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Ronny Rössler, Anne-Laure Decombeix, Jean Galtier, Rodrigo Neregato, Sandra Niemirowska, et al..
The limits of life revealed in a silicified micro-ecosystem: Sphenophyllum stems, leaves, and roots
trapped inside an arthropod boring in a Permian calamitalean. *Palaeontographica Abteilung B*, 2021,
302 (1-6), pp.3-35. 10.1127/palb/2021/0073 . hal-03271054

HAL Id: hal-03271054

<https://hal.inrae.fr/hal-03271054v1>

Submitted on 14 Oct 2021

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The limits of life revealed in a silicified micro-ecosystem: *Sphenophyllum* stems, leaves, and roots trapped in an arthropod boring in a Permian calamite

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Abstract

One of the youngest known occurrences of anatomically preserved *Sphenophyllum* Brongniart 1828 is reported from the Permian Motuca Formation, Parnaíba Basin, central-north Brazil. At least 31 stems, densely interwoven to each other and associated with tiny roots and leaves of this extinct herbaceous sphenopsid, were found in a silica-petrified state. Originally grown upright, they squeezed into in the pith of the arborescent calamite *Arthropitys barthelii* NEREGATO et al. 2017, which was additionally caved by putative xylophagous herbivores. Although restricted within natural limits, the *Sphenophyllum* organs show different developmental stages that encompass a majority of juvenile stems and a few ones with initial secondary growth. The stems are of circular to elliptical outline and consist of a central triarch actinostele made of primary vascular tissues and a variable amount of wood. Extraxylary tissues comprise a narrow innermost zone with putative phloem, internal periderm made of rectangular cells arranged in radial files, inner parenchymatous cortex, outer sclerenchymatous cortex, and small-celled layers of bounding tissue. Moreover, *Sphenophyllum* is exhibited to be a frequent climber on the trunk surface of *Psaronius*, *Tietea* and *Grammatopteris* tree ferns or trapped among their adventitious aerial roots. In addition, *Sphenophyllum* cauline members were also found dispersed with other plant organs in a particular type of fossil-rich silicified fluvial sandstone or chert reflecting rapid fossilisation of parautochthonous aspects. These fossil assemblages disclose an underestimated facet of seasonally influenced, densely vegetated riparian forests bordering extended distal fluvial discharges in low-latitude Gondwana. Nevertheless, due to their similar development of major anatomical characteristics, the taxonomic delimitation of late Paleozoic sphenophylls based on vegetative axes alone remains challenging and underlines unexpected long-term stability of especially primary cauline anatomy and vascular architecture in general.

Keywords: *Sphenophyllum*, Anatomy, Animal-Plant-Interaction, Climber, Silicification, Parnaíba Basin, Permian

1 Introduction

Sphenophyllales are an extinct group of herbaceous, climbing or ground-covering equisetophytes, whose stratigraphic occurrences span from the Late Devonian up to the Early Triassic with abundance in the peat-forming Pennsylvanian tropics (TAYLOR et al. 2009). These plants were widely distributed in different palaeogeographic regions, such as the palaeoequatorial areas of Euramerica and Cathaysia (STORCH 1966, 1980; BATENBURG 1977, 1982; HAVLENA 1982, DE-MING WANG et al. 2005) but also extending into higher latitude floral realms of Gondwana (WALTON 1929, ARCHANGELSKY 1960, ANDERSON & ANDERSON 1985, SRIVASTAVA & RIGBY 1983, MCLOUGHLIN 1992, CUNEO et al. 1993) and Angara (NAUGOLNYKH 2003). RÖSLER (1974) reported the first *Sphenophyllum* remains from the Permian of Brazil, discovered in the Parana Basin. Later, RÖSLER & ROHN (1984) figured several leafy shoots likewise preserved as compressions. Besides first indications of *S. thonii* MAHR in Brazil, a large-leaved characteristic form previously documented from Euramerica (MAHR 1868, ABBOTT 1958, BARTHEL 2003), Angara (MEYEN 1978, NAUGOLNYKH 2003, 2015), Cathaysia (HALLE 1927, ASAMA 1970), and African Karroo (LACEY & HUARD-MOINE 1966), they introduced *S. paranaensis*, and underlined a nearly cosmopolitan distribution of sphenophyllaleans.

Sphenophyllum, the first genus of the group, was erected by BRONGNIART (1828) and remained the most common and widespread member. Besides, it is a genus that comprises both compressions/impressions and anatomically preserved petrifications/permineralisations (BATENBURG 1982), whereas convincing correlation at species level remains challenging. Sphenophyllalean species are quite frequent and morphologically diverse in compression/impression preservation (KERP 1984, GALTIER & DAVIERO 1999) up to their epidermal characteristics (ABBOTT 1958, PANT & MEHRA 1963, MEYEN 1970, BARTHEL 1997), and roots (LEGGEWIE 1933, STORCH & BARTHEL 1980, BATENBURG 1982). The mode of circumferential enlargement of the vascular cambium seems to be unique to sphenophyllaleans as the considerable length of their conducting elements is, both sharply contrasting to other wood-forming plants, fossil and extant (CICHAN & TAYLOR 1982). Reproductive organs are reported both from compressions (REMY 1955, KERP 1984, WANG, Y. 1993; DE-MING WANG 2005; BEK et al. 2009) and preservational states that offer 3D aspects, such as coal balls or tuffs (BINNEY 1871, BOUREAU 1964, BARTHEL 1976, 2016, RIGGS & ROTHWELL 1985, ZODROW & GAO 1991, LIBERTÍN et al. 2008). In contrast, petrified/permineralised species that provide detailed anatomical information on vegetative sphenophyllalean organs remain rare and obviously less differentiated (RENAULT 1873, 1876; WILLIAMSON 1874, FELIX 1886, BAXTER 1948, REED 1949, SNIGIREVSKAYA 1959, COQUEL & DANZÉ-CORSIN 1964, BATENBURG 1981, CICHAN & TAYLOR 1982, CICHAN 1985, SCHABILION 1975, WANG et al. 2009, TERREAUX DE FELICE et al. 2019).

Here we document petrified *Sphenophyllum* organs from western low-latitude Gondwana. In recent times, anatomically preserved *Sphenophyllum* has been mentioned repeatedly

from the Permian of the Parnaíba Basin. The stems that are easily recognisable by their characteristic triangular stele not only appeared in densely silicified sandstones or cherts, in which they washed together with fern pinnules or gymnosperm woods and roots (DERNBACH et al. 2002, RÖBLER & NOLL 2002, RÖBLER 2006). *Sphenophyllum* was also found preserved in growth position among adventitious aerial roots of different tree ferns, like *Grammatopteris freitasii* (RÖBLER & NOLL 2002) or *Tietea singularis* (RÖBLER et al. 2019). However, briefly discussed and illustrated by RÖBLER et al. (2020) because of its palaeoecological meaning, *Sphenophyllum* from central-north Brazil remained to be documented in more detail. In this contribution, we describe Permian material showing *Sphenophyllum* plants that once entered the interior of an upright standing calamitalean tree (NEREGATO et al. 2017).

2 Material and Methods

The material studied herein was found in the southern part of the Parnaíba Basin (Text-fig. 1a), between Filadélfia and Araguaína cities, State of Tocantins. The fossil-bearing strata in the north of Tocantins belong to the Motuca Formation of the Balsas Group (Text-fig. 1b) (DIAS-BRITO et al. 2007). The latter is divided from the basis up to the top into the Piauí, Pedra de Fogo, Motuca and Sambaíba formations (GÓES & FEIJÓ 1994). The exact stratigraphy of the host strata remains debated until now and need to be resolved in the future. Summarising all biostratigraphic indications, we consider a Permian age (Cisuralian to Guadalupian) most likely (IANNUZZI et al. 2018). Regarding detailed information on palaeogeographical and geological settings and taphonomic aspects, we refer to CAPRETZ & ROHN (2013), NEREGATO et al. (2015, 2017) and IANNUZZI et al. (2018).

The fossil has been found embedded in well-rounded, well-sorted, and medium-grained fluvial quartz sandstone of which a rim adheres to the stem due to largely silicified pore space (TRÜMPER et al. 2019). The specimen was cut with a trimming saw to reveal both transverse and longitudinal sections. Resulting surfaces were ground and polished with standard procedures and subsequently examined and photographed under reflected light using a Nikon DS-5M-L1 digital camera attached to Nikon Eclipse ME 600 and Nikon SMZ 1500 microscopes. Photomicrographs were processed by NIS-Elements D software version 3.2. Overview images were digitised using an Epson Perfection 4870 Photo scanner. Composite images were created using Corel Draw version X6 and corrected only for contrast and colour. Fossil material described and illustrated in this contribution is stored in the Museum für Naturkunde Chemnitz, Germany, identified with labels K or F and collection number, in the Grand'Eury Collection, MNHN Paris/France, identified with label GE, in the Palaeontological Collection of the Museum für Naturkunde Berlin, identified with label PB, in the Senckenberg Natural History Collection Dresden, identified with label MMG, and in the private collections of SANDRA NIEMIROWSKA, Warsaw/Poland, and HANS-JÜRGEN WEIß, Rabenau/Germany.

3 Description of the material

3.1 General features

A calamite stem assigned to as *Arthropitys barthelii* NEREGATO et al. (2017) is represented by one slice, 11 mm thick and 116 mm in maximum diameter. This species usually shows small piths surrounded by soft parenchyma-rich homogeneous wood (Neregato et al. 2017). In the present specimen, however, an asymmetric hole, running from the pith, is extended laterally into the wood. At least 31 *Sphenophyllum* axes, attaining 4–9 mm in diameter, and many tiny roots had been preserved in that calamite's interior (Pl. 1, Fig. 1, 2). Various *Sphenophyllum* organs took possession of the wood cavity and started simultaneous growth (Pl. 1, Fig. 2). The unusual hole shows an irregular outline in transverse section. Some of the innermost segments of the calamite wood were affected and cut in favour of a progressively widened cavity. At the interface between the wood and the cavity, abundant small spherical coprolites of 40–60 μm diameter reveal the putative cause of damage, most likely xylophagous animal boring (Pl. 1, Figs 4, 5). The special microhabitat inside the calamite obviously supported and sheltered the early development of likely one generation of juvenile *Sphenophyllum* axes and associated leaves and roots as well. Preservation of the stems is quite detailed, including primary and secondary vascular tissues, different extraxylary tissues, attached branches, leaves, and roots as well (Pl. 2–5). Probably due to a varying growth rate, the single *Sphenophyllum* stems show a slight variation in their ontogenetic stages, whereupon juvenile ones prevail due to the limits provided by the microhabitat. Due to the limited thickness of the available calamite specimen, we cannot decide whether the aerial stems had grown separate or, at least in part, diverged from each other. In contrast to the longitudinally ridged appearance of many published *Sphenophyllum* stems, our axes show an exclusively circular to elliptical outline in transverse section, both in nodal or internodal regions. Although both the developmental stage and preservation quality vary in the presented *Sphenophyllum* organs, the following description will summarise the most significant characteristics documented.

3.2 Anatomy of primary vascular tissues

The primary xylem is actinostelic and triangular, whereas the arms include an angle of approximately 120° . Protoxylem elements are circular in transverse section, 19 (12–25) μm in diameter. In some cases, they seem to entirely surround a lacuna of ca. 53–85 μm diameter (Pl. 3, Fig. 6). In other cases, however, the protoxylem seems restricted to a crescent-shaped area on the inner side of the lacuna (Pl. 2, Fig. 2; Pl. 4, Fig. 3). The outer side of the lacuna is surrounded by larger cells that are interpreted as secondary xylem based on their continuity with layers of secondary xylem in the interfascicular regions (Pl. 2, Fig. 2). Primary xylem maturation is exarch. In transverse section, the metaxylem is made of circular to polygonal elements mainly elongated perpendicularly to the arms in the transverse section (Pl. 2, Fig. 3). They average 48 (24–125) μm in diameter with the largest ones in the middle of the triangle. Metaxylem elements show lignified walls and spiral thickenings (Pl. 2, Figs 1, 2).

In places, between tracheids of the metaxylem triangle and along the concave metaxylem arms, in the interspace between metaxylem and secondary xylem, thin-walled, small-celled parenchyma can be recognised (Pl. 4, Fig. 3, white arrows).

3.3 Anatomy of secondary vascular tissues

Initial secondary xylem is recognised in all stems of K6040. Fascicular segments with generally smaller tracheid diameters averaging 58 (32–91) μm and more tracheids per file (9–12) can be distinguished from interfascicular parts that show larger tracheid diameters averaging 110 (69–148) μm and fewer tracheids (5–8) per file (Pl. 2, Fig. 3). The formation of secondary xylem tracheids appears to have started in the interfascicular regions (Pl. 2, Fig. 2; Pl. 4, Fig. 3; Pl. 6, Fig. 5). Nevertheless, secondary growth in both the fascicular and interfascicular regions shows a regular concentric arrangement relating to the overall stem (Pl. 2, Fig. 3). The majority of stems show radial files of secondary xylem of only 1–4 tracheids, only in one stem up to 8–12 tracheids per file are recognisable. Secondary xylem tracheids are mainly of a square to circular outline in transverse section and rarely flatten radially against adjoining tracheids. They have circular to elliptical pits (Pl. 2, Fig. 5), are elongated considerably in an axial direction to reach several millimetres in length and show tapering end walls. Due to the limited size of the specimen, we were not able to measure the exact length of the tracheids.

Especially in the fascicular segments, tracheid files are separated by uni- to biseriate rays up to 80 μm wide (Pl. 2, Fig. 3). The secondary xylem also contains parenchymatous cells averaging 28 (20–36) μm in diameter that occur isolated or in clusters between the tracheids, forming a network of parenchyma within the wood (Pl. 2, Figs 1–3; Pl. 3, Fig. 6; Pl. 4, Fig. 3, black arrows).

3.4 Extraxylary tissues

All *Sphenophyllum* stems recognisable in K6040, irrespective their developmental stage, are bounded by an epidermis (EL at Pl. 2, Figs 1, 2). Beneath the latter, there is a conspicuous subepidermal layer two-cells thick and averaging 25 (40–55) μm , made of thin-walled isodiametric to polygonal cells, in transverse section ca. 15–35 μm in diameter (Pl. 2, Figs 1, 3; Pl. 3, Figs 7, 8: black arrows).

Beneath this outer layer, there are fibre-like, longitudinally elongated cells with thickened walls (“Cs” on Pl. 2, Figs 1–3, 6; Pl. 3, Figs 7, 8). In contrast to adjoining tissues, they are dark-brown coloured. In transverse section, they are circular to polygonal with a diameter of 13–32 μm . In longitudinal sections, they show oblique end walls and reach ca. 1 mm in length (Pl. 2, Fig. 6).

The next layer that adjoins centripetally is made of thin-walled (? parenchymatous) cells, 230–540 μm long, with rectangular to oblique end walls (“Cp” on Pl. 2, Figs 1–3, 6; Pl. 3, Figs 7, 8). In transverse section, these cells show circular to polygonal outlines and

average 52 (25–72) μm in diameter. Further centripetally, these cells are often heavily compressed in a radial direction (Pl. 2, Fig. 4).

Centripetally to the latter there is a layer of periderm ca. 140–300 μm in radial width and recognisable in all stems (“PD” on Pl. 2, Figs 1–4; Pl. 3, Fig. 8). It consists of rectangular cells, averaging 64–70 μm tangentially and 25–30 μm radially. These cells are arranged in radial files extending to a maximum of 8 cells per file (Pl. 2, Figs 1–4). In longitudinal section, they average 104 (77–125) μm in length (Pl. 2, Fig. 6).

Between the last layer and the periphery of the secondary xylem, there are a few thin-walled cells of circular to elliptical outline in transverse section. They average 25–50 μm in diameter and could represent phloem (Pl. 3, Figs 5, 6).

To sum up, we would like to stress that all *Sphenophyllum* stems trapped in the calamite’s cavity seem to be in a stage prior to decortication. Primary cortex and bounding tissues are still mostly intact and have not been sloughed off. However, periderm formation has already started and resulted in more or less compaction among large-celled cortex parenchyma (Pl. 2, Fig. 4).

3.5 Leaves

A few stems show thickened nodes with whorls of attached dichotomously veined leaves (Pl. 1, Fig. 3; Pl. 3, Fig. 4; Pl. 4, Figs 4–6). In one transverse section, six lens-shaped bases of initial leaves were counted close to the stem periphery (Pl. 3, Figs 1, 4). At this position they are ca. 300 μm thick, vascularised by 3–6 tiny bundles that are embedded in the mesophyll, associated to cells with brownish contents (? fibres). The section figured in Pl. 3, Fig. 4 shows the leaves cut slightly above their departure. Longitudinal sections exhibit the leaves arched upwards and closely spaced against the stem (Pl. 1, Fig. 3; Pl. 4, Fig. 4), according to the limited space available between adjoining *Sphenophyllum* organs inside the cavity. All leaf remains attached to anatomically preserved *Sphenophyllum* stems in the present material (Pl. 3, Figs 1, 4, 5; Pl. 4, Figs 4, 6), including those found among the aerial roots of a *Tiетеa singularis* trunk (Pl. 6, Figs 4–5) show relatively broad, rapidly widening laminae. No recognisable division of the laminae was observed, which points to rather broad-leaved, entire-margined leaves in contrast to bifid or linear types. Based on the general organisation of leaves at the node (Pl. 3, Fig. 1), they likely departed in pairs opposite each of the three primary xylem arms (Pl. 3, Fig. 5). Small structures leaving with a slightly downwards orientation below the leaves could correspond to rootlets (Pl. 4, Fig. 4).

3.6 Roots

Spaces between *Sphenophyllum* stems are densely filled by associated roots, which even crowd into the softer rays between wood fascicles of the host plant (Pl. 1, Fig. 4; Pl. 4, Fig. 4; Pl. 5, Figs 2–3, 7). In transverse section, they are of circular outline averaging 550

(270–950) μm in diameter. A central vascular bundle reaching 100 to 200 μm in diameter is diarch and made of up to 20 tracheids (Pl. 5, Figs 4–6). The smallest elements, probably representing protoxylem, are 10 μm in diameter; the larger ones measure 20–30 μm in diameter. Tracheid wall structure or pitting was not discernable. A darker coloured well-defined endodermal layer, ca. 20–50 μm wide, separates the vascular bundle from the parenchymatous cortex (Pl. 5, Figs 5–7). The latter is made of elliptical to polygonal cells averaging 40–80 μm . Roots in the present material do not show any secondary growth and, thus, may represent only juvenile ones.

4 Discussion

4.1 Occurrence, preservation, and growth of Permian *Sphenophyllum* species from Brazil and other sites

The first mention of *Sphenophyllum* in Brazil was provided by RÖSLER (1974), who introduced *S. brasiliensis* based on compression material from the Permian (Sakmarian/Artinskian) Rio Bonito Formation of Cambuí Coal Mine at Figueira, Paraná State. Later, again from the Paraná Basin, RÖSLER & ROHN (1985) introduced *S. paranaensis* based on isolated leaves, verticils, and articulated stems from the Permian (Wordian) Rio do Rasto Formation at Dorizon. Moreover, RÖSLER & ROHN (1985) illustrate additional material from the same site identified as *Sphenophyllum* cf. *S. thonii* and emphasised its similarity to *S. thonii* described from the Karoo Basin in southern Zimbabwe, Africa (LACEY & HUARD-MOINE 1966), and to *S. thonii* var. *minor* STERZEL from the Black Forest, SW Germany (STERZEL 1895). Based on the general outline, size, and venation of the leaves, *S. thonii* var. *minor* could be included in *Lilpopia raciborski* (LILPOP) CONERT et SCHAARSCHMIDT 1970, a heterophyllous sphenophyll with reproductive organs alternating with leaves at the nodes from the early Permian travertine of Karniowice, Poland (LIPIARSKI 1972), and Sobernheim, SW Germany (KERP 1984). Beyond its type locality in the early Permian of Thuringia, central Germany (MAHR 1868, BARTHEL 2003), *Sphenophyllum thonii* MAHR 1868 and closely related forms are widely distributed in the late Pennsylvanian and early Permian of several floral realms such as Euramerica (ABBOTT 1958), Angara (MEYEN 1978, NAUGOLNYKH 2003, 2015), and Cathaysia (HALLE 1927, ASAMA 1970). Although the occurrence of sphenophylls in Brazil confines to compression taxa until now, there are several characters of the early Permian “*S. thonii* group”, which would correspond to single features of the new material presented in this study (see Pl. 3, Figs 1, 4, 5; Pl. 4, Fig. 6). Among them are (1) the number of veins (four to five) entering individual leaves, (2) the broad-triangular wedge-shaped leaves without any deep incision of the lamina, (3) the number (six) of leaves attached to every node, (4) the slightly sexangular but not deeply ribbed stems, and (5) the wide intercontinental occurrence of the “*S. thonii* group” forms. Recently, impressions identified as *Sphenophyllum thonii* were also illustrated from central-north Brazil. Among callipterids similar to *Rhachiphyllum schenkii* (HEYER) KERP and a few other pteridophytes they were reported from the Pedra de Fogo Formation (IANNUZZI et al. 2018: figs 4, 5).

Here, we document in-depth the first anatomically preserved *Sphenophyllum* organs found among the increasing Permian fossil record of the Parnaíba Basin (NEREGATO et al. 2017). This material kept a “life snapshot”, which reveals an interesting ecological relationship between a tree-sized calamite and its surrounding supposed ground cover or climbers. The unusual habitat, the pith cavity of the calamite, was initially further caved by putative xylophagous animals. *Sphenophyllum* is usually regarded as a common constituent of the understorey in late Paleozoic swamp environments (TAYLOR et al. 2009). Although the majority of occurrences seem to confirm this ecological preference and even point to peat-forming conditions, our new material enlarges the variety of potential habitats to mineral stands of floodplains accompanying large rivers. Since there is no evidence of peat-forming swamps in the Permian of the Parnaíba Basin (CAPRETZ & ROHN 2013, NEREGATO et al. 2015), we would like to interpret the sphenophylls presented here as hygrophilous climbers growing in densely vegetated riparian forests and thus being part of the azonal vegetation of an extended fluvio-lacustrine discharge system (TRÜMPER et al. 2020).

Growth strategies recognised in sphenophyllaleans are manifold and reach from the ground cover to non-self-supporting scramblers or climbers. Among all of them, the latter was certainly more competitive in gaining light. As indicated by the presence of climber hooks attached to *Sphenophyllum* twigs (BARTHEL 1997) and the presence of *Sphenophyllum* stems among aerial roots on the surface of usually tall tree ferns (MICKLE 1984, RÖBLER et al. 2020), the climbing sphenophyte was documented to reach also higher levels in the forest beyond the ground cover vegetation.

In the Parnaíba Basin of Brazil, *Sphenophyllum* was evidenced to climb up on different tree fern trunks and, hence, became occasionally trapped among aerial roots (Pl. 6, Figs 1–4). As tiny *Sphenophyllum* roots anchored the emerging axes at the tree fern root mantle, was recognised in *Tietea singularis* and, likewise, in *Grammatopteris freitasii* fern trunks (RÖBLER et al. 2020). As the preservational places on the outer surface or between aerial roots of tree fern trunks suggest, the sclerenchyma in the cortex of the *Sphenophyllum* stems underlines that our forms could have attained climbing growth. Although relatively abundant in the Permian of the Parnaíba Basin and already illustrated by RÖBLER & NOLL (2002), until now the species of the sphenophylls remained to be identified.

Based on a few transverse coal ball sections from China, WANG et al. (2009) erected three new fossil species, *S. guizhouense* from the upper Permian (Changhsingian) Wangjiazhai Formation of Liupanshui City, Guizhou Province, *S. taiyuanense*, and *S. truncatum* from the lower Permian (Asselian–Sakmarian) Taiyuan Formation in Taiyuan City, Shanxi Province. The first species seems to show a juvenile axis having an unusual enlargement of the distal primary xylem arms apparently forking into two protoxylem strands each. Such character would be noteworthy and is usually not known from *Sphenophyllum*. However, even the authors were not sure about this feature writing in the species diagnosis “Probably each tip of the arm with two protoxylem strands” but provided only one transverse section photograph at low magnification. Furthermore, the illustrated *S. guizhouense* axis shows only 50% of the transverse section with adequate cell preservation, excluding the recognition of further detail. The figured specimen shows

remnants of a parenchymatous cortex but lacks the striking periderm layer and any secondary growth recognisable in both the classical material of *S. stephanense* (RENAULT 1873) and our new material from Brazil. Accordingly, it could probably result from a very juvenile stage. *S. truncatum* also reflects an early stage of development. However, the “nearly parallel edges” of the primary xylem arms as highlighted in the species diagnosis are rather cone-shaped judging from the provided figs 19C, D and are only recognisable at fig. 20A but contrasting the former figures. Anyway, two xylem arms of the latter specimen are incompletely preserved. As the single *S. guizhouense* axis, the two figured specimens of *S. truncatum* lack both periderm and secondary growth. In contrast, *S. taiyuanense* represent a more mature axis with several layers of secondary xylem tracheids. Any variation resulting from both the ontogeny and taphonomy was unfortunately not considered or substantiated by any illustration. Judging from the published photographs at low magnification, it remains challenging to approve species-diagnostic characters in the three species. Even though *S. guizhouense* is not reproducible as a new fossil species, the only figured specimen is probably the youngest anatomically preserved representative of the genus.

Compared to the Pennsylvanian coal-ball material, anatomically preserved *Sphenophyllum* organs from the Permian remain rare. Although figured or touched upon in several publications as a component of fossil floras or prominent fossil assemblages (e.g., BARTHEL et al. 2002, GALTIER et al. 2011, BARTHEL 2016), they represent single petrified or permineralised finds made in cherts or pyroclastics (HILTON et al. 2001; BARTHEL et al. 2001, pl. 1, fig. 5; BARTHEL 2002: fig. 10; GALTIER et al. 2011, fig. 5G; BARTHEL 2016: figs 40–44). However, neither cellular detail nor ontogenetic variation or taphonomic specifics was documented in detail. In some cases, only a few single rubble stones were available (Pl. 8, Fig. 3), in other cases, preservation did not allow closer study (Pl. 8, Figs 5, 6). They had mostly been attributed to the forest ground cover to some extent consisting of zygopterid or anachoropterid ferns and sphenophylls (WANG et al. 2012; BARTHEL 2016). Despite their possible identification at the generic level, recognition and delimitation of species seem challenging. This is mostly due to taphonomic limitations, the scarcity of material, or the absence of appropriate anatomical differences. Accordingly, is it noteworthy to emphasise that the Autun specimens (RENAULT 1876) and the new stems described in this study constitute to date the only Permian representatives of *Sphenophyllum* for which the anatomy is documented in closer detail. Nevertheless, despite their excellent anatomical preservation, any discernible anatomical differences are mostly due to ontogenetic variation.

4.2 *Sphenophyllum* organs compared

The leaves of *Sphenophyllum* are predominantly wedge- or fan-shaped to bifid, multiveined, and of highly morphological diversity comprising both heterophylly and even considerable intraspecific variability (GALTIER & DAVIERO 1999; BASHFORTH & ZODROW 2007). They are borne superposed at thickened nodes of slim, diversely branched, upright axes up to one centimetre in diameter. Accordingly, many taxa have been proposed on the basis of differences in leaf size, shape, and venation characteristics, but hardly represent

natural species (SCHABILION & BAXTER 1971). The leaves revealed in different sections of our material (Pl. 3, Figs 1, 4, 5; Pl. 4, Figs 4, 6; Pl. 6, Figs 4–5) appear to characterise broad-leaved sphenophylls without deep incision of the lamina. In contrast, the leaves of the well-reputed species *S. plurifoliatum* WILLIAMSON et SCOTT 1895 are described as of the linear type, a significant reason that these leaves have initially been assigned to *Asterophyllites* (WILLIAMSON 1874). While WILLIAMSON & SCOTT (1895) mention that the number of leaves in their new species from Oldham, England, should not have been less than 18, BAXTER (1948) referring to specimens from the USA summarised the number of leaves to six.

S. stephanense RENAULT 1873 from the Upper Pennsylvanian of Grand-Croix, France, was the first species that provided more insight into the vascular architecture of vegetative axes and confirmed the association with the well-known fan-shaped leaves and ribbed axes (GALTIER 2008). Minor differences between *S. stephanense* and the later introduced *S. quadrifidum* RENAULT 1876 could represent variability within the same species, and *S. stephanense* has priority in terms of taxonomic treatment (DOUBINGER et al. 1995). In our material, the stems are of circular outline and not ribbed with concave emarginations at all, but the appearance of attached leaves resemble those illustrated by RENAULT (1876). Other characters such as different types of parenchyma in the stele or the cortex are also very similar to RENAULT's material (compare Pl. 4, Fig. 3 with Pl. 8, Fig. 2). However, probably due to the plane of the section close to the next node, *S. stephanense* shows leaf traces to six leaves inside the cortex (Pl. 8, Fig. 1). These leaf traces occur as two pairs associated with arm A, as bifurcate and trifurcate traces at arm B or as trifurcate and probably quadrifurcate at arm C (Pl. 8, Fig. 1). Considering a slight obliquity of the stem, the leaf traces divide once or twice, and probably result in four and not "three or four" veins, which was the primary criterion to distinguish *S. stephanense* from *S. quadrifidum*. This variation may question the distinction between the two species. Finally, most of the figured specimens (BOUREAU 1964: figs 86 A–B; DOUBINGER et al. 1995: fig. 80) show leaves with three lobes. Nonetheless, in our material from Brazil, the number of vein-like strands seem to be four or five (Pl. 3, Figs 1, 4; Plate 4, Fig. 6) but may also vary according to differences in the plane of the section or as a result of natural variability.

Decorticated *Sphenophyllum* stems from the Permian of Autun (RENAULT 1873: pl. 2, figs 6, 9) show more homogeneous metaxylem without any parenchyma between the tracheids compared with those from Grand Croix (Pl. 8, Fig. 2) or in the new material from Brazil (Pl. 4, Fig. 3). Otherwise, the appearance of the Autun material, published by RENAULT without any specific epithet, resembles in its triangular protoxylem arms with the decorticated specimen from the Permian of Freital in both relatively homogeneous metaxylem and the very small protoxylem lacunae (Pl. 8, Fig. 3).

In contrast to the leaves, anatomically preserved vegetative axes of the Sphenophyllales show a considerable morphological and anatomical similarity and, therefore, complicate species delimitation since ages (GOOD 1973). Nevertheless, BOUREAU (1964) listed seven species of permineralised *Sphenophyllum* based on minor cauline anatomical differences. A triarch actinostele characterises typical stems, such as the differing amount of secondary growth and, especially in juvenile axes, a large portion of extraxylary tissues do.

Due to its differences in secondary growth, compared to other wood-forming plants, *Sphenophyllum* was several times subjected to detailed study for revealing function and differentiation of its apical and lateral meristems (GOOD & TAYLOR 1972, CICHAN & TAYLOR 1982). Nevertheless, several workers underlined that internodal anatomy representing the majority of investigated sections does not yield reliable characteristics for species segregation (e.g., BAXTER 1948).

S. plurifoliatum, a common form from the Early to Late Pennsylvanian of Euramerica, is known in hundreds of specimens yielding various stages of branching. It is highly variable and probably comprises the majority of decorticated examples with extensive secondary development and includes several orders of branching (BAXTER 1948, SCHABILION & BAXTER 1971, GOOD 1973). In contrast, *S. constrictum* PHILLIPS 1959 and *S. multirame* (DARRAH 1968) GOOD represent small shoots with little secondary growth. They were reported in organic connection to *S. plurifoliatum* (DARRAH 1968, SCHABILION 1969). *S. constrictum* has small bifid leaf tips, whereas *S. multirame* differs from others in having linear leaves that show lobes with a distinct abaxial furrow and are without superimposed arrangement (GOOD 1973). However, due to the wide leaf shape variation in *Sphenophyllum*, slight morphological differences seem to be a vague taxonomic feature. *S. reedae* GOOD 1973 is considered the only species of the genus showing apical cell segmentation in a dextrorse direction (GOOD 1973).

One of the characteristics revealing differences in anatomically preserved species is the pitting in the secondary xylem. The characteristic reticulated-scalariform wall structure of the large secondary xylem tracheids was first mentioned, but not illustrated, by DAWSON (1865) from the Pennsylvanian of Nova Scotia, Canada. While the Pennsylvanian/Permian forms seem to share groups of crowded elliptical to circular bordered pits (e.g., RENAULT 1873, WILLIAMSON & SCOTT 1895, BAXTER 1948, CICHAN 1985), the Mississippian forms show scalariform pits (GALTIER 1970, TERREAUX DE FELICE et al. 2019). However, the oldest known sphenophyllalean forms with preserved anatomy from the Late Devonian of China, such as *Hamatophyton* LI et al. 1995, *Rotafolia* WANG et al. 2005, and *Pleurorhizoxylon* ZHANG 2018 show various transitions from radially elongated “scalariform” to multiscalariform or elliptical bordered pits (LI et al. 1995, DE-MING WANG 2005, ZHANG et al. 2018). In *S. plurifoliatum*, not only the secondary xylem but also the metaxylem shows elliptical bordered pits (BAXTER 1948). In our material, in contrast, the metaxylem seems to exhibit spiral thickenings, but the availability of longitudinal sections was too limited to be sure in that case. Moreover, the stem diameter of *S. plurifoliatum* identified among North American specimens is reported as not exceeding 4 mm (BAXTER 1948), whereas WILLIAMSON & SCOTT (1895) reported mature stems up to 1 cm.

Notable is also the peculiar system of stelar parenchyma revealed in *S. plurifoliatum* and even existing in our material. After a long debate, CICHAN (1985) confirmed the existence of a real ray system in *Sphenophyllum* wood, although with significant differences compared to other wood-forming plants. Besides, there is axial parenchyma between tracheids of the primary and secondary xylem and within the secondary xylem (Pl. 4, Fig. 3).

S. insigne WILLIAMSON et SCOTT 1895 was first reported from the Mississippian of Scotland and formally differs in having more prominent rays in the interfascicular wood, showing scalariform pits in the radial tracheid walls, the presence of large “sieve cells” in the phloem, and the presence of protoxylem lacunae. The latter is also common in our material and, according to BAXTER (1948), even in *S. plurifoliatum*. Confirming previously described anatomical characteristics, TERREAUX DE FELICE et al. (2019) assigned new material from the Montagne Noire, France, and Saalfeld, Germany, to *S. insigne*. However, the existence of protoxylem lacunae could also depend on the plane of section, the stage of growth extension in the stem, or only preservation rather than representing any specific differences. Specimens representing very early stages of ontogenetic development often lack any lacunae (Pl. 8, Fig. 4) or show the beginning formation of them (Pl. 8, Fig. 2). The new specimens from Brazil display different anatomies of the lacunae. In some instances, the lacunae are apparently “closed” on the exterior side by a layer of secondary xylem (e.g., Pl. 4, Fig. 3), while in others there seem to be primary xylem all around the lacunae (e.g., Pl. 3, Fig. 6). Regardless of their particular developmental stage, specimens from other occurrences also exhibit differences in manifesting lacunae or not (Pl. 8, Figs 3–4). In some of these, the formation of protoxylem lacunae even differs in the same section (Pl. 8, Fig. 2).

In contrast to the primary and secondary vascular tissues, also extraxylary tissues could reveal features of specific value. Nevertheless, the recognition of both similar ontogenetic stages and changes in the latter remains critically. Differences are reported in the sclerotisation of the outer stem cortex. Except for *S. constrictum* (PHILLIPS 1959) and *S. reedae* (GOOD 1973) which show an exclusively parenchymatous cortex, many *Sphenophyllum* stems have an outer cortex made of thick-walled sclerenchymatous cells, so that this character is often linked to mature axes and excluded for younger ones (GOOD & TAYLOR 1972, BATENBURG 1982). Otherwise, mature axes have already sloughed off their primary cortex and developed an early initiated multi-layered periderm. Although our *Sphenophyllum* axes represent relatively young shoots, a fibrous outer cortex is already recognisable, as well as a juvenile periderm. This stage of development allows us to view the organisation of the primary cortex and the secondary tissues and shows that the specimen likely could develop further. The epidermis of *Sphenophyllum* stems is mostly designated thick-walled (RENAULT 1885: Pl. D, 5; REED 1949, DARRAH 1968), except that in *S. constrictum* which is described as thin-walled parenchymatous (PHILLIPS 1959). In our material, the epidermis is made of small, rather thin-walled cells, but beneath it one to two layers of subepidermal cells are recognisable. Leaf anatomy with vascular bundles and accompanying fibre-like cells mostly resembles those figured by RENAULT (1876).

Due to the lack of reproducible anatomical characters, we refrain from naming the studied specimens keeping in mind that characters relevant for systematics and particular species distinction are hardly recognisable from cauline members alone. Nevertheless, we see some relationships to compressions of the “*Sphenophyllum thonii*” group, which is nearly globally distributed during the early Permian.

6 Conclusions

- 1 We report the first anatomically preserved *Sphenophyllum* from Permian low-latitude gondwanan riparian forests of the southwestern Parnaíba Basin, central-north Brazil.
- 2 The material consists of 31 stems, several attached leaves, and many small roots, all of them representing early developmental stages. The various *Sphenophyllum* tissues were found silica-petrified in excellent cellular detail filling the pith cavity of the arborescent calamite *Arthropitys barthelii* NEREGATO et al. 2017.
- 3 Prior to colonisation with *Sphenophyllum* organs, the pith cavity was asymmetrically enlarged by putative animal boring but, nevertheless, spatially restricted the lifetime of intruding plant organs. Due to small spherical coprolites close to the smooth cut front, the boring is attributed to xylophagous arthropods.
- 4 Although the *Sphenophyllum* stems show slightly different stages of secondary growth, they remained corticated. Thus, various tissues surround the xylem, including putative phloem, initial periderm, differentiated cortex, subepidermal layers, and epidermis.
- 5 *Sphenophyllum* stems were additionally found as putative climbers on the surface of tree fern stems, trapped mostly among their exposed aerial roots, or floating in a particular type of fossil-rich silicified fluvial sandstone or chert. Besides other plant remains such as fertile pinnae or axes of ferns such fossil assemblages provide more in-depth insight into usually hidden elements of the azonal vegetation bordering extended distal fluvial discharges.
- 6 *Sphenophyllum* stems of both the Pennsylvanian and Cisuralian closely resemble in their internal organisation. Despite the lack of adequate stratigraphic control for the Brazilian specimens, unexpected long-term stability of primary cauline anatomical characteristics can be concluded. Accordingly, the taxonomic delimitation of anatomically preserved sphenophylls based on vegetative axes alone remains challenging.

Acknowledgements

We are indebted to Rosemarie Rohn, Rio Claro, and Zhuo Feng, Kunming, for providing literature and Dario De Franceschi, Paris, for access to the Grand'Eury Collection (MNHN Paris). Frank Lócse, Uhlsdorf, Manfred Barthel (†), Berlin, and Lutz Kunzmann, Dresden, are acknowledged for their help with several collection enquiries. Mathias Merbitz, Volker Annacker, both Chemnitz, ensured detailed preparations. Ireneusz Niemirowski, Warsaw, provided additional photomicrographs, and Evgeniy Potievsky kindly digitised some overview images. Finally, we would like to thank for the financial support offered by the Deutsche Forschungsgemeinschaft (DFG grant RO 1273/4-1 to RR).

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Text-Figure 1 and explanation

- a: Map of Brazil with the position of Tocantins State (TO), Maranhão State (MA) and Piauí State (PI).
- b: Detailed map showing the municipalities close to the fossil sites. In orange, outcrops of the Pedra de Fogo Formation and in blue, the Motuca Formation (modified from IANNUZZI et al. 2018).
- c: Stratigraphic column of the Balsas Group of the Parnaíba Basin, northern of Brazil (modified after VAZ et al. 2007 and MENZIES et al. 2018).

Plates 1–8 and explanations

Plate 1

Diverse *Sphenophyllum* organs preserved in a cavity inside a calamite stem (*Arthropitys barthelii* NEREGATO et al. 2017), K6040, Permian of northern Tocantins, central-north Brazil.

Fig. 1 Calamite stem in transverse section showing *Sphenophyllum* stems, leaves, and roots anatomically preserved in the pith cavity (PC), which was deepened by putative animal boring (arrows). Scale bar: 10 mm.

Fig. 2 Detail of Fig. 1 showing *Sphenophyllum* stems at slightly different growth stages. The rectangle indicates a closeup view given in Fig. 4. Scale bar: 5 mm.

Fig. 3 *Sphenophyllum* stem in longitudinal-radial section showing extraxylary tissues (ET) and one thickened node with two upwards departing leaves (L). Scale bar: 1 mm.

Fig. 4 Detail of Fig. 2 showing the area between a *Sphenophyllum* stem (*) and the cut calamite's pith margin with fascicular wedges (FW) and interfascicular rays (IR). A dense tangle of *Sphenophyllum* roots (R) gaining every space even between wood fascicles. Clusters of small spherical coprolites (arrows) suggest xylophagy. Scale bar: 500 μm .

Fig. 5 Detail of the cut calamite wood with intruding *Sphenophyllum* roots (R) and small spherical coprolites (arrow). Scale bar: 100 μm .

Plate 2

Diverse *Sphenophyllum* organs preserved in a cavity inside a calamite stem (*Arthropitys barthelii* NEREGATO et al. 2017), K6040, Permian of northern Tocantins, central-north Brazil.

Fig. 1 *Sphenophyllum* stem with most secondary growth in both transverse (above) and longitudinal sections. Preserved tissues show protoxylem (PX) surrounding small lacunae, central metaxylem arms (MX) surrounded by secondary xylem (SX), periderm (PD), inner parenchymatous cortex (Cp), outer sclerenchymatous cortex (Cs), the epidermis and underlying layer (EL). Scale bar: 500 μm .

Fig. 2 *Sphenophyllum* stem with less secondary growth in both transverse (above) and longitudinal sections. Preserved tissues show protoxylem (PX) surrounding small lacunae, one central metaxylem arm (MX) surrounded by secondary xylem (SX) and some axial parenchyma (P), periderm (PD), inner parenchymatous cortex (Cp), outer sclerenchymatous cortex (Cs) and epidermal layer (EL). Scale bar: 200 μm .

Fig. 3 *Sphenophyllum* stem with most secondary growth in transverse section. Protoxylem lacunae (arrows) lie at the ends of the metaxylem arms (MX), fascicular wood (SX_f) shows uni- to biseriate rays (white arrowhead), interfascicular wood (SX_i) shows largest tracheids. Interspaces between tracheids are often filled with small-celled parenchyma. External to the xylem there lies the cambial region, ?phloem (Ph), periderm (PD), cortex and epidermal layer (EL). Scale bar: 500 μm .

- Fig. 4 Area between one xylem arm with protoxylem lacuna (arrow), periderm arranged in files (PD) and inner parenchymatous cortex (Cp). Scale bar: 100 μm .
- Fig. 5 Secondary xylem tracheids in longitudinal radial section. Note the circular to elliptical pitting that is only patchy recognisable due to ferric staining. Scale bar: 100 μm .
- Fig. 6 Extraxylary tissues in longitudinal section. Periderm (PD), inner parenchymatous cortex (Cp), outer sclerenchymatous cortex (Cs), epidermal layer (EL). Scale bar: 200 μm .

Plate 3

Diverse *Sphenophyllum* organs preserved in a cavity inside a calamite stem (*Arthropitys barthelii* NEREGATO et al. 2017), K6040, Permian of northern Tocantins, central-north Brazil.

- Fig. 1 *Sphenophyllum* stem in a transverse section surrounded by six leaves borne on a node below the plane of section. The rectangle indicates a closeup view given in Fig. 4. Scale bar: 1 mm.
- Fig. 2 *Sphenophyllum* stem in oblique longitudinal section showing closely-spaced nodes with initial appendages. Scale bar: 1 mm.
- Fig. 3 *Sphenophyllum* stem in longitudinal view showing terminal shoot with tiny leaves. Scale bar: 1 mm.
- Fig. 4 Leaf in transverse section showing mesophyll and four to five vein-like strands (arrows). Scale bar: 500 μm .
- Fig. 5 *Sphenophyllum* stem with stele, less secondary growth and extended cortex. Two still attached leaves (arrows) depart at the side of one xylem arm from the stem. Scale bar: 500 μm .
- Fig. 6 External to the interfascicular region of the xylem of a *Sphenophyllum* stem, there is a layer of circular elements representing probable phloem and phloem parenchyma (Ph). Scale bar: 200 μm .
- Fig. 7 Tissues external to the xylem in a more mature stem. SX: secondary xylem, Ph: phloem, PD: periderm, Cp: parenchymatous cortex, Cs: sclerenchymatous cortex, EL: epidermis and subepidermal cell layers. The black arrow points to the subepidermal layer. Scale bar: 100 μm .
- Fig. 8 Tissues external to the xylem in a less mature stem. SX: secondary xylem, PD: periderm, Cp: parenchymatous cortex, Cs: sclerenchymatous cortex, EL: epidermis and subepidermal cell layers. The white arrow indicates a possible leaf trace crossing the cortex; the black arrow points to the subepidermal layer. Scale bar: 100 μm .

Plate 4

Diverse *Sphenophyllum* organs preserved in a cavity inside a calamite stem (*Arthropitys barthelii* NEREGATO et al. 2017), K6040, Permian of northern Tocantins, central-north Brazil.

Fig. 1 *Sphenophyllum* stem with a departing lateral branch (arrow). Scale bar: 1 mm.

Fig. 2 Detail of Fig. 1 showing the tip of the lateral branch. Scale bar: 200 μ m.

Fig. 3 *Sphenophyllum* stele with only two layers of secondary xylem tracheids. Note the axial parenchyma (white arrows) between tracheids of the primary and secondary xylem and within the secondary xylem (black arrows) Scale bar: 100 μ m.

Fig. 4 Periphery of a stem with two departing leaves in both transverse (above) and longitudinal sections. Note the vein-like strands in the attached leaf (black arrows). The tiny appendages departing slightly downwards (white arrows) could represent rootlets. Scale bar: 500 μ m.

Fig. 5 Stem periphery with thickened node and one departing leaf with a slightly recurved tip. Scale bar: 500 μ m.

Fig. 6 Leaf in transverse section showing three to four vein-like strands (arrows). Scale bar: 100 μ m.

Plate 5

Diverse *Sphenophyllum* organs preserved in a cavity inside a calamite stem (*Arthropitys barthelii* NEREGATO et al. 2017), K6040, Permian of northern Tocantins, central-north Brazil.

Fig. 1 *Sphenophyllum* stem in transverse section showing several roots (R) that penetrated the stem cortex. A leaf (L) is seen over the top of the stem. Scale bar: 1 mm.

Fig. 2 Several roots in transverse view are densely filling the space between *Sphenophyllum* stem (bottom) and the cut calamite wood (top). Scale bar: 500 μ m.

Fig. 3 Roots in both longitudinal and transverse views. Scale bar: 300 μ m.

Fig. 4 Root in transverse section showing small vascular bundle (arrow) and extended root cortex (RC). Scale bar: 200 μ m.

Fig. 5 Root in transverse section showing central vascular bundle, well-defined endodermis (arrow) and root cortex (RC). Scale bar: 200 μ m.

Fig. 6 Root in transverse section showing diarch vascular bundle in the centre, endodermis (arrow) and root cortex (RC). Scale bar: 200 μ m.

Fig. 7 Root in longitudinal view with well-defined endodermis (arrow) and root cortex (RC). Scale bar: 100 μ m.

Plate 6

Sphenophyllum remains preserved on the outer surface or among aerial roots of tree ferns. Permian of northern Tocantins, central-north Brazil.

Fig. 1 Juvenile *Sphenophyllum* stem preserved at the periphery of a *Grammatopteris freitasii* trunk. The triarch stele (S) in the centre is still without secondary xylem and surrounded by large parenchymatous cortex (Cp) and epidermal layer (arrow), K4969c. Scale bar = 1 mm.

Fig. 2 *Tietea singularis* trunk showing two juvenile *Sphenophyllum* stems once climbing on the tree fern and later became overgrown by aerial fern roots (the rectangle indicates a closeup view given in Fig. 3). Coll. Sandra Niemirowska, Warsaw, number 2546. Scale bar: 20 mm.

Fig. 3 Detail of Fig. 2 showing two *Sphenophyllum* stems each with stele and cortex (arrows). Scale bar: 1 mm.

Fig. 4 *Sphenophyllum* stem recognised on the backside of the same slice as in Fig. 2. Note the closely adjoining thin leaves (arrows) and oval micro-coprolites in the cortex cavity (CC). Scale bar: 1 mm.

Fig. 5 *Sphenophyllum* stem with stele showing one tangential row of secondary xylem tracheids (black arrow), periderm (PD) and primary cortex (C) preserved at the periphery of another slice of the same *Tietea singularis* trunk as in Fig. 2. Note the attached thin leaves (white arrows). Coll. Sandra Niemirowska, Warsaw, number 2562. Scale bar: 1 mm.

Fig. 6 Two *Sphenophyllum* stems preserved among aerial roots in the next following slice of the same tree fern trunk as in Figs 2 and 5. The left stem is showing central stele, periderm (PD), and cortex (C). Primary xylem arms do not show lacunae. Coll. Sandra Niemirowska, Warsaw, number 2561. Scale bar: 1 mm.

Fig. 7 *Sphenophyllum* stem with central stele showing one protoxylem lacuna (arrow) and one layer of secondary xylem tracheids, internal periderm layer (PD) and primary cortex (C) with parenchymatous and sclerenchymatous cells. Coll. Sandra Niemirowska, Warsaw, number 2562. Scale bar: 500 µm.

Plate 7

Sphenophyllum remains preserved in silica-cemented highly mature quartz sandstone. Permian of northern Tocantins, central-north Brazil.

Fig. 1 Three-dimensionally preserved plant fossil organs entombed in densely silicified fluvial sandstone. Among them a *Sphenophyllum* stem (arrow) with vascular tissues and a remnant of the primary cortex. F13972f. Scale bar: 1 mm.

Fig. 2 Detail of Fig. 1 showing one *Sphenophyllum* stem with a few layers of secondary xylem tracheids. Scale bar: 500 µm.

Fig. 3 Detail of Fig. 2 showing the stele with only two metaxylem arms having small protoxylem lacunae (white arrows), three to four tangential rows of secondary xylem tracheids and axial parenchyma (black arrow). Scale bar: 200 µm.

Fig. 4 *Sphenophyllum* stem with triarch stele (arrow) and only one row of secondary xylem tracheids and a surrounding remnant of the primary cortex (C). Transverse to slightly oblique section. The majority of extraxylary tissues are replaced by sand grains. F13972b. Scale bar: 1 mm.

Fig. 5 Remnant of a juvenile *Sphenophyllum* stele “floating” in fluvial sandstone. Transverse to slightly oblique section. Scale bar: 500 μ m.

Fig. 6 *Sphenophyllum* stem with triarch stele showing one row of secondary xylem tracheids, an initial layer of internal periderm (PD) and primary cortex (C). Transverse to slightly oblique section. F13972d. Scale bar: 1 mm.

Fig. 7 Detail of Fig. 6 showing the stele. The arrow indicates the position of one protoxylem lacuna. The cavity external to the wood is filled with quartz crystallites. Scale bar: 200 μ m.

Plate 8

Sphenophyllum stems from other late Paleozoic occurrences.

Fig. 1 *Sphenophyllum stephanense* from the Upper Pennsylvanian of Grand-Croix, France. The transverse section shows an actinostelic stem with three primary xylem arms (A, B, C), less secondary growth and leaf traces in the cortex (arrows). Grand'Eury Collection GE327, MNHN Paris. Scale bar: 1 mm.

Fig. 2 Detail of Fig. 1 showing the three protoxylem poles (arrows) with only one preserved as a small lacuna. Scale bar: 500 μ m.

Fig. 3 *Sphenophyllum* sp. from the early Permian of Freital, SE Germany. The transverse section shows a decorticated actinostelic stem with three primary xylem arms (arrows) with small lacunae distally, up to seven layers of secondary xylem (SX) but lacking any extraxylary tissues. Coll. Weiß, Rabenau, number H3-83. Scale bar: 1 mm.

Fig. 4 *Sphenophyllum* sp. from the Pennsylvanian (Moscovian) Coal Measures of the U.K. The transverse section shows an actinostelic stem with three primary xylem arms (arrows) without any lacunae but a developmental stage comparable to Fig. 2, one to two layers of secondary xylem, and parenchymatous primary cortex (C) of a ribbed axis. Coll. Sandra Niemirowska, Warsaw, number 3366. Scale bar: 1 mm.

Fig. 5 *Sphenophyllum* sp. from the early Permian of Freital, SE Germany. The transverse section shows an actinostelic stele in the centre of a ribbed stem (arrow) with two lateral branches (B). Carbonised preservation in fine-grained pyroclastics caused some shrinkage and thus limited cell preservation. Coll. MfN Berlin PB2012/664. Scale bar: 1 mm.

Fig. 6 *Sphenophyllum* sp. from the early Permian of Freital, SE Germany. Ribbed stem in transverse section with poorly preserved cauline tissues and at least three bifurcated leaves. Senckenberg Dresden MMG BU-144. Scale bar: 1 mm.

















