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Micro-CT investigation of a seed fern (probable medullosan) fertile pinna from the Early Permian Petrified Forest in Chemnitz, Germany



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ABSTRACT

A new bipinnate fertile pinna, *Sterzelitheca chemnitzensis*, bearing alternate synangia, is described from the Chemnitz Petrified Forest, Germany. The specimen occurs in the basal volcanic ash of the Zeisigwald Tuff Horizon, Leukersdorf Formation, Lower Permian. Because it is partially embedded in the tuffaceous matrix, X-ray micro-computer tomography was employed to investigate the complete morphology without mechanical preparation of the hand specimen. The pinna is 66 mm long and branched once at least, the ultimate pinnae alternately positioned on the penultimate axis at angles of 45–55°. Stalked synangia are bell-like, borne alternately on both the terminal portion of the penultimate axis and the ultimate axes at angles of 25–60°. The smooth walled stalk is 3–7 mm long, 1–1.5 mm wide. Individual synangia are up to 6.5 mm in diameter and 10 mm long, and bear 12–14 elongated sporangia. Tubular sporangia are thin walled, circular in transverse section, arranged at the rim of the circular synangial pad around a central hollow. The unique preservational mould of the studied specimen is neither a permineralisation nor a compression–impression. It is three-dimensionally preserved, but lacks any organic remains. We provide the first detailed three-dimensional features of a probable medullosan male reproductive organ from the Chemnitz Fossil Lagerstätte. The relatively simple structure of the specimen offers a better understanding of the Palaeozoic seed ferns.

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1. Introduction

Palaeozoic seed ferns or pteridosperms are a very heterogeneous group of extinct plants that possess mostly fern-like compound fronds but bear seeds (Millay and Taylor, 1979). The Medullosaceae is one of the most diverse clades of seed ferns based on dispersed vegetative and reproductive organs documented from the Lower Carboniferous up to the Permian (Millay and Taylor, 1977; Stidd, 1981; Taylor et al., 2009). They are reconstructed as free-standing or lax-stemmed small trees (Pfefferkorn et al., 1984; Wnuk and Pfefferkorn, 1984), or vine/liana-like forms with a climbing growth habit (Dunn et al., 2003; Dunn, 2006).

The Medullosaceae have a noteworthy variety of pollen producing organs assigned to them (Schopf, 1948; Baxter, 1949; Millay and Eggert, 1970; Millay and Taylor, 1977). These pollen organs exhibit a considerable range of structural patterns, arrangement of sporangia, and pollen types that suggest a heterogeneous group evolving in different ways (Millay and Taylor, 1979). To date, nearly twenty genera of pollen organs with distinct structural–morphological features have been attributed to the Medullosales. However, most of the comprehensive

interpretations of medullosan reproductive organs are mainly obtained from sporadic permineralised materials, and few from compression–impression fossils (Serbet et al., 2006). Very few specimens show both three-dimensional preservation and attachment to pinnate fronds, thus, the morphological organisation and homology of medullosan reproductive organs are not well understood.

Here we describe a three-dimensional but non-permineralised reproductive pinna from the type locality of *Medullosa* Cotta 1832. X-Ray micro-Computer Tomography examination shows the Early Permian fertile pinna possessing a simple architecture, and indicates it has a probable medullosan affinity. The morphological features obtained from the specimen enhance our understanding of the seed fern fertile organs.

2. Material and method

The reproductive organ described here occurs in the Early Permian (Sakmarian) Petrified Forest of Chemnitz, Germany. This Fossil Lagerstätte represents an *in situ* preserved subtropical forest ecosystem, which was buried in a relatively short period of time (Feng et al., 2012; Rößler et al., 2012a,b). Recently, a precise 3D-coordinated excavation has been performed in a site of 24 × 18 m for the Chemnitz Fossil Lagerstätte. More than 1800 plant remains and diverse animal specimens were obtained. Among them are fifty-three trunk bases,

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including calamitaleans, psaroniaceous tree ferns, medullosan seed ferns, cordaitaleans and some unidentified gymnospermous stems still standing upright in their growth positions and rooting in the original palaeosol. This not only offers a unique insight into an early Permian non-peat-forming forest habitat with a dense hygrophilous vegetation of pteridophytes and gymnosperms, but also provides information on its community structure and vegetational density (Rößler et al., 2012b).

The geological settings and volcanic taphonomy of the Chemnitz fossil site has been recently investigated in detail by Rößler et al. (2012b). Sub-units S1 to S6 of the Chemnitz Hilbersdorf section are recognized as different litho-facies. The specimen studied here was buried in the lower part of Unit S5, a fossil-rich layer at the base of the Zeisigwald Tuff Horizon, Leukersdorf Formation. This so called leaf horizon is an approximately 15–20 cm thick, weakly horizontally-bedded and moderately sorted, fine to medium-grained, non-welded purple-red coloured ash-tuff. This deposit, composed of several normal-graded units, rests sharply upon a variegated palaeosol, and represents a succession that resulted from low-concentration pyroclastic density currents and accompanying fallout during an early stage of volcanic activity in the investigation area. This deposit was caused by an explosive magmatic to phreatomagmatic eruption, where the volcanic ashes covered the standing vegetation. As a result, many trees had the leaves ripped from them, to be found embedded in a characteristic leaf horizon near the base of Unit S5, close to just before the final pyroclastic flow entombed the whole ecosystem. Along with leafy shoots, pinnate fronds, detached intact and fragmentary leaves, this horizon has also yielded the first outstanding faunal remains (Rößler et al., 2012b).

The specimen described here was investigated with the aid of X-ray micro-tomography; a Computer Tomography scan was conducted on a Phoenix v|tome|x s at the Steinmann Institute, Bonn University, Germany. The part and counterpart of the specimen, having already been split, were placed back together for X-ray examination. The specimen was immobilised by wrapping in household plastic wrap and mounted in a florist foam block for stability; both materials have very low X-ray attenuation and were thus readily distinguishable from the specimen. Ca. 1500 projections with a 1 mm copper filter were obtained at 140 kV and 150 mA. Three-dimensional reconstructions were produced by using imaging software Amira v. 5.4.2.

SEM was employed to examine *in situ* pollen on both the part and the counterpart of the specimen. Unfortunately the reproductive organ lacks any *in situ* pollen.

Hand specimen photographs were made by using a Nikon D3x camera with a AF-S Micro Nikkor 60 mm 1:2.8G lens. Composite images were created using Adobe Photoshop CS v. 8.0.

3. Results

Systematic Palaeontology

? Order Medullosales

? Family Medullosaceae

Sterzelitheca Feng et Roessler gen. nov.

Type species: *S. chemnitzensis* Feng et Roessler gen. nov. et sp. nov.

Generic diagnosis: Fertile pinna without sterile foliage, at least bipinnate and bearing numerous pendulous stalked synangia. Ultimate pinnae alternately arranged on the penultimate axis. Individual synangia are bell-like, slightly longer than broad, consisting of numerous tubular sporangia attached to a circular synangial pad.

S. chemnitzensis Feng et Roessler gen. nov. et sp. nov.

Specific diagnosis: At least bipinnate fertile pinna, nearly 66 mm long. The penultimate axis is 3.3 mm broad at the base. Seven ultimate pinnae alternately arranged and having numerous stalked synangia along their entire lengths. Stalk is smooth walled, 3–7 mm long, 1–1.5 mm wide. Pendulous synangia are bell-like, borne alternately on both the penultimate axis and ultimate axes at angles of 25–60°. Synangia are up to 6.5 mm in diameter and 10 mm long, bearing 12–14 elongated

sporangia. Tubular sporangia are thin walled, circular in transverse section, arranged at the rim of the circular synangial pad and surrounding a hollow central region.

Etymology: The former portion of the generic name *Sterzelitheca* is proposed to honour the career and inspiring works of Johann Traugott Sterzel, the founding director of Natural History Collections in Chemnitz, Germany, the latter portion refers to the Greek *theke*, a container for which we use the equivalent Latin spelling of *theca*. The specific name is derived from the city of Chemnitz, where the type specimen was collected.

Holotype: Specimen TA0201a and b (part and counterpart). Figs. 1–3.

Repository: Museum für Naturkunde Chemnitz, Germany.

Type locality: 50°51'58.68" N, 12°57'32.54" E, the city of Chemnitz, Germany.

Type Stratum: Zeisigwald Tuff Horizon, Leukersdorf Formation, Lower Permian.

Age: Ca. 290 million years, Early Permian (Sakmarian).

4. Description

One specimen including a part and counterpart is available for study (Fig. 1A and B). The fertile pinna is partially visible on the randomly split rock surface; the other portions are still hidden and embedded in the sediment, which could only be seen by the X-ray images. The synangia attached on the fertile pinna are three-dimensionally preserved, but slightly compressed, possibly prior to preservation. Original organic material is lacking.

4.1. General features of the fertile pinna

The fertile pinna is characterised by a slender penultimate axis bearing several laterally attached ultimate pinnae that appear approximately in the same plane (Fig. 2A and B). The penultimate axis is somewhat broader than those of the ultimate axes. There is no sterile foliage present on the pinna. The pinna is at least 66 mm long, with a smooth rachis. The penultimate axis is 3.3 mm broad at the base, and becomes gradually narrower distally. The uppermost portion of the penultimate axis is unbranched, but bears five distinct synangia. Seven ultimate pinnae are preserved that are alternately borne on the lower portion of the penultimate axis at angles of 45–55°. Each ultimate pinnae has a different length and bears a different number of pendulous synangia. The lowermost pinna is the longest one (39.5 mm long, 2.8 mm broad at the base) and exhibits the largest number (eight) of borne synangia. The morphology and organisation of synangia on the ultimate axes resemble those on the penultimate axis.

4.2. Morphology of the synangia and sporangia

Nearly fifty synangia are available for examination. The campanulate synangia are alternately arranged on the pinna, 2.2–7.3 mm (av. = 4.3) apart, with short stalks (Fig. 1C, arrow). The stalk is smooth walled, ranging from 3 to 7 mm long, 1–1.5 mm wide, arise from the axes at angles of 25–60° (av. = 40°). The distal portion of the stalk is bent and conspicuously expanded, fused with a flattened circular synangial pad, which bears numerous pendant elongate sporangia (Fig. 3A, arrows). The synangia vary from 5 to 6.5 mm in diameter, and up to 10 mm in length, probably representing different maturation stages. The appressed sporangia are arranged in a ring at the rim of the synangial pad and around a hollow centre (Fig. 3B). The sporangia bend towards the centre of the synangium at the middle portion, and then slightly bend outwardly. The distal portion of the sporangia is inwardly curved and forms a hook-like tip (Fig. 3C). The number of sporangia in each ring varies from 12 to 14 (Fig. 3B). The diameter of the sporangia measures 1 to 1.5 mm, their length measures up to 8 mm. Adjacent sporangia are commonly connected to each other by thin tissue (Fig. 3D). In several instances, they are separated from each

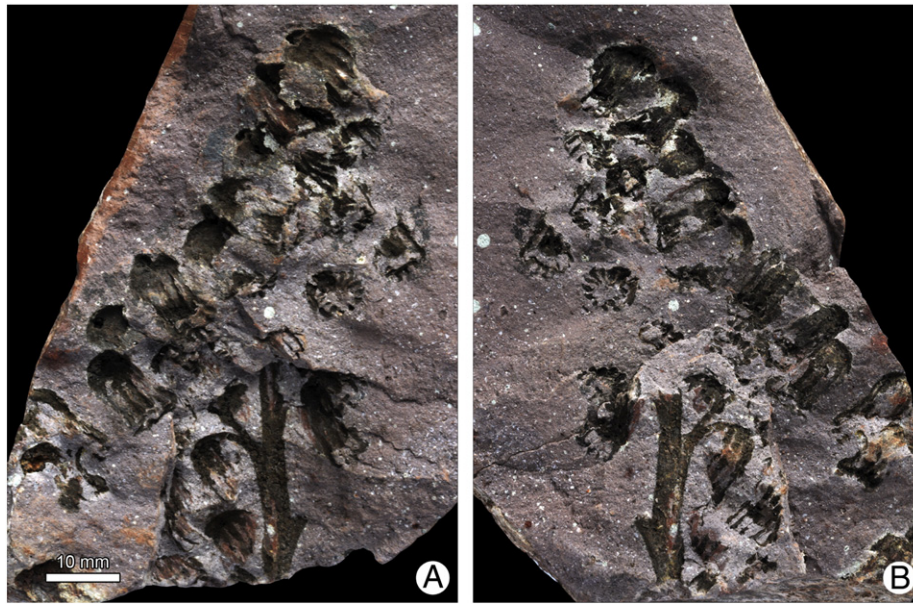


Fig. 1. *Sterzelitheca chemnitzensis* gen. nov. et sp. nov., from the Early Permian Petrified Forest in Chemnitz, Germany. A and B are part and counterpart, respectively, showing the gross morphology of the fertile pinna.

other at the main bodies, but connected partially at the distal tips by a thin membrane like structure (Fig. 3E and F, arrows). However, sometimes they are totally separated from each other (Fig. 3C). The connection and the separation of adjacent sporangia may indicate the manner of the maturation process of the sporangial walls. Transversely, the individual sporangia are circular in outline, showing a central cavity surrounded by a thin smooth sporangial wall (Fig. 3G, arrows). No consistent feature could be found to suggest the manner of sporangial dehiscence.

5. Discussion

5.1. Assignment of *S. chemnitzensis*

Reproductive organs are not only important to classify fossil plants, they are also essential in documenting the biodiversity and evolutionary trends of plant lineages (Serbet et al., 2006). Our specimen provides the first seed fern reproductive pinna with detailed 3-D information from the Early Permian Chemnitz Fossil Lagerstätte. Due to its length (66 mm long), our specimen may represent a terminal portion of a pinnate frond; therefore a complete frond is probably larger with more branches. Whether the fertile portion was borne on the terminal portion of a vegetative frond remains unknown. Superficially, the gross morphology of our material, especially the circular synangial pad and the marginal attachment of the numerous sporangia, is comparable to both the addressed lyginopteridalean *Crossotheca* Zeiller, 1883 and some simple medullosan pollen organs.

Kidston's (1906, 1923) authoritative studies indicated that *Crossotheca* represents the terminal or basal portions of frond segments in which the rachis bears alternately arranged pinnae that terminate in a reduced fertile pinnule. Basal portions of the frond bear sterile pinnules of the *Pecopteris*, *Sphenopteris*, or *Rhodia* type (Stur, 1883). The synangium of *Crossotheca* is characterised by consisting of free bilocular sporangia arranged around the periphery of a reduced fleshy pinnule (Kidston, 1906).

The vast majority of non-permineralised materials assigned in the past to *Crossotheca* are probably preserved in a way that precludes the determination of the bilocular condition of the sporangia. Eggert and Taylor (1971) pointed out that the subsequently assigned

Crossotheca species may be more imaginary than real. Unless a complete reinvestigation of *Crossotheca* is carried out, the generic name should be used for any forms in which evidence of a reduced or modified pinnule and bilocular sporangia is clearly present (Eggert and Taylor, 1971). Therefore, permineralised materials are commonly referred to by different generic names, such as *Feraxothea*, a permineralised lyginopterid pollen organ that represents a different preservational state of *Crossotheca* (Millay and Taylor, 1977, 1978). Although our material is not permineralised, it is also not in a compression–impression condition (*sensu* Bateman, 1991). More importantly, real bilocular sporangia are not present in our specimen. Thus, we establish the new name *Sterzelitheca* for our material based on the detailed three-dimensional morphology and the attachment pattern of the synangia.

Crossotheca is regarded as a reproductive organ belonging to a typical Carboniferous lyginopterid (Taylor et al., 2009). Although *Heterangium* from the Early Permian of Autun, France is interpreted as the youngest representative of the lyginopteridaleans (Galtier, 2008, 2013), there is no evidence of a lyginopteridalean being present in the Chemnitz flora. However, a variety of petrified medullosan stems and petiole remains have been recovered from the Chemnitz fossil site. In the recently excavated site, among the 53 *in situ* preserved stem-bases, 17 show medullosan affinity. In addition to the stems, the same bed that the *Sterzelitheca* specimen came from, yields diverse medullosan foliages, such as *Alethopteris schneideri*, *Neurocallipteris planchardii* and *Neurocallipteris* sp. (Rößler et al., 2012b). Therefore, it is more likely that the fertile pinna described here belongs to a medullosan plant.

5.2. Comparison of *S. chemnitzensis* with proposed medullosan pollen organs

Previously reported genera of medullosan pollen organs include *Whittleseyia* (Newberry, 1853; Halle, 1933), *Aulacotheca* (White, 1900; Halle, 1933; Jongmans, 1937; Hemingway, 1941; Arnold, 1949; Tidwell, 1967; Eggert and Kryder, 1969; Mickle and Leary, 1984), *Codonothea* (Sellards, 1903, 1907; Stidd and Leisman, 1985), *Dolerotheca* (Halle, 1933; Schopf, 1948; Baxter, 1949; Rothwell and Eggert, 1986), *Schopfitheca* (Delevoryas, 1964), *Goldenbergia* (Halle, 1933), *Rhetinothea* (Leisman and Peters, 1970; Rothwell and Mickle, 1982), *Sullitheca* (Stidd et al., 1977), *Halletheca* (Taylor, 1971; Taylor and Millay, 1981;

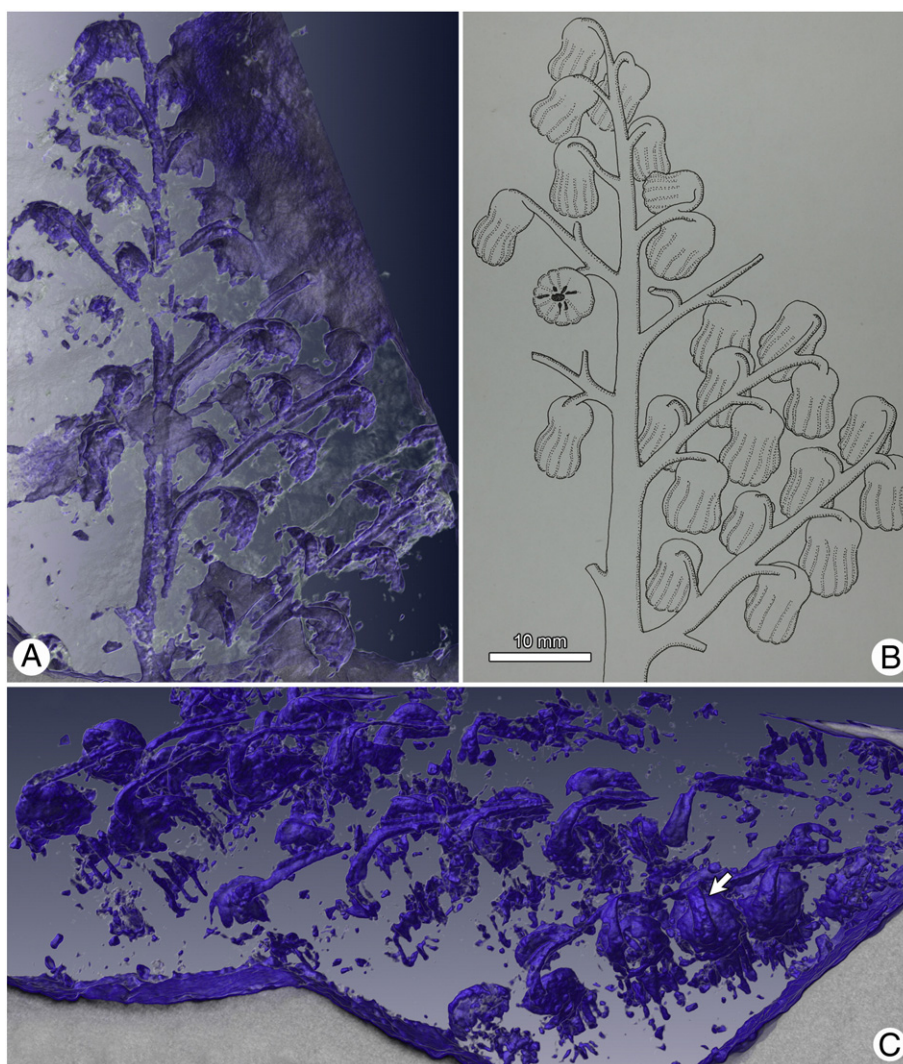


Fig. 2. X-ray micro-Computer Tomography images and drawing reconstruction of *Sterzelitheca chemnitzensis* gen. nov. et sp. nov., from the Early Permian Petrified Forest in Chemnitz, Germany. A, dorsal view of the pinna, showing the branching pattern and the alternate arrangement of synangia. B, drawing reconstruction of the pinna. C, oblique side view of the pinna, showing the arrangement of the stalked synangia (arrow).

Mapes, 1982), *Stewartiotheca* (Eggert and Rothwell, 1979), *Boulayatheca* (Taylor and Kurmann, 1985), *Bernaltia* (Rothwell and Eggert, 1986), *Saharatheca* (Stidd, 1991) and *Murielatheca* (Serbet et al., 2006), consisting of more than twenty species which have been attributed to this group. The comparative characters of selected genera and species are summarized in Table 1 to show the major structural distinctions.

Besides the aforementioned genera, two additional taxa, *Parasporotheca* (Dennis and Eggert, 1978) and *Potoniea* (Stidd, 1978; Schultka, 1995) have also been attributed to Medullosaceae. Because the former produces grains with vestigial sacci and the latter produces trilete pollen, their affinity to the Medullosaceae remains controversial (Schopf, 1948; Stidd, 1978, 1981; Taylor, 1988).

The previously described taxa of medullosan pollen organs, *Dolerotheca*, *Bernaltia*, *Schopfitheca*, *Rhetinotheca*, *Halletheca*, *Sullitheca*, *Stewartiotheca*, *Saharatheca* and *Murielatheca* are permineralised and mainly come from the North American Pennsylvanian coal ball floras. These taxa provide detailed information of the vascular organisation, configuration of sporangia, cell structure and even the *in situ* pollen grains of the synangia. Because of the nature of preservation and the absence of sufficient anatomical characters to define *Sterzelitheca*, this taxon is difficult to compare adequately with these permineralised

taxa. However, the basic morphology of *Sterzelitheca* and those of adpressed medullosan pollen organs is similar.

By using ingenious softening and embedding techniques, Halle (1933) successfully sectioned the coalified specimens and reconstructed the three-dimensional configurations of *Whittleseyia*, *Boulayatheca*, *Aulacotheca*, *Goldenbergia* and *Codonotheca*. These compressed genera were described as being cupulate, and having sporangial tubes arranged in a cyclic pattern around a central hollow. Halle (1933) characterised these genera as possessing large monolete spores contained in long tubular sporangia embedded in vegetative tissue, and attributed these pollen organs to the subtribe Whittleseyinae. The pollen-bearing organs obviously show a general structural plan that involves elongated sporangia in varying degrees of fusion (Schopf, 1948). The organisation of these medullosan pollen organs is similar to that in *Sterzelitheca*.

Schopf (1948) established the subtribe Dolerothecinae to place the complex pollen organs within, which are typified by *Dolerotheca*. The basic organisation of *Dolerotheca* is interpreted as a highly plicated pollen organ composed of multiple units, each unit corresponding to a single synangium (Dennis and Eggert, 1978). Rothwell and Eggert (1986) proposed *Bernaltia* for those showing both external morphology and internal organisation, and retained *Dolerotheca* for the poorly

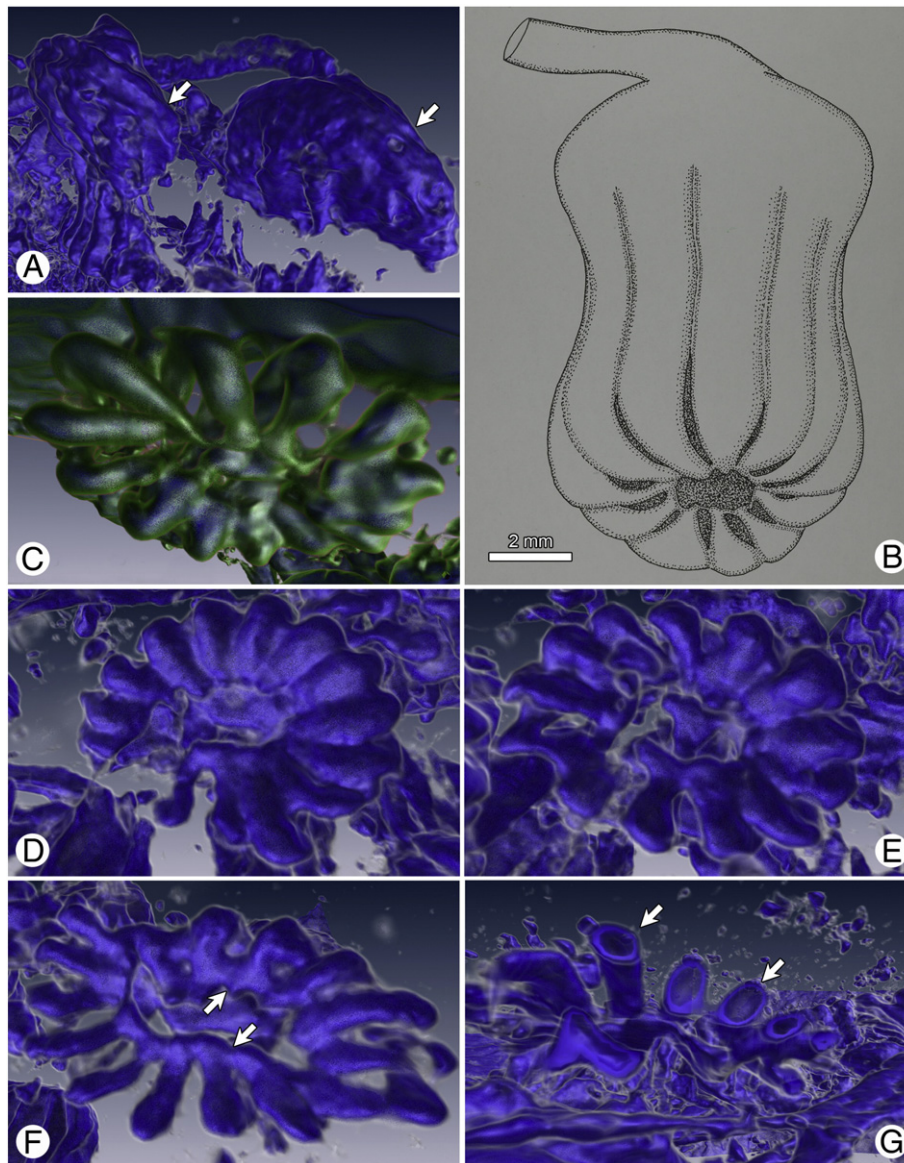


Fig. 3. X-ray micro-Computer Tomography images and drawing reconstruction of *Sterzelitheca chemnitzensis* gen. nov. et sp. nov., from the Early Permian Petrified Forest in Chemnitz, Germany. A, side view of two synangia with tubular sporangia, arrows indicating the circular synangial pad. B, drawing reconstruction of a synangium. C, oblique ventral view of synangium, showing the hook-like distal tips of sporangia around a hollow centre. D, ventral view of synangium, showing adjacent sporangia completely connected by thin tissue. E, ventral view of synangium, showing adjacent sporangia connected or free positioned. F, ventral view of synangium, arrows indicating only the sporangial tips connected. G, transverse section near the middle portion of a synangium, arrows indicating the thin-walled sporangia with central cavities.

known forms. The most complex form, *Bernalthia formosa*, is up to 45 mm in diameter, includes more than 1200 individual sporangia fused into four plicated synangial units (Rothwell and Eggert, 1986). Our specimen has sporangia arranged in a peripheral ring, which is very different to the members of the complex Dolerothecinae.

Three forms of medullosan pollen organs, e.g., simple, aggregate and compound synangiate types have been recognised based on the morphological features and the internal structures (Millay and Taylor, 1979). The simple forms include the adpression (impression–compression) genera *Whittleseya*, *Aulacotheca*, *Boulayatheca*, *Codonotheca*, *Goldenbergia* and *Schopfitheca*, and the anatomically preserved genera *Halletheca*, *Sullitheca* and *Murielatheca*. Of these, our taxon is more comparable to the adpressed genera, which show a central hollow surrounded by sporangia.

The basic form of the simple group is exemplified by the Westphalian *Codonotheca* type (Millay and Taylor, 1979), as its sporangia are arranged in a ring with the individual sporangia fused in the proximal

third of the organ (Sellards, 1903, 1907; Halle, 1933). *Aulacotheca* shows individual pollen sacs fused along its entire length, and includes the largest number of species. In this taxon, closely appressed sporangia are fused laterally to form a ring-like structure around a central hollow region (Halle, 1933). *Whittleseya* and *Goldenbergia* possess a ring of fused sporangia around a large central hollow that forms a cup-shaped pollen organ, open at the distal end (Sellards, 1903, 1907; Halle, 1933). However, the sporangial number of *Whittleseya* is about 50–60, much higher than in our specimen, whereas, the sporangial number of *Goldenbergia* is 12–16 (Halle, 1933), very close to that of our material. *Boulayatheca* and *Schopfitheca* are poorly preserved, and do not provide more information.

The permineralised simple forms, e.g., *Halletheca* (Taylor, 1971), *Saharatheca* (Stidd, 1991), *Rhetinotheca* (Leisman and Peters, 1970; Rothwell and Mickle, 1982) and *Murielatheca* (Serbet et al., 2006) exhibit a central core of sclerenchymatous tissue extended to varying degrees, and different from our species.

Table 1
Comparative characteristics of the simple forms (type I) of the proposed medullosan pollen organs.

Taxon	Synangium (size and shape)	Sporangial organisation	<i>In situ</i> pollen	Preservation type and remarks	Horizon and age	Locality	reference
<i>Whittleseya elegans</i>	Campanulate, or urn-shape; 50 × 25 mm (L × D.)	Numerous (ca. 50–60 ^a) tubular concrescent sporangia (1 mm in Diam.) embedded in thick ground tissue, and arranged in a ring around a hollow centre.	<i>Monoletes</i> , 200–250 × 140–160 μm	Compressed	Pottsville Fm., Middle Pennsylvanian;	Tallmadge, Ohio, USA; UK	Newberry (1853); Halle (1933); Schopf (1948)
<i>Codonotheca caduca</i>	Stalked, elongated cup or bell-shape; covered with dense hairs; 30–50 × 11.3 mm	6 elongated, lamina-like sporangia (1.5–2 mm in Diam.) that united at the base and were free at tips, around a hollow centre.	<i>Monoletes</i> , 276–351 × 183–262 μm	Compressed	Carbondale Fm.; Middle Pennsylvanian	Mazon Creek flora, Illinois, USA	Sellards (1903, 1907); Halle (1933); Drinnan and Crane (1994)
<i>Boulayatheca fertilis</i>	Clevate-pyriform, round triangular in cross section; 10–16 × 6 ^a mm	Concrescent sporangia zone surround a hollow centre.	<i>Monoletes</i> , 210–280 × 60–190 μm	Compressed	Westphalian	France, Germany, Holland; UK	Carpentier (1914, 1925); Halle (1933); Kurmann and Taylor (1984); Taylor and Kurmann (1985) Halle (1933)
<i>Aulacotheca elongata</i> (= <i>Aulacotheca hemingwayi</i>)	Clavate to elongate cylindrical; 15–20 × 3.6–4 mm	9 circular or wide elliptical (0.5–0.7 mm in Diam.) concrescent sporangia surround a hollow centre, inner wall is thinner.	<i>Monoletes</i> , 140–150 × 90–100 μm	Compressed	Lower Yorkian, Upper Carboniferous	Yorkshire, Scotland	
<i>Aulacotheca idelbergeri</i>	Cylindrical; 30–35 × 6–7 mm	6–9 strong longitudinal ribs represent the sporangia.		Impressed	Westphalian A	Westphalia, Gelsenkirchen, Zeche Holland	Halle (1933)
<i>Aulacotheca iowensis</i>	Spatulate; 5 × 1.5 mm	3–4 tubular sporangia.	<i>Monoletes</i> , 88–165 × 44–121 μm	Compressed	Cherokee Gr.; Middle Pennsylvanian	Redfield, Iowa, USA	Eggert and Kryder (1969)
<i>Goldenbergia glomerata</i>	Obovoid; covered with hairs; 6–8 × 3–4 mm	12–16 tubular concrescent sporangia embedded in thick ground tissue surrounding a hollow centre.	<i>Monoletes</i> , 300–400 × 200–300 μm	Compressed, Synangia arranged in one row along rachis	Westphalian, Pennsylvanian	Dudweiler, Saarbrücken, Germany	Halle (1933)
<i>Schopfitheca boulayoides</i>	Stalked, Clavate-pyriform; covered with dense hairs; 16–27 × 8.5–14 mm		<i>Monoletes</i> , 461–544 × 321–416 μm	Compressed	Carbondale Fm., Middle Pennsylvanian	Will County, Illinois, USA	Delevoryas (1964); Drinnan and Crane (1994)
<i>Rhethinotheca tetrasolenata</i>	Rectangular parallelepiped-shaped; 2–3.6 × 0.7–1.2 mm	4 tubular sporangia (0.4 in Diam.) around a central column of thick-walled elongate cells.	<i>Monoletes</i> , 245–275 × 112–173 μm	Permineralised, may represent <i>A. iowensis</i> .	Carbondale Fm., Middle Pennsylvanian	Williamson County Illinois, UAS	Leisman and Peters (1970)
<i>Halletheca reticulatus</i>	Elongate; 15 × 5 mm	5 thick-walled tubular sporangia embedded in parenchymatous tissue with few secretory canals, around a pentagonal central column of thick walled cells at half length.	<i>Monoletes</i> , 320–450 × 200–260 μm	Permineralised	Calhoun Coal, Mattoon Fm., Late Pennsylvanian;	Berryville, Lawrence County, Illinois, USA	Taylor (1971)
<i>Sullitheca dactylifera</i>	Obpyriform or urceolate; 25 × 10 mm	Ca. 40 tubular sporangia (1 × 10 mm) formed 8–12 groups; each group contains 4–6 sporangia that embedded in ground tissue and extends centripetally.	<i>Monoletes</i> , 440–560 × 330–440 μm	Permineralised	Staunton Fm., Middle Pennsylvanian	Indiana, Iowa, Kansas, USA	Stidd et al. (1977)
<i>Sterzelitheca chemnitzensis</i>	Stalked, bell-shaped; 10 × 4.5–9 mm	12–14 tubular sporangia arranged in a ring around a central hollow, sporangia either free positioned or connected with each other by thin tissue.		3-d preserved, without cell structure; Synangia alternately arranged on axis	Leukersdorf Formation, Early Permian	Chemnitz, Germany	This paper

^a Counted or measured from the original illustration; L, Length; D=Diam., Diameter; Gr., Group; Fm., Formation.

According to the morphological variety of their pollen organs, the medullosan seed ferns have been recognised as the most diverse group of pteridosperms (Millay and Taylor, 1977; Serbet et al., 2006). These organs exhibit a variety of structural patterns, arrangement of sporangia and pollen types. The relationship between most of these genera is not clear at present, and to discuss this matter in detail is beyond the scope of this contribution. *Sterzelitheca* not only adds to a growing list of supposed medullosan pollen organs, but also represents an excellent example of three-dimensional information provided by using X-ray micro-Computer Tomography.

Although numerous medullosan fertile and sterile organs have been described, relatively few organs have been found in organic connection (Serbet et al., 2006). Our Micro-CT study of *S. chemnitzensis* indicates that in this species the pollen organs were borne alternately on the pinnate axes unlike those of *Aulacotheca iowensis* that were borne in clusters on a planated branching system (Eggert and Kryder, 1969). Other Medullosaceae pollen organs such as *Bernaltia* and *Alethopteris norinii* are borne on fronds in the place of a penultimate pinna (Ramanujam et al., 1974) or ultimate pinnule (Seyfullah and Hilton, 2009). Although some pollen organs were borne singly, others like *Rhetinotheca* were arranged in clusters (Leisman and Peters, 1970).

5.3. Functional mould and evolutionary implication of *S. chemnitzensis*

The sporangia of *Sterzelitheca* show both free positions and connections to each other, probably representing different maturation stages. Therefore, we speculate that during the indehiscent stage, the sporangia are enclosed and connected with each other by thin tissues, while during their maturation, the thin tissues progressively withered until only the tips of the sporangia were connected. Finally the tips of the sporangia separated, exposing the distal parts of the synangia, which is helpful for the sporangia releasing pollen grains into air. In this case, it may be speculated that sporangia were coordinated into an organ that served to reduce desiccation and protect against predation, while still providing an efficient method for the release of pollen. Although there is no cellular structure preserved in our material, the thickness of both the inner facing and outer facing sporangial walls show no difference in transverse section. The possibility exists that, as pollen organs matured, cells of the central tissues broke down so that pollen release was toward the centre of the synangium.

The abundance and variety of medullosan seed ferns in the Chemnitz Petrified Forest indicate clearly that this group was one of the most dominant and wide-spread clades. The wide range in anatomical features exhibited by Chemnitz medullosan stems certainly may represent a large plant group rather than variety expressed by one genus. Accordingly, it is not surprising to find corresponding diversity from this site in foliage types and pollen organs associated with and regarded as belonging to the Medullosaceae.

The most complex permineralised medullosan pollen organs, such as *Sullitheca*, *Stewartiotheca*, *Bernaltia* and *Dolerotheca* are considered to have evolved from a similar type of cup-shaped organ with a single ring of pollen sacs, broadly open distally, and with a central hollow (Eggert and Rothwell, 1979). The structural organisation of *Condonotheca* has been interpreted as ancestral to several other types of medullosan pollen organs (Stidd, 1981; Taylor, 1988). The small pollen organ *Halletheca* is also presumed to demonstrate features of the basic ancestral medullosan type (Taylor and Millay, 1981). Although some authors have suggested evolutionary patterns in medullosan pollen organs that have involved an increasing number of pollen sacs and synangial dimension, the validity of these patterns within a phylogenetic context is uncertain. Although our specimen exhibits a relatively simple structure, it should be noted that it occurs in the lowermost Permian, stratigraphically much younger than the structurally more complicated genera.

Our current understanding of the evolutionary development of the seed ferns continues to be incomplete. Specimens like *S. chemnitzensis* are significant to our knowledge of the group because they provide a

basis for extending the morphological range of reproductive organs. More importantly, specimens like the one described in this paper afford an excellent opportunity to determine precisely how certain types of fructifications were borne on pinnate pinna.

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