock 2002). The forest consisted of large cordaitalean, calamitalean, and sporadic conifer trees forming the canopy (<30-m height), as well as abundant medullosan seed ferns and psaroniacean tree ferns in the shaded understory (<15-m height). The supposed small dimensions of *Cycadodendron* give reason to assume that it was growing in the lower understory (<5-m height?) and therefore probably under light-deficient conditions.

An interesting aspect of plant association in the habitat is the co-occurrence of *C. galtieri* with medullosan pteridosperms. The evolutionary proximity of medullosans and cycads has been repeatedly discussed in older literature but also recently (Renault 1896; Worsdell 1896; Bancroft 1914; Chamberlain 1920; Dele-

voryas 1982; Stewart and Rothwell 1993; Nixon et al. 1994; Hilton and Bateman 2006; Luthardt et al. 2021). Even though they have not yet been found together in situ, the existence of both groups in the same eco-space is likely. The resulting similar environmental specialization of both clades might be regarded as the result of their supposed evolutionary proximity.

Evolution of Late Paleozoic Cycads

The advent of cycadophytes reported from the fossil record falls in a period of tremendous environmental change on the late Paleozoic Earth. At this time, highly dynamic landscape formation was triggered by significant tectonic activity, resulting in the supercontinent formation of Pangea (e.g., Kroner and Romer 2013). Extensive glaciation of the Late Paleozoic Ice Age, accompanied by millennial-scale climate fluctuations, further contributed to a general trend of aridification and pronounced seasonality in terrestrial ecosystems of the low latitudes (e.g., Montañez and Poulsen 2013; DiMichele 2014; Kent and Muttoni 2020). In the framework of late Paleozoic landscapes, seasonally dry upland environments were extended and are regarded as plant evolution laboratories (Looy et al. 2014). During the Carboniferous and Permian, the vegetation of the paleotropics underwent a gradual turnover, characterized by the disappearance of ancient elements such as the lycophytes; the adaptation of well-established forms such as calamitaleans and medullosans (Barthel and Rößler 2012); and the rise of new clades such as the Peltaspermales, Ginkgoales, large-leaved conifers, and the Cycadales (e.g., Kerp 2000; DiMichele et al. 2001, 2005). *Cycadodendron galtieri* represents one of the most ancient cycads that was growing in a seasonally dry forest of an intramontane basin, which is in accordance with the ecological affinity not only proposed for early Cycadales in the late Paleozoic but also for the vast majority of modern cycads (Norstog and Nichols 1997; Whitelock 2002).

The temporal and spatial evolution framework of cycads is still under debate. The oldest cycad-like reproductive structures were described from the lower Pennsylvanian of North America, associated with the leaf type *Lesleya* sp. (Leary 1990). *Lesleya* sp. is known from the Mississippian, but it might not be assigned to cycadales alone (Taylor et al. 2009). More convincing evidence

of cycad-like reproductive structures dates back to the upper Pennsylvanian in North America (Cridland and Morris 1960; Taylor 1970). In Europe, the leaf type of *Pterophyllum* first occurs in Gzhelian–Kasimovian strata at several fossil localities and can be seen as a clear indication of the presence of cycads in late Carboniferous terrestrial ecosystems (e.g., Zeiller 1906). Another leaf type, *Plagiozamites*, already occurs in the Moscovian, for example, *P. carbonarius* Potonié 1893 (syn. *Zamites* sp. Renault 1890), but might be less clearly solely assignable to cycads (Šimůnek and Bek 2003). In the lower Permian, the fossil record already provides diverse evidence of ancient cycads, encompassing leaves and megasporophylls (Kerp 1983; Gillespie and Pfefferkorn 1986; Gao and Thomas 1989) and with *Cycadodendron* the first anatomically preserved fossil stem. An interesting aspect that has been pointed out by Spiekermann et al. (2021) is that cycad fossils of the lower Permian are known from various places in the world, encompassing North and South America, Europe, China, and at least since the mid-Permian even Russia (Naugolnykh et al. 2021). This implicates a global occurrence of cycads in nearly all major floral provinces of that time, encompassing Angara, Cathaysia, Euramerica, Gondwana, and Mid-North Brazil (Iannuzzi et al. 2018). Considering the reproduction strategies of extant cycads, the global extension of ancient relatives in the lower Permian appears surprising for two reasons. First, cycads can be evaluated among plants as K-strategists, as they produce small amounts of high-cost seeds, reproducing only at a late ontogenetic stage. Combined with their dioecious nature and a long and complex fertilization process in the ovules (Whitelock 2002; Brenner et al. 2003), the reproduction rate of cycads is generally low. Second, seed dispersal of most cycads is spatially restricted, in some reported cases only a few meters away from the mother plant (Tang 1988). Cycad seeds occur in a wide range of sizes but are generally large enough to be unfavorable for wind transportation. Water flotation is known for those cycads with spongy tissue in their seeds (e.g., Dehgan and Yuen 1983). Animal dispersal is known from several examples (Eckenwalder 1980; Malaisse et al. 1990; Norstog and Nicholls 1997; Schneider et al. 2002; Monson et al. 2003; Salgado et al. 2017; Yáñez-Espinosa et al. 2021), even though most cycads produce harmful neurotoxins but not in the sarcotesta (Schneider et al. 2002; Brenner et al. 2003). Altogether, the seed dispersal of cycads is predominantly spatially restricted, which might also explain the unusual continent-specific distribution patterns of extant genera (Greguss 1968). Consequently, the spatial dispersal and migration potential of cycads are generally low. Assuming similar reproductive strategies of ancient cycads, their global distribution in the lower Permian might have lasted several millions of years, implicating a distinctly earlier origin than the first unequivocal evidence reflects. Despite their early global distribution, cycads remain sparse in the fossil record of Permian terrestrial ecosystems. Their radia-

tion begins with the decline of ancient lineages, such as most seed ferns associated with the end-Permian global mass extinction.

Conclusions

1. *Cycadodendron galtieri* gen. nov. et sp. nov. represents a petrified cycad stem of early Permian age providing the oldest-known evidence of cycad anatomy.
2. Although found in a gravel pit, the specimen's association with the Chemnitz Fossil Lagerstätte, a volcanically preserved, autochthonous assemblage 291 million years old, was indicated by using UV luminescence patterns of the petrified wood.
3. The broad anatomical similarities of *C. galtieri* with other fossil and extant cycads demonstrate the early evolution of various cycad-specific anatomical features in the lower Permian, including a wide pith, medullary bundles both scattered in the pith and traversing the vascular segments, and successive vascular segments (polyxyly) with araucarioid-type pitting in the secondary xylem tracheids.
4. The occurrence of successive vascular segments in *C. galtieri* reveals that the ability to form successive cambia during ontogenesis was an early-derived feature in the cycad clade and might have had a functional role in increasing drought tolerance.
5. The plant is supposed to have been self-supported and arborescent with a slender stem, possessing generally small dimensions.
6. *Cycadodendron galtieri* was growing in low-energy alluvial plain settings of intramontane basins in the seasonally dry paleoclimate of the Pangean tropical belt. The forest habitat was characterized by a shaded understory and well-drained, alkaline mineral soil reflecting moist local conditions due to near-surface groundwater.

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