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Medullosan seed ferns of seasonally-dry habitats: old and new perspectives on enigmatic elements of Late Pennsylvanian–early Permian intramontane basinal vegetation

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ABSTRACT

The medullosans represent a diverse group of pteridosperms that was widely distributed in forested landscapes of the late Paleozoic. These plants became widely known from the extensive tropical lowland basins of Euramerica, where they grew as slender plants with large fronds and fern-like foliage. Besides, there also exist medullosans of Late Pennsylvanian–early Permian intramontane basins of Central Europe, which have been out of research focus for more than a century. They had bigger stems with larger amounts of secondary xylem and a modified organisation organization of the vascular system. We provide an overview on taxonomy, anatomy and palaeoecology of these medullosans from the most important fossil localities, encompassing Chemnitz (Germany), the type locality for most taxa, Autun (France), Nová Paka (Czech Republic) and others.Late Pennsylvanian–early Permian medullosans of intramontane basins were thriving under seasonally-dry palaeoclimate on wet clastic soils showing proximity to the groundwater level. In forested landscapes, they occurred mostly sub-ordinated as part of the forest understorey. The plants' architecture and taphonomical inferences point to a (semi-)self-supporting growth habit of most of the taxa presented here. Plant architectural and anatomical peculiarities suggest a high water-conducting potential of these plants, raising questions on their ecological role in early Permian habitats. Anatomical differences with tropical relatives of Carboniferous age might reflect an evolutionary process that was driven by environmental changes during the late Paleozoic. The unusual arrangement of their stem tissues addresses the question of their role in seed plant evolution, e.g., their potential relationship with cycads.

1. Introduction

The medullosans (Class: *Pteridospermopsida*; Order: *Medullosales*; Family: *Medullosaceae*; Genus: *Medullosa* Cotta, 1832) depict a widely distributed and diverse group of enigmatic and highly complex plants belonging to the pteridosperms sensu stricto (Hilton and Bateman, 2006). Pteridosperms are a paraphyletic plexus of basal seed plants sharing compound leaves and originating in the Late Devonian (Gillespie et al., 1981; Fairon-Demaret and Scheckler, 1987; Serbet and Rothwell, 1992). After a first diversification event in the Mississippian, several groups of pteridosperms flourished during the Pennsylvanian and Permian, colonising various terrestrial ecosystems for at least 120 Ma. Mesozoic orders of pteridosperms persisted up to the Late Cretaceous (e.g., Kerp, 2000) or putatively even to the Cenozoic (McLoughlin et al., 2008).

The late Paleozoic was a time of significant global change strongly affecting terrestrial ecosystems (Quie et al., 2019; Richey et al., 2020). In these ecosystems, pteridosperms may be regarded as sensitive vegetational elements indicating relationships between plant evolution and environmental change (DiMichele et al., 2006b; Wilson et al., 2015). Among them, the medullosans are suggested to have been highly adaptive to various environment types, which resulted in a broad spectrum of different growth forms and natural species (e.g., Stidd, 1981). They may, therefore, have played a key role as a link in the evolution of modern seed plants (e.g., Worsdell, 1906; Bancroft 1914; Doyle, 2006).

First approaches on medullosans were published during the 19th century on anatomically preserved fossil material from the post-

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Variscan intramontane basins of Central Europe (Cotta, 1832; Brongniart, 1849; Mougeot, 1852; Göppert, 1865; Göppert and Stenzel, 1881; Schenk, 1889; Renault, 1875, 1878, 1893, 1896; Weber and Sterzel, 1896; Solms-Laubach, 1897; Potonié, 1904). They provided the initial spark for following extensive research on earlier medullosans of the Carboniferous coal swamp basins of North America and Europe (e.g., Scott, 1899, 1914; Bancroft 1914; De Fraine, 1914; Seward, 1917). During the last decade, the research focus has remarkably shifted towards their physiological and functional properties, by applying novel geochemical approaches and water flow modelling (e.g., Wilson and Knoll, 2010; Wilson and Fischer, 2011; Wilson et al., 2008, 2015).

In contrast to growth forms occurring in the Carboniferous lowland basins, scientific progress on the younger growth forms from European intramontane basins stagnated for a long time. As a result, these complex and peculiar plants remained enigmatic regarding their anatomy, tissue-functional traits, palaeoecological affinities and evolutionary pathways. However, promising fossil material from both new excavations and old collections from the Chemnitz Fossil Lagerstätte (Rößler et al., 2012b; Luthardt et al., 2016), the type locality of *Medullosa stellata* Cotta and other stem taxa of early Permian age (Cotta, 1832; Göppert and Stenzel, 1881; Schenk, 1889), will provide a basis for ongoing scientific progress.

By returning to the early roots of palaeobotany, we aim to shed light on this distinct group of seed ferns, which had been out of focus for more than a century. Based on the current state of knowledge, we present a comparison of these medullosans with their earlier relatives from the Carboniferous. Moreover, we address new and old questions and hypotheses regarding medullosan systematics, functionality, palaeoecology and evolution, to give a preview for near-future research.

2. Stratigraphy and the fossil record

The Medullosales originated in the early–middle Carboniferous and were exposed to major global change around the Carboniferous–Permian transition (Fig. 1). Their stratigraphic occurrence is strongly linked to stem fossils but further supported by assigned foliage and reproductive organs. Among the non-arborescent early pteridosperms, the Calamopityaceae are recorded since the earliest Tournaisian (Early Mississippian; e.g., Beck et al., 1992; Galtier and Meyer-Berthaud, 1989). They may be closely allied to the medullosans as both share specific characteristics, like the manoxylic wood. This type of wood is defined as a secondary tissue showing wide tracheids that may exceed 200 μm in diameter, as well as broad, tall rays with comparable values in calamopityans and the early medullosan *Quaestora* (Galtier, 1992). The Calamopityales and the Medullosales also share a sclerenchymatised hypodermis and wide petiole bases containing numerous vascular strands, whose number is related to the size of their leaves (Galtier, 1988). However, calamopityans and medullosans differ in their stelar organisation ranging from protostelic to eustelic in the formers, whereas the medullosans are supposed to be only eustelic (Beck et al., 1982). In addition, leaf traces of calamopityans originate from one (*Calamopitys* and *Stenomyelon*), rarely two (*Diichnia*) or three (*Triichnia*) sympodial bundles, whilst those of the medullosans seem to originate from two or more sympodia.

Neuropterid foliage is known since the upper Tournaisian (Stewart and Delevoryas, 1956; Stidd, 1981; Hübers et al., 2014), but its particular affinity to medullosans was doubted (Gensel, 1988). Thus, the first occurrence of medullosans was evidenced by slender stems of *M. steinii*, which is of Late Mississippian age (Serpukhovian; Dunn et al., 2003; Fig. 1). After their rise in the early–middle Carboniferous, medullosans occurred as a subordinated plant group in the humid, low-

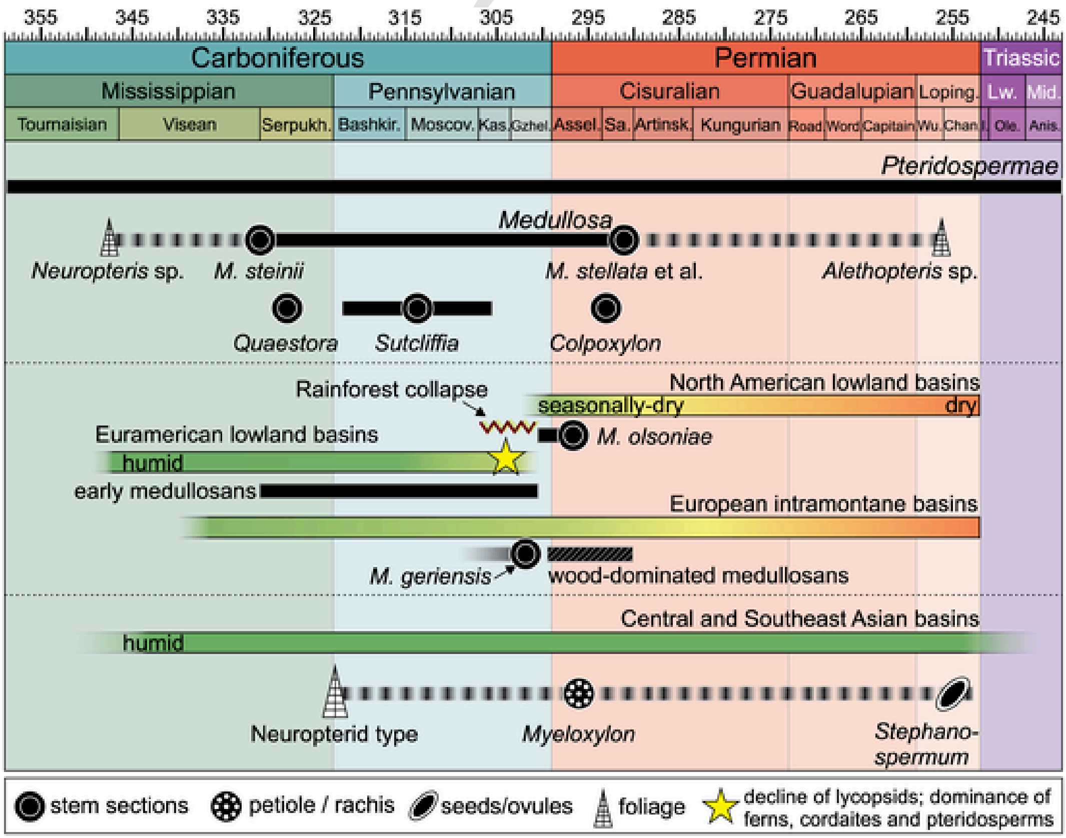

Fig. 1. Stratigraphy and fossil record of the *Medullosales* in the context of palaeogeographic and palaeoclimatic developments in the late Paleozoic (see text for references; upper scale in million years).

latitude forest ecosystems of the extended coal-forming foreland basins of Euramerica (e.g., Galtier, 2008). In the glacial cycles of North American coal strata, they frequently occurred at the initial phases of rainforest vegetation (DiMichele et al., 2006b). Later, during the Middle–Upper Pennsylvanian, they became more dominant in the tropical forest ecosystems together with other pteridosperms and ferns, most probably as a result of environmental change towards more seasonally pronounced palaeoclimate and/or the uplift of the Variscan orogen, coinciding with the significant decline of lycopsids in Euramerica (Phillips, 1981; Pfefferkorn and Thomson, 1982; Phillips et al., 1985; Kerp, 2000; Cleal et al., 2009). With the stepwise disappearance of coal-forming ecosystems in the Late Pennsylvanian, the taphonomic window favouring anatomical preservation of medullosans became successively smaller. The youngest structurally preserved medullosan stem from North America is of earliest Permian age and represented by *M. olseniae* Roberts et Barghoorn (Figs. 1 + 2). However, the record of compression flora indicates that the medullosans persisted during the collapse of the vast tropical forests in the early Permian by adapting to seasonally-dry conditions along with river courses or in lake proximity in so-called “wet-spot” habitats (e.g., Kerp, 1996; DiMichele et al., 2006a; Bashforth et al., 2016; DiMichele et al., 2018).

In Europe, five early medullosan taxa, *M. centrofilis* de Fraine, *M. geriensis* Boureau, *M. pusilla* Scott, *M. primaeva* Baxter, and *M. anglica* Scott, occurred in Pennsylvanian coal-bearing strata, from which only *M. primaeva* Baxter and *M. anglica* Scott also occurred in North America (Fig. 2). After the disappearance of the major coal-forming environments in Europe, the taphonomic record of medullosans became mainly restricted to the post-Variscan intramontane basins, where volcanic activity favoured their anatomical preservation in spatially restricted taphonomic windows (e.g., Cotta, 1832; Mougeot, 1852; Renault, 1875; Rößler et al., 2012b; Opluštil et al., 2013). Among these, the Chemnitz Fossil Lagerstätte recently provided the youngest evidence of medullosan stems (Sakmarian, 291 ± 2 Ma; Luthardt et al., 2018).

Nevertheless, medullosans are supposed to have survived in a wide palaeogeographic range up to the Permian–Triassic boundary (Fig. 1), which is indicated by alethopterid foliage of late Permian age (Wuchiapingian) from Central Europe (Kustatscher et al., 2014). Based on fossil foliage, it seems likely that medullosans of Euramerican “coal ball” floras spread eastward, into the humid coal basins of the Russian platform (e.g., Donets Basin; Boyarina, 2010), as well as into those of Southeast Asia. In South Asian strata, they appear subordinated and are known from the frequent occurrence of neuropterid foliage, since the lower Namurian (e.g., Laveine, 1997; Laveine et al., 2003). Anatomically preserved fossils are represented by *Myeloxylon* petioles and rachises of early Permian age (Seyfullah et al., 2009) and *Stephanospermum* seeds in “coal balls” of Lopingian age (late Permian) from Southern China (Spencer et al., 2013). However, evidence from anatomically preserved stems is still lacking. The only known specimen from Central Asia may represent *Medullosa ludwigii*, which was described from Pawlodar, Kazakhstan (Göppert and Stenzel, 1881; Schenk, 1889). However, its affinity to medullosans was questioned by Solms-Laubach (1897). Medullosans have not been found in Mesozoic strata, so far, suggesting that they might have declined at the Permian–Triassic transition.

3. Medullosans of Carboniferous palaeo-tropical lowland basins

The early lowland medullosans are diverse in architecture and reproductive biology, whereas whole-plant reconstructions are rare (DiMichele et al., 2006b). Most of the plants had slender stems with diameters of 2–5 cm, whereas some grew up to 20 cm wide and were probably more than 10 m high (Delevoryas, 1955; Wnuk and Pfefferkorn, 1984). They had large fronds and adventitious roots (e.g., Stewart and Delevoryas, 1956; Laveine, 1997). The plants exhibited different growth habits encompassing self-supporting trees, liana-like climbers or vines, scramblers and probably cormose plants (e.g., Stewart and Delevoryas, 1956; Stidd, 1981; Pfefferkorn et al., 1984; Wnuk and Pfefferkorn, 1984; Galtier, 1997, 2008; Krings et al., 2003; Zodrow, 2003; Dunn, 2006; DiMichele et al., 2006b; Wilson and Fischer, 2011). From Mississippian–Pennsylvanian strata of North America (NA) and Europe (EU), including “coal balls” or fossiliferous cherts, nine different stem taxa are known (NA: *M. endocentrica* Baxter, *M. noei* Steidtmann, *M. olseniae* Roberts et Barghoorn, *M. steinii* Dunn et al., and *M. thompsonii* Andrews; EU: *M. centrofilis* de Fraine, *M. geriensis* Boureau, and *M. pusilla* Scott; NA/EU: *M. primaeva* Baxter, and *M. anglica* Scott). *M. olseniae* represents the only specimen recorded from earliest Permian strata of North America (Roberts and Barghoorn, 1952). It is similar in anatomy to the Carboniferous coal ball forms, and thus included here. Other genera close to *Medullosa* are *Sutcliffia* Scott and *Quaestora* Mapes et Rothwell (Taylor et al., 2009).

3.1. Stem anatomy

Stems consist of ground and conducting tissues with a variable number of cauline vascular segments (see no. 1–9 in Fig. 2). Medullosans are distinguished from most of the other pteridosperms by their mode of leaf trace production in which terete strands are formed from two or more vascular segments (Mapes and Rothwell, 1980; Hamer and Rothwell, 1986; Dunn, 2006; Taylor et al., 2009). The medullosan stem was initially thought to be polystelic (Delevoryas, 1955). However, today it is regarded as eustelic, in which the cauline vasculature of *Medullosa* consists of interconnected primary vascular segments, each surrounded by concentrically arranged secondary tissues (Basinger et al., 1974; Beck et al., 1982). Number (2–23), shape and size of vascular segments is variable among stem taxa. In some taxa, additional segments occur in the stem centre, from which no leaf traces emerge. These segments are here described as “central accessory strands”. Manoxylic wood is characteristic for all medullosans. The secondary phloem is characterised by tangential bands of fibres, except for *M. steinii* (Smoot, 1984; Dunn et al., 2003). Stem anatomy can vary in individuals from base to top, as demonstrated by various stem sections of *M. noei* (Delevoryas, 1955) and probably *M. thompsonii* (no. 2 + 3 in Fig. 2).

3.2. Petioles, rachises and foliage

Petioles and rachises of the medullosans are of the *Myeloxylon* type, which was first described as the stem taxon *M. elegans* by Cotta (1832). It was Grand'Eury (1877) who later recognised its foliar identity. *Myeloxylon* fronds are helically arranged around the stem. Some medullosans had up to 20 functional fronds (Wnuk and Pfefferkorn, 1984). Their anatomy is characterised by a peripheral hypodermis composed of a parenchymatous tissue interlaced with numerous longitudinally oriented, non-anastomosing groups of sclerenchyma plates and a parenchymatous ground tissue with immersed secretory canals and numerous scattered vascular strands (Seward, 1917; Fig. 3 F + G). Petiole cross-sections can be more than 12 cm wide and are proximally oval to triangular-shaped, becoming distally narrower and more circular (Ramanujam et al., 1974). The fronds were commonly bifurcating and produced rachises with several orders of pinnae attached (Krings et al., 2006; Laveine and Oudoire, 2009). Pinnae and pinnules are characterised by their fern-like appearance and have been early identified as the corresponding foliage of medullosans (Renault, 1875; Grand'Eury, 1877; Pryor, 1990). Based on pinna morphology and whole-frond architecture, three major groups are differentiated at family level by Laveine (1997), from which two are assigna-

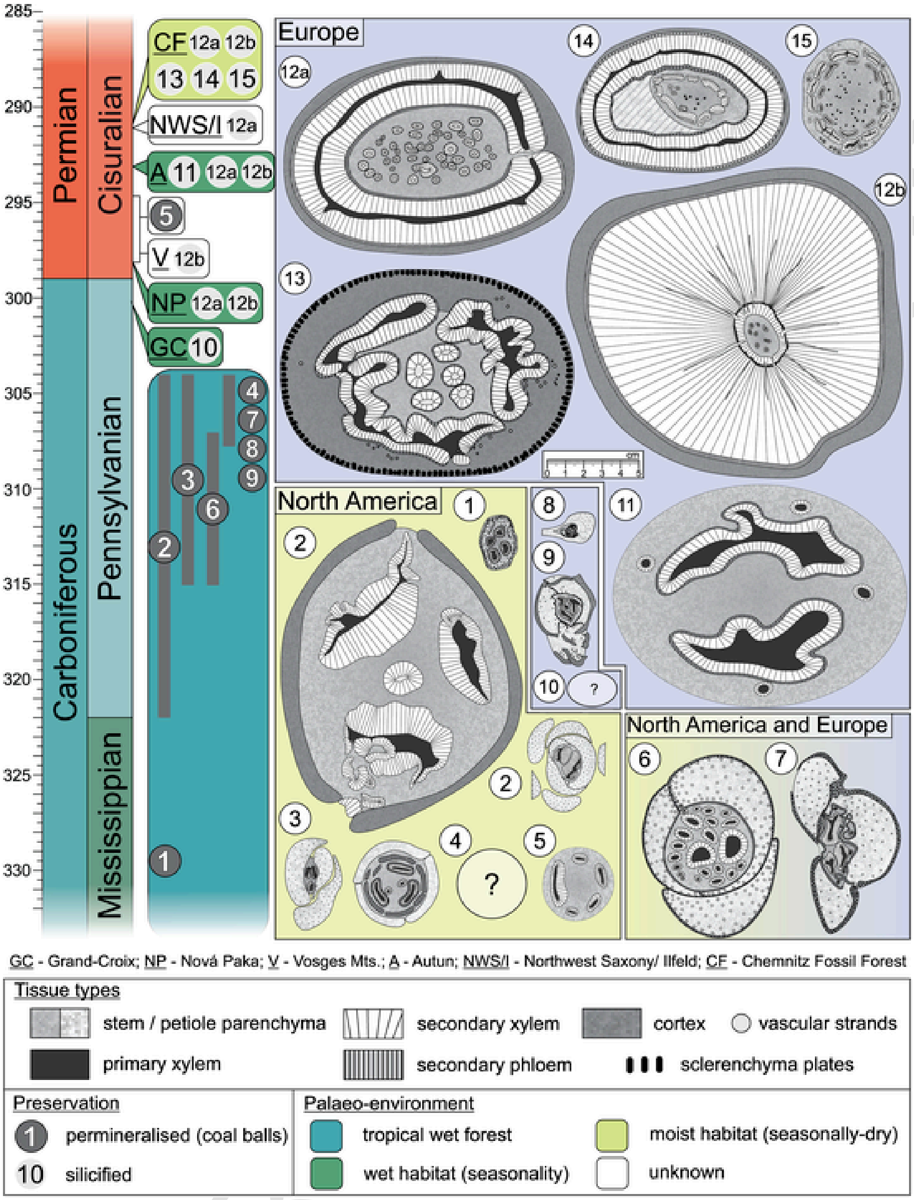

Fig. 2. Transverse sections of stem taxa of medullosans with information on their stratigraphy, (palaeo-) geographic origin, taphonomy and palaeo-environment. Note that all specimens are to scale. 1 – *M. steinii* Dunn et al. (redrawn from Dunn, 2006); 2 – *M. noei* Steidtmann encompassing two varieties, which probably represent different ontogenetic stages (redrawn from Basinger et al., 1974 for the small specimen and Delevoryas, 1955 for the large specimen); 3 – *M. thompsonii* Andrews, again two varieties, probably representing different ontogenetic stages (redrawn from Basinger et al., 1974, left, and Steidtmann, 1944, right); 4 – *M. endocentrica* Baxter, from which no drawing exists; 5 – *M. olsoniae* Roberts et Barghoorn (drawn from photography provided by Roberts and Barghoorn, 1952); 6 – *M. primaeva* Baxter (redrawn from Stewart and Delevoryas, 1956); 7 – *M. anglica* Scott (drawn from photography provided by Scott, 1899); 8 – *M. centrofilis* de Fraine (redrawn from De Fraine, 1914); 9 – *M. pusilla* (redrawn from Scott, 1914); 10 – *M. geriensis* (Scott) Boureau, from which no drawing exists; 11 – *Colpoxylon aeduense* Brongniart (redrawn from Stewart and Delevoryas, 1956, cortex not represented); 12a – *M. stellata* (Cotta) var. *typica* Weber et Sterzel (redrawn from Weber and Sterzel, 1896); 12b – *M. stellata* (Cotta) var. *lignosa* Weber et Sterzel (specimen K4496 from the collection of the Natural History Museum Chemnitz); 13 – *M. leuckartii* Göppert et Stenzel (redrawn from Weber and Sterzel, 1896); 14 – *M. porosa* Cotta (redrawn from Weber and Sterzel, 1896); 15 – *M. solmsii* Schenk (redrawn from Weber and Sterzel, 1896).

ble to medullosans. The Neuralethopteridaceae (e.g., *Alethopteris*, *Lonchopteris* and *Neuralethopteris*) were bifurcating fronds and are among the largest known, with documented dimensions of up to 7.4 × 4.2 m (Laveine, 1997). The Neurodontopteridaceae represent bifurcate, semi-pinnate fronds and were subdivided by Cleal and Shute, 2003) into the Neurodontopteridaceae sensu stricto (e.g., *Neuropteris*, *Odontopteris*, *Macroneuropteris*) and the Cyclopteridaceae (*Laveineopteris*, *Margaritopteris*, *Callipteridium*). Some of the neuropterids were clearly attached to medullosan stem taxa (Beehler, 1983). Large strap-shaped foliage of the *Taeniopteris* type may also be assigned to late Paleozoic seed ferns (Taylor et al., 2009), and thus potentially to medullosans.

3.3. Reproductive organs

Among pteridosperms, medullosans reveal the highest diversity of reproductive organs. Their synangiate pollen organs were attached to the rachises and produced prepollen of the *Monoletes* type (Serbet et al., 2006). Pollen organs are highly diverse, including different forms attached to the same foliage types (Stidd, 1981). Among the most common genera are *Aulacotheca, Bernaultia, Codonotheca*, *Dolerotheca*, *Halletheca*, *Potoniea, Rhetinotheca*, *Sullitheca* and *Whittleseya* (e.g., Ramanujam et al., 1974; Stidd, 1981; Zodrow, 2007). Medullosan

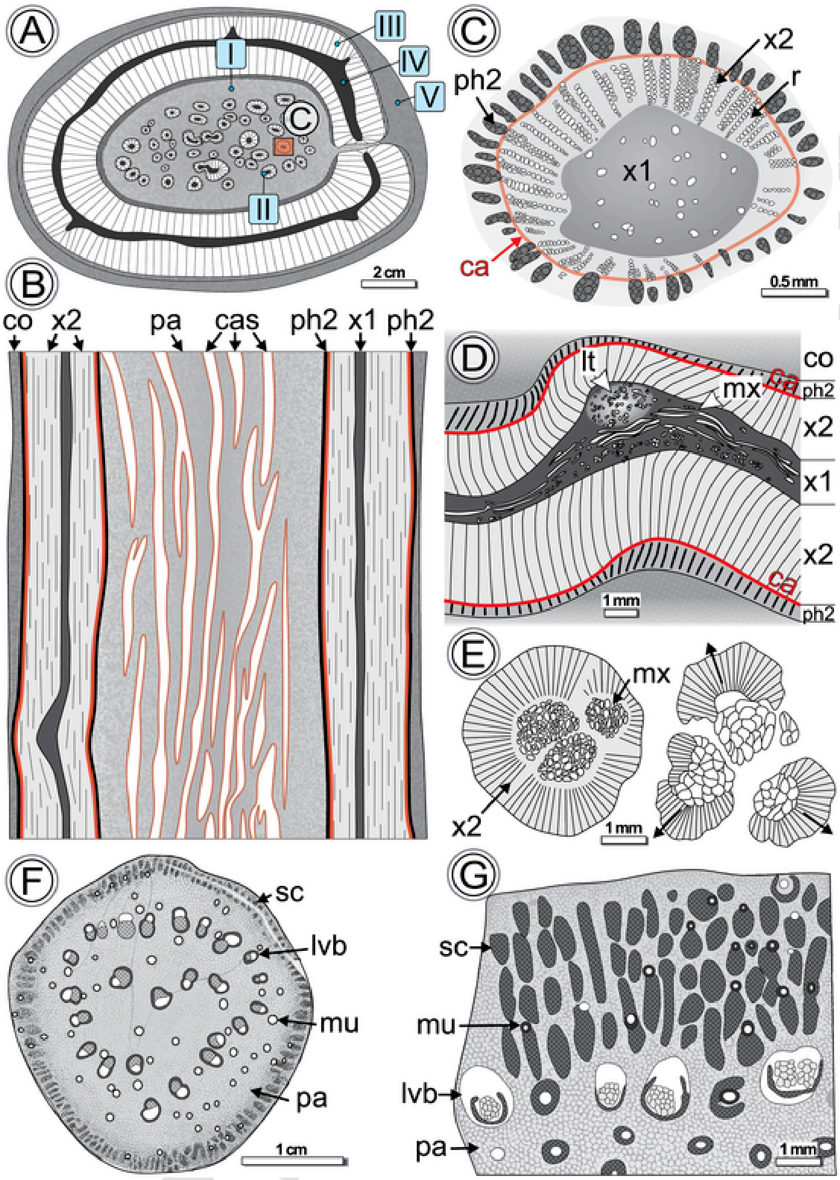

Fig. 3. Idealised sketches on general anatomical characteristics of early Permian medullosans from intramontane basins. A – cross-section of *M. stellata* var. *typica* illustrating main anatomical elements: I – central parenchymatous cylinder, II – central accessory strands, III – cylindrical-shaped peripheral vascular segment with secondary xylem and phloem, IV – primary xylem with emerging leaf traces, V – cortex (redrawn from Weber and Sterzel, 1896; see Fig. 2 for tissue signatures); B – longitudinal section through a stem showing branching central accessory strands and zones of cambial activity (red lines); C – anatomical details of a central accessory strand showing the zone of cambial activity; D – cross-section through part of the peripheral vascular segment with an emerging leaf trace from the primary tissue, in which horizontal metaxylem tracheids are present; E – branching leaf trace on its way through the outer wood, redrawn from Weber and Sterzel (1896) and Solms-Laubach (1897); F – cross-section through a *Myeloxylon landriotii* rachis, redrawn from Renault (1875); G – close-up of the outer part of a *Myeloxylon* foliar axis with sclerenchymatous outer cortex, redrawn from Renault (1875). abbreviations: pa – parenchyma, mx – metaxylem, x 1 – primary xylem, x 2 – secondary xylem, ph 2 – secondary phloem, ca – active cambial zone; r –rays, sc – sclerenchyma strand, co – cortex, cas – central accessory strands, lvb – leaf vascular bundles, lt – leaf trace, mu – mucilage canals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ovules are also very diverse. They were acupulate and attached to the rachises (e.g., Zodrow and McCandlish, 1980). Among them, *Trigonocarpus* and its permineralized or petrified equivalent *Pachytesta* are the most common types. Some *Pachytesta* forms are among the largest known in the Carboniferous (Taylor, 1965; Cichan and Taylor, 1981; Stidd, 1981). Other ovules referred to medullosans are *Hexapterospermum* (Taylor, 1966), *Stephanospermum* (Leisman and Roth, 1963), *Polypterospermum*, *Polylophospermum*, *Codonospermum* and *Colpospermum* (Combourieu and Galtier, 1985).

3.4. Roots

Peatland medullosans had adventitious roots attached to their stems (e.g., Stewart and Delevoryas, 1956; Wnuk and Pfefferkorn, 1984). These roots show an exarch actinostele with four protoxylem strands, which is usually surrounded by secondary tissues (Taylor et al., 2009). Secondary xylem is either continuous around the primary xylem or arranged in cross-shaped wedges opposite the metaxylem (Steidtmann, 1944; Rothwell and Whiteside, 1973). Secondary phloem consisting of sieve cells and rays occurs at the periphery of the xylem.

3.5. Diversity and palaeoecology

The diversity of natural species remains shrouded as long as whole-plant reconstructions are rare. Up to now, only the high number of different reproductive organs may reflect the assumed high species diversity. Morphological and anatomical variations among both foliage and stem taxa may represent ecomorphotypes or ontogenetic varieties (e.g., Krings et al., 2008; Cleal and Shute, 2012) and should therefore be evaluated with care.

Palaeoecological inferences on medullosans of the Carboniferous are mainly derived from compression floras. Due to their high abundance, ecomorphological variations were statistically evidenced (e.g., Laveine, 1997; Cleal, 2008; Cleal and Shute, 2012; Raymond et al., 2014). A comprehensive overview of medullosan palaeoecology is given by DiMichele et al. (2006b). Medullosans of palaeo-tropical lowlands are supposed to have preferred wet clastic substrates along rivers and on alluvial plains, tolerating slight seasonal fluctuations of water availability (e.g., Wnuk and Pfefferkorn, 1984; Falcon-Lang, 2009; Raymond et al., 2014; D'Angelo and Zodrow, 2016). Peaty substrates with standing water bodies were unfavourable for them (DiMichele et al., 2006b), although the majority of anatomically preserved stem fossils is related to permineralised peat substrates ("coal balls"). Adventitious roots might be regarded as an adaptation to wet soils. Xeromorphic leaf-morphological features were re-interpreted as an adaptation to high-humid conditions, suggesting that medullosans preferred both sunny and shaded localities (Cleal and Shute, 2012; Stull et al., 2012). As medullosans were predominant components of the understorey in the Lower–Middle Pennsylvanian rainforests, their huge leaf mass and climbing growth habits may be seen as light-catching strategies. Their diverse stem tissues, different secretions such as resin or mucilage, as well as high biomass production, made them the most carbon-consumptive plant group in the palaeo-tropical rainforests (Baker and DiMichele, 1997; DiMichele et al., 2006b). Dispersal of prepollens and seeds could have involved wind, water and animals, the latter demonstrated by the discovery of numerous pollen grains on a leg segment of an arthropleurid, which could have represented a potential pollinator (Scott and Taylor, 1983). The *Codonospermum* seeds revealed a large basal air chamber, probably in adaptation to floating (Combourieu and Galtier, 1985). Statistical analyses on foliage types suggest specific niche segregation between alethopterids and neuropterids, whereas alethopterids may have been more meso- to xerophilous, and neuropterids more abundant during wet phases of glacial cycles in the palaeo-tropics (Wnuk and Pfefferkorn, 1984; Cleal and Shute, 1995). Extensive formation of tyloses in the secondary tissues of medullosans is reported from *M. olseniae* (Roberts and Barghoorn, 1952).

4. Medullosans of Late Pennsylvanian–early Permian intramontane basins

From these medullosans, five stem taxa are known, *M. stellata* Cotta, *M. leuckartii* Göppert et Stenzel, *M. solmsii* Schenk, *M. porosa* Cotta, and *M. gigas* Renault. They differ in anatomy and overall vascular organisation from their early relatives of the Carboniferous tropical lowlands (Fig. 2; Table 2). Permian medullosans had somewhat more massive stems with peripheral vascular segments surrounded by considerable portions of secondary xylem, a high average number of central accessory strands, as well as voluminous crowns, some of them with massive petiole bases. In the fossil record of intramontane basins, anatomically preserved medullosans remain scarce and are known from a few localities in Central Europe (e.g., Mougeot, 1852; Renault, 1875; Solms-Laubach, 1897; Sterzel, 1886; Opluštil et al., 2013; see Table 1). Among them, the Chemnitz Fossil Forest depicts a rich assemblage of these plants and is the type locality for four of the five *Medullosa* species (e.g., Cotta, 1832; Weber and Sterzel, 1896; Rößler et al., 2012b). Until today, no whole-plant reconstructions exist.

4.1. Medullosans from the Chemnitz Fossil Forest

The Chemnitz Fossil Forest in central-east Germany represents a so-called T^0 fossil assemblage, as the arborescent vegetation was buried in growth position in a geological instant by silicic pyroclastic deposits of the Zeisigwald Volcanic Complex (e.g., Rößler et al., 2012b). The latter is intercalated in the Leukersdorf Formation, which is part of the sedimentary succession of the post-Variscan intramontane Chemnitz Basin(Schneider et al., 2012). The entombing tuff revealed an age of 291 ± 2 Ma (Sakmarian/Artinskian transition, early Permian), radio-isotopically constrained by magmatic zircons (Luthardt et al., 2018). The particular taphonomy of the fossil assemblage bears the potential to find in-situ medullosans with various organ connections of stems with roots, petioles and rachises, foliage and probably reproductive or-

Table 1
Overview on fossil localities of anatomically preserved medullosan taxa (and *Colpoxylon*) from the Upper Pennsylvanian–early Permian intramontane basins including stratigraphic age and sedimentological environment.

Locality	Geological structure	Medullosan taxa	Sedimentary environment	Palaeoclimate	Stratigraphy
Chemnitz Fossil Forest (Germany)	Chemnitz Basin	*M. stellata* *M. leuckartii* *M. porosa* *M. solmsii*	Alluvial plain, clastic soil and near-surface groundwater level	Sub-humid; pronounced seasonally-dry	291 ± 2 Ma, Leukersdorf-Formation, Sakmarian/Artinskian transition, early Permian
NW Saxony (Germany)	NW Saxony Volcanic Complex	*M. stellata* var. *typica*	Unknown	Unknown	Asselian–Sakmarian, early Permian
Ilfeld (Germany)	Saar-Nahe Basin	*M. stellata* var. *typica*	Unknown	Unknown	Early Permian
Nová Paka (Czech Republic)	Krkonoše Piedmont Basin	*M. stellata* var. *typica*/ var. *lignosa*	Alluvial plain, wet clastic soil, lacustrine proximity	Sub-humid; slightly seasonally-dry	Semily-Formation, late Gzhelian, late Upper Pennsylvanian
Autun (France)	Autun Basin	*M. stellata* var. *typica*/var. *lignosa* *M. gigantea* *Colpoxylon*	Alluvial plain, fluvial proximity?	(Sub-) humid; slightly seasonally-dry	Millery-Formation, Asselian–Sakmarian, early Permian
Val d'Ajol (France)	Val-d'Ajol Basin	*M. stellata* var. *lignosa*	Unknown	Unknown	Asselian?, early Permian
Rive de Gier (France)	Saint-Etienne Basin	*M. geriensis*	Peaty substrate?	Unknown	Upper Pennsylvanian

gans (Rößler, 2021). Stems, foliar organs and roots were petrified by silica and calcium fluorite.

The Chemnitz medullosans were first described by Cotta (1832) who established three taxa, among them the type species of the genus, *M. stellata*. Later, more detailed studies on anatomical characteristics of the medullosans led to some revision and reorganisation of the taxonomic concepts, e.g., by Solms-Laubach (1897) or Göppert and Stenzel (1881), who designated medullosans as fossil cycads. The most comprehensive study at that time was published by Weber and Sterzel (1896), which is still state of the art in documenting available growth forms. The taxonomic classification only based on several stem sections remains questionable and requires verification by more complete fossil material.

4.1.1. Stem anatomy and variation in medullosan taxa

Medullosans, in part preserved in situ, show a high growth form diversity (Fig. 2). Some trunks were of slender-columnar stature, and others were short and thick. Up to 5-m-long stem segments possess more or less constant diameters. Most sections have diameters of < 10 cm, several exhibit wider diameters of 15–30 cm, and only a few reach diameters up to 48 cm. The general stem anatomy encompasses a central parenchyma ("I" in Fig. 3 A) embedding central accessory strands ("II" in Fig. 3 A), a ring of one or several peripheral vascular segments ("III" in Fig. 3 A) with primary xylem ("IV" in Fig. 3 A) surrounded by secondary xylem and phloem, and a more or less prominent cortex with sclerenchyma ("V" in Fig. 3 A). Although it was called "pith" in earlier publications (e.g., Weber and Sterzel, 1896), we prefer to use the term "central parenchyma", due to significant differences of the medullosan stelar architecture compared to other seed plants.

The central accessory strands embedded in the central parenchyma (also called "star rings" or "plate rings" by Weber and Sterzel, 1896) are built up of metaxylem surrounded by secondary xylem and marginal phloem (Fig. 3 C; Plate I, 4,+5). They do not show any protoxylem strands. The number of accessory strands varies within some individuals between one and more than 100 (Plate I, 2). Otherwise, their number seems to remain nearly constant within a single stem. Minor changes are due to anastomoses of the bundles forming a network of conducting tissue (Fig. 3 B). Also, the shape of the accessory strands is highly variable in cross-section, ranging from (sub-) circular to oval and tubular. Shape and arrangement of these strands were originally regarded as of taxonomic value (Cotta, 1832; Weber and Sterzel, 1896).

The vascular segments are composed of primary xylem, including parenchyma, protoxylem strands and metaxylem tracheids. Metaxylem tracheids are frequently horizontally oriented (Fig. 3 D; Plate I; Plate III; Rudolph, 1922). Leaf traces originate from protoxylem strands (Schenk, 1889) and divide on their way out of the stem towards the petioles (Plate III, 5). Vascular segments are surrounded by abundant secondary xylem and phloem, resulting in secondary growth both to the centre and the periphery of the stem (Fig. 3 A–D). The width of secondary xylem varies from 1 to 25 cm, representing the dominating tissue type in many stems. It is composed of loosely-arranged radial tracheid rows and thick parenchymatous rays (Plate I, 10,+11). Tracheids are long and wide (≤ 220 μm in diameter) compared to those of pycnoxylic gymnosperms and have circular lumina and comparably thick cell walls. Pits in the secondary xylem tracheids are multiseriate and densely arranged (Text-Fig. 2 in Weber and Sterzel, 1896; Plate I, 11). Some specimens of *M. stellata* show indistinct growth rings, especially in the outer wood zone (Luthardt et al., 2017). Secondary phloem occurs at the outer margins of the secondary xylem (Fig. 3 D). The stems are bounded externally by a parenchymatous cortex layer, which is thickened around the petiole attachments. The presence of a periderm was not evidenced, so far.

4.1.2. Taxonomic descriptions

Class: PTERIDOSPERMOPSIDA
Order: MEDULLOSALES
Family: MEDULLOSACEAE
Genus: **Medullosa** Cotta, 1832
Species: Medullosa stellata Cotta, 1832

Syntypes: Cotta (1832) figured three specimens (Pl. XIII, 1, 2, 4) but did not select any holotype or paratype. We propose to choose specimen MfNC K3004 (Cotta, 1832, Pl. XIII, 4) as lectotype. From the same stem, there remained a few more slices. Among them is a large thin-section preparation (K3004DS) and an additional polished slice: MB.Pb 2011/0950.

Repository: Natural History Museum of Chemnitz (MfNC); Leibniz Institute for Biodiversity - Natural History Museum of Berlin (MB).

Type locality: Chemnitz Fossil Forest, Chemnitz-Hilbersdorf

Stratigraphic horizon: Zeisigwald Volcanic Complex, Leukersdorf Formation

Age: 291 ± 2 Ma, early Permian (Luthardt et al., 2018)

Specific diagnosis: original diagnosis was presented by Cotta (1832, p. 65), here completed by additional data provided from literature (e.g., Weber and Sterzel, 1896); central parenchyma with a variable number of accessory strands showing radially arranged secondary tissues; nearly continuous cylinder of a peripheral vascular segment separated by narrow, occasional openings unrelated to leaf trace emission; vascular segment with centrifugally and centripetally grown manoxylic wood and secondary phloem; parenchymatous cortex; see Fig. 3 A–D and Plate I.

Description: The taxon represents the most frequent stem type in the Chemnitz Fossil Forest. Several growth varieties were distinguished (Göppert and Stenzel, 1881; Weber and Sterzel, 1896), but their taxonomic significance was questioned (Schenk, 1889). *Medullosa stellata* var. *typica* exhibits wide central parenchyma with many accessory strands, a peripheral vascular segment with comparably thin wood and a thin cortex or periderm layer (Plate I, 1–3). The outer wood zone is not distinctly wider or even thinner than the inner one. Secondary tracheids are 75–110 μm wide. Growth rings are indistinct and occur predominantly irregularly (Luthardt et al., 2017). Petiole bases show numerous sclerenchyma fibres in the thickened cortex, and vascular bundles with a concentric zone of secondary xylem (Weber and Sterzel, 1896, p. 57, Text-Fig. 7). *Medullosa stellata* var. *corticata* and var. *incrassata* probably represent different growth stages, which might occur in the same plant.

Medullosa stellata var. *lignosa* is characterised by narrow central parenchyma with only a few accessory strands (⌀ 1–10; ≤ 31) and a particularly thick outer zone of secondary xylem around the peripheral vascular segment (Plate I, 7, 8). Secondary tracheids are 90–110 μm wide. Indistinct, but regular growth rings occur in the outer zone, suggesting periodic secondary growth from a lateral meristem, which is referred to as seasonally driven cambial activity (Luthardt et al., 2017). Secondary growth leads, in part, to considerable stem diameters up to 34 cm with more than 95% of wood. Small leaf traces are observed on the inner edge of the outer wood zone (Plate I, 9).

Medullosa stellata var. *gigantea* is represented only by a few specimens and exhibits the largest stem diameters of all medullosans known so far (48 × 45 cm). Therefore, this variety most likely represents basal sections of old individuals (Weber and Sterzel, 1896). In contrast to most other medullosans, var. *gigantea* is characterised by multiple consecutive cylinders of wood surrounding the central parenchyma (Plate II, 1). These wood cylinders are separated by wavy-shaped rows of secondary phloem and parenchyma (Plate II, 3). Accessory strands of two different size classes (a: ⌀ 25 mm; b: ⌀ 5 mm) frequently occur in the central parenchyma (Plate II, 2).

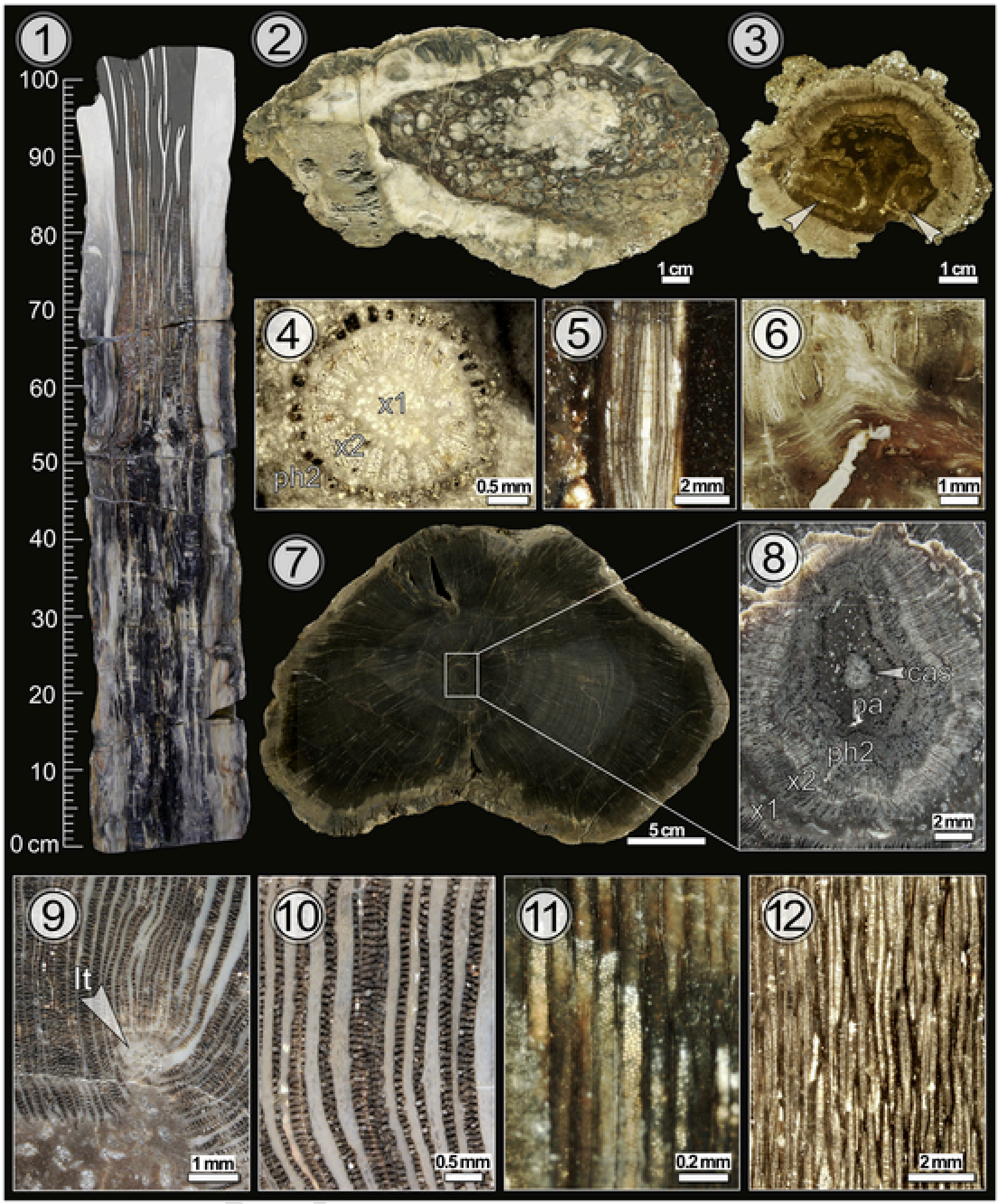

Plate I. Anatomical details of *M. stellata* var. *typica* (1–6) and var. *lignosa* (7–12) from the Chemnitz Fossil Forest (collection of the Natural History Museum Chemnitz). 1. Longitudinal section of a one-metre-long stem segment (K4019, with sketch of peripheral vascular segment, central parenchyma and accessory strands at the top); 2. cross-section of an adult stem showing more than 100 central accessory strands (K109); 3. historical thin section of a smaller specimens showing central accessory strands forming two rings in the central parenchyma (indicated by arrows, M1?); 4. central accessory strand in cross-section with primary xylem (x 1), secondary xylem (x 2) and secondary phloem (ph 2) in K4999; 5. central accessory strands in longitudinal section (KH0196); 6. leaf trace in the primary xylem zone of the peripheral vascular segment showing several horizontally oriented metaxylem tracheids (K2595); 7. *M. stellata* var. *lignosa* cross-section showing vascular segment with abundant secondary xylem and narrow central parenchyma (K6042); 8. magnification of Fig. 7 showing the central parenchyma (pa) with one central accessory strands (cas) and the inner wood of the peripheral vascular segment; 9. leaf trace (lt) emerging from the primary tissue zone of the peripheral vascular segment (K6042); 10. secondary xylem with narrow tracheid rows (dark) and abundant ray parenchyma (light grey) in K6042; 11. longitudinal section showing multiseriate pits in tracheids of secondary xylem (K6042); 12. secondary xylem in tangential section showing typical arrangement of tracheid rows and ray parenchyma (K6042).

Remarks: Any further subdivision of the species *M. stellata* as suggested by several authors (Göppert and Stenzel, 1881; Weber and Sterzel, 1896) needs to be evaluated in more detail in forthcoming publications.

Class: Pteridospermopsida

Order: Medullosales

Family: Medullosaceae

Genus: **Medullosa** Cotta, 1832

Species: Medullosa porosa Cotta, 1832

Holotype: The specimen figured by Cotta (1832: pl. XII, 6) is lost. Additional polished stem segments, more complete than the holotype, and three thin-section preparations of the same stem are stored at MfNC (K2965, K309, K2581, K5618).

Repository: Natural History Museum of Chemnitz (MfNC)

Type locality: Chemnitz Fossil Forest, Chemnitz-Hilbersdorf

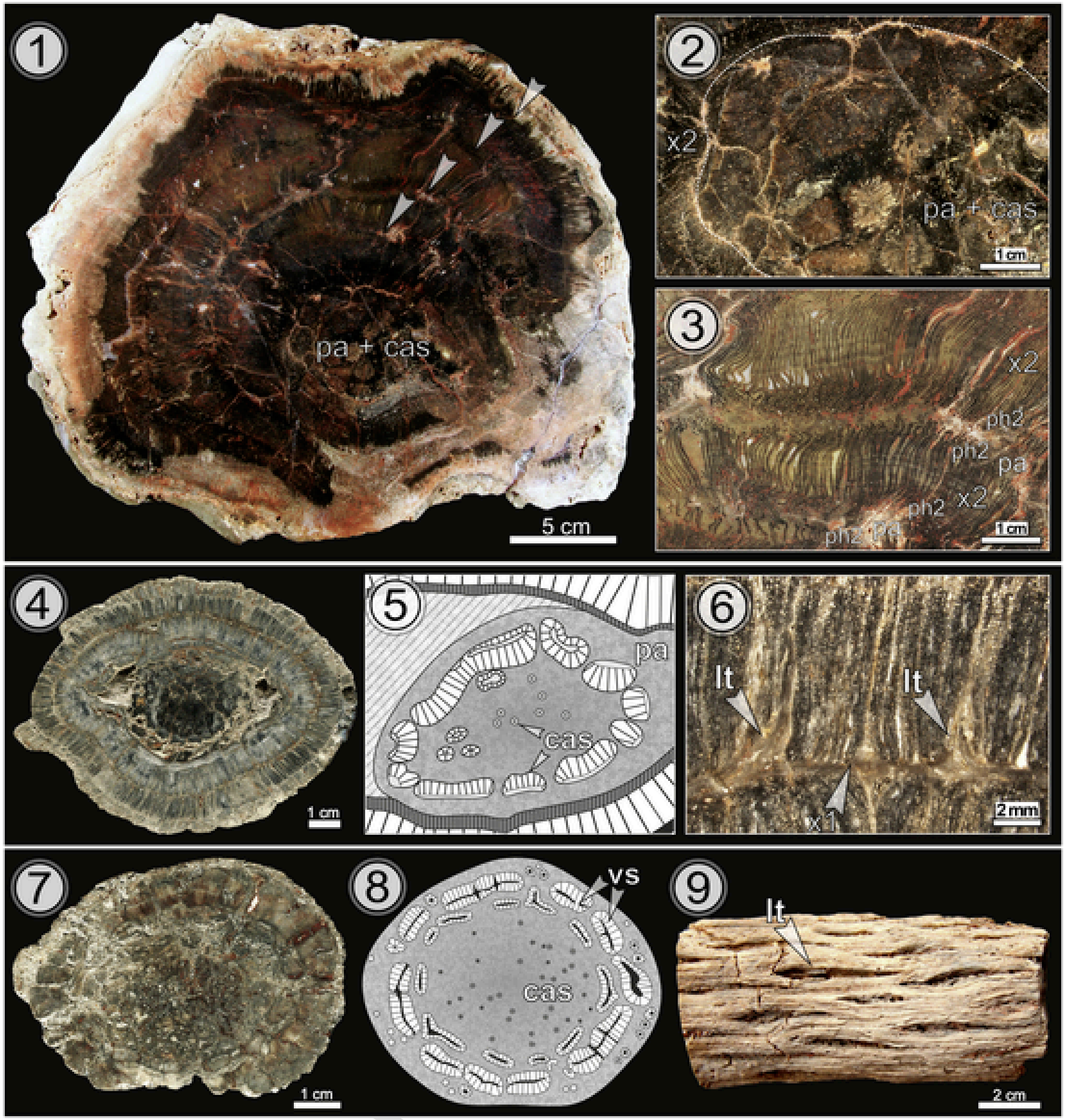

Plate II. Anatomical details of *M. stellata* var. *gigantea* (Figs. 1–3), *M. porosa* (Figs. 4–6) and *M. solmsii* (Figs. 7–8) from the Chemnitz Fossil Forest (collection of Natural History Museum Chemnitz). 1. Cross-section of *M. stellata* var. *gigantea* showing several consecutive cylinders of vascular segments in K7510b (see arrows; pa – central parenchyma, cas – central accessory strands; courtesy R. Noll); 2. close-up of the central parenchyma with accessory strands (courtesy R. Noll); 3. close-up showing consecutive vascular segments with centripetal and centrifugal secondary xylem (x 2) and phloem (ph 2) separated by parenchyma (pa), courtesy R. Noll; 4. cross-section of *M. porosa* (K2581); 5. sketch of central accessory strands which show the typical centripetal growth of secondary xylem; 6. vascular segment with two leaf traces (lt) emerging from the primary tissue (2581); 7. cross-section of *M. solmsii* (K5597); 8. sketch of anatomical details of *M. solmsii* with an outer ring of about 10 vascular segments (vs) and central accessory strands (see Fig. 2 for tissue signatures); 9. surface of the wood cylinder of a decorticated stem segment showing numerous openings (lt), corresponding to the intervals between the adjacent peripheral vascular segments, as shown on Fig. 8 (K5596b).

Stratigraphic horizon: Zeisigwald Volcanic Complex, Leukersdorf Formation

Age: 291 ± 2 Ma, early Permian (Luthardt et al., 2018)

Specific diagnosis: original diagnosis was presented by Cotta (1832, p. 63), here completed by additional data provided from literature (e.g., Weber and Sterzel, 1896); anatomy similar to *M. stellata*, but central accessory strands (Plate II, 4, 5) are organised in an inner and an outer zone; outer accessory strands frequently tangentially elongated and anastomosing, forming a discontinuous "ring"; secondary xylem of outer accessory strands was preferentially growing centrifugally; leaf traces may be emitted in pairs (Plate II, 6).

Description: Only a few sections exist of this taxon and preservation is insufficient to provide more detailed anatomical characteristics. The sections have diameters around 10 cm.

Remarks: The justification of a separate species *M. porosa* is still questioned and needs to be substantiated.

Class: PTERIDOSPERMOPSIDA

Order: MEDULLOSALES

Family: MEDULLOSACEAE

Genus: **Medullosa** Cotta, 1832

Species: Medullosa solmsii Schenk, 1889.

Holotype: The specimen figured by Schenk (1889: Taf. III, fig. 49) at MfNC numbered as K3021.

Repository: Natural History Museum of Chemnitz (MfNC)

Type locality: Chemnitz Fossil Forest, Chemnitz-Hilbersdorf

Stratigraphic horizon: Zeisigwald Volcanic Complex, Leukersdorf Formation

Age: 291 ± 2 Ma (early Permian; Luthardt et al., 2018)

Specific diagnosis: original diagnosis was presented by Schenk (1889, pp. 539–541), here completed by additional data provided from literature (e.g., Weber and Sterzel, 1896); central parenchyma with tiny accessory strands (⌀ 1 mm, distinctly smaller compared to *M. stellata*); many peripheral vascular segments with radially arranged secondary tissues; vascular segments form one or several consecutive rings (for M. *solmsii* var. *lignosa*), in cross-section (Plate II, 8).

Description: Specimens are rather poorly preserved concerning anatomical structures. Stem sections of *M. solmsii* are rare and show diameters that never exceed seven centimetres, suggesting that they represent a small medullosan species (Plate II, 7). Vascular segments vary in size and exhibit a dense structure with thin parenchyma rays. Externally, the decorticated stem shows the surface of the outer ring with numerous openings corresponding to the intervals between adjacent peripheral vascular segments (Plate II, 9), probably with paired leaf traces (Weber and Sterzel, 1896; Sterzel, 1918).

Class: Pteridospermopsida

Order: Medullosales

Family: Medullosaceae

Genus: **Medullosa** Cotta, 1832

Species: Medullosa leuckartii Göppert et Stenzel 1881

Holotype: The specimen figured by Göppert and Stenzel (1881: Taf. III, figs. 13, 14) at MfNC numbered as K3017a, b.

Repository: Natural History Museum of Chemnitz (MfNC)

Type locality: Chemnitz Fossil Forest, Chemnitz-Hilbersdorf

Stratigraphic horizon: Zeisigwald Volcanic Complex, Leukersdorf Formation

Age: 291 ± 2 Ma (early Permian; Luthardt et al., 2018)

Specific diagnosis: original diagnosis was presented by Göppert and Stenzel (1881, pp. 13–16), here completed by additional data provided from literature (e.g., Weber and Sterzel, 1896); elongated and sinuously shaped peripheral vascular segments around the central parenchyma; central accessory strands are mostly (sub) circular, but variable in shape and possessing a broad central zone with metaxylem clusters (Plate III, 2, 7, 9); massive petiole bases of *Myeloxylon elegans* Brongniart; thick parenchymatous cortex with sclerenchyma plates and mucilage canals.

Description: Few, wide stem sections (≤ 26 cm) of *M. leuckartii* have been found, suggesting a short and thick growth habit. The most significant specimen (Plate III, 1–6) is represented by a large stem portion with several attached massive petiole bases of the *Myeloxylon elegans* Brongniart type (Sterzel, 1918; Plate III, 1). The central accessory strands are probably connected to the peripheral vascular segments (Weber and Sterzel, 1896). The secondary xylem of *M. leuckartii* exhibits abundant parenchyma in wide medullary rays. Secondary tracheids are 80–220 μm wide. Secondary phloem is arranged in wavy-shaped rows (Plate III, 8), occurring relatively abundant at the periphery of vascular segments and accessory strands.

Attached petioles of the *Myeloxylon elegans* Brongniart type are helically arranged and have more than 20 cm wide, triangular bases (Plate III, 3). They probably bifurcate and are similar to the *M. landriotii* and *M. radiatum* foliar axes described from Autun (Renault, 1875; Zeiller, 1890). Sclerenchyma plates and mucilage canals are abundant at the petiole periphery (Plate III, 11). The leaf vascular bundles are collateral, circular in cross-section, with an endarch primary xylem and primary phloem (Plate III, 10). It is assumed that the sclerenchyma in the outer cortex and decurrent petiole bases mostly insured the mechanical support of the parenchymatous stem (Weber and Sterzel, 1896).

Remarks: A formal revision of this unquestionably separate species is needed and should include more complete finds such as that figured by Sterzel (1918: pl. 5, fig. 72).

4.1.3. Foliage and reproductive organs

Due to the T^0 character of the Chemnitz Fossil Lagerstätte (Rößler et al., 2012b; Luthardt et al., 2018), stem and foliage taxa assigned to the medullosans originate from the same thanatocoenosis. The record of foliage adpressions with medullosan affinity encompasses *Alethopteris schneideri*, *Neurocallipteris planchardii*, *Neurocallipteris neuropteroides* and *Taeniopteris abnormis* (Plate IV), which were found frequently in the basalmost fallout horizons of the Zeisigwald pyroclastics (Rößler et al., 2012b; Rößler, 2021). In addition, Sterzel (1918) describes *Noeggerathia zamitoides* Sterzel (Plate IV, 5), which is of unclear affinity, but might be close to medullosans.

The attachment of *Myeloxylon elegans* specimens, exceeding 20 cm in width, to a *M. leuckartii* stem was reported by Sterzel (1918). The connection of *Taeniopteris abnormis* foliage to this specimen is supposed, based on large fronds found in the adhering tuff (Plate III, 4,+5, Sterzel, 1918). The Hilbersdorf excavation (2008–2011) revealed *T. abnormis* foliage frequently occurring in taphonomic proximity to an upright-standing *M. leuckartii* stem. Further potential organ connections were reported from an in-situ stem of *M. stellata* var. *typica*, which was surrounded by *A. schneideri* fronds (Weber and Sterzel, 1896, therein described as *Callipteris weberi*) with basal *Cyclopteris* pinnae. This association is evidenced from the Hilbersdorf excavation, where a *M. stellata* upper stem portion shows multiple organ connections with at least 10 large frond bases and attached fronds of *A. schneideri* (Rößler et al., 2012b). The material from the Chemnitz-Hilbersdorf excavation generally bears a high potential for recognising further organ connections, e.g., *Neurocallipteris planchardii* currently found in taphonomic proximity to *M. stellata* var. *lignosa*.

The record of medullosan reproductive organs is restricted to a few exceptional specimens, like the three-dimensionally preserved pollen organ *Sterzelitheca chemnitzensis* (Feng et al., 2014). Ovules are generally rare, and proof of their medullosan affinity is still missing. Thus, reproduction strategies of these early Permian medullosans remain speculative.

4.1.4. Roots

The Hilbersdorf excavation revealed the first morpho-anatomical details of root systems from several in-situ petrified specimens (Rößler et al., 2012b; Luthardt et al., 2016). Medullosan roots seem to penetrate the siliciclastic soil not deeper than 70 cm. At least three of the specimens with the largest stem diameters exhibit silicified vertical taproots, from which numerous lateral roots emerged. In smaller specimens, no tap roots were found, but only lateral roots preserved as adpressions (Luthardt et al., 2016 for more details). Thus, there are potentially two different types of root systems, which might be of specific value, but could also reflect different ontogenetic stages or preservation effects. Some medullosan root systems show bushy appendages (Rößler et al., 2012b, fig. 5 F; Rößler, 2021, pl. I, fig. 2), reminding the coralloid roots of modern cycads. No adventitious roots were found in the stem sections of any taxon.

4.1.5. Plant distribution patterns and palaeo-environment

Medullosans of the Chemnitz Fossil Forest were colonising a mineral substrate on an alluvial plain of the post-Variscan intramontane Chemnitz Basin. They were growing together with large cordaitalean trees, psaroniaceous tree ferns, arborescent calamitaleans and probably walchian conifers, which all co-existed with various faunal elements (e.g., Feng et al., 2012; Rößler et al., 2012a, 2012b; Dunlop et al., 2016; Luthardt et al., 2016; Spindler et al., 2018; Rößler, 2021). The forest community was thriving under a sub-humid local palaeoclimate characterised by distinct dry and wet phases, whereas the habitat likely benefited from a local near-surface groundwater level (Luthardt et al., 2016; Luthardt et al., 2017).

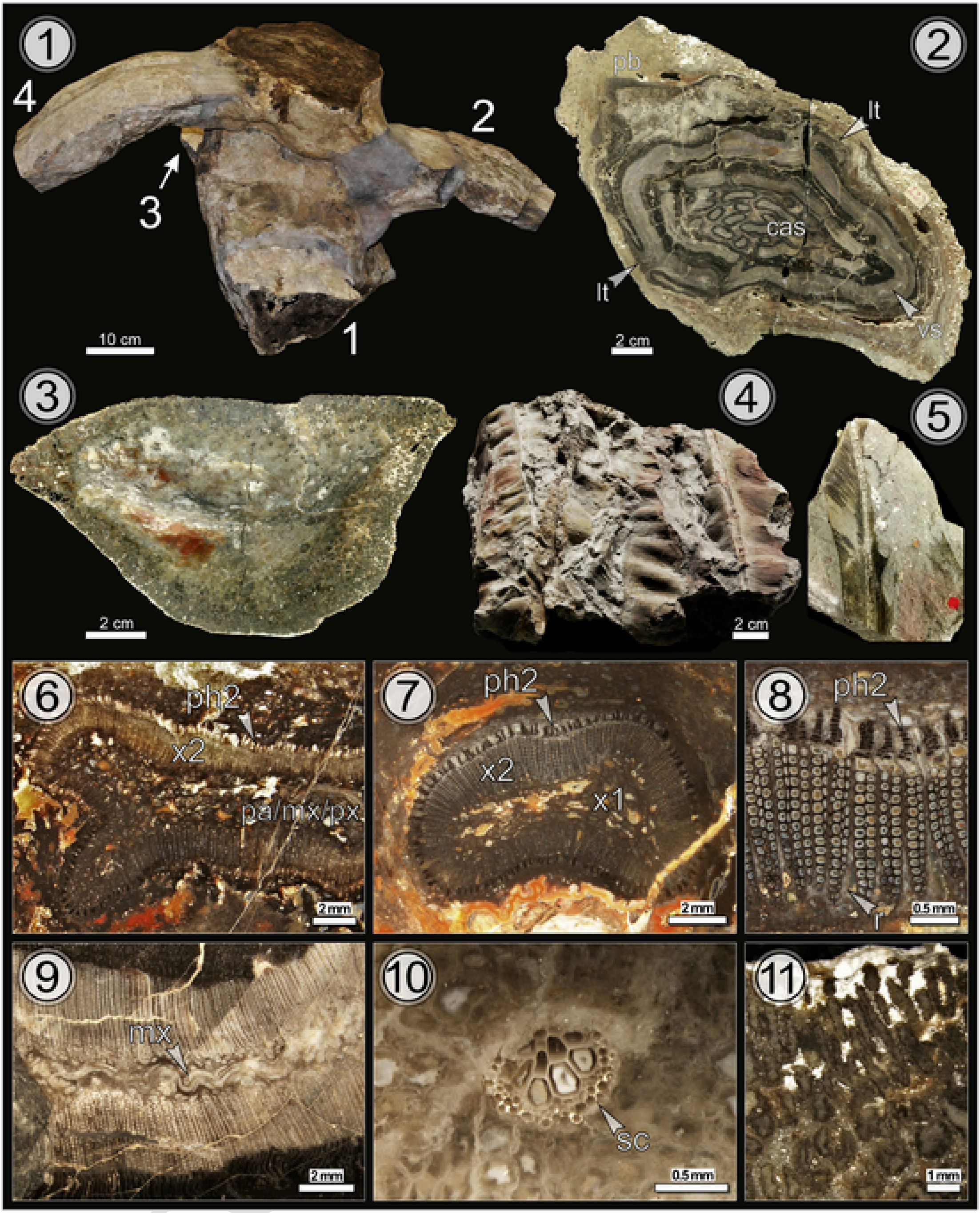

Plate III. Anatomical details of *M. leuckartii* from the Chemnitz Fossil Forest (collection of the Natural History Museum Chemnitz). 1. Segment of a huge leafy stem showing the bases of several attached petioles, first described by Sterzel (1918); 2. cross-section of the same specimen from its upper part showing the characteristic arrangement of vascular segments and accessory strands, and the thickened cortex where petioles were attached (K3037); 3. cross-section of a massive *Myeloxylon landriotii* petiole, once attached to the specimen shown in Fig. 1; 4. foliage adpressions of *Taeniopteris abnormis* preserved in tuff and found in taphonomic proximity to the foliated stem segment of Fig. 1; 5. close-up of *T. abnormis* preserved in tuff; 6. peripheral vascular segment showing parenchyma, metaxylem, and protoxylem, surrounded by secondary xylem and phloem (type specimen K3017); 7. central accessory strands (type specimen K3017); 8. detail of secondary tissues of a central accessory strand (type specimen K3017); 9. horizontally oriented metaxylem tracheids in a wood segment as part of the vascular segment (K3037); 10. leaf vascular bundle in the *Myeloxylon landriotii* petiole of) (3) with primary tracheids partly surrounded by sclerenchyma fibres; 11. outer cortex of the same petiole showing the characteristic morphology of sclerenchyma fibres. Abbreviations: pa – parenchyma, mx – metaxylem, px – protoxylem, x 1 – primary xylem, x 2 – secondary xylem, ph 2 – secondary phloem, r –rays, sc – sclerenchyma, cas – central accessory strands, vs – vascular segment, pb – petiole base.

Among the fossil localities in the outcrop area of the entombing pyroclastics, the Chemnitz-Hilbersdorf site provides the majority of medullosan fossils where they made up to 35% of all identified in-situ stems. In the whole fossil lagerstätte, medullosans represented 29% of the specimens (n = 3340) stored in the two largest local collections (Chemnitz Natural History Museum, private collection of Bernd Tunger, Chemnitz) (Rößler, 2021). In the Hilbersdorf excavation, medullosans were probably dominating among the in-situ preserved plants (35% medullosans, 30% pycnoxylic gymnosperms, 22% psaroniaceous tree ferns, 13% calamitaleans). Here, they colonised a well-drained and well-aerated siliciclastic soil (Luthardt et al., 2016). At the Hilbersdorf locality, medullosans are among the smallest plants (≤ 10 m),

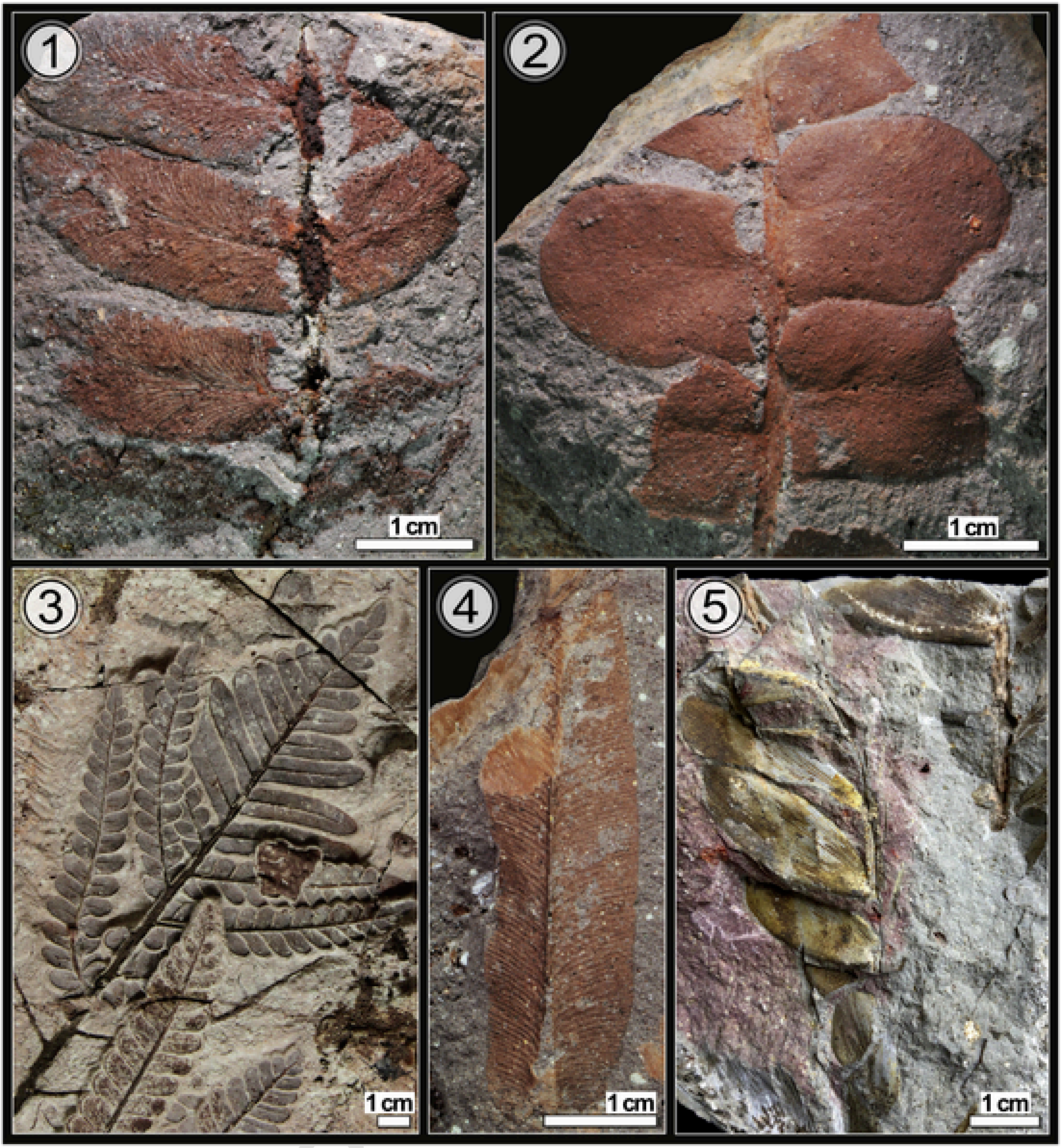

Plate IV. Foliage types with medullosan affinity from the Chemnitz Fossil Lagerstätte (specimens of Fig. 1–4 from the Chemnitz-Hilbersdorf excavation). 1. pinnules of *Neurocallipteris planchardii* (TA0849c); 2. pinnules of *Neurocallipteris neuropteroides* with partly preserved fine venation (TA0317); 3. second-order pinna of *Alethopteris schneideri* with pinnules of different orders; 4. pinnule of *Taeniopteris abnormis* (TA1044a) with putative affinity to *M. leuckartii*; 5. historical specimen of *Noeggerathia zamitoides* (K4113), which was first described by Sterzel (1918) and may have an association to medullosan stems.

sharing the understorey of the forest with psaroniaceous tree ferns, and being shaded by the distinctly higher cordaitalean and calamitalean trees. This canopy architecture was already supposed by Weber and Sterzel (1896), who found small medullosan stems (< 13 cm ⌀) together with large cordaitalean trees in a temporary outcrop, close to the current excavation site.

Medullosan fossils from other localities in the city of Chemnitz are rare, especially from the Sonnenberg locality, where many stems have been found of pycnoxylic gymnosperms, but also psaroniaceous tree ferns and calamitaleans. The low number of medullosans at this locality is remarkable compared to their dominance at the Hilbersdorf locality.

4.2. Medullosans from Autun (France)

The Autun Basin, located in central-east France, represents another post-Variscan intramontane basin filled by Carboniferous–Permian continental strata. In contrast to the Chemnitz Fossil Forest, silicified plant material is derived from a wide area within the basin, originating from various taphocoenoses of different stratigraphic levels from the Igornay to the Millery Formations (Renault, 1896). These formations are now known to range from the late Gzhelian to late Asselian age (Pellenard et al., 2017), where medullosans are known from compression floras. However, silicified medullosans have been found only in the Millery Formation (Asselian), which encompasses claystones with numerous oil-shale beds and one boghead bed near the top. The stems are supposed to have grown in swamp environments. However, their taphonomy is still incompletely understood.

The majority of medullosans and corresponding taxa is stored in the collections of the Muséum National d'Histoire Naturelle de Paris (MNHNP) and of the Muséum d'Histoire Naturelle d'Autun (MHNA). The medullosans, including their *Myeloxylon* foliar components, and some other stem taxa that are closely related to medullosans, such as *Colpoxylon*, *Ptychoxylon* and *Cycadoxylon*, have been first described in the 19th century (Brongniart, 1849; Renault, 1875, 1879, 1881, 1893, 1896).

4.2.1. Medullosan stem sections

Medullosans are rare in the MHNA collection material. Nevertheless, six almost complete stem sections, or fragments with parts of the central parenchyma preserved, are documented (Plate V). In addition, several wood fragments of *Palaeoxylon* type are present, which are attributed to medullosans based on the arrangement of medullary rays and the multiseriate pitting of secondary xylem tracheids (Brongniart, 1849; Renault, 1896; Plate V, 7 + 8). A large fragment of *Palaeoxylon* is supposed to have been part of a 45–50 cm wide medullosan stem, thus leading Renault (1896) to introduce the species *M. gigas*. However, as no specimen with central parenchyma exists for *M. gigas*, the taxon remains questionable, as it could also represent part of a massive *M. stellata* stem. Almost all complete sections of medullosans range within 12–17.5 cm in diameter and resemble *M. stellata* from Chemnitz. Three of them exhibit a peripheral vascular segment with considerable amounts of centrifugal wood, and narrow central parenchyma with few or no central accessory strands. They are comparable to *M. stellata* var. *lignosa* (Plate V, 1–3). At least 20 regular growth rings occur in the wood of MHNA-PAL-2020-0002 (Plate V, 3). In this specimen, secondary xylem tracheids are 70–200 μm in diameter. Sections with less wood around the peripheral vascular segment and more abundant accessory strands in wide central parenchyma are similar to *M. stellata* var. *typica* (Plate V, 2 + 4). According to Renault (1896), horizontal metaxylem tracheids occur in the peripheral vascular segments (compare to Rudolph, 1922). In the cortex, mucilage canals and numerous leaf vascular bundles occur at the level of petiole attachment (Renault, 1896).

4.2.2. Other stem genera close to medullosans

Renault (1896) recognised the genera *Colpoxylon*, *Ptychoxylon,* and *Cycadoxylon* as closely related to the medullosans. He put them all together in a group, the Cycadoxylées. The genus *Colpoxylon* Brongniart is represented by the single species *C. aeduense* and is known from very few specimens, e.g., from a ca. 15.5 × 12.5 cm wide section (Plate V, 5) described by several authors (Brongniart, 1849; Renault, 1881, 1896; Grambast, 1962). It is characterised by a wide central parenchyma, which is surrounded by one or two narrow, sinuous peripheral vascular segments with secondary xylem and phloem. The primary xylem of the segments is associated with parenchyma and includes variously oriented metaxylem tracheids (Grambast, 1962), comparable to metaxylem tracheids in the Chemnitz medullosans. Noticeable features include the broad parenchymatous cortex, the broad primary xylem (Fig. 2, no. 11) and the absence of accessory strands in the central parenchyma. Leaf traces frequently emerge from the peripheral vascular segment(s), originating from protoxylem strands in the primary tissue. The secondary xylem consists of tracheids arranged in rows up to four cells wide, separated by thick files of ray parenchyma. The cortex of *Colpoxylon* is distinctly thickened at the level of petiole attachment. Petiole bases are narrow, rectangular and 5–6 cm wide, according to Grambast (1962). They show a single row of tangentially aligned leaf vascular bundles and mucilage canals surrounded by sclerenchyma. They further possess dense, radially elongated sclerenchyma plates at the periphery and are therefore similar in several features to *Myeloxylon*. The proximity of *Colpoxylon* to the medullosans, especially to *M. leuckartii* has been suggested (Brongniart, 1849; Schenk, 1889; Grambast, 1962), although central accessory strands are missing in *Colpoxylon*, as emphasized by Delevoryas (1955). Grambast (1962) also illustrated cross-field pitting with oculipores contrasting with single oopores in the wood of the associated *Medullosa gigas* and *M. stellata*.

Cycadoxylon and *Ptychoxylon,* respectively described by Renault (1879, 1896), are very rare and have been generally ignored in the literature with a few exceptions (Broutin et al., 1999; Gand et al., 2015). They have been collected at the "Champ des Borgis" locality, stratigraphically above the Boghead bed in the Millery Formation. It is one of the youngest deposits of silicified plants in the Autun Basin (Gand, personal communication). Specimens of both plants are only 2–6 cm in diameter and characterised by rings and arcs of very loose manoxylic wood embedded in a parenchymatous tissue. The wood consists of thin tracheid rows that are interlaced by wide medullary rays. The tracheids have multiseriate pits. Anatomically, *Cycadoxylon* and *Ptychoxylon* show affinities to cycads. Their relationships with medullosans are unclear.

4.2.3. Myeloxylon petioles and rachises

Petioles and rachises of the *Myeloxylon* type are relatively abundant and, at least in part, well-preserved at the cell level. *Myeloxylon* sections are usually oval-shaped and constituted of parenchymatous tissue in which numerous leaf vascular strands are embedded (Plate I, 6 + 7; Plate V, 6 + 9). The latter consist of endarch primary xylem and phloem, partially surrounded by sclerenchyma (Fig. 3 G). The number of vascular bundles increases towards the outer part of the petioles and rachises where they tend to form a ring, whereas they appear more scattered in the centre. Additionally, mucilage canals mantled by fusiform sclerenchyma occur in the parenchyma (Fig. 3 G). At the periphery of the petioles and rachises, a dense ring of circular to elongated and radially arranged sclerenchyma plates is presently forming a characteristic outer cortical zone (Fig. 3 G; Plate V, 9). Based on the morphology of these sclerenchyma plates, Renault (1875) differentiated *M. radiata* (elongated plates) from *M. landriotii* (circular plates), each with different varieties. However, any distinction between these taxa remains challenging in many specimens. Both "species" could likely represent growth variations in petioles and rachises of the same plant. Some specimens show relicts of the epidermis and emerging secondary rachises (Renault, 1875). Nearly nothing is known on the dimensions and architecture of these fronds, and which foliage had been attached. Complete specimens of the MHNA collection have diameters of 2–9.5 cm (9.5 × 6.5 cm; Plate V, 6). The largest specimen kept in the MNHNP collections is a representative of *Myeloxylon radiatum* with a diameter of 11 × 14 cm in diameter (Zeiller, 1890). *Myeloxylon* organs less than 5 cm diameter certainly correspond to portions of the frond above the petiole bifurcation and should be designated as rachises.

4.2.4. Foliage

The compression flora of the Autun Basin shows a general transition from the more ancient 'Stephanian/Gzhelian' flora, which is stepwise replaced by 'Autunian/Asselian' floral elements. Foliage with medullosan affinity is represented by alethopterid, neuropterid, odontopterid and taeniopterid forms. However, no alethopterid foliage was documented from the Muse and Millery Formations (Gand et al., 2015). The latter fact is surprising as *Alethopteris* is one of the most common foliage types of medullosans. Equally, medullosan reproductive structures such as *Dolerotheca fertilis* or *Pachytesta gigantea* are only recorded from the Pennsylvanian strata (Gand et al., 2015). Moreover, the presence of *Sphenozamites*, *Plagiozamites planchardii* and *Pterophyllum cambrayi*, all with cycad affinities, have to be mentioned in the strata of the Autun Basin (Zeiller, 1890; Renault, 1896).

4.3. Medullosans from Nová Paka (Czech Republic)

Medullosans from the Czech Republic originate from Gzhelian age (Late Pennsylvanian) red beds of the intramontane Krkonoše-Piedmont Basin. They occur in a fluvial sandstone horizon of the Semily Forma-

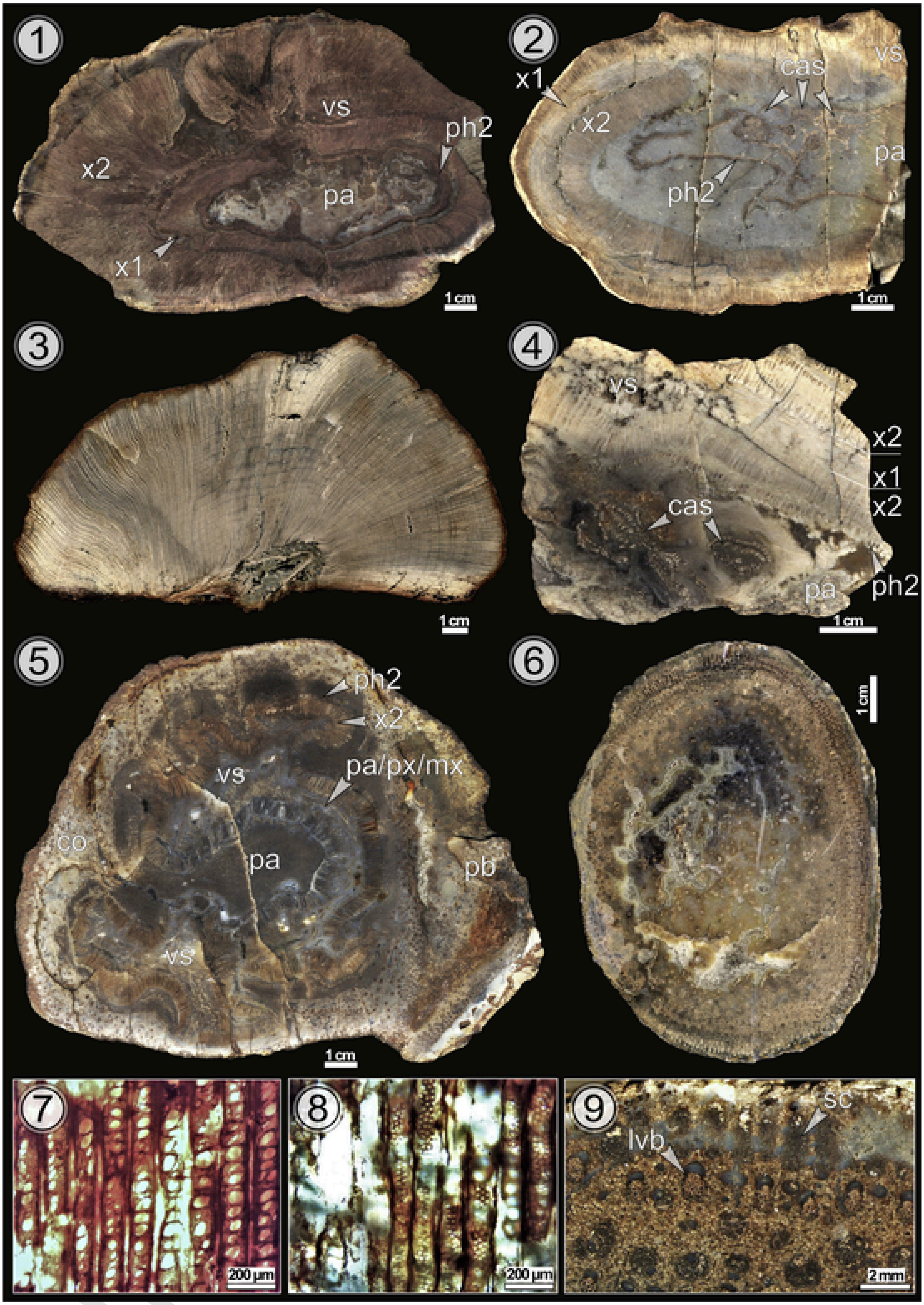

Plate V. Medullosan stem sections and foliar axes from the Autun fossil locality (Autun Basin, France; collection of the Natural History Museum Autun). 1. Cross-section of *M. stellata* var. *lignosa* showing a vascular segment with abundant secondary xylem, central parenchyma with accessory strands is not preserved (sp. no. 141); 2. cross-section of *M. stellata* var. *typica* with thin vascular segment and accessory strands preserved in the central parenchyma, the secondary phloem seems to be detached from the inner part of the vascular segment (sp. no. 25); 3. cross-section of *M. stellata* var. *lignosa* with a poorly preserved central parenchyma and a vascular segment with abundant wood showing at least 20 growth rings (sp. no. MHNA-PAL-2020-0002); 4. fragment of *M. stellata* var. *typica* with parts of the vascular segment and central parenchyma with accessory strands (sp. no. 151); 5. *Colpoxylon aeduense* showing stem section with abundant parenchyma, an undulating vascular segment, thick cortex and a petiole base (sp. no. 148); 6. cross-section of massive *Myeloxylon* type petiole with numerous leaf vascular bundles and sclerenchymatous outer cortex (sp. no. 158); 7. historical thin section from the Renault collection of medullosan wood in radial orientation showing cross field-pitting of tracheids with broad oopores; 8. same thin section highlighting multiseriate bordered pits of the tracheids; 9. outer part of a *Myeloxylon* type foliar axis showing leaf vascular bundles and sclerenchyma plates in the outer cortex. Abbreviations:: pa – parenchyma, mx – metaxylem, px – protoxylem, x 1 – primary xylem, x 2 – secondary xylem, ph 2 – secondary phloem, sc – sclerenchyma, cas – central accessory strands, vs – vascular segment, pb – petiole base.

tion, connected to the lacustrine Ploužnice Horizon, which provides evidence of a rich compression flora and fauna, as well (e.g., Opluštil et al., 2013). Deposition of this stratigraphic unit was accompanied by volcanic activity and contains layers of acid tuffs and basaltic bodies (Pešek, 2004). The silicified flora is most likely sub-autochthonous to allochthonous and more varied within the basin, encompassing stems of sphenopsids, psaroniaceous tree ferns, and pycnoxylic gymnosperms.

Medullosan stems are comparably scarce (Matysová et al., 2010), represented by a few stem fragments about 8–25 cm in diameter (Plate VI). They exhibit a wide central parenchyma with numerous central accessory strands. The cylindrical peripheral vascular segment is up to 10 cm thick, including secondary xylem. Accessory strands are 2–5 mm wide and bounded by secondary xylem and phloem with parenchymatous rays, similar to the accessory strands described for both the Chemnitz and Autun specimens. Secondary xylem tracheids are on average 90 μm wide and mostly arranged in files 2–4 cells wide, which are separated by wide rays. Four stem segments (Plate VI, 1–4) show an affinity to *M. stellata* var. *typica*. Specimens of Figs. 1–3 (Plate VI) might represent juvenile stem parts due to the thin wood of their peripheral vascular segment, whereas specimen of Fig. 4 (Plate VI) depicts the basal part of an older stem, indicated by its large diameter and extended wood. Specimen of Fig. 5 (Plate VI) has wide outer wood and a distinctly narrower central parenchyma with only three central accessory strands, thus showing affinities to *M. stellata* var. *lignosa*.

Medullosan foliage found in the underlying Ploužnice Horizon is represented by neuropterids (e.g., *Neurocallipteris neuropteroides* (Goeppert) Cleal, Shute et Zodrow) and odontopterids (Opluštil et al., 2013). From the same stratigraphic level, pteridosperms of the Líně Formation from western and central Bohemia colonised mineral substrates of wetlands or wet spot environments on an alluvial plain temporarily flooded by a lake (Opluštil et al., 2013). The palaeoclimate at this stratigraphic interval is interpreted as moist sub-humid to dry sub-humid (Opluštil et al., 2013).

4.4. Medullosans from other localities

Additional fossil material of early Permian medullosans originates from volcanically-influenced strata of other small intramontane basins in Germany and France.

From the Northwest Saxony Volcanite Complex, stem sections of *M. stellata* and *M. porosa* were described by Cotta (1832). These specimens probably originate from the Rüdigsdorf Tuff, a pyroclastic horizon at the base of the Kohren Formation, revealing a biostratigraphic and radiometric age near the Carboniferous–Permian boundary

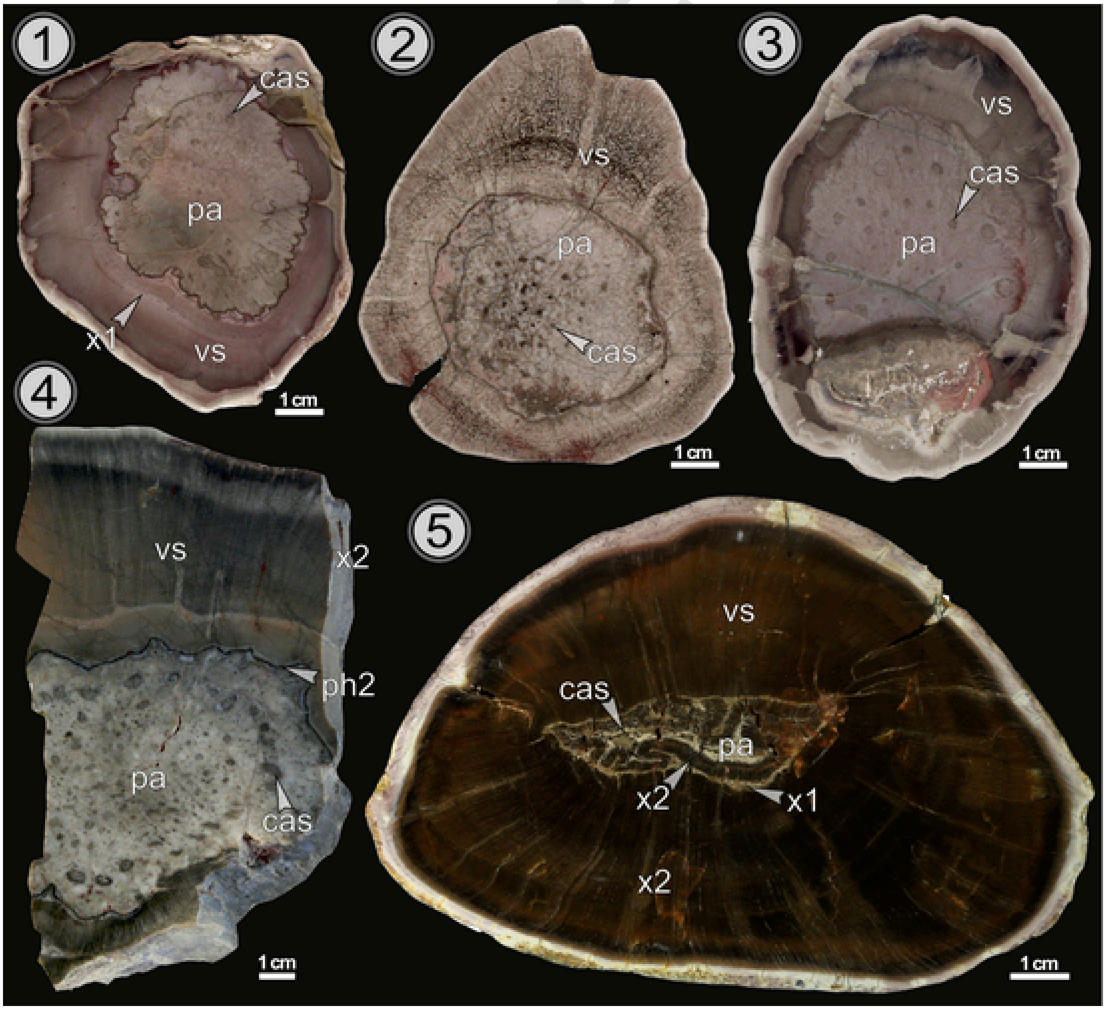

Plate VI. Medullosan stem sections from the Nová Paka fossil locality. 1–3. Cross-sections of *M. stellata* var. *typica*, probably juvenile specimens (collection of the Museum Nová Paka); 4. fragment of a large *M. stellata* var. *typica* stem (collection of the National Museum of Prague); 5. cross-section with affinity to *M. stellata* var. *lignosa* (private collection, courtesy Stanislav Vlačiha). Abbreviations: pa – parenchyma, x 1 – primary xylem, x 2 – secondary xylem, ph 2 – secondary phloem, cas – central accessory strands, vs – vascular segment.

(Barthel, 1976; Hoffmann et al., 2012). The presence of medullosans in these pyroclastic deposits is further evidenced by alethopterid foliage and *Myeloxylon* foliar axes (Sterzel, 1886; Barthel, 1976). Other specimens of *M. stellata* var. *typica* are known from the Ilfeld Basin in central Germany, which also yielded neuropterid and alethopterid foliage (Sterzel, 1901a, 1901b).

In eastern France, Permian strata of the Vosges Mountains occur in a complex of several small depocentres, such as the Val d'Ajol "basin". A medullosan stem section was described by Mougeot (1852) and shows affinity to *M. stellata* var. *lignosa*. It was found in a pyroclastic deposit, together with psaroniaceous tree ferns, pycnoxylic gymnosperms and calamitaleans, probably resembling an in-situ fossil assemblage (Durand, 1994). The stratigraphic level is supposed to be of early Permian age (Velain, 1885; Feys and Greber, 1970).

Finally, there is a single specimen of *Medullosa geriensis* (Scott) Boureau from the Rive de Gier formation (early Late Pennsylvanian) in the Saint-Etienne Basin in France, which yielded also the contemporaneous silicified peat of Grand-Croix from the Late Pennsylvanian Grand-Croix locality in the Saint-Etienne Basin in France (Boureau, 1951; Doubinger et al., 1995; Galtier, 2008). *M. geriensis* represents a stem with two (or probably three) vascular segments with primary xylem mainly consisting of broad metaxylem tracheids up to 500 μm in diameter. The primary xylem is surrounded by a mainly endocentric secondary xylem, 5–12 mm in radial thickness. Secondary xylem tracheids are 180–300 μm in diameter and show up to four rows of seriate pits. The stem is bounded externally by an up to 12 cells thick periderm. Interestingly, this specimen is anatomically similar to the early medullosans (*Medullosa anglica* type) of Carboniferous lowland basins, but the Saint-Etienne Basin is clearly interpreted as an intramontane-type basin. Besides, the Grand-Croix permineralised flora bears an exceptionally high diversity of medullosan ovules (Galtier, 2008) and of foliage including small *Myeloxylon* rachises in connection with *Alethopteris* pinnules (Doubinger et al., 1995).

5. Discussion

Despite the rich fossil material, crucial questions on the medullosans from the classical sites Chemnitz, Autun, Nová Paka and a few other localities in Central Europe have remained unanswered until today. The organisation of tissue types in the stems of medullosans of Late Pennsylvanian–early Permian intramontane basins is highly complex and differs from that seen in other late Paleozoic gymnosperms (e.g., Decombeix et al., 2019). Important scientific questions refer to plant development, including primary and secondary growth, the functionality of conducting tissues, biomechanical features concerning growth habits and the role in gymnosperm evolution.

5.1. Taxonomic significance of stem anatomical features

For all medullosans, the taxonomic classification based on wood anatomical characters remains challenging, as long as evidence of connection with foliar and reproductive parts is missing. On the one hand, the same stem anatomy may be shared by different natural species (e.g., Serbet and Rothwell, 1995). On the other hand, significant morphological variations may occur within the same plant, as shown by several varieties introduced for the Chemnitz taxa (e.g., Göppert and Stenzel, 1881). Variations most probably refer to different ontogenetic positions in the stem (Weber and Sterzel, 1896). Other varieties could represent natural species, such as *M. stellata* var. *lignosa*, which has been suggested to represent the provisory species *Medullosa sturii* (Schenk, 1889). Improving the taxonomy of medullosans will be based on: 1) whole-plant reconstructions taking into account large stem sections with attached foliage, reproductive organs and roots, 2) reconstruction of the primary vascular system architecture, i.e., that of stems and leaves, as suggested for medullosans of the Carboniferous lowland basins (see Basinger et al., 1974; Beeler, 1983; Dunn et al., 2003), and 3) statistical analysis of quantifiable stem anatomical parameters, such as wood thickness in peripheral vascular segments, the width of the central parenchyma and number of central accessory strands.

5.2. Palaeoecology

The stratigraphic occurrence of intramontane medullosans extends over more than 10 Ma, from the Gzhelian to latest Sakmarian, including the Carboniferous–Permian transition. Medullosans may have been subordinated (to sub-dominant) in the forested landscapes of the intramontane basins, compared to more exposed plant groups, such as the cordaitales, calamitales, and psaroniaceous tree ferns. Alethopterid, neuropterid and odontopterid foliage seem to have been more abundant than other foliage type, and occur in palustrine, lacustrine and alluvial environments of intramontane basins (e.g., Barthel, 2009; Barthel and Rößler, 2012; Opluštil et al., 2013; Barthel and Brauner, 2015; Barthel, 2016). The Hilbersdorf locality of the Chemnitz Fossil Lagerstätte might represent a diversity hotspot, as it depicts a high abundance and diversity of stem taxa. Their locally restricted dominance at Chemnitz-Hilbersdorf could be due to site-specific conditions, e.g., soil properties and groundwater availability.

Medullosans favoured wet to well-drained clastic soils of intrabasinal localities with a near-surface groundwater table, preferably in the proximity of lakes or on alluvial plains (Opluštil et al., 2013; Luthardt et al., 2016). In forest ecosystems, they likely colonised more shaded areas of the sub-canopy. To increase their drought resistance, they developed different adaptations: 1) seasonally-induced cambial dormancy, evidenced by faint tree rings in *M. stellata* (var. *typica* + var. *lignosa*); 2) water-storing tissue represented by central and ray parenchyma, which is abundant in medullosan stems. Nevertheless, an increased environmental sensitivity compared to pycnoxylic gymnosperms is indicated by higher ring width variations and the occurrence of traumatic "event rings" (Luthardt et al., 2017).

5.3. Vascular architecture and water conductivity

The vascular system of medullosans is complex and probably highly efficient. The mostly horizontal orientation of metaxylem tracheids in the vascular segments of *M. stellata, M. porosa*, *M. leuckartii* and *Colpoxylon* is rarely observed in plants. Its functional significance remains poorly understood. Rudolph (1922) suggested similarities with the girdling leaf traces of modern cycads and suggested a water storage function. We think that these tracheids were rather involved in hydraulic conduction, enabling water transport to leaf traces, which were made of primary tracheids and partially surrounded by secondary xylem. Leaf traces cross the cortex and branch into the numerous bundles of the petiole bases (Fig. 3 D+E; Plate I, 6+9; Weber and Sterzel, 1896; Solms-Laubach, 1897; Rothwell, 2020).

Medullosan stems show secondary vascular tissues around the vascular segments and central accessory strands (Fig. 3; Plate I, 4; Plate III, 7+8). The secondary xylem of the vascular segments may be thick, increasing the water-conducting potential of stems. The secondary xylem exhibits densely-pitted tracheids with exceptional lengths, and diameters mostly exceeding 100 μm on average (up to 220 μm). The largest tracheid diameters known from medullosans were measured in *Medullosa geriensis* with 500 μm for metaxylem tracheids and up to 300 μm for secondary xylem tracheids. These characteristics suggest that medullosan wood was much more efficient in water transport than the wood of other late Paleozoic gymnosperms (Wilson et al., 2015).

The network of central accessory strands might have provided additional transport for water in stems. However, its functional role and development are still poorly understood. Connection of the accessory strands with the vascular segments was not demonstrated in *M. stellata* and *M. porosa*, but is likely in *M. leuckartii*. The number of strands remains nearly constant in long stems suggesting that their network architecture does not change markedly during ontogenesis.

5.4. Ecophysiological approaches

Water and nutrient transport, as well as storage capacity, are significant functions of stem tissues, which are developed in adaptation to the physical environment of a plant. Preliminary results on leaf and stem hydraulic properties of Carboniferous medullosans have suggested an unexpectedly high water-flow potential similar to that of some extant tropical angiosperms (Wilson et al., 2008, 2015). In addition to the highly conductive vascular system of stems, the large photosynthetic surfaces of the leaves and their elevated vein and stomata densities point to a high evapotranspirational potential for these plants. This hypothesis raises the question of their drought tolerance with regard to the seasonally-dry Late Pennsylvanian–early Permian intramontane ecosystems. A high hydraulic capacity increases the risk of cell embolism under water-deficient conditions and makes a plant vulnerable to droughts (Wilson et al., 2008; Wilson and Knoll, 2010; Wilson et al., 2015). Hence, in the context of modelling a plant's hydraulic capacity, evaluation of its water use efficiency with regard to drought-resistance mechanisms is important, as well. In future research, whole-plant models are expected to provide more robust data (Wilson et al., 2015). An essential step was made by developing a whole-tissue model for quantifying hydraulic properties (Tanrattana et al., 2019). However, whole-plant water flow models are challenging, as they encompass multiple anatomical parameters from the roots, stem tissues, fronds and pinnae (e.g., Ogle et al., 2004; Sperry and Hacke, 2004; Brodribb et al., 2007; Wilson et al., 2008; Boyce et al., 2009; Raymond et al., 2014).

Hydraulic and gas exchange capacities of medullosans might be of crucial importance to understand their role in forcing microclimate on the ecosystem scale, but also concerning late Paleozoic palaeo-atmospheric conditions (see White et al., 2020). It is hypothesised that their highly efficient gas exchange mechanisms represented an evolutionary advantage compared to other plants growing under the same atmospheric conditions (Wilson et al., 2017). Thus, their radiation in the Late Pennsylvanian–early Permian might be coupled to exceptionally low rates of atmospheric $p\text{CO}_2$ during the climax of the Late Paleozoic Ice Age (LPIA; Richey et al., 2020).

5.5. Biomechanical inferences

The stem-anatomical peculiarities of the Late Pennsylvanian–early Permian medullosans gave rise to various hypotheses regarding their growth habits. On the one hand, some of them are supposed to represent climbing vines similar to older species, such as *M. steinii* (Göppert and Stenzel, 1881; Dunn et al., 2003; Rothwell, 2020). Climbing plants are recognised by the following features: 1) the small diameter of stems compared to frond dimensions; 2) the unusual arrangement of secondary tissues; 3) the high amount of (ray) parenchyma and large tracheid size; 4) the co-occurrence of relatively small fronds and long internodes (e.g., Krings and Kerp, 2006). However, no medullosan stem has ever been found attached to another non-medullosan stem. Additionally, most in-situ medullosans from Chemnitz-Hilbersdorf (mainly *M. stellata*) were found free-standing in a straight upright position. Concerning biomechanics, *M. stellata*, *M. leuckartii,* and *M. solmsii* exhibit an arrangement of their strengthening elements suggesting that they were actually self-supporting (Mosbrugger, 1990). The abundance of secondary xylem might have favoured such a growth habit. Biomechanical approaches based on tissue characteristics from different parts of the stem (e.g., Rowe and Speck, 1998; Masselter et al., 2007) are promising tools to assess more reliably the growth habits of medullosan species.

5.6. Evolutionary pathways

Anatomically preserved medullosans from “coal balls” of the Carboniferous tropical lowland basins and those from the European intramontane basins of the Late Pennsylvanian–early Permian differ by their stem anatomical characteristics, growth habits and palaeoecological preferences (Fig. 2; Table 2). The Carboniferous lowland medullosans are considered as the more pristine forms with regard to tissue organisation (e.g., Delevoryas, 1955). They likely colonised the first Central European intramontane basins during the Mississippian, which is known from numerous medullosan foliage types in several intramontane basins (e.g., Cleal et al., 2009; Opluštil et al., 2009; Löcse et al., 2013; Opluštil et al., 2013; Cleal and Cascales-Miñana, 2019). The stem taxon *M. geriensis* from the Saint Étienne Basin (Doubinger et al., 1995; Galtier, 2008) indicates that lowland-type medullosans occurred in intramontane basin at least to the Pennsylvanian. However, according to Cleal (2008) the composition of medullosan foliage types of intramontane and lowland basins already differed significantly in the Moscovian. These changes may have been driven by increasing palaeogeographic isolation and major changes in their physical environment. As a result, the medullosans became generally larger with more massive stems (Fig. 2) and most species adapted to a self-supporting growth habit. The vascular system evolved from a few segments with low amounts of secondary tissues to a cylindrical system with abundant secondary tissues and wide central parenchyma. The complexity and possible efficiency of the vascular system were further increased by the formation of abundant central accessory strands.

Table 2
Comparison of early medullosans of Carboniferous lowland basins with their Upper Pennsylvanian–early Permian relatives from intramontane basins (references indicated in the text).

Character	Lowland forms	Intramontane forms
Max. stem diameter	20 cm	48 cm
Cauline vascular segments	2–8 in most taxa, but rarely up to 23	≥ 1, mostly cylindrical-shaped
Central accessory strands	Mostly absent, rarely more than one	Frequent in most taxa (1–>100)
Predominant orientation of wood growth	Endocentric	Exocentric
Amount of secondary xylem	Low–medium	Medium–high
Secondary tracheids	≤ 300 µm, thin-walled	≤ 220 µm, thin- to thick-walled
Leaf trace production	From single or paired protoxylem strands at the periphery of vascular segments	From two or more protoxylem strands at the periphery of vascular segments
Periderm	Present	No evidence
Root type	Adventitious	Taproots and laterals, coralloid?
Growth habits	Climbing (vines/lianas), leaning, scrambling, (semi-) self-supporting	Predominantly self-supporting, (climbing vines?)
Palaeoecology	Wet tropical to slightly seasonal palaeoclimate; poorly-drained peat and mineral substrates; along rivers and on alluvial plains	Sub-humid, seasonally-dry palaeoclimate; mineral substrates on moist to well-drained clastic soils of alluvial plains

During the late Paleozoic, the early lowland medullosans migrated eastwards to the coal-forming basins of Central and Southeast Asia (e.g., Seyfullah et al., 2009), while the intramontane forms may have survived up to the latest Permian in Central Europe (Kustatscher et al., 2014). Beyond the restricted taphonomic windows, the occurrence and evolution of medullosans in seasonally-dry ecosystems, e.g., of North America, remains speculative and is predominantly documented by foliage remains, e.g., taeniopterid type leaves as part of a Middle Pennsylvanian age dryland vegetation (Bashforth et al., 2016).

5.7. Similarities and relations to other plant groups

Although the medullosan anatomy is unusual among gymnosperms, some ancient and modern plant groups show interesting similarities, potentially pointing to phylogenetic relationships. In the fossil record, the medullosan affinities of *Colpoxylon aeduense* are discussed (Brongniart, 1849; Schenk, 1889; Grambast, 1962; Dunn, 2006; Taylor et al., 2009). This taxon shares several stelar and cortex features with the medullosans, such as a dissected vascular anatomy, a manoxylic wood, horizontal metaxylem tracheids and the potential possession of *Myeloxylon* petioles and rachises. A difference is the absence of central accessory strands in *Colpoxylon*.

Medullosans, especially those of Late Pennsylvanian–early Permian age have been repeatedly compared to modern cycads (e.g., Renault, 1896; Worsdell, 1906; Bancroft 1914; Delevoryas, 1955). Cycads are supposed to have originated in the late Paleozoic (Mamay, 1969, 1976). Early cycadophyte foliage, such as *Plagiozamites, Noeggerathia zamitoides*, *Pterophyllum* or *Taeniopteris* (Gillespie and Pfefferkorn, 1986), as well as cycad-like stem taxa such as *Ptychoxylon* and *Cycadoxylon* (Autun, France) already co-occurred with the medullosans during the Late Pennsylvanian–early Permian. Both groups share several anatomical and ecological features: 1) stem anatomy characterised by wide central parenchyma or pith surrounded by one to multiple vascular segments and a cortex; 2) the possession of central accessory strands in stems, which occurs in some juvenile cycads (Worsdell, 1906); 3) secondary xylem with abundant ray parenchyma, long tracheids with multiseriate bordered pits and an intrafascicular cambium; 4) similar ovules, which are attached to reduced leaves (Stewart and Delevoryas, 1956); 5) cycad-like megasporophylls whose distal parts are of *Taeniopteris* type (Mamay, 1969, 1973; Gillespie and Pfefferkorn, 1986; Axsmith et al., 2003). *Taeniopteris* is supposed to be the foliage of some medullosans (e.g., *M. leuckartii*). Even the root systems of cycads are comparable to those of in-situ medullosans from Chemnitz (Luthardt et al., 2016). The most conspicuous difference might be seen in the frond anatomy and foliage morphology. However, taeniopterid leaves are supposed to provide a link between pteridosperms and ancestral cycads (Axsmith et al., 2003; Taylor et al., 2009), and are found at the Hilbersdorf locality closely associated with *M. leuckartii*. The large number of distinctive characters common to the Medullosales and the Cycadales suggests that these characters may have evolved in a common ancestor and that these two groups may have been phylogenetically closer than hypothesised in current cladistic analyses of seed plants including fossils (Hilton and Bateman, 2006; Doyle, 2006; Magallón, 2010).

6. Summary and perspectives

Our contribution aims to highlight Late Pennsylvanian–early Permian medullosan seed ferns of Central European intramontane basins, which have been out of research focus for more than 100 years. These plants have either slender or thick stems with large alethopterid or neuropterid fronds bearing massive petiole bases. They possess an unusual stem architecture with a complex cauline vascular system. Medullosans grew subordinated in the shaded understorey of forest ecosystems that existed on wet clastic soils with a near-surface groundwater level. They are supposed to have been adapted to seasonal droughts. Nevertheless, their vascular system might have revealed high water-conducting potential and the large fronds with densely veined pinnules a high evapotranspiration potential. We have shown that there exist several anatomical and architectural differences compared to medullosans of Carboniferous tropical lowland basins, encompassing modifications of the vascular system, amount of secondary tissue and growth habits. This heterogeneity most probably reflects significant evolutionary diversification. A linkage between major palaeo-environmental changes in the late Paleozoic and evolution of medullosans is likely and provides the potential for future studies that shed light on plant evolution and climate change in the late Paleozoic.

The research potential on Late Pennsylvanian–early Permian medullosans is based on detailed anatomical studies from the 19th century, combined with new fossil material from the Chemnitz Fossil Lagerstätte. The material provides various opportunities for future investigations following both traditional, modern and novel branches of palaeobotany. The taphonomic particularity of organ connections allows for whole-plant reconstructions, which permits the application of current approaches in the fields of plant physiological modelling and biomechanics. Due to their remarkable anatomy and architecture, medullosans might be of crucial importance to understand the functioning of seasonally-dry, late Paleozoic vegetated ecosystems. Deciphering the evolution of medullosans might provide new inferences on the evolution of seed plants in the late Paleozoic, such as the origin of cycads.

Uncited references

Declaration of Competing Interest

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organisation or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

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References

Axsmith, B.J., Serbet, R., Krings, M., Taylor, T.N., Taylor, E.L., Mamay, S.H., 2003. The enigmatic Paleozoic plants *Spermopteris* and *Phasmatocycas* reconsidered. Am. J. Bot. 90 (11), 1585–1595.

Baker, R.A., DiMichele, W.A., 1997. Biomass allocation in late Pennsylvanian coal-swamp plants. Palaios 12, 127–132.

Bancroft, N., 1914. Pteridosperm anatomy and its relation to that of the cycads. New Phytol. 13 (1–2), 41–68.

Barthel, M., 1976. Die Rotliegend-Flora Sachsens. Abh. Staatl. Mus. Min. Geol. Dresden 24, 1–190.

Barthel, M., 2009. Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Special Issue 2009.

Barthel, M., 2016. The Lower Permian (Rotliegend) flora of the Döhlen Formation. Geol. Saxonica 61 (2), 105–238.

Barthel, M., Brauner, S., 2015. Die Rotliegendflora des Thüringer Waldes – Supplementum. Semana 30, 3–37.

Barthel, M., Rößler, R., 2012. Pflanzen und Pflanzengesellschaften des Rotliegend. In: Lützner, H., Kowalczyk, G. (Eds.), Stratigraphie von Deutschland X. Rotliegend. Part I: Innervariscische Becken. In: Schriftenr. Deu. Ges. Geowiss. 61. pp. 79–97 Hannover.

Bashforth, A.R., DiMichele, W.A., Eble, C.F., Nelson, W.J., 2016. Dryland vegetation from the Middle Pennsylvanian of Indiana (Illinois Basin): The dryland biome in glacioeustatic, paleobiogeographic, and paleoecologic context. J. Paleontol. 90 (5), 785–814.

Basinger, J.F., Rothwell, G.W., Stewart, W.N., 1974. Cauline vasculature and leaf trace production in medullosan pteridosperms. Am. J. Bot. 61 (9), 1002–1015.

Beck, C.B., Schmid, R., Rothwell, G.W., 1982. Stelar morphology and the primary vascular system of seed plants. Bot. Rev. 48 (4), 692–913.

Beck, C.B., Galtier, J., Stein, W.E., 1992. A reinvestigation of *Diichnia* Read from the New Albany Shale of Kentucky. Rev. Palaeobot. Palynol. 75, 1–32.

Beehler, H.E., 1983. Anatomy and frond architecture of *Neuropteris ovata* and *N. scheuchzeri* from the Upper Pennsylvanian of the Appalachian Basin. Can. J. Bot. 61 (9), 2352–2368.

Boureau, E., 1951. Sur un nouveau *Medullosa* du Stéphanien de Rive-de-Gier. Bull. Soc. Geol. France 6 (1), 419–423.

Boyarina, N., 2010. Late Gzhelian pteridosperms with callipterid foliage of the Donets Basin, Ukraine. Acta Palaeontol. Polon. 55 (2), 343–359.

Boyce, C.K., Brodribb, T.J., Feild, T.S., Zwieniecki, M.A., 2009. Angiosperm leaf vein evolution was physiologically and environmentally transformative. Proc. R. Soc. B 276 (1663), 1771–1776.

Brodribb, T.J., Feild, T.S., Jordan, G.J., 2007. Leaf maximum photosynthetic rate and venation are linked by hydraulics. Plant Phys. 144 (4), 1890–1898.

Brongniart, A., 1849. Tableau des genres de végétaux fossiles considérés sous le point de vue leur classification botanique et de leur distribution géologique. Dictionnaire Uinv. Hist. Nat. 13, 1–127.

Broutin, J., Châteauneuf, J.-J., Galtier, J., Ronchi, A., 1999. L'Autunien d'Autun reste-t-il une référence pour les dépots continentaux du Permien inférieur d'Europe? Apport des données paléobotaniques. Geol. France 2, 17–31.

Cichan, M.A., Taylor, T.N., 1981. On the structure and morphology of the seed *Pachytesta muncii* N. SP. (Medullosales). Rev. Palaeobot. Palynol. 34 (3–4), 359–367. doi:10.1016/0034-6667(81)90051-8.

Cleal, C.J., 2008. Palaeofloristics of Middle Pennsylvanian medullosaleans in Variscan Euramerica. Palaeogeogr. Palaeoclimatol. Palaeoecol. 268, 164–180.

Cleal, C.J., Cascales-Miñana, B., 2019. The floristic relationship between the upland and lowland Carboniferous wetlands of Variscan Euramerica – Evidence from some medullosalean pteridosperm fronds. J. Palaeogeogr. 8 (14), 1–12.

Cleal, C.J., Shute, C.H., 1995. A synopsis of neuropterid foliage from the Carboniferous and Lower Permian of Europe. Bull. Nat. Hist. Mus. Geol. 51 (1), 1–52.

Cleal, C.J., Shute, C.H., 2003. Systematics of the Late Carboniferous medullosalean pteridosperm *Laveinopteris* and its associated *Cyclopteris* leaves. Palaeontology 46, 353–411.

Cleal, C.J., Shute, C.H., 2012. The systematic and palaeoecological value of foliage anatomy in Late Paleozoic medullosan seed-plants. J. Syst. Paleontol. 10 (4), 765–800.

Cleal, C.J., Opluštil, S., Thomas, B.A., Tenchov, Y., 2009. Late Moscovian terrestrial biotas and palaeoenvironments of Variscan Euramerica. Neth. J. Geosci. 88 (4), 181–278.

Combourieu, N., Galtier, J., 1985. Nouvelles observations sur *Polypterospermum*, *Polylophospermum*, *Colpospermum* et *Codonospermum*, ovules de Ptéridospermales du Carbonifère supérieur français. Palaeontogr. Abt. B 196, 1–29.

Cotta, B., 1832. Die Dendrolithen in Bezug auf ihren inneren Bau. Arnoldische Buchhandlung, Leipzig, Dresden, p. 89.

D'Angelo, J.A., Zodrow, E.L., 2016. 3D chemical map and a theoretical life model for *Neuropteris ovata* var. *simonii* (index fossil, Asturian, Late Pennsylvanian, Canada). Int. J. Coal Geol. 153, 12–27.

De Fraine, F.L.S., 1914. On *Medullosa centrofilis*, a new species of *Medullosa* from the lower coal measures. Ann. Bot. 28 (110), 251–264.

Decombeix, A.-L., Boura, A., Tomescu, A.M.F., 2019. Plant hydraulic architecture through time: lessons and questions on the evolution of vascular systems. IAWA J. 40 (3), 387–420.

Delevoryas, T., 1955. The Medullosae – structure and relationships. Palaeontogr. Abt. B 97, 114–167.

DiMichele, W.A., Tabor, N.J., Chaney, D.S., Nelson, W.J., 2006a. From wetlands to wet spots: The fate and significance of Carboniferous elements in Early Permian coastal plain floras of North-Central Texas. In: Greb, S., DiMichele, W.A. (Eds.), Wetlands through Time. In: Geol. Soc. Am. Spec. Publ..

DiMichele, W.A., Phillips, T.L., Pfefferkorn, H.W., 2006b. Paleoecology of Late Paleozoic pteridosperms from tropical Euramerica. J. Torrey Bot. Soc. 133 (1), 83–118.

DiMichele, W.A., Hook, R.W., Kerp, H., Hotton, C.L., Looy, C.V., Chaney, D.S., 2018. Chapter 6 - Lower Permian Flora of the Sanzenbacher Ranch, Clay County, Texas. In: Krings, M., Harper, C.J., Cúneo, N.R., Rothwell, G.W. (Eds.), Transf. Paleobot. Academic Press, pp. 95–126. doi:10.1016/b978-0-12-813012-4.00006-1.

Doubinger, J., Vetter, P., Langiaux, J., Galtier, J., Broutin, J., 1995. La flore fossile du bassin houiller de Saint-Etienne. Mém. Mus. Nat. Hist. Nat. Paris 164, 1–357.

Doyle, J.A., 2006. Seed ferns and the origin of angiosperms. J. Torrey Bot. Soc. 133 (1), 169–209.

Dunlop, J.A., Legg, D.A., Selden, P.A., Fet, V., Schneider, J.W., Rößler, R., 2016. Permian scorpions from the Petrified Forest of Chemnitz, Germany. BMC Evol. Biol. 16 (1), 72. doi:10.1186/s12862-016-0634-z.

Dunn, M.T., 2006. A review of permineralized seed fern stems of the Upper Paleozoic. J. Torrey Bot. Soc. 133 (1), 20–32.

Dunn, M.T., Krings, M., Mapes, G., Rothwell, G.W., Mapes, R.H., Keqin, S., 2003. *Medullosa steinii* sp. nov., a seed fern vine from the Upper Mississippian. Rev. Palaeobot. Palynol. 124, 307–324.

Durand, M., 1994. Le Permien des Vosges. Livret-Guide. Associations des Géologues du Permien.

Fairon-Demaret, M., Scheckler, S.E., 1987. Typification and redescription of *Moresnetia zalesskyi* Stockmans, 1948, an early seed plant from the Upper Famennian of Belgium. Bull. Inst. R. Sci. Nat. Belg. Sci. Terre 57, 183–199.

Falcon-Lang, H.J., 2009. A *Macroneuropteris scheuchzeri* tree preserved in growth position in the Middle Pennsylvanian Sydney Mines Formation, Nova Scotia, Canada. Atl. Geol. 45, 74–80.

Feng, Z., Zierold, T., Rößler, R., 2012. When horsetails became giants. Chin. Sci. Bull. 57, 2285–2288.

Feng, Z., Rößler, R., Annacker, V., Yang, J.-Y., 2014. Micro-CT investigation of a seed fern (probable medullosan) fertile pinna from the Early Permian Petrified Forest in Chemnitz, Germany. Gondwana Res. 26, 1208–1215.

Feys, R., Greber, Ch., 1970. Pour une synthèse du Permien en France. Propositions pour un programme de recherches. Direction du Service Géologique National, p. 83.

Galtier, J., 1988. Morphology and phylogenetic relationships of early pteridosperms. In: Beck, C.B. (Ed.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 135–176.

Galtier, J., 1992. On the earliest arborescent gymnosperms. Cour. Forschungsinst. Senckenb. 147, 119–125.

Galtier, J., 1997. Coal-ball floras of the Namurian–Westphalian of Europe. Rev. Palaeobot. Palynol. 95 (1), 51–72. doi:10.1016/S0034-6667(96)00027-9.

Galtier, J., 2008. A new look at the permineralized flora of Grand-Croix (Late Pennsylvanian, Saint-Etienne basin, France). Rev. Palaeobot. Palynol. 152, 129–140.

Galtier, J., Meyer-Berthaud, B., 1989. Studies of the early Carboniferous pteridosperm *Calamopitys* – A redescription of the type material from Saalfeld (GDR). Pal. B 213, 1–36.

Gand, G., Galtier, J., Broutin, J., Van Waveren, I., 2015. Guidebook for Field-Trip in the Autun Basin. Agora Paleobotanica Conference, Autun, p. 27.

Gensel, P., 1988. On *Neuropteris* Brongniart and *Cardiopteridium* Nathorst from early Carboniferous Price Formation, Southwest Virginia, U.S.A. Rev. Palaeobot. Palynol. 54, 105–119.

Gillespie, W.H., Pfefferkorn, H.W., 1986. Taeniopterid lamina on *Phasmatocycas* megasporophylls (Cycadales) from the lower Permian of Kansas, U.S.A. Rev. Palbot. Palynol. 49, 99–116.

Gillespie, W.H., Rothwell, G.W., Scheckler, S.E., 1981. The earliest seeds. Nature 293 (5832), 462–464.

Göppert, H.R., 1865. Die fossile Flora der Permischen Formation. Theodor Fischer Verlag, Kassel., p. 465.

Göppert, H.R., Stenzel, G., 1881. Die Medulloseae. Eine neue Gruppe der fossilen Cycadeen. Theodor Fischer Verlag, Kassel, pp. 1–17.

Grambast, L., 1962. *Colpoxylon aeduense* – Ptéridospermée remarquable due Permien d'Autun. Bull. Soc. Hist. Nat. Autun. 21, 9–13.

Grand'Eury, C.F., 1877. Flore Carbonifère du Départment de la Loire et du Centre de la France. Prémiere Partie-Botanique. Imprimerie Nationale, Paris, p. 624.

Hamer, J.J., Rothwell, G.W., 1986. The vegetative structure of *Medullosa endocentrica* (Pteridospermopsida). Can. J. Bot. 66, 375–387.

Hilton, J., Bateman, R.M., 2006. Pteridosperms are the backbone of seed-plant phylogeny. J. Torrey Bot. Soc. 133 (1), 119–168.

Hoffmann, U., Breitkreuz, C., Breiter, K., Sergeev, S., Stanek, K.P., Tichomirowa, M., 2012. Carboniferous–Permian volcanic evolution in Central Europe—U/Pb ages of volcanic rocks in Saxony (Germany) and northern Bohemia (Czech Republic). Int. J. Earth Sci. 102, 73–99.

Hübers, M., Bomfleur, B., Krings, M., Pott, C., Kerp, H., 2014. A reappraisal of Mississippian (Tournaisian and Visean) adpression floras from central and northwestern Europe. Zitteliana A 54, 39–52.

Kerp, H., 1996. Post-Variscan late Palaeozoic Northern Hemisphere gymnosperms: the onset to the Mesozoic. Rev. Palaeobot. Palynol. 90, 263–285.

Kerp, H., 2000. The modernization of landscapes during the Late Paleozoic-Early Mesozoic. In: Gastaldo, R.A., DiMichele, W.A. (Eds.), Phanerozoic Terrestrial Ecosystems. In: Paleontol. Soc. Pap, 6. pp. 79–113.

Krings, M., Kerp, H., 2006. *Neuropteris attenuata*, a narrow-stemmed, leaning or lianescent seed fern from the Upper Pennsylvanian of Lower Saxony, Germany. Flora 201 (3), 233–239.

Krings, M., Kerp, H., Taylor, T.N., Taylor, E.L., 2003. How Paleozoic vines and lianas got off the ground: on scrambling and climbing Carboniferous–Early Permian pteridosperms. Bot. Rev. 69, 204–244.

Krings, M., Klavins, S.D., Taylor, T.N., Taylor, E.L., Serbet, R., Kerp, H., 2006. Frond architecture of *Odontopteris brardii* (Pteridospermopsida, ?Medullosales): new evidence from the Upper Pennsylvanian of Missouri, U.S.A. J. Torrey Bot. Soc. 133 (1), 33–45.

Krings, M., Kerp, H., Bomfleur, B., 2008. Zur Wedelentwicklung und Heterophyllie bei Pteridospermen aus dem Oberkarbon und Unterperm. Abh. Westf. Mus. Naturk. 70 (3/4), 453–464.

Kustatscher, E., Bauer, K., Butzmann, R., Fischer, T.C., Meller, B., van Koijnenburg-van Cittert, J.H.A., Kerp, H., 2014. Sphenophytes, pteridosperms and possible cycads from the Wuchiapingian (Lopingian, Permian) of Bletterbach (Dolomites, Northern Italy). Rev. Palaeobot. Palynol. 208, 65–82.

Laveine, J.-P., 1997. Synthetic analysis of the Neuropterids. Their interest for the decipherment of Carboniferous palaeogeography. Rev. Palaeobot. Palynol. 95, 155–189.

Laveine, J.P., Oudoire, T., 2009. Symmetrical bifurcation of the *Alethopteris urophylla* frond. Rev. Esp. Paleont. 24 (2), 121–131.

Laveine, J.-P., Zhang, S., Liu, L., Gu, F., Liu, Y., Wen, J., Lemoigne, Y., 2003. The late Carboniferous floras of the Delingha area (Wulan County, Qinghai Province, Northwest China). Rev. Paleobiol. 22, 567–651.

Leisman, G.A., Roth, J., 1963. A reconsideration of *Stephanospermum*. Bot. Gaz. 124, 231–240.

Löcse, F., Meyer, J., Klein, R., Linnemann, U., Weber, J., Rößler, R., 2013. Neue Florenfunde in einem Vulkanit von Flöha – Querschnitt durch eine ignimbritische Abkühlungseinheit. Veröff. Mus. Nat. Chemnitz 36, 85–142.

Luthardt, L., Rößler, R., Schneider, J.W., 2016. Palaeoclimatic and site-specific conditions in the early Permian fossil forest of Chemnitz – Sedimentological, geochemical and palaeobotanical evidence. Palaeogeogr. Palaeoclimatol. Palaeoecol. 441, 627–652.

Luthardt, L., Rößler, R., Schneider, J.W., 2017. Tree-ring analysis elucidating palaeo-environmental effects captured in an in situ fossil forest – The last 80 years within an early Permian ecosystem. Palaeogeogr. Palaeoclimatol. Palaeoecol. 487, 278–295.

Luthardt, L., Hofmann, M., Linnemann, U., Gerdes, A., Marko, L., Rößler, R., 2018. A new U–Pb zircon age and a volcanogenic model for the early Permian Chemnitz Fossil Forest. Int. J. Earth Sci. 107, 2465–2489.

Magallón, S., 2010. Using fossils to break long branches in molecular dating: A comparison of relaxed clocks applied to the origin of angiosperms. Syst. Biol. 59, 384–399.

Mamay, S.H., 1969. Cycads: fossil evidence of late Paleozoic origin. Science 164, 295–296.

Mamay, S.H., 1973. *Archaecycas* and *Phasmatocycas* – new genera of Permian cycads. J. Res. US Geol. Survey 1 (6), 687–689.

Mamay, S.H., 1976. Paleozoic origin of the cycads. Geol. Surv. Prof. Paper 934, 1–47.

Mapes, G., Rothwell, G.W., 1980. *Quaestora amplecta* gen. Et sp. nov., a structurally simple medullosan stem from the Upper Mississippian of Arkansas. Am. J. Bot. 67 (5), 636–647.

Masselter, T., Rowe, N.P., Speck, T., 2007. Biomechanical reconstruction of the Carboniferous seed fern *Lyginopteris oldhamia*: implications for growth form reconstruction and habit. Int. J. Plant Sci. 168 (8), 1177–1189.

Matysová, P., Rössler, R., Götze, J., Leichmann, J., Forbes, G., Taylor, E.L., Sakala, J., Grygar, T., 2010. Alluvial and volcanic pathways to silicified plant stems (Upper Carboniferous–Triassic) and their taphonomic and palaeoenvironmental meaning. Palaeogeogr. Palaeoclimatol. Palaeoecol. 292, 127–143.

McLoughlin, S., Carpenter, R.J., Jordan, G.J., Hill, R.S., 2008. Seed ferns survived the end-Cretaceous mass extinction in Tasmania. Am. J. Bot. 95 (4), 465–471.

Mosbrugger, V., 1990. The tree habit in land plants. In: Bhattacharji (Ed.), et al., Lecture notes in Earth sciences 28. Springer, p. 161.

Mougeot, A., 1852. Essai d'une flore du nouveau Grès Rouge des Vosges – description des végétaux silicifiés. Annales de la Société d'Émulation du Dep. des Vosges 183–232.

Ogle, K., Wolpert, R.L., Reynolds, J.F., 2004. Reconstructing plant root area and water uptake profiles. Ecology 85 (7), 1967–1978.

Opluštil, S., Pšenička, J., Libertín, M., Bek, J., Dašková, J., Šimůnek, Z., Drábková, J., 2009. Composition and structure of an in situ Middle Pennsylvanian peat-forming plant assemblage buried in volcanic ash, Radnice Basin (Czech Republic). Palaios 24, 726–746.

Opluštil, S., Šimůnek, Z., Zajíc, J., Mencl, V., 2013. Climatic and biotic changes around the Carboniferous/Permian boundary recorded in the continental basins of the Czech Republic. Int. J. Coal Geol. 119, 114–151. doi:10.1016/j.coal.2013.07.014.

Pellenard, P., Gand, G., Schmitz, M., Galtier, J., Broutin, J., Steyer, J.-S., 2017. High-precision U-Pb zircon ages for explosive volcanism calibrating the NW European continental Autunian stratotype. Gondwana Res. 51, 118–136.

Pešek, J., 2004. Late Paleozoic limnic basins and coal deposits of the Czech Republic. Folia Musei rerum naturalis Bohemiae occidentalis – Geologica, Edittio Specialis 1, 1–188.

Pfefferkorn, H.W., Thomson, M.C., 1982. Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages. Geology 10 (12), 641–644.

Pfefferkorn, H.W., Gillespie, W.H., Resnick, D.A., Scheihing, M.H., 1984. Reconstruction and architecture of medullosan pteridosperms (Pennsylvanian). The Mosasaur 2, 1–8.

Phillips, T.L., 1981. Stratigraphic occurrences and vegetational patterns of Pennsylvanian pteridosperms in Euramerican coal swamps. Rev. Palaeobot. Palynol. 32 (1), 5–26. doi:10.1016/0034-6667(81)90073-7.

Phillips, T., Peppers, R.A., DiMichele, W.A., 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. Int. J. Coal Geol. 5, 43–109.

Potonié, H., 1904. Abbildungen und Beschreibungen fossiler Pflanzen-Reste der paläozoischen und meszoischen Formationen. In: Lieferung I-XI, 1–180. Königlich Preußische Geologische Landesanstalt und Bergakademie, Berlin.

Pryor, J.S., 1990. Delimiting species among permineralized medullosan pteridosperms: A plant bearing *Alethopteris* fronds from the Upper Pennsylvanian of the Appalachian Basin. Can. J. Bot. 68 (1), 184–192. doi:10.1139/b90-025.

Quie, W., Algeo, T.J., Luo, G., Herrmann, A., 2019. Global events of the Late Paleozoic (Early Devonian to Middle Permian): A review. Palaeogeogr. Palaeoclimatol. Palaeoecol. 531. doi:10.1016/j.palaeo.2019.109259.

Ramanujam, C.G.K., Rothwell, G.W., Stewart, W.N., 1974. Probable attachment of the *Dolerotheca eampanulum* to a *Myeloxylon-Alethopteris* type frond. Am. J. Bot. 61, 1057–1066.

Raymond, A., Wehner, M., Costanza, S.H., 2014. Permineralized *Alethopteris ambigua* (Lesquereux)White: A medullosan with relatively long-lived leaves, adapted for sunny habitats in mires and floodplains. Rev. Palaeobot. Palynol. 200, 82–96.

Renault, B., 1875. Recherches sur les Végéteaux silificés d'Autun. II – Étude du genre *Myelopteris*, Mém. prés. par Divers Savants à l'Acad. des. Sciences 22 (10).

Renault, B., 1878. Recherches sur la structure et les affinités botaniques des végétaux silicifiés regueillis aux environs d'Autun et de St. Étienne. Publ. Soc. Éduenne, Autun, p. 216.

Renault, B., 1879. Structure comparée de quelques tiges de la flore carbonifère. Thèse d'Etat Sciences naturelles, Paris, Faculté des sciences 213–349.

Renault, B., 1881. Cours de botanique fossile fait au Muséum national d'Histoire naturelle, première année, Paris.

Renault, B., 1893. Bassin houiller et Permien d'Autun et d'Épinac. Fasc IV, Flore fossile, deuxième partie. In: Études des Gîtes Minéraux de la France, Atlas, 89 pl. Imprimerie nationale, Paris.

Renault, B., 1896. Bassin houiller et Permien d'Autun et d'Épinac. Fasc IV, Flore fossile, deuxième partie. In: Études des Gîtes Minéraux de la France, Texte. Imprimerie nationale, Paris, p. 578.

Richey, J.D., Montañez, I.P., Goddéris, Y., Looy, C.V., Griffins, N.P., DiMichele, W.A., 2020. Influence of temporally varying weatherability on CO$_2$-climate coupling and ecosystem change in the late Paleozoic. Clim. Past 16, 1759–1775. doi:10.5194/cp-16-1759-2020.

Roberts, D.C., Barghoorn, E.S., 1952. *Medullosa olseniae*: a Permian medullosa from North Central Texas. Bot. Mus. Leaflets 13 (7), 191–200.

Rößler, R., 2021. The most entirely known terrestrial permian ecosystem on Earth – kept by explosive volcanism. Palaeontographica Abt. B 302 (1–3), xx–xx. In press.

Rößler, R., Feng, Z., Noll, R., 2012a. The largest calamite and its growth architecture—*Arthropitys bistriata* from the Permian petrified forest of Chemnitz. Rev. Palaeobot. Palynol. 185, 64–78.

Rößler, R., Zierold, T., Feng, Z., Kretzschmar, R., Merbitz, M., Annacker, V., Schneider, J.W., 2012b. A snapshot of an Early Permian ecosystem preserved by explosive volcanism: New results from the petrified forest of Chemnitz, Germany. Palaios 27, 814–834.

Rothwell, G.W., 2020. Cauline vasculature and leaf trace production of *Medullosa leuckartii* Göppert & Stenzel (Medullosaceae), a Paleozoic gymnospermous vine. Int. J. Plant Sci. 181 (4), 464–472.

Rothwell, G.W., Whiteside, K.L., 1973. Rooting structures of the Carboniferous medullosan pteridosperms. Can. J. Bot. 52, 97–102.

Rowe, N.P., Speck, T., 1998. Biomechanics of plant growth forms: the trouble with fossil plants. Rev. Palaeobot. Palynol. 102, 43–62.

Rudolph, K., 1922. Zur Kenntnis des Baues der Medullosen. Beih. Bot. Zentralbl. 39, 196–222.

Schenk, 1889. Über *Medullosa* Cotta und *Tubicaulis* Cotta. Abh. Math.-Phys. Cl. Königl. Sächs. Ges. Wissensch. 15, 523–558.

Schneider, J.W., Rößler, R., Fischer, F., 2012. Rotliegend des Chemnitz-Beckens (syn. Erzgebirge-Becken). In: Lützner, H., Kowalczyk, G. (Eds.), Stratigraphie von Deutschland X. Rotliegend. Part I: Innervariscische Becken, 61. Schriftenr. Deu. Ges. Geowiss, Hannover, pp. 530–588.

Scott, D.H., 1899. On the structure and affinities of fossil plants from the Paleozoic rocks, III. On *Medullosa anglica*: a new representative of the Cycadofilices. Ann. Bot. 13 (49), 183–187.

Scott, D.H., 1914. Studies in fossil Botany, Part II, on *Medullosa pusilla*. Proc. R. Soc., Ser. B 87, 221–228.

Scott, A.C., Taylor, T.N., 1983. Plant/animal interactions during the Upper Carboniferous. Bot. Rev. 49, 259–307.

Serbet, R., Rothwell, G.W., 1992. Characterising the most primitive seed ferns. I. A Reconstruction of *Elkinsia polymorpha*. Int. J. Plant Sci. 153 (4), 602–621.

Serbet, R., Rothwell, G.W., 1995. Functional morphology and homologies of gymnospermous ovules: evidence from a new species of *Stephanospermum* (Medullosales). Can. J. Bot. 73, 650–661.

Serbet, R., Taylor, T.N., Taylor, E.L., 2006. On a medullosan pollen organ from the Pennsylvanian of North America. Rev. Palaeobot. Palynol. 142, 219–227.

Seward, A.C., 1917. Fossil plants. 3. Cambridge University Press, Cambridge.

Seyfullah, L.J., Hilton, J., Wang, S.-J., Galtier, J., 2009. Anatomically preserved pteridosperm stems and rachises from Permian floras of China. Int. J. Plant Sci. 170 (6), 814–828.

Smoot, E.L., 1984. Phloem anatomy of the Carboniferous pteridosperm *Medullosa* and evolutionary trends in gymnosperm phloem. Bot. Gazette 145, 550–564.

Solms-Laubach, H., 1897. Über *Medullosa leuckarti*. Bot. Zeitschrift 55, 175–292.

Spencer, A.R.T., Wang, S.-J., Dunn, M.T., Hilton, J., 2013. Species of the medullosan ovule *Stephanospermum* from the Lopingian (late Permian) floras of China. J. Asian Earth Sci. 76, 59–69.

Sperry, J.S., Hacke, U.G., 2004. Analysis of circular bordered pit function. I. Angiosperm vessels with homogenous pit membranes. Am. J. Bot. 91, 369–385.

Spindler, F., Werneburg, R., Schneider, J.W., Luthardt, L., Annacker, V., Rößler, R., 2018. First arboreal 'pelycosaurs' (Synapsida: Varanopidae) from the early Permian Chemnitz Fossil Lagerstätte, SE-Germany, with a review of varanopid phylogeny. Pal. Z. 92 (1), 315–364.

Steidtmann, W.E., 1944. The anatomy and affinities of *Medullosa noei* Steidtmann, and associated foliage, roots and seeds. Contrib. Mus. Paleontol., Univ. Michigan 6, 131–166.

Sterzel, J.T., 1886. Die Flora des Rothliegenden im nordwestlichen Sachsen. Palaeontolog. Abh. 3 (4), 237–370 Berlin.

Sterzel, J.T., 1901a. Die Flora des Rothliegenden von Ilfeld am Harz. Centralblatt für Min. Geol. u. Palaeont. in Verbindung mit dem Neuen Jahrbuch für Min. Geol. u. Palaeont. 417–427.

Sterzel, J.T., 1901b. Weitere Beiträge zur Revision der Rothliegendflora der Gegend von Ilfeld am Harz. Centralblatt für Min. Geol. u. Palaeont. in Verbindung mit dem Neuen Jahrbuch für Min. Geol. u. Palaeont. 590–598.

Sterzel, J.T., 1918. Die organischen Reste des Kulms und Rotliegenden der Gegend von Chemnitz. Abh. math.-phys. Kl. sächs. Ges. Wiss. 35.

Stewart, W.N., Delevoryas, T., 1956. The Medullosan pteridosperms. Bot. Rev. 45–80.

Stidd, B.M., 1981. The current status of Medullosan seed ferns. Rev. Palaeobot. Palynol. 32, 63–101.

Stull, G.W., DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J., Elrick, S., 2012. Palaeoecology of *Macroneuropteris scheuchzeri*, and its implications for resolving the paradox of 'xeromorphic' plants in Pennsylvanian wetlands. Palaeogeogr. Palaeoclimatol. Palaeoecol. 331–332, 162–176.

Tanrattana, M., Barczi, J.-F., Decombeix, A.-L., Meyer-Berthaud, B., Wilson, J.P., 2019. A new approach for modelling water transport in fossil plants. IAWA J. 40, 466–487. doi:10.1163/22941932-40190243.

Taylor, T.N., 1965. Paleozoic seed studies: a monograph of the American species of *Pachytesta*. Palaeontogr. Abt. B 117, 1–46.

Taylor, T.N., 1966. Paleozoic seed studies: on the genus *Hexapterospermum*. Am. J. Bot. 53, 185–192.

Taylor, T.N., Taylor, E.H., Krings, M., 2009. Paleobotany: The Biology and Evolution of Fossil Plants. second edition Academic Press, New York, p. 1252.

Velain, C., 1885. Le Permien dans la région des Vosges. Bull. Soc. Géol. France 13, 536–564.

Weber, O., Sterzel, J.T., 1896. Beiträge zur Kenntnis der Medulloseae. Berichte der Naturwissenschaftlichen Gesellschaft zu Chemnitz 13, 44–143.

White, J.D., Montañez, I.P., Wilson, J.P., Poulsen, C.J., McElwain, J.C., DiMichele, W.A., Hren, M.T., Macarewich, S., Richey, J.D., Matthaeus, W.J., 2020. A process-based ecosystem model (Paleo-BGC) to simulate the dynamic response of late Carboniferous plants to elevated O_2 and aridification. Am. J. Sci. 320 (7), 547–598.

Wilson, J.P., Fischer, W.W., 2011. Geochemical support for climbing habit within the Paleozoic seed fern genus *Medullosa*. Int. J. Plant Sci. 172, 586–598. doi:10.1086/658929.

Wilson, J.P., Knoll, A.H., 2010. A physiologically explicit morphospace for tracheid-based water transport in modern and extinct seed plants. Paleobiology 36, 335–355. doi:10.1666/08071.1.

Wilson, J.P., Knoll, A.H., Holbrook, N.M., Marshall, C.R., 2008. Modeling fluid flow in *Medullosa*, an anatomically unusual Carboniferous seed plant. Paleobiology 34, 472–493. doi:10.1666/07076.1.

Wilson, J.P., Montañez, I.P., White, J.D., DiMichele, W.A., McElwain, J.C., Poulsen, C.J., Hren, M.T., 2017. Dynamic Carboniferous tropical forests: newviews of plant function and potential forphysiological forcing of climate. Ne Phytologist 215 (4), 1–21. doi:10.1111/nph.14700.

Wilson, J.P., White, J.D., DiMichele, W.A., Hren, M.T., Poulsen, C.J., McElwain, J.C., Montañez, I.P., 2015. Reconstructing extinct plant water use for understanding vegetation-climate feedbacks: Methods, synthesis, and a case study using the Paleozoic-era Medullosan seed ferns. Pal. Soc. Pap. 21, 167–196.

Wnuk, C., Pfefferkorn, H.W., 1984. The life habits and paleoecology of Middle Pennsylvanian medullosan pteridosperms based on an in situ assemblage from Bernice Basin (Sullivan County, Pennsylvania, U.S.A.). Rev. Palaeobot. Palynol. 41, 329–351.

Worsdell, W.C., 1906. The structure and origin of the Cycadaceae. Ann. Bot. 20 (78), 129–159.

Zeiller, C.R., 1890. Bassin houiller et Permien d'Autun et d'Épinac. In: Fasc II, Flore fossile, premiere partie. Études des Gîtes Minéraux de la France, Paris.

Zodrow, E.L., 2003. The "medullosan forest" at the Lloyd Cove Seam (Pennsylvanian, Sydney Coalfield, Nova Scotia, Canada). Atl. Geol. 39, 177–195.

Zodrow, E.L., 2007. Reconstructed tree fern *Alethopteris zeilleri* (Carboniferous, Medullosales). Int. J. Coal Geol. 69, 68–89.

Zodrow, E.L., McCandlish, K., 1980. On a *Trigonocarpus* species attached to *Neuropteris* (*Mixoneura*) *flexuosa* from Sydney Coalfield, Cape Breton Island, Nova Scotia, Canada. Rev. Palaeobot. Palynol. 30, 57–66.