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Pleurorhizoxylon yixingense gen. et sp. nov., a euphyllophyte axis with anatomically preserved adventitious roots from the Late Devonian of South China

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Running head: ZHANG ET AL.—LATE DEVONIAN ADVENTITIOUS ROOTS

Keywords: Upper Devonian, wood, mesarch protostele, adventitious root trace, Wutong Formation.

Premise of research. Rooting structures were major contributors to Devonian global change, but anatomically preserved plant roots are rare from this period. We report a new type of plant axis from the Upper Devonian strata of South China that contains a protostele, relatively extensive secondary xylem and adventitious root traces.

Methodology. The original specimens were fragmentary coalified axes, most of which were embedded in Epon resin, sectioned transversely and longitudinally, and ground into thin sections. The sections were observed and imaged with the light microscope. A few were observed directly with a Scanning Electronic Microscope (SEM).

Pivotal results. The axis of this new plant, named *Pleurorhizoxylon* gen. nov., consists of a three-ribbed protostele and thick secondary xylem; the primary xylem is of apparent mesarch maturation, with a single protoxylem lacuna near the end of each rib. The secondary xylem has variable rays composed of parenchyma cells and has scalariform to elliptical bordered pits on both radial and tangential walls of the tracheids. The adventitious root traces are located opposite each primary xylem rib going through the wood, they are accompanied by large rays and cause significant accommodation (knotting) in the wood. Extra-xylary portions are poorly preserved, and no cambium or secondary phloem has been found.

Conclusion. The new plant has a unique combination of characters and demonstrates the anatomical basis for adventitious root growth present in a Devonian moniliform plant for the first time.

Introduction and Background

The euphyllophytes originated in the late Silurian-early Devonian and had reached high diversity and disparity by the end of Devonian. Several groups are recognized, including sphenophytes, early fernlike plants, progymnosperms and seed plants (Taylor et al. 2009). Based on the arrangement of protoxylem in the primary xylem, the euphyllophytes are divided into the Moniliformopses and Radiatopses (Beck and Stein 1993; Kenrick and Crane 1997).

Well-developed secondary xylem generated by a bifacial cambium is commonly thought characteristic of the lignophyte lineage (progymnosperms and seed plants) within the Radiatopses (Doyle and Donoghue 1986). However, in members of sphenophytes and early fernlike plants included in the Moniliformopses, secondary xylem produced by a bifacial or unifacial cambium has also been reported, e.g. *Rotafolia* Wang, Hao et Wang 2005, *Sphenophyllum* Brongniart 1828, *Metacladophyton* Wang et Geng 1997 and *Shougangia* Wang et al. 2015 (Baxter 1948; Cichan 1985; Wang DM and Lin 2007; Wang DM et al. 2005, 2006a, 2017). Traces found in anatomically preserved specimens in the Devonian are usually recognized as branch/leaf traces in aerial parts of the plant. In early Moniliformopses the traces derive from protoxylem poles permanently located towards the periphery of the xylem ribs. In early Radiatopses traces ultimately derive from a protoxylem strand located in the center of the stele, and travel outwards along the mid-plane of the ribs (Beck and Stein 1993; Kenrick and Crane 1997).

Anatomically preserved roots or root traces are more rarely seen, particularly in woody taxa. Trees with complex rooting systems in the Devonian are regarded to have contributed significantly to global geochemical cycles that consequently led to a 90% decline in atmospheric CO_2 levels through the Palaeozoic as the Earth became increasingly forested (Morris et al. 2015).

In this paper, we describe a new type of plant axis, *Pleurorhizoxylon yixingense* gen. et sp. nov., based on anatomically preserved materials from the Upper Devonian of South China, with apparent Moniliformopses protostele and extensive secondary xylem. Emission of adventitious root traces perpendicular to the length of the stem, that may supply aerial or underground adventitious roots, are recognized in an anatomically preserved Devonian woody plant for the first time.

Material and methods

Fossils were collected from the Upper Devonian Wutong Formation. The profile is exposed in Nanshan Hill (GPS data: 31º13′57.48″N, 119º49′32.18″E) about 2 km southwest of Dingshu Town, Yixing City, Jiangsu Province, China (fig. 1). The Wutong Formation comprises the Guanshan Member, including thick quartz sandstone and conglomerate layers, and above it the Leigutai Member, which contains interbedded sandstone and mudstone. According to Li et al. (1984), the Guanshan Member is early Famennian and the Leigutai Member late Famennian in age based on megafossils, spore assemblages and sedimentary deposits. Other authors have suggested the Guanshan Member is of mid-late Famennian (Fa2b-c) age and the Leigutai Member spans from the latest Famennian into the early Carboniferous (Ouyang 2000; Hou and Qi 2006). The specimens in this paper were found in the mudstone interlayers among the thick quartz sandstone and conglomerate layers in the Guanshan Member, associated with some fossil plant compressions including *Hamatophyton* Gu et Zhi 1974, *Sphenophyllum* and *Eviostachya* Stockmans 1948.

All the fragmentary coalfied plant axes were preserved in light-gray mudstone (some shown in fig. S1). It is possible to distinguish six different taxa based on anatomical characters, but only the one which shows definitive adventitious root structure is described in this paper. Most of the specimens were embedded in Epon resin, sectioned transversely or longitudinally at about 1 mm intervals, and ground. The sections were made into slides, observed and photographed with the light microscope (LM). Some other fragments were examined and photographed with a scanning electron microscope (SEM). Sections that show well-preserved anatomical structures are labeled (see below) and housed in the School of Earth and Space Sciences, Peking University, Beijing, China.

Systematic Paleobotany

Subdivision Euphyllophytina—Kenrick and Crane 1997

? Infradivision Moniliformopses—Kenrick and Crane 1997

Class, Order and Family—Incertae sedis

Genus—*Pleurorhizoxylon* Zhang et al. gen. nov.

Etymology. Pleuro-, from the Greek *πλευρά* – side; rhizo-, from the Greek *ῥίζα* – root; and -xylon, from the Greek *ξύλον* – wood, meaning a woody axis with laterally borne roots.

Generic diagnosis. Anatomically preserved plant axes consisting of a three-ribbed protostele and substantial secondary xylem. Primary xylem mesarch with a single protoxylem lacuna located near the end of each rib. Metaxylem tracheids possessing scalariform to elliptical bordered pits, or 2- to 3-seriate circular bordered pits. Secondary xylem consists of rays, short or high, and tracheids with scalariform to elliptical bordered pits on both tangential and radial walls. Adventitious root traces located opposite each primary xylem rib in larger axes, accompanied by large rays and causing conspicuous accommodation in adjacent wood of the parent axis.

Type species—*Pleurorhizoxylon yixingense* Zhang et al. sp. nov.

Holotype designated here. Specimen PKUB15204 (Fig. 3*a-c*, *f-i*; Fig. 4*a-h*; Fig. 10*a-i*; Fig. 12*f*)

Paratypes. Specimen PKUB15208 (Fig. 7*d-i*; Fig. 11*a-i*; Fig. 12*a-e*)

Specimens examined here. PKUB15201-PKUB15209; slides PKUB15201/02-15201/03, PKUB15202/02-15202/06, PKUB15204/T01-15204/T02, PKUB15204/L01-15204/L06, PKUB15205/T01-15205/T04, PKUB15205/L01-15205/L06, PKUB15206/02-15206/06, PKUB15207/01, 15207/03-15207/06, PKUB15208/01-15208/09, PKUB15209/08-15209/10.

Repository. All slides are housed in the School of Earth and Space Sciences, Peking University, Beijing, China.

Locality. Nanshan Hill, about 2 km southwest of Dingshu Town, Yixing City, Jiangsu Province, China. GPS location 31º13′57.48″N, 119º49′32.18″E.

Stratigraphic horizon. Wutong Formation, Upper Devonian (Famennian).

Etymology. *yixingense* – named after its type locality, Yixing City, Jiangsu Province, China.

Specific diagnosis. Larger axes 2.1-8.7 mm wide in transverse section, primary xylem 0.4-1.4 mm wide. Protoxylem lacuna up to 36 μm in diameter. Metaxylem tracheids 11- 62 μm in diameter. Secondary xylem up to 61 cells thick, tracheids 11 to 113 μm in radial diameter and 10-153 μm in tangential diameter. Rays 1-4 cells wide and 1 to at least 41 cells high. Smaller axes 0.8-3.0 mm wide, primary stele 0.3-0.9 mm wide. Protoxylem or early metaxylem tracheids possessing helical to scalariform thickenings. Metaxylem tracheids 13-47 μm in diameter. Secondary xylem up to 20 cells thick, tracheids 8.2-176 μm in radial diameter and 5.3-139 μm in tangential diameter. Adventitious root traces emitted usually perpendicularly and composed of a xylem bundle with tracheids, oval in transverse view and 0.9 x 1.0 mm in diameter.

Description

Nine fragmentary carbonized specimens, 5-19 mm wide and 5-24 mm long, contain axes assignable to *Pleurorhizoxylon yixingense*. In transverse view, all specimens include a larger axis, some include in addition distinctly smaller axes which are described separately below (Table 1). Generally, axes consist of a small protostele and relatively extensive secondary xylem, where some trace emissions can be seen. Only the xylem tissue has good cellular preservation, and neither phloem nor cambium has been found. Some sections exhibit a thick extra-xylary portion that is poorly preserved, with few cortical or epidermal structures detected. Longitudinal sections demonstrate primary xylem, secondary xylem, and traces. Three of the specimens show larger axes without traces (PKUB15201, PKUB15202, PKUB15203), one is a larger axis with traces (PKUB15204), two include larger and unconnected smaller axes (PKUB15207, PKUB15209), and two have a larger axis with traces and unconnected smaller axes (PKUB15205, PKUB15208). There seems to be no causal relation between the diameter of an axis and whether it produces traces or is accompanied by smaller axes.

Larger axes

Primary xylem. In transverse section, the larger axes are 2.1-8.7 mm wide, in which the primary body is 0.4-1.4 mm wide. The primary xylem is three-ribbed with each rib tapering (fig. 2*c*, 2*e*, 3*b*). The ridges of three ribs invaginate to form shallow to moderate concave sides, the distance from the stelar center to the end of each rib is 0.2-0.7 mm; the three lacunae of the primary body constitute a triangle whose angles vary from 31° to 100°. The maturation of primary xylem is mesarch, with the position of protoxylem inferred from the presence of one lacuna near the end of each primary xylem rib (fig. 2*f*, 2*g*). Only one possible division of a protoxylem strand is observed (fig. 2*h*), but the trace cannot be followed distally as there are no other sections available. The protoxylem lacunae, inferred to have been produced by the stretching of protoxylem tracheids (Scheckler et al. 2006), are noticeable in all transverse sections and are longitudinally continuous. The diameter of the lacuna is up to 36 μm. Probable protoxylem or early metaxylem tracheids around the lacunae are small and circular to oval (fig. 2*f*, 2*g*), and vary from 2.4 to 9.4 μm in diameter. Other metaxylem tracheids range from 11 to 62 μm in diameter, usually smaller at the margins of the primary body and larger in the middle of the ribs and center and are of various shapes in transverse view (oval, elongate, triangular, rectangular, polygonal and irregular). Longitudinal sections through the primary body show that the metaxylem tracheids are slender, with acute tips (fig. 3*g*). Scalariform to elliptical bordered pits, or 2- to 3-seriate circular bordered pits are present (fig. 3*h*). The scalariform bars are 3.0-7.8 μm high; the elliptical bordered pits are 10-45 μm in long axis and 5.0-10 μm in short axis; the circular ones are 5.5-12 μm in diameter. The apertures are elliptical, horizontally oriented or slightly inclined, 2.9-36 μm wide and 0.7-5.3 μm high (fig. 3*i*).

Secondary xylem. The secondary xylem is composed of tracheids and rays in various shapes. In transverse view, files of secondary xylem tracheids arise from the periphery of the primary body and extend outwards to 0.4-4.5 mm, up to 63 cells thick (fig. 3*a*). Tracheid sizes increase along the file centrifugally, ranging from 11 to 113 μm in radial diameter and 10-153 μm in tangential diameter. Like the metaxylem tracheids, the secondary xylem tracheids have various shapes in transverse section, e.g., circular, oval, square, rectangular, elongate, polygonal or irregular, but are usually identical in the same file. The tracheid files are crowded in early development because of their origination from the concave margin of the primary xylem, which leads to the distortion of some tracheids and the termination of some files (fig. 2*e*, right arrow; 3*c*, arrow). As the secondary xylem extends outwards, some early files disappear, and new files initiate between the original rows. Some areas of the secondary xylem show tracheid files being interrupted and then resumed by a greater number of new files with smaller tracheids (fig. 2*b*, square; 3*e*). Each 2-6 files of tracheids are separated by thin gaps where rays are barely visible. Tracheid files are occasionally separated by cracks, some 2-3 tracheids wide, where broken ray cells are sometimes visible (fig. 3*a*, arrows; 3*f*). In serial transections of specimen PKUB15208, the secondary xylem cylinder of the larger axis exhibits a noticeable, nearly continuous boundary at the position of about half radius; the tracheids that form the boundary are smaller relative to those of each side, which probably indicates some sort of abrupt change but then resumption of normal growth (fig. 11*a*-11*c*, arrows).

Longitudinal sections demonstrate both tangential and radial facets of the secondary xylem (fig. 4*a*, 4*e*). Tracheids in longitudinal sections have tapering ends, the maximum measured tracheid length is about 3.9 mm. The pits on the tangential and radial walls of tracheids are nearly identical, they are scalariform to elliptically bordered with horizontal or slightly oblique apertures (fig. 4*c*, 4*d*, 4*f*, 4*g*, 4*i*-4*k*). Pits are 1- to 3-seriate. The scalariform bars are 3.9-9.4 µm high, and the elliptical bordered pits measure 7.2-34 µm in long axis and 4.5-12 µm in short axis. The apertures are 4.0-40 µm wide and 1.4-5.6 µm high. In tangential section, rays are abundant among tracheids, 1 to at least 41 cells (1.1 mm) high and 1-4 cells (0.1 mm) wide (fig. 4*a*, 4*b*); ray cells are thin-walled, round, oval to elongate, measuring 6.2-83 µm in width or height. Sometimes the parenchyma walls are so broken that cells are uncountable. In radial view, some rays are horizontally arranged and minor, only 3-10 cells high and up to at least 6 cells long; ray cells appear rectangular, long axis 26-120 µm and short axis 11-40 µm (fig. 4*h*). Other rays are higher, up to 118 cells (2.3 mm) and irregular in shape because of the nonuniform directions of the tracheid files and the obliquity of the rays with respect to the section, where the ray cells are often too broken to count (fig. 4*e*, 9, gray regions). Pits in cross fields were not observed.

Smaller axes

Some transverse sections exhibit distinct smaller axes that are terete, 0.8-3.0 mm diameter, differing from the larger axis in the same section mainly in size (fig. 5, 6, 7*a*, 7*e*). In the serial transverse sections of a specimen, the relative position of the smaller axis/axes to the larger axis shift dramatically (fig. 5, 6). The xylem architecture of smaller axes resembles that of larger axes, with a small three-ribbed protostele of 0.3-0.9 mm wide and relatively extensive secondary xylem (fig. 7*h*, 7*i*). The maturation of the primary xylem is mesarch (fig. 7*c*, 7*f*), except in specimen PKUB15209 where protoxylem lacunae are not visible (fig. 8*h*). The tracheids of the protoxylem or early metaxylem are circular to oval in transverse section, 4.2-11 µm in diameter. Scalariform thickenings can be observed on the metaxylem tracheid walls from an oblique transverse section of the smaller axis (fig. 7*g*). Most metaxylem tracheids are large, 13-47 µm in diameter and various in shape, while the outermost are usually small and form a clear boundary between the primary body and the secondary xylem (fig. 7*b*).

The secondary xylem of the smaller axis reaches 20 cells (1.2 mm) thick, occupying a prominent proportion in transverse section, which is nearly identical to, though not as extensive as, that of the larger axis. 1 to 4 tracheid files are separated by slits which are possibly filled with rays (fig. 7*i*). The tracheid sizes increase centrifugally, 8.2-176 μm in radial diameter and 5.3-139 μm in tangential diameter. In transverse section, shapes of tracheids vary from oval to square. No longitudinal sections show structures of smaller axes, while an obliquely cut section exhibits scalariform to elliptical bordered pits in secondary xylem tracheid walls (fig. 8*a*, 8*c*-8*e*).

Adventitious root traces

Adventitious root traces are only observed in the larger axes. Clear evidence comes from a series of longitudinal sections L02-L06 (fig. 9) cut from specimen PKUB15204 (fig. 3*a*). Traces are either observed directly (fig. 9, t1, t2, t3) or by the presence of xylem cells of the axis which have been reorientated to accommodate the passage of the trace (fig. 9, t4, t5). Complementary transverse sections were cut from specimen PKUB15208 (fig. 11*a*-11*c*).

An oblique longitudinal view of the adventitous root trace (t3 in fig. 9) is seen in fig. 10*a*; it is intruded by a horizontal crack which extends into the center of the parent axis. Proximally (on the right in the photograph), the central tracheids are perpendicular to those of the parent axis, whereas those above and below curve inward, and all become parallel distally (left side). The trace is approximately 0.3 mm high (diameter). The tracheids are 6.6-20 μm in width. A second trace (t1 in fig. 9) is seen in fig. 10*b* which crosses the plane of section over a more extended distance. The proximal (on the left in the photograph), central xylem cells are perpendicular to those of the parent axis, whereas those above and below curve inwards symmetrically to become parallel to the trace. Annular to scalariform thickenings are observed on some tracheid walls (fig. 10*c*). A third trace (t2 in fig. 9) seen in transverse view (tangential to the parent axis) is shown in two adjacent sections (fig. 10*e*, 10*f*); it is oval and 0.9-1.0 mm in diameter. The primary stele is not visible in the traces (e.g. fig. 10*e*), certainly no three-lobed stele with protoxylem lacunae is present. Some tracheids of the trace are aligned in slightly meandering files radiating from the center, probably representing secondary xylem. Most are 11-22 μm in diameter, but other tracheids are significantly larger and up to 62 μm in diameter (fig. 10*e*).

The passage of some traces which are not directly intersected by the planes of our sections can only be interpreted from the conspicuous knotting of the parent axis wood. These areas, where xylem cell orientation is rotated by up to 90° in the tangential plane, accommodate the trace growth. They are much larger than the traces themselves, and are observed in both longitudinal (fig. 10*g*, 10*h*, 10*i*) and transverse (fig. 11*e*, 11*i*, 12*c*, 12*d*) sections. When tracheids adjacent to the trace are rotated at right angles to the parent axis, pits are visible on the walls (fig. 11*f*). Big splits between tracheid files filled with probable parenchyma ray cells in transverse section of the parent axis (fig. 8*b*) may also indicate the position of adventitious root traces. In longitudinal section of the parent axis, large rays often accompany traces (fig. 10*g*, 10*h*, arrows), and adjacent rotated xylem tracheids even appear as files as in transverse view (fig. 10*b*, 10*g*-10*i*). These rays associated with the traces are distinct from other rays in the parent axis wood and might be the result of the fusion of several rays in disturbed wood. In some extant lignophytes, unusually large rays are believed to be linked with the production of adventitious roots (Fink 1982).

It is uncertain whether the adventitious root traces are connected to the primary stele or not, and it is rarely possible to infer a set pattern of trace emission. In transverse sections of the parent axis, root traces are usually located opposite the primary xylem ribs, occasionally very close to the protoxylem strand (fig. 11*d*); in most cases, traces appear to have arisen from a more outward position in the secondary xylem of the parent axis (fig. 8*b*). In some locations, two traces were produced opposite one primary xylem rib (fig. 11*g*), rather than the more common situation with a single trace. Serial longitudinal sections of an axis around 8.3 mm long show three definite traces (t1-t3) and two locations (t4-t5) where traces have passed close by (fig. 9, 10). Here traces t2-t4 occur at approximately the same level but t1 and t5 are isolated. Trace t1, t2 and t3 are probably emitted perpendicularly to the parent axis, whereas trace t4 and t5 appear to ascend and descend through the wood from their points of origin.

Extra-xylary structures

Some specimens contain a notable proportion of extra-xylary tissue, though most are distorted, degraded or lost, and are generally replaced by a region of vitrinite-like materials (fig. 7*d*, 8*f*). No phloem is observed. A few parenchyma cells external to xylem are detectable in some transverse and tangential sections and may represent cortex (fig. 7*d*, arrows; 12*e*, 12*f*). These thin-walled cells are 54-206 µm in diameter in transverse section and 20-157 µm in longitudinal section and are largely broken. Furthermore, some unrecognizable cellular tissues are observed; they form irregular shapes and are severely broken (fig. 8*f*, arrows).

Discussion

Stelar architecture & systematic position

Pleurorhizoxylon has a three-ribbed primary xylem strand, broadly triangular in outline with concave sides, and the protoxylem is located near the ends of the ribs only. This immediately sets it apart from basal members of Radiatopses including aneurophytalean progymnosperms such as *Aneurophyton* and *Triloboxylon*, where protoxylem strands are found along the mid-plane of the ribs, aneurophytes being absent from South China anyhow (Wang Y et al. 2007; Wang DM and Liu 2015). *Yiduxylon* Wang DM and Liu 2015, a putative precursor of seed plants from the Famennian of Hubei province, has peripheral mesarch protoxylem strands, but the three narrow ribs are narrowest near the center of the stele, quite distinct from the broad triangle of *Pleurorhizoxylon*, and no protoxylem lacunae are found (Wang DM and Liu 2015).

The triangular primary xylem at first glance recalls that of *Sphenophyllum*, a plant first known from the Late Devonian and best known from the Carboniferous. *Sphenophyllum* is recognized primarily from compressions of their wedge-shaped leaves which are arranged in whorls, and as a small understory plant. Most *Sphenophyllum*, where the anatomy is known, such as *S. plurifoliatum*, have exarch protoxylem maturation (Baxter 1948; Zhao 1989), the protoxylem distributed at the extremity of the corners of the primary stele. This form is clearly distinct from the apparent mesarch protoxylem found in *Pleurorhizoxylon*. However, in a second type currently referred to *Sphenophyllum*, represented by *S. insigne* (Williamson and Scott 1895), an apparent 'protoxylem canal' or lacuna is seen at each corner of the triangle, completely surrounded by xylem cells which are considerably smaller than the bulk of the metaxylem. According to Williamson and Scott (1895, p. 927) these are 'spiral tracheids' (i.e. protoxylem) but this is not illustrated. They also stated that fragments of spiral tracheids are also found in the canal itself. The lacuna is also illustrated by Solms-Laubach (1896), where the smaller cells appear to form the inner extent of radial files of secondary xylem. Both these interpretations suggest that the xylem maturation is more or less exarch despite the presence of the mesarch protoxylem lacunae, but exact interpretation would depend on extremely good preservation and unambiguous preparation of the very small protoxylem area. Baxter (1948) also recognised protoxylem lacunae in some of the specimens he attributed to S. *plurifoliatum* from the Carboniferous of Iowa. *Sphenophyllum perforatum* also has apparent protoxylem lacunae and is distinguished from *S. insigne* by the narrowness of the xylem ribs (Koopmans 1928).

Several other sphenophylls with anatomy have been reported from the Late Devonian of South China; these are *Hamatophyton verticillatum* Gu et Zhi 1974, *Rotafolia songziensis* Wang, Hao et Wang 2005 and *Eviostachya hoegii* Stockmans 1948. They differ from *Pleurorhizoxylon yixingense* because of clearly exarch maturation of the primary xylem and the absence of mesarch protoxylem lacunae (Wang Y 1993; Li et al. 1995; Wang DM et al. 2005, 2006a, 2006b). The genus *Sphenophyllum* has also been found in the Late Devonian of South China but only as compression/impression specimens. Compression specimens found at the same locality have a maximum axis diameter of 2 mm only.

The stelar architecture of *Pleurorhizoxylon* seems closer to the “permanent protoxylem” group, termed “Moniliformopses” by Kenrick and Crane (1997) that includes iridopteridaleans, most cladoxylopsids and probably sphenopsids (Beck and Stein 1993). The classification of these Middle to Late Devonian plants referred to as fernlike plants or as preferns (Taylor et al. 2009) remains highly problematic. Two subgroups were recognized in the Cladoxylopsida by Berry and Stein (2000) which is employed by Taylor et al. (2009), the Iridopteridales that possess a solid primary xylem containing “permanent” peripheral protoxylem strands near rib tips, and the Pseudosporochnales that can be recognized by the presence of stelar systems with radially directed, deeply bifurcate/trifurcate (or more complexly divided) primary ribs in branches, and simpler radial plates in trunks. In terms of this framework, *Pleurorhizoxylon* has a primary body that accords with the features of the Iridopteridales, but is distinctive from any other group members e.g. *Ibyka* Skog et Banks 1973, *Iridopteris* Arnold 1940, *Arachnoxylon* Read 1938, *Asteropteris* Dawson 1881 and *Compsocradus* Berry et Stein 2000 that either have bifurcate xylem ribs or have a more highly ribbed stele (Skog and Banks 1973; Stein 1981, 1982; Berry and Stein 2000; detailed comparisons are shown in Table 2).

The mesarch protoxylem strand of euphyllophytes has been discussed by Scheckler et al. (2006) who distinguished mainly two types. Type one is a "peripheral loop" that has a core of thin-walled parenchyma surrounded by protoxylem tracheids. *Langoxylon asterochlaenoideum* Stockmans 1968, *Stenokoleos holmesii* Matten 1972 and *Rotoxylon dawsonii* Cordi et Stein 2005 have this type. The authors didn't consider this structure comparable to those of Late Devonian *Rhacophyton* (Dawson) Krausel et Weyland 1941 or Carboniferous Zygopteridales that have also been called "peripheral loops", because the xylem parenchyma in the former may be better interpreted as immature or degraded tracheids (Cordi and Stein 2005). Another distinction is the peripheral loops of *Rhacophyton* open during the departure of traces (Scheckler 1974). The second type is a "protoxylem lacuna" or "protoxylem cavity" that is found in iridopteridaleans such as *Ibyka*, *Iridopteris*, *Arachnoxylon*, *Asteropteris* and *Compsocradus*, and in the cladoxylopsid *Rhymokalon* Scheckler 1975, and forms a conspicuous cavity by stretching and destruction of the innermost (first formed) tracheids of a mesarch protoxylem strand during early development. We prefer that the protoxylem lacunae near the end of xylem ribs in *Pleurorhizoxylon* are more likely a result of the stretching or degradation of the central tracheids of protoxylem as no parenchyma cells are seen in the cavity on the transverse section, and therefore might be included in the second type. Unfortunately, however, we are unable to provide a longitudinal view of the protoxylem strand in *Pleurorhizoxylon yixingense* to confirm the absence of xylem parenchyma cells. We agree that the "peripheral loop" or "protoxylem lacuna/cavity", though remaining unsupported by histological evidence (Cordi and Stein 2005), is a real existing structure and may eventually have some significance for unraveling the phylogeny of Devonian euphyllophytes (Scheckler et al. 2006). The tangential division of a protoxylem strand in fig. 2*h* may indicate the emission of a trace, or bifurcation of a xylem rib, but the next adjacent section is not available for study. Both iridopteridalean and sphenophyllalean axes would be expected to demonstrate nodal anatomy with long internodes. As our longest specimen is 24 mm with no sign of a node (fig. 6), we conclude that we have only internode material available to study.

One question that remains would be how different developmentally the protoxylem lacunae of *Pleurorhizoxylon* is from those of iridopteridaleans and *Sphenophyllum*, and indeed from the exarch state of most specimens of *S. plurifoliatum*? In some iridopteridalean specimens, the mesarch protoxylem strand is surrounded on all sides by metaxylem cells that are substantially bigger than the protoxylem (e.g. figure 6 of Stein et al. 1983). However, in many others, including many *Iridopteris* and *Arachnoxlon* specimens, the outer border of the lacuna is contained by only very small xylem cells (Stein 1981, 1982). This suggests there might also be a continuum of forms in *Sphenophyllum* between the completely exarch and apparently mesarch, dependant on the number, and area made up, of protoxylem cells, and the exact position of the first-formed protoxylem which may be ruptured during early development to form the lacuna.

Secondary wood

Older stems of *Sphenophyllum plurifoliatum* have abundant secondary xylem that is differentiated into fascicular and interfascicular regions. The fascicular regions are opposite the three primary ridges with tracheid diameter increasing in a distinct centrifugal pattern, while the interfascicular regions between the primary ridges have tracheids whose width appears to be relatively constant (Baxter 1948; Cichan 1985). In the fascicular areas, multiseriate vascular rays are present in the wood, sometimes extending across the entire zone, and areas of parenchyma strands occur in the angles between tracheids. These parenchyma strands are oriented both radially and tangentially, and this latter feature is apparently unique to the secondary xylem of the genus (Eggert and Gaunt 1973). In the interfascicular secondary wood, the parenchymatous system is composed of upright cells with radial processes and upright cells that lack such outgrowths and was believed to be a true ray system (Cichan 1985). The tracheids of *Sphenophyllum* are extremely long with tapering end walls and lateral bordered pitting that is crowded and circular to elliptical (Eggert and Gaunt 1973; Cichan and Taylor 1982).

Wood of the *S. insigne* type is best illustrated by Williamson (1874, Part V fig 23), in an axis approaching 10 mm in diameter. It is divided clearly into narrow files in the fascicular areas and wider files in the interfascicular areas. Inception of new files is more common than in the *plurifoliatum* type. A notable boundary is present just outside the diameter of the primary stele, where the number of files of cells increases suddenly and the diameter of all cells decreases. Outside this zone rays are common and reach across the remaining radius of the axis.

Chinese Devonian exarch sphenophylls *Hamatophyton* and *Rotafolia* have wood that is not divided into fascicular and interfascicular zones, and rays are either absent or inconspicuous. They also have tracheids with scalariform thickenings or scalariform to elliptical/circular bordered pits on the walls (Wang DM et al. 2005, 2006a, 2006b).

Some Devonian fernlike plants also developed wood, the most striking example exists in Cladoxylopsida, *Xinicaulis lignescens* Xu, Berry et Stein 2017, that possesses concentric secondary xylem, including rays and growth increments, around many primary xylem plates in the trunk. Others include the Middle-Late Devonian gerera *Calamophyton* Kräusel et Weyland 1925, *Xenocladia* Arnold 1940, and *Rhacophyton*, which have secondary xylem, sometimes up to 20 cells thick, composed of radially aligned tracheids and narrow or inconspicuous rays (Arnold 1952; Dittrich et al. 1983; Giesen and Berry 2013). Three Chinese Devonian fernlike plants, *Polypetalophyton* Geng 1995, *Metacladophyton* and *Shougangia*, were described as having secondary xylem (or putative) with indistinct or narrow rays, and scalariform thickenings or bordered pits on the tracheid walls (Hilton et al. 2003; Wang DM and Lin 2007; Wang DM et al. 2017).

As shown in Table 3, none of the above taxa have secondary xylem identical to that in *Pleurorhizoxylon*. Firstly, the secondary xylem of *Pleurorhizoxylon* is very well-developed and much broader than most of them, up to 63 cells thick. Secondly, the secondary xylem in most members of fernlike plants or early ferns and sphenophytes (except for *Sphenophyllum*) contain indistinct or narrow rays, while *Pleurorhizoxylon yixingense* has 1-4 seriate rays in tangential section, some are short, and others can be as high as 41 cells. However, to some extent, the tracheids in *Pleurorhizoxylon* have a similar pitting pattern to that in many of these genera (*Polypetalophyton*, *Shougangia*, *Hamatophyton* and *Rotafolia*), with scalariform thickenings and bordered pits.

Lignophytes, including progymnosperms and seed plants, have a characteristic bifacial cambium that produces secondary xylem towards the inside and secondary phloem towards the outside (Crane 1985; Doyle and Donoghue 1986), although something similar is also reported in *Sphenophyllum* (Eggert and Gaunt 1973; Cichan and Taylor 1982). It is not possible to infer the presence of a bifacial cambium in *Pleurorhizoxylon yixingense* since no phloem is observed. The characters of the secondary xylem in Devonian lignophytes were summarized by Momont et al. (2016) as follows. In Aneurophytales, tracheids have multiseriate circular to elliptical bordered pits on all walls; rays are at least 20 cells high, typically 1-seriate, multiseriate rays are sometimes present (Dannenhoffer et al. 2007). *Callixylon* (Archaeopteridales) has tracheids with grouped circular bordered pits on radial walls only, with some pitting on the tangential walls of late wood; rays are highly variable amongst species (Beck 1960, 1970, 1981; Orlova and Jurina 2011). The wood of seed plants shows a trend to the restriction of the pitting to the radial walls and increasing width of rays (Galtier and Meyer-Berthaud 2005). Some early seed plants have circular bordered pits on all tracheid walls; rays are highly variable, up to 6-seriate, 10 to 60 cells high (Barnard and Long 1975; Serbet and Rothwell 1992; Galtier and Meyer-Berthaud 1996). *Brabantophyton* Momont et al. 2016, a member of the Stenokoleales from the Middle-Late Devonian, was thought close to early seed plants based on wood characters, having 2-6 seriate bordered pits on the tangential walls and 2-10 seriate bordered pits on the radial walls (Momont et al. 2016). The broad secondary xylem of *Yiduxylon* has very high biseriate rays in the wood and multiserate bordered pits of oval shape on both tangential and radial walls of secondary xylem tracheids (Wang DM and Liu 2015).

Despite the fact that *Pleurorhizoxylon* has a broad secondary xylem comparable to that in *Brabantophyton* and *Yiduxylon*, as well as in some aneurophytes, we do not think the wood is identical to any in the lignophyte lineage, because the secondary xylem tracheids of *Pleurorhizoxylon* have scalariform thickenings and most commonly uniseriate bordered pits on both the tangential and radial walls, as well as 1-4 seriate rays up to at least 41 cells high.

It is worth noting that the circumferential augmentation of wood tracheids (doubling of xylem rows) is considered by some authors (Donoghue 2005; Gerrienne et al. 2011) to be a characteristic of the lignophyte clade. Because of the similarity of the primary structure with that of *Sphenophyllum*, we must however consider that the increase in the number of xylem files radially might be caused rather by increase in the length of individual xylem cells and their fusiform initials (Cichan and Taylor 1982). Whether this process alone could account for the expansion of our largest axes cannot be determined with the material to hand.

Adventitious root trace

Anatomically preserved roots have been relatively rarely found in Devonian plants. We now demonstrate the presence of adventitious root traces in a plant with primary anatomy most similar to Iridopteridales or mesarch forms of *Sphenophyllum*. Adventitious roots have not yet been clearly demonstrated in iridopteridaleans. Amongst the closely related moniliforms, in *Denlongia* (compressions) small aerial rootlets have been found below the nodes on the small main axes (Xue and Hao 2008; Xue et al. 2010) and in *Shougangia*, with a dissected stele and frond-like branches from the Wutong Formation, adventitious roots were found only on one side of a (horizontal) stem (Wang DM et al. 2015, 2017).

In Carboniferous *Sphenophyllum*, narrow adventitious roots are demonstrated (e.g. Storch and Barthel 1980) associated with leaf whorls in compression fossils. No Devonian sphenophytes yet show roots.

The Middle and Late Devonian tree-formed cladoxylopsids have basal roots and roots which emerge from the lower sides of the erect trunk. For example, small adventitious roots occur in the proximal part of the stem in *Pietzschia* levis Soria, Meyer-Berthaud et Scheckler 2001 that are observed as three-five lobed vascular bundles with exarch protoxylem poles in cross sections (Soria et al. 2001). These adventitious roots are arranged all around the axis and depart at an acute angle downward, in a direction opposite to that of the lateral organs. They originated from the surface of the many xylem strands which form a ring near the outside of the trunk, grew long and branched dichotomously from the tip. Similar but woody roots are also seen in *Xinicaulis* (Xu et al. 2017).

Because of the presence of a significant amount of secondary wood in the parent axis, the adventitious root traces of *Pleurorhizoxylon* are perhaps more comparable with those found in woody roots of lignophytes. The root traces in *Pleurorhizoxylon yixingense* are frequently accompanied by large rays and led to accommodation in the parent axis wood that are conspicuous in both transverse and longitudinal section, and both features are well recognized in the anatomy of some lignophyte roots (Barnard 1962; Li 1986; Meyer-Berthaud et al. 2013; Decombeix et al. 2017). In the probable root of *Protopitys*/*Stauroxylon*, Decombeix et al. (2017) found conspicuous and non-permanent structures crossing the secondary xylem of the axis radially and interpreted them as traces to lateral roots. The traces are typically located in the areas facing the protoxylem strands, sometimes with two traces facing a single protoxylem strand, and appear either as large traces that occupy a whole sector of the axis or as smaller structures that superficially resemble an unusually large ray. This description is comparable with that in *P. yixingense*. A definite trace was not observed in *Protopitys*/*Stauroxylon*'s roots, nor is the structure of the trace described (Decombeix et al. 2017). Some major and minor traces in archaeopterid roots in Meyer-Berthaud et al. (2013), though well documented, are not preserved as actual traces but are interpreted from the deviation of the secondary xylem tracheids around the trace as they crossed the wood, or are represented by cavities. Lateral rootlets perpendicular to an *Archaeopteris* root have also been illustrated in Figure 4f in Algeo and Scheckler (1998) in near median longitudinal view and cross-section view of the lateral rootlet. These structures were not described in detail, but the elongate and incurved tracheids in the proximal side perpendicular to the parent axis seem the same as in *P. yixingense*.

For further comparative material we also made observations in transverse sections of *Amyelon* Williamson 1894, root of cordaites, from Carboniferous coal balls from the UK in Cardiff University collections and compared our results with those seen in Plate 33. 4 in Barnard (1962) and Plate III. 4 in Li (1986), where longitudinal sections show transverse views of lateral roots. In transverse sections we observed disruption of the secondary xylem cells close to the trace, comparable to that observed in transverse section in *P. yixingense*. In transverse view with respect to the rootlet, Barnard (1962) shows a very similar structure to our trace in fig. 10*e*.

Pleurorhizoxylon is therefore so far unique in being a Devonian plant with anatomically preserved adventitious roots, outside of cladoxylopsid trunks.

Conclusion

Anatomically preserved remains of Devonian rooting systems are very rare. *Pleurorhizoxylon* joins *Archaeopteris* as the only Devonian plants currently shown to have anatomically well-preserved perpendicular root traces. The axis of *Pleurorhizoxylon* has a three-ribbed protostele that is, because of the mesarch maturation and permanent lacuna located near the end of each primary xylem rib, most similar to euphyllophytes of the Moniliformopses group (e.g. Iridopteridales) and to *Sphenophyllum insigne*. The well-developed secondary xylem of *Pleurorhizoxylon* possesses scalariform to elliptical bordered pits on both tangential and radial walls of tracheids, more similar with those in the Moniliformopses group rather than those in contemporaneous Radiatopses. Because of the broadly triangular protostele, and the presence of significant secondary wood, *Pleurorhizoxylon* is perhaps closer to *Sphenophyllum insigne* than to Iridopteridales. An obvious difference from *Sphenophyllum* is that *Pleurorhizoxylon* wood is not divided into fascicular and interfascicular zones, but this is also true of the other Chinese Devonian sphenophylls. Therefore, the new genus *Pleurorhizoxylon* is erected to accommodate this new combination of characters. It demonstrates the anatomical basis for formation of adventitious roots otherwise only so far known from Cladoxylopsids in the Devonian.

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Fig. 1 Location map of the fossil site.

Fig. 2 *Pleurorhizoxylon yixingense* Zhang et al. gen. et sp. nov. *a*, *b*, Transverse sections of two larger axes showing the small primary stele surrounded by extensive secondary xylem. PKUB15201/03, PKUB15202/03. *c*, Enlargement of the center in fig. 2*a*, showing a three-ribbed primary stele, with the protoxylem lacunae located near the end of each rib. *d*, Enlargement of secondary xylem tracheid files in fig. 2*a* (rectangle) separated by a crack. *e*, The three-ribbed primary stele of axis in fig. 2*b* in a different section. Right arrow shows termination of an early tracheid file. PKUB15202/02. *f*, *g*, Enlargements of the primary rib end in fig. 2*c* (arrow) and fig. 2*e* (left arrow), respectively, showing the protoxylem lacuna and mesarch maturation. *h*, The same rib end as in fig. 2*g* in a different section, showing a protoxylem strand dividing into two. PKUB15202/06. Scale bars = 1 mm (*a*, *b*), 200 μm (*c*-*e*) or 100 μm (*f*-*h*).

Fig. 3 *Pleurorhizoxylon yixingense* Zhang et al. gen. et sp. nov. *a*, Transverse section of a larger axis showing a small primary stele surrounded by extensive secondary xylem. Arrows point to cracks between secondary tracheid files. Dashed lines L01-L06 represent the positions where the same axis was cut longitudinally. PKUB15204/T01. *b*, Enlargement of the central primary stele in fig. 3*a*, with protoxylem lacunae placed near the end of each rib. Dashed line L04 represents the same cut as in fig. 3*a*. *c*, Enlargement of early secondary xylem in fig. 3*a* (upper left rectangle), arrow points to the termination of a tracheid file. *d*, Secondary xylem of the same axis as in fig. 2*b* in a different section, showing augmentation (doubling) of tracheid files. Outside of axis to the left. PKUB15202/04. *e*, Secondary xylem in the same slide in fig. 2*h*, showing an interruption in wood growth and initiation of a large number of rows of small diameter cells. Outside of axis to the right. PKUB15202/06. *f*, Enlargement of tracheid files in fig. 3*a* (lower right rectangle) separated by a wide crack with ray cells (arrow). *g*, Metaxylem in the longitudinal section (radial, L04 in fig. 3*a*, 3*b*) of the same axis as in fig. 3*a*, showing metaxylem tracheids slender with acute tips. PKUB15204/L04. *h*, Scalariform to bordered pits on the tracheid walls of metaxylem in the same section in fig. 3*g*. *i*, Bordered pits on metaxylem tracheid walls in fig. 3*g* (arrow). Scale bars = 2 mm (*a*), 200 μm (*b*-*f*), 50 μm (*h*) or 20 μm (*i*).

Fig. 4 *Pleurorhizoxylon yixingense* Zhang et al. gen. et sp. nov. *a*, Secondary xylem in longitudinal section (tangential, L03 in fig. 3*a*). PKUB15204/L03. *b*, Rays and pit pairs in tangential section (the same section in fig. 4*a*). *c*, *d*, Scalariform thickenings to bordered pits on the tracheid walls of secondary xylem in tangential section (the same section as in fig. 4*a*). *e*, Secondary xylem in longitudinal section (radial, L04 in fig. 3*a*, the same section in fig. 3*g*), showing tracheids and rays. *f, g*, Scalariform thickenings to bordered pits on the tracheid walls of secondary xylem in radial section (the same section as in fig. 3*g*). *h*, Rectangular parenchyma ray cells in radial section (the same section as in fig. 3*g*). *i*-*k*, Secondary xylem tracheids observed under SEM, showing bordered pits and pit apertures. PKUB15203. Scale bars = 200 μm (*a, e*), 50 μm (*b, h*), 20 μm (*c, d, f, g, i*), 10 μm (*j*) or 5 μm (*k*).

Fig. 5 Line drawings of serial transverse sections (T1-T4) of specimen PKUB15205, showing changes to the relative position of the larger (l) and smaller (s) axes. Dashed lines represent inferred outlines.

Fig. 6 Line drawings of serial transverse sections (T1-T9) of specimen PKUB15208, showing changes to the relative positions of the larger (l) and two smaller (s1and s2) axes. Dashed lines represent inferred outlines.

Fig. 7 *Pleurorhizoxylon yixingense* Zhang et al. gen. et sp. nov. *a*, Transverse section of a larger axis (l) with a smaller axis (s) in the same specimen. PKUB15207/06. *b*, Enlargement of the three-ribbed primary stele in the smaller axis (s) in fig. 7*a*, with protoxylem lacunae located near the end of each rib (arrows). *c*, Enlargement of a primary rib in fig. 7*b* (square), showing the protoxylem lacuna and mesarch maturation. *d*, Transverse section of a larger axis (l) with two smaller axes (s1 and s2) in the same specimen (T1 in Fig. 6). Arrows point to parenchyma cells in presumed cortex. PKUB15208/01. *e*, Enlargement of a part of a smaller axis (s1) in fig. 7*d* (lower right rectangle), showing a primary xylem rib. *f*, Enlargement of the primary xylem rib end in fig. 7*e* (rectangle), showing the protoxylem lacuna surrounded by early metaxylem tracheids. *g*, Enlargement of the metaxylem tracheid walls in fig. 7*f* (arrow), showing scalariform thickenings. *h*, The primary stele of the other smaller axis (s2) in fig. 7*d* in a different section (T6 in fig. 6). PKUB15208/06. *i*, Enlargement of the secondary xylem in s2 in fig. 7*d* (upper left square). Scale bars = 2 mm (*a*, *d*), 500μm (*e*), 200 μm (*b, h, i*), 100 μm (*c, f*), 20 μm (*g*).

Fig. 8 *Pleurorhizoxylon yixingense* Zhang et al. gen. et sp. nov. *a*, Transverse section (T3 in fig. 5) of a larger axis (l) with a smaller axis (s) in the same specimen. PKUB15205/03. *b*, Enlargement of a part of the secondary xylem in the larger axis in fig. 8*a* (lower square), possibly indicating passage of an adventitious root trace. *c*, Enlargement of the smaller axis (s) in fig. 8*a* (upper square), showing the obliquely cut secondary xylem. *d*, *e*, Enlargement of the tracheid walls of secondary xylem in fig. 8*a* (rotated, right and left arrows respectively), showing the elliptical and circular bordered pits and pit pairs. *f*, Transverse section of a larger axis (l) with a smaller axis (s), a large protostele (p) and some unrecognizable cellular portions (arrows) in the same specimen. PKUB15209/09. *g*, The larger axis (l) in fig. 8*f* in a different section, showing a three-ribbed primary stele and wide secondary xylem. PKUB15209/08. *h*, Enlargement of the smaller axis (s) in fig. 8*f*, showing a triangular primary stele where protoxylem lacunae are not visible. Scale bars = 1 mm (*a*, *f*), 500 μm (*g*, *h*), 200 μm (*b*, *c*) or 20 μm (*d*, *e*).

Fig. 9 Simplified sketches of serial longitudinal sections (L02-L06, corresponding to the same cut in fig. 3*a*) of specimen PKUB15204, showing adventitious root traces t1-t5 going through the wood that caused notable accommodation. Gray regions represent parenchyma rays.

Fig. 10 Adventitious root traces of *Pleurorhizoxylon yixingense* Zhang et al. gen. et sp. nov. in longitudinal sections. *a*, A trace in tangential section (dashed line L03 in fig. 3*a* and tagged as t3 in fig. 9), showing an oblique longitudinal view of the trace (radial to the parent axis). Outside of axis to the left. *b*, A second trace on the same section (dashed line L03 in fig. 3*a* and tagged as t1 in fig. 9), showing an oblique longitudinal view of the trace (sub-radial to the parent axis). Note the parenchyma areas above and below the trace, and the xylem tracheid files of the parent axis that appear a transverse view. *c*, Enlargement of trace tracheids in fig. 10*b* (rectangle), showing the proximal, central xylem cells perpendicular to those of the parent axis. *d*, Englargement of trace tracheids in fig. 10*a* (rectangle), showing the central tracheids perpendicular to those of the parent axis, whereas those above and below curve inward. *e*, *f*, A third trace on two obliquely cut serial tangential sections (dashed lines L05 and L06 in fig. 3*a* and tagged as t2 in fig. 9), respectively showing a transverse view and a possible oblique transverse view. PKUB15204/L05, PKUB15204/L06. *g*, *h*, An inferred fourth trace on two serial longitudinal sections (dashed lines L03 and L04 in fig. 3*a* and tagged as t4 in fig. 9). Note xylem tracheid files of the parent axis that are identical to those in the transverse view, as well as the wide ray area below (arrows). *i*, An inferred fifth trace on the radial section (dashed line L04 fig. 3*a* and tagged as t5 in fig.9). Note the obliquely aligned xylem tracheid files and the parenchyma area above them (arrow). Scale bars = 500 µm (*a*, *b*, *e*-*h*) or 200 µm (*c*, *d*).

Fig. 11 *Pleurorhizoxylon yixingense* Zhang et al. gen. et sp. nov. *a*-*c*, Three serial transverse sections (T1-T3 in fig. 6) of a larger axis (specimen PKUB15208), with three adventitious root traces or trace remnants (t1, t2 and t3). Arrows point to abrupt changes in the secondary xylem growth. *d*, Enlargement of a part of t1 in fig. 11*a* (square) that is close to a primary rib. *e*, Enlargement of t1 in fig. 11*a*, showing tangential orientated xylem tracheids in the parent axis affected by trace growth. *f*, Enlargement of tangential orientated tracheids in fig. 11*e* (rectangle), showing the scalariform pits on the walls. *g*, Enlargement of t1 area in fig. 11*b*, where two traces arise from the same location. *h*, Enlargement of a part of t1 (1) in fig. 11*g* (square), showing the tangential orientated proximal tracheids. *i*, Enlargement of t1 area in fig. 11*c*, showing elongate xylem tracheids in the parent axis affected by trace growth. Scale bars = 1 mm (a-c), 200 µm (*d*, *e*, *g*-*i*) or 50 µm (*f*).

Fig. 12 *Pleurorhizoxylon yixingense* Zhang et al. gen. et sp. nov. *a*, Enlargement of t2 in fig. 11*b*, showing a xylem bundle with an open area in the center. *b*, Enlargement of a part of the trace in fig. 12*a* (square), showing proximal tracheids aligned radially with respect to the parent axis. *c*, Enlargement of t2 area in fig. 11*c*, showing tangential orientated xylem tracheids in the parent axis affected by trace growth. *d*, Enlargement of t3 area in fig. 11*b*, showing disturbance of xylem cells adjacent to the trace(s). *e*, Enlargement of extra-xylary tissues fig. 7*d* (lower left arrow), showing some broken parenchyma cells inferred to be part of the cortex. *f*, Parenchyma cells of extra-xylary tissues in the tangential section (L02 in fig. 9) that are inferred to be part of the cortex. PKUB15204/L02. Scale bars = 200 µm (*a*, *c*-*e*) or 100 µm (*b*, *f*).

Fig. S1 Some of the original specimens collected from the Wutong Formation, Yixing, Jiangsu Province, China. *a*, Overall morphology of plant axes described in this paper. *b*, *c*, Two of the specimens showing bifurcation (arrows). Scale bars = 1 cm.

Table 1

Specimens Used to Describe the Anatomy of *Pleurorhizoxylon yixingense* gen. et sp. nov..

Specimen	No. of slides*	Where placed	Branch order	Axis diameter in transverse sections (mm)
PKUB15201	2 TS	Fig. 2*a*, 2*c*, 2*d*, 2*f*	Larger axis	4.6 x 3.5
PKUB15202	5 TS	Fig. 2*b*, 2*e*, 2*g*, 2*h*; Fig. 3*d*, 3*e*	Larger axis	7.5 x 6.0
PKUB15203	/	Fig. 4*i*-4*k*	Larger axis	4.2 x 3.0
PKUB15204#	2 TS, 6 LS	Fig. 3*a*-3*c*, 3*f*-3*i*; Fig. 4*a*-4*h*; Fig. 10*a*-10*i*; Fig. 12*f*	Larger axis	8.7 x 6.3
PKUB15205#	4 TS	Fig. 8*a*-8*e*	Larger axis	6.1 x 2.9
			Smaller axis	3.6 x 1.8
PKUB15207	5 TS	Fig. 7*a*-7*c*	Larger axis	5.3 x 2.3
			Smaller axis	3.0 x 1.7
PKUB15208#	9 TS	Fig. 7*d*-7*i*; Fig. 11*a*-11*i*; Fig. 12*a*-12*e*	Larger axis	5.7 x 3.5
			Smaller axis	4.3 x 1.7
			Smaller axis	1.8 x 1.4
PKUB15209	3 TS	Fig. 8*f*-8*i*	Larger axis	3.1 x 2.1
			Smaller axis	1.5 x 0.8

*TS = transverse sections; LS = longitudinal sections.

Axes that produce traces.

/ Specimen prepared for SEM observation.

Table 2

Comparisons on the primary xylem of *Pleurorhizoxylon* gen. nov. with *Yiduxylon*, iridopterids and sphenophylls.

	Genus	Stelar shape	Maturation	Protoxylem lacunae	Metaxylem tracheids	References
	Pleurorhizoxylon	three ribbed	mesarch	yes	scalariform to elliptical/circular bordered pits; 1- to 3- seriate	this paper
	Yiduxylon	three ribbed	mesarch	no	/	Wang DM and Liu 2015
iridopterids	*Ibyka*	three main arms which often bifurcate	mesarch	yes	scalariform thickenings to ovate/circular pitting	Skog and Banks 1973
	Iridopteris	five ribbed	mesarch	yes	circular to elliptical/scalariform bordered pit pairs	Stein 1982
	Arachnoxylon	six or seven ribbed	mesarch	yes	scalariform to elliptical/circular bordered pit pairs	Stein 1981

	Asteropteris	ten to twelve ribbed	mesarch	yes	/	Stein 1981
	Compsocradus	six ribbed	mesarch	yes	uniseriate elliptical bordered pits	Berry and Stein 2000
sphenophylls	*Sphenophyllum plurifoliatum*	three ribbed	exarch	no	reticulate bordered pits	Williamson and Scott 1895; Baxter 1948; Zhao 1989
	Sphenophyllum insigne	three ribbed	exarch	yes	oval, transversely elongated pits, approach the scalariform type	Williamson and Scott 1895; Solms-Laubuch 1896; Galtier 1970
	Hamatophyton	three ribbed	exarch	no	reticulate thickenings and simple/bordered pits	Li et al. 1995; Wang DM et al. 2006a

Rotafolia	three or four ribbed	exarch	no	scalariform pits and/or bordered pits	Wang DM et al. 2005, 2006b
Eviostachya	three ribbed	exarch	no	reticulate thickenings and elliptical bordered pits	Wang Y 1993

/ Information unknown.

Table 3

Comparisons of the secondary xylem of *Pleurorhizoxylon* gen. nov., with *Yiduxylon*, fernlike plants & sphenophylls.

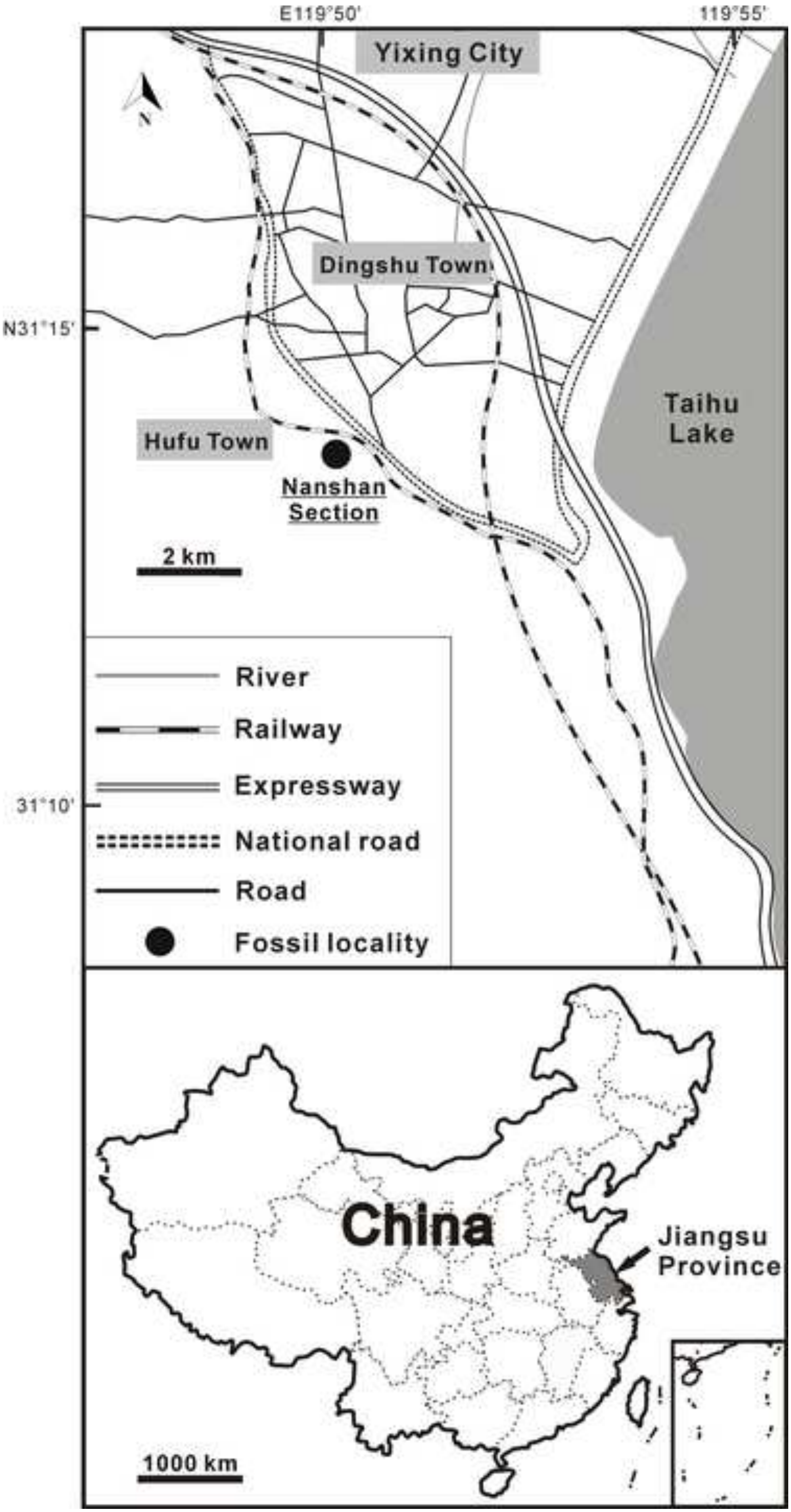
	Genus	Secondary xylem	Rays	Tracheids	References
	Pleurorhizoxylon	well-developed and broad	1-4 cells wide; sometimes abnormally large	have scalariform thickenings and elliptical boredered pits, 1- to 3-seriate	this paper
	Yiduxylon	well-developed and broad	usually 2 and sometimes up to 6 cells wide	multiseriate pits of circular and oval shape	Wang DM and Liu 2015
fernlike plants or early ferns	*Polypetalophyton*	putative, about 15 cells thick	narrow slits resembling rays	have circular and scalariform bordered pits in uniseriate and biseriate arrangements	Hilton et al. 2003
	Metacladophyton	well-developed	uiseriate and two to six cells high	have elliptical or circular bordered pits	Wang DM and Lin 2007
	Shougangia	well-developed	uniseriate to triseriate	have with scalariform thickenings and multiseriate elliptical bordered pits	Wang DM et al. 2017
	Calamophyton	up to at least 20 cells thick	/	/	Giesen and Berry 2013

	Xenocladia	compact	inconspicuous; have no visible parenchyma	have uniseriate or biseriate bordered pits	Arnold 1952
	Rhacophyton	up to 10 cells thick	uniseriate and 1-7 cells high	have scalariformly bordered pitting, or scalariform-reticulate patterns	Dittrich et al. 1983
sphenophylls	*Sphenophyllum plurifoliatum*	differentiated into fascicular and interfascicular regions	a true ray system	have crowded and circular to elliptical bordered pits	Baxter 1948; Eggert and Gaunt 1973; Cichan and Taylor 1982; Cichan 1985
	Sphenophyllum insigne	differentiated into fascicular and interfascicular regions	continuous medullary rays	have scalariform thickenings at least on the radial walls and only a few small rounded pits on the tangential walls	Williamson and Scott 1895

Hamatophyton	divided by the primary ribs	/	have scalariform thickenings or scalariform to elliptical bordered pits	Wang DM et al. 2006a
Rotafolia	homogeneous	present	have scalariform thickenings or scalariform to elliptical/circular bordered pits	Wang DM et al. 2005, 2006b

/ Information unknown.

Figure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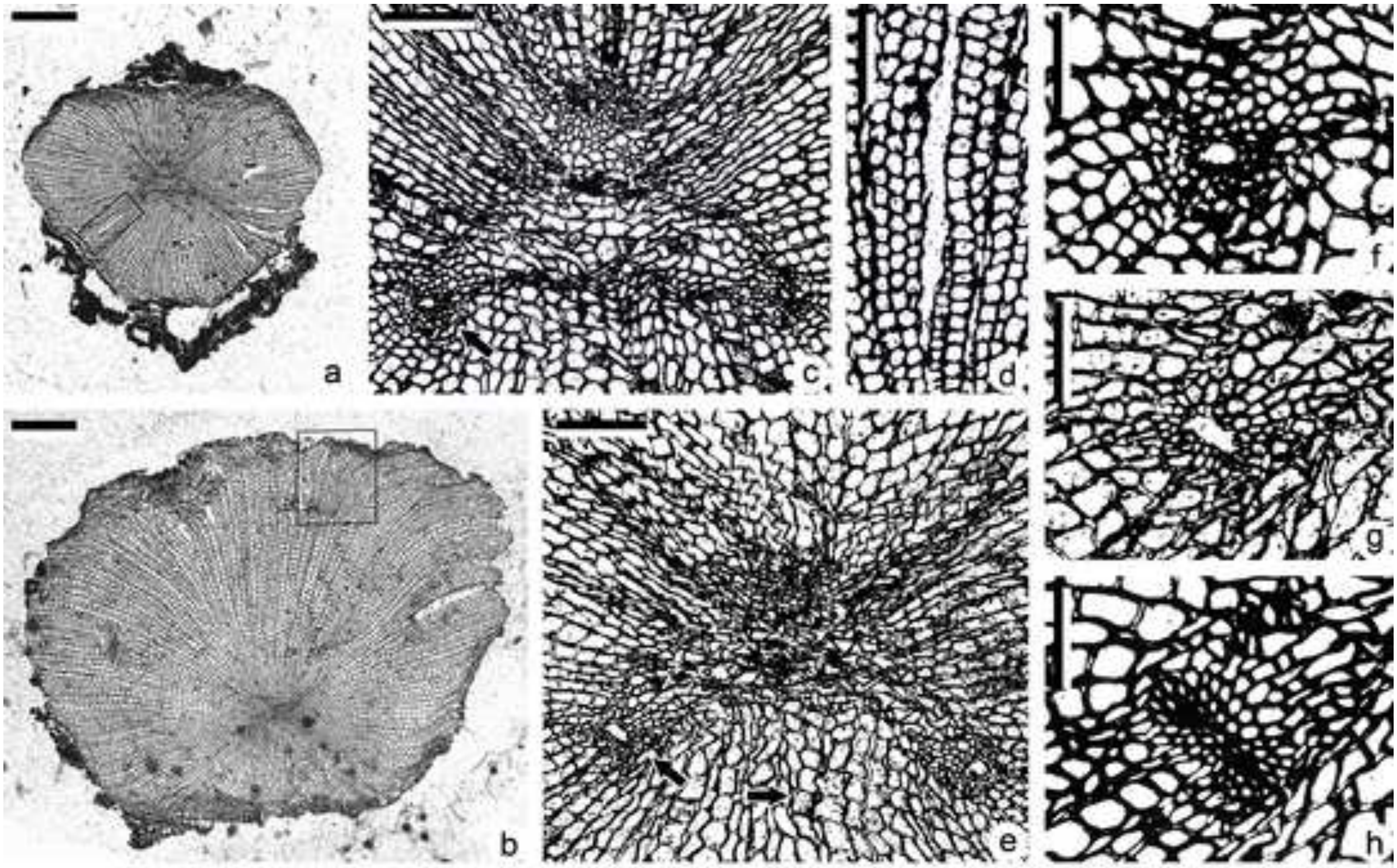
Fossil locality
China
Jiangsu Province
1000 km

Figure



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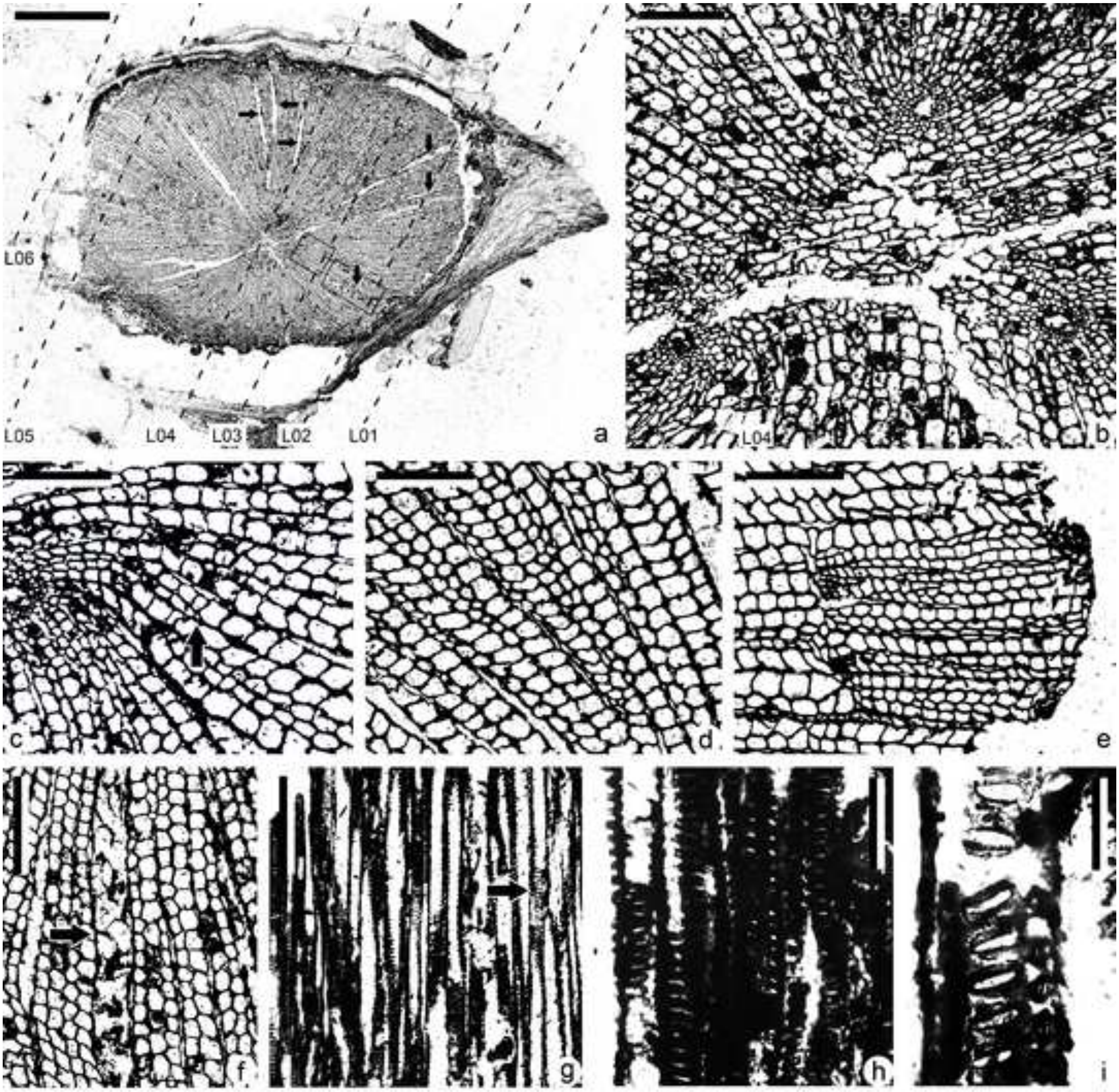

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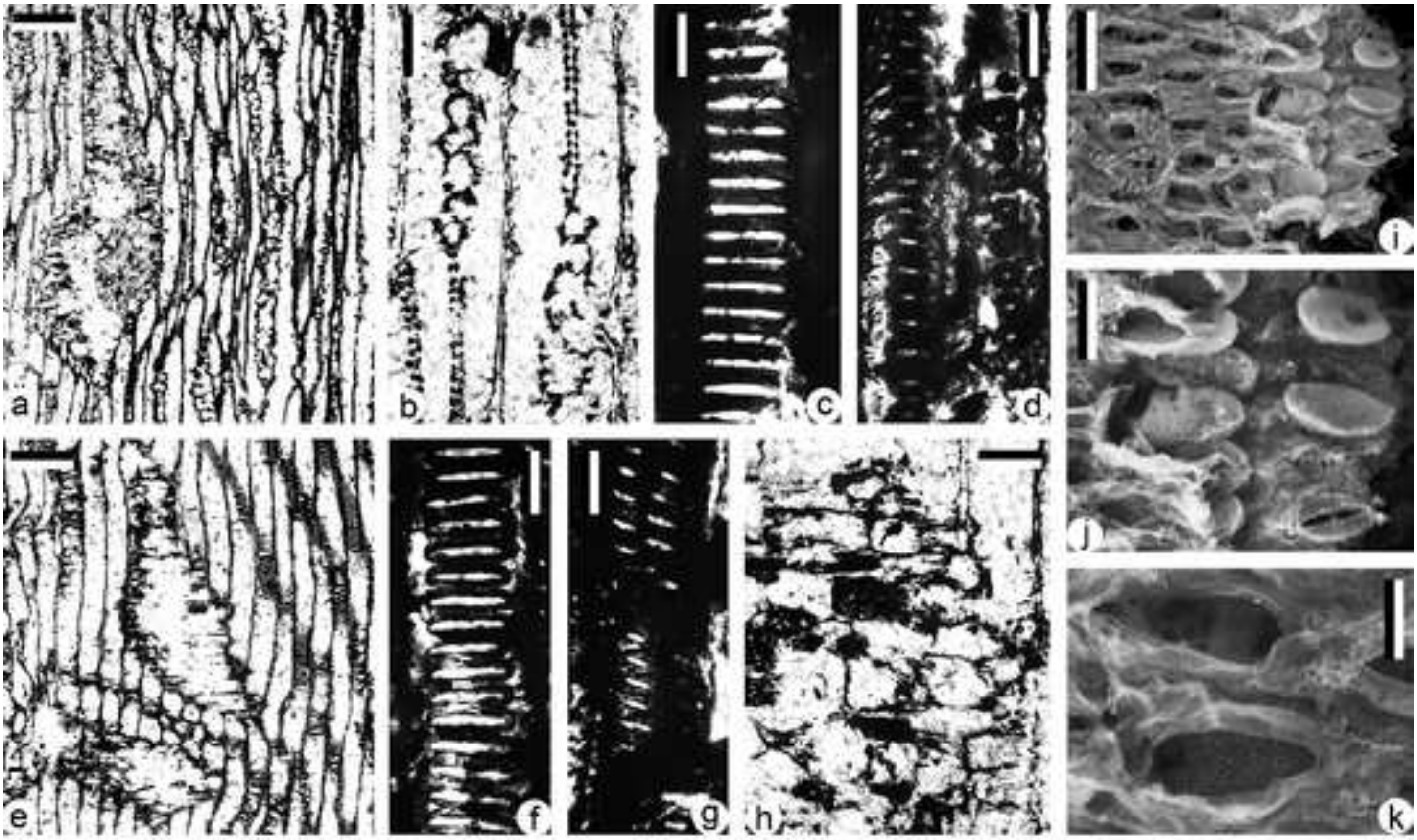

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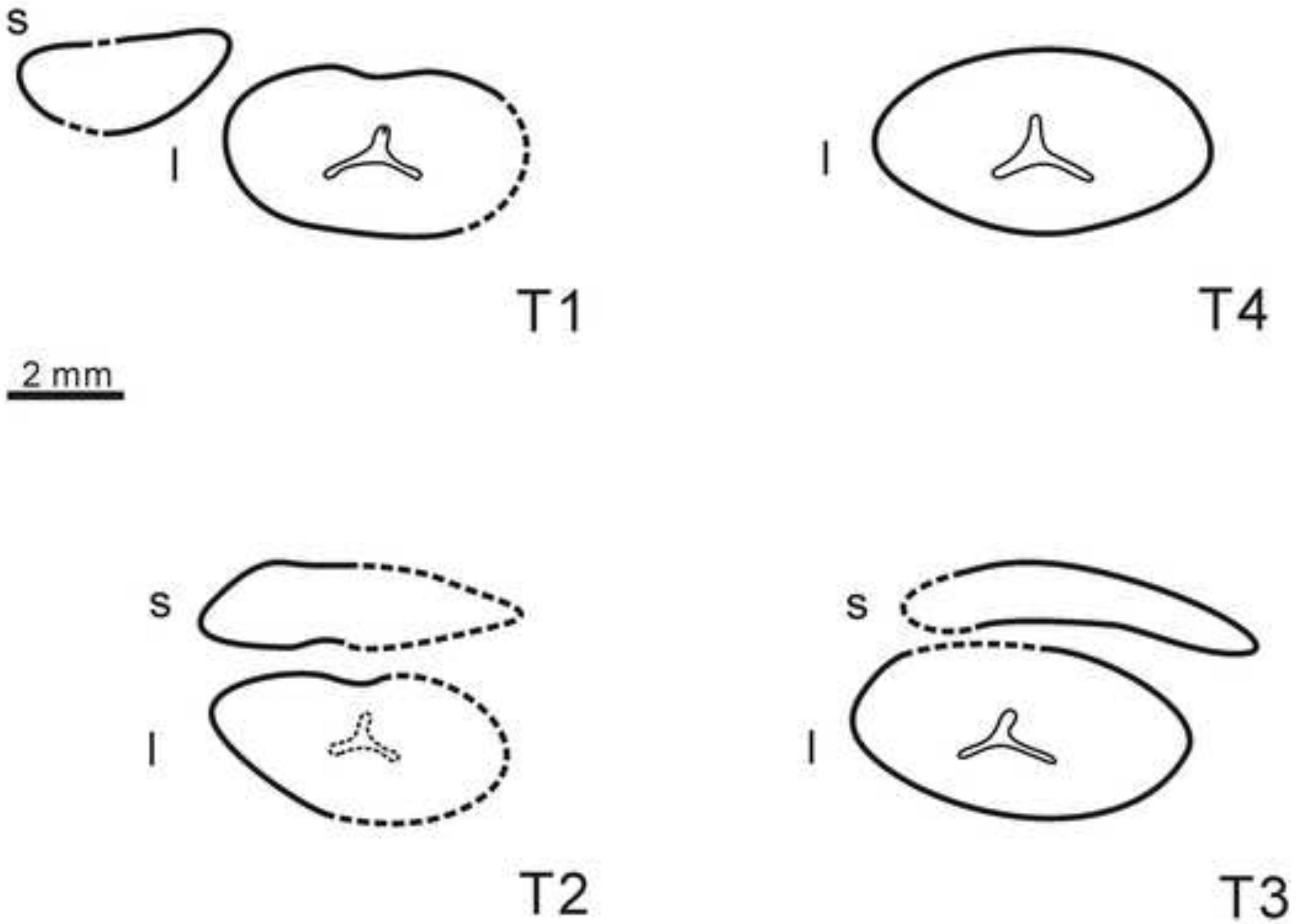

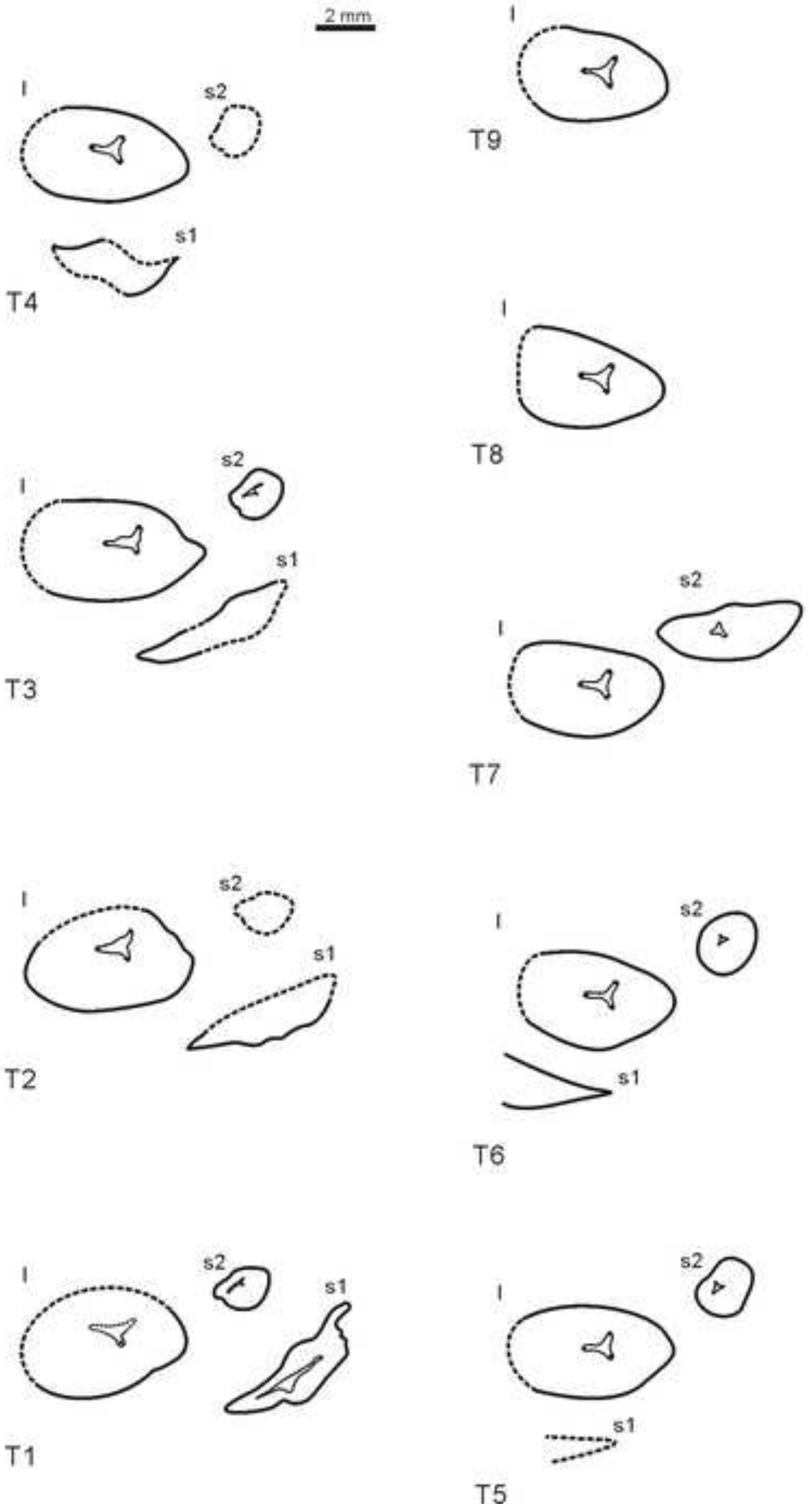
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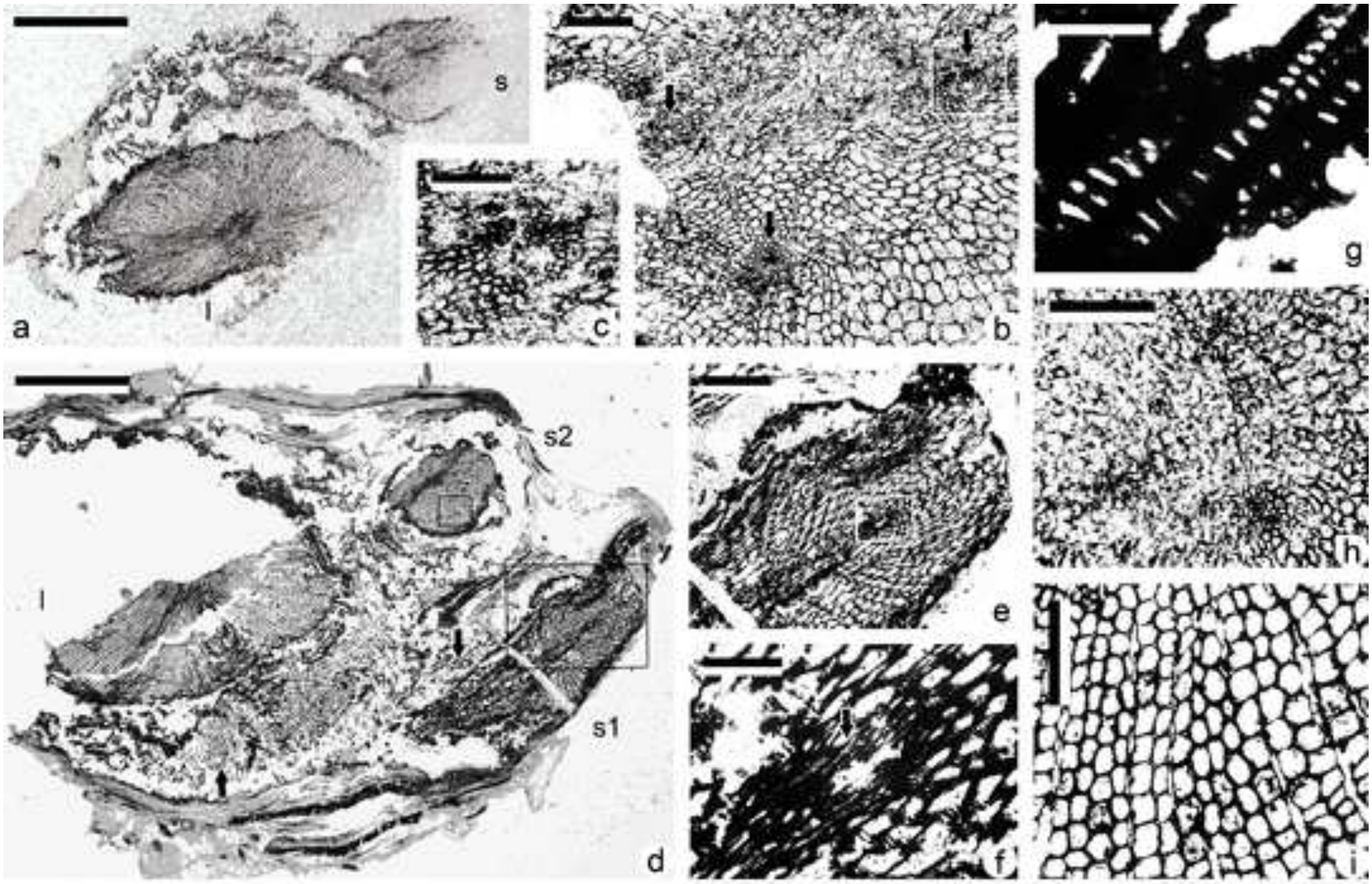

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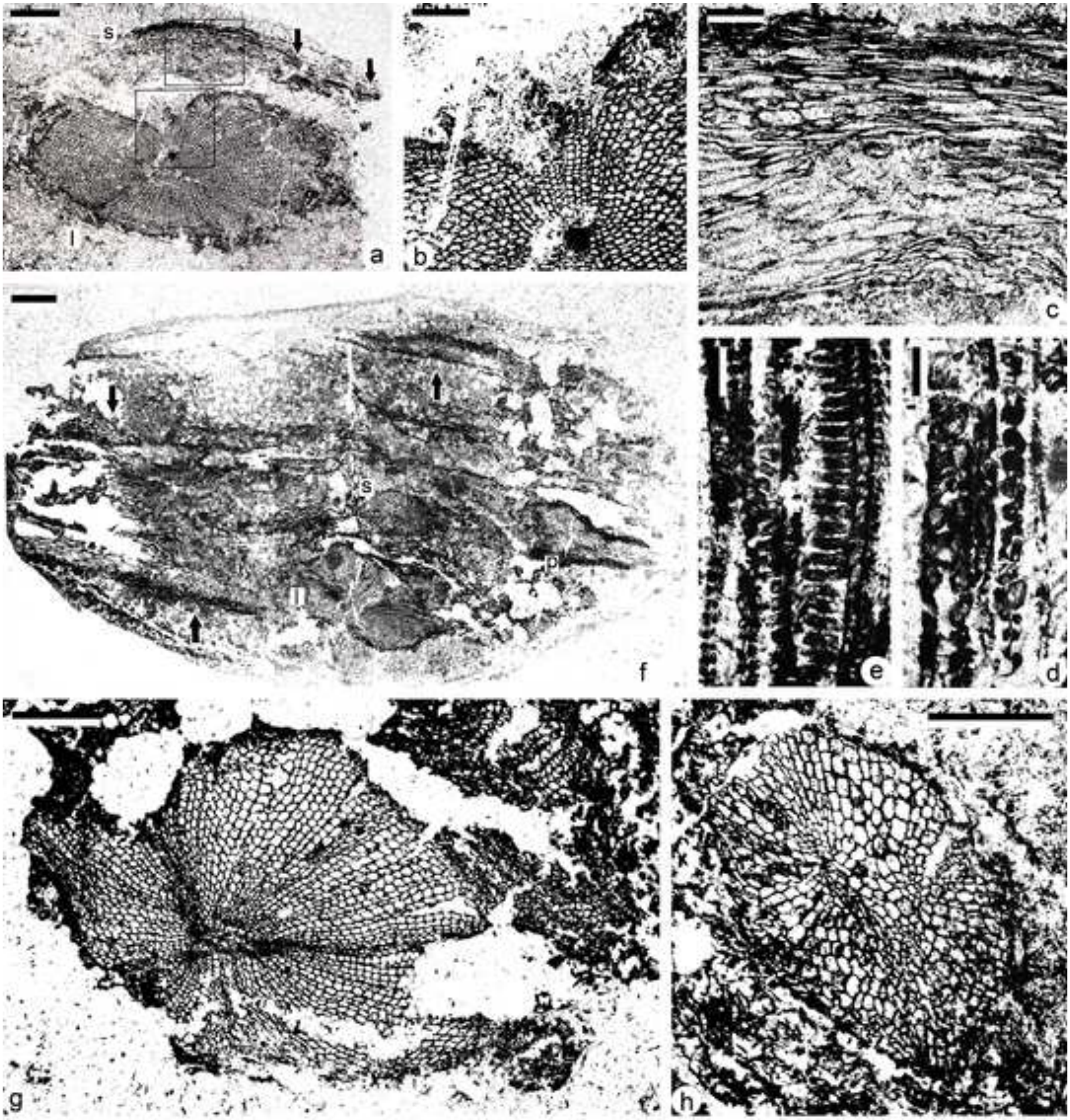

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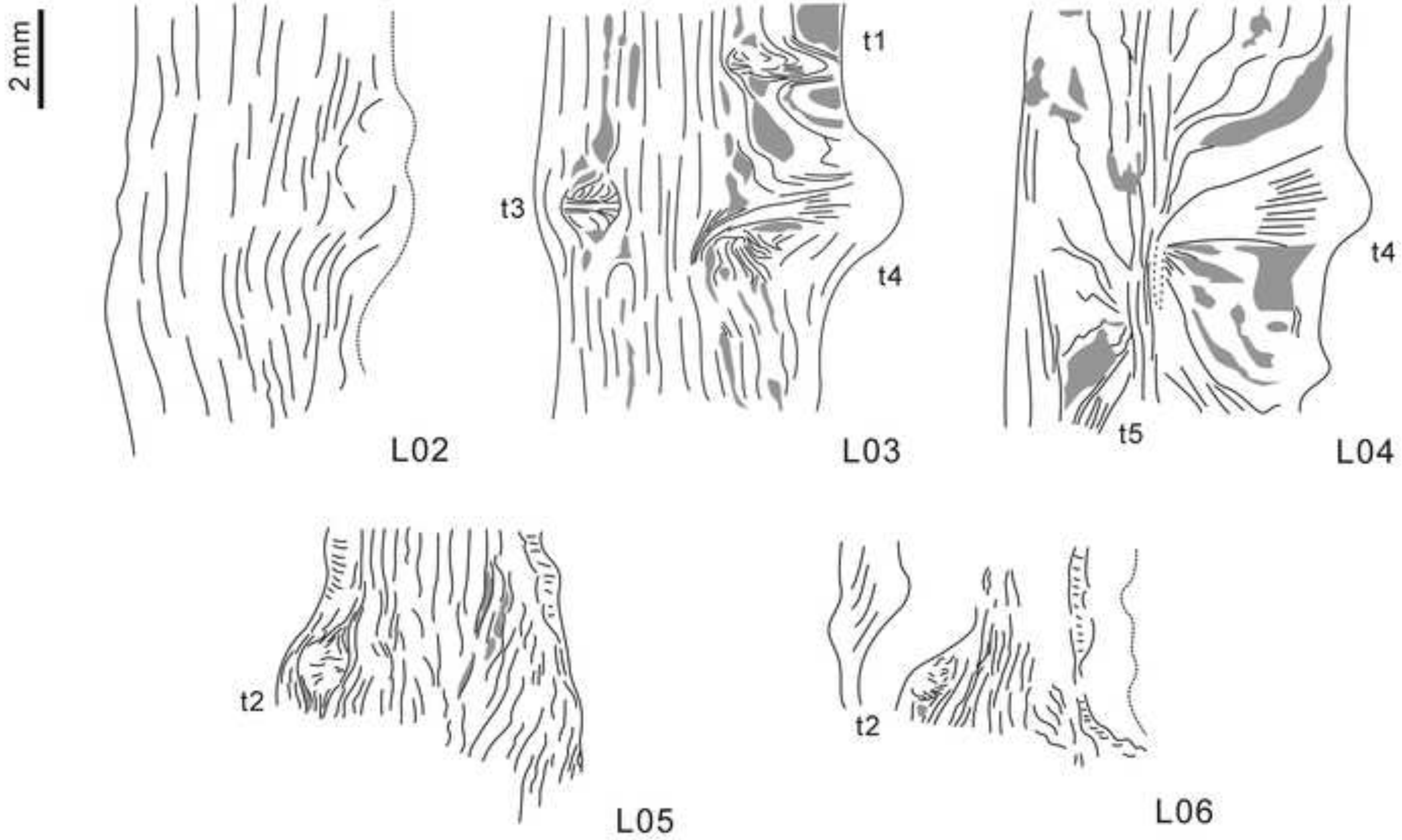

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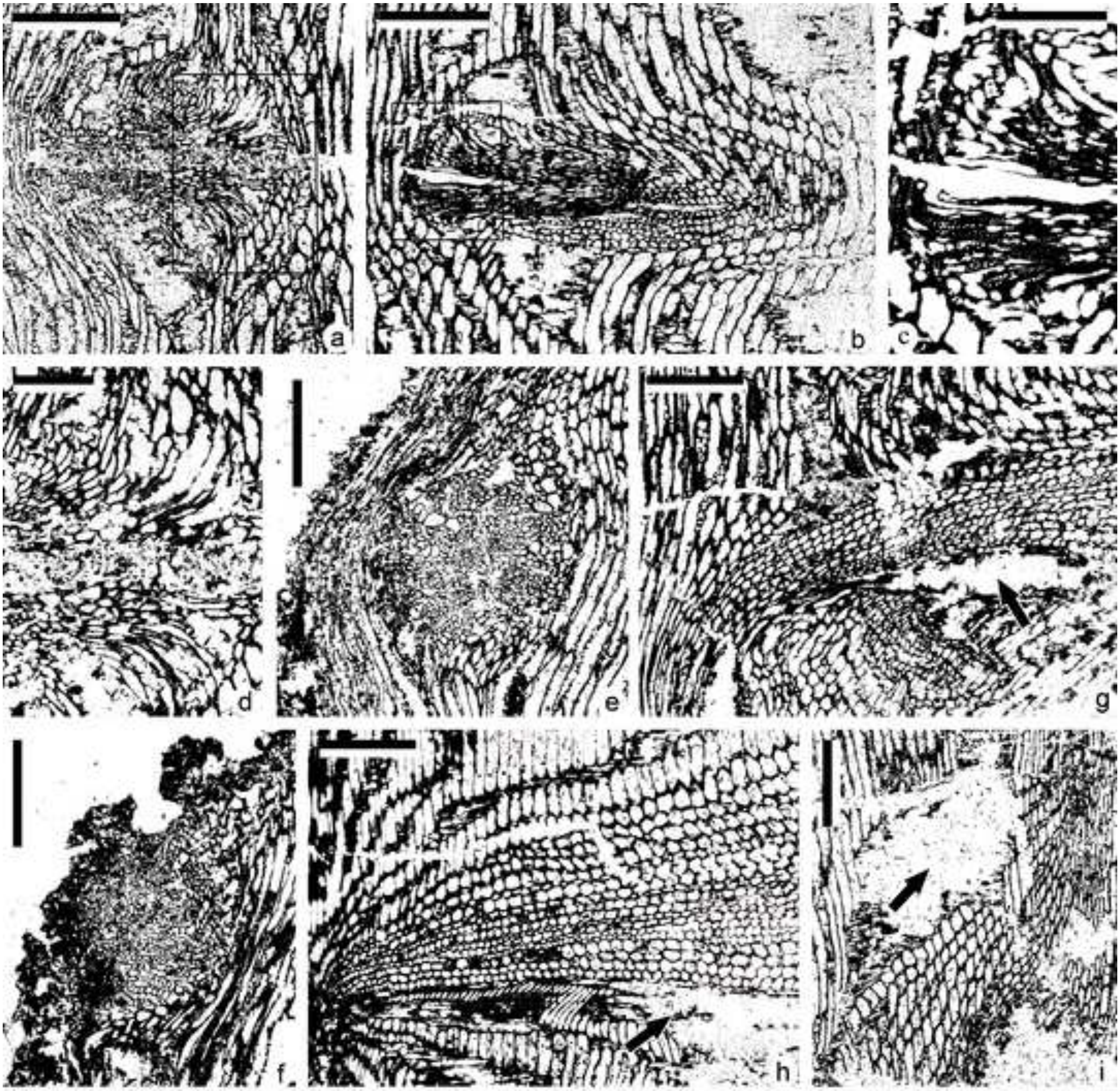

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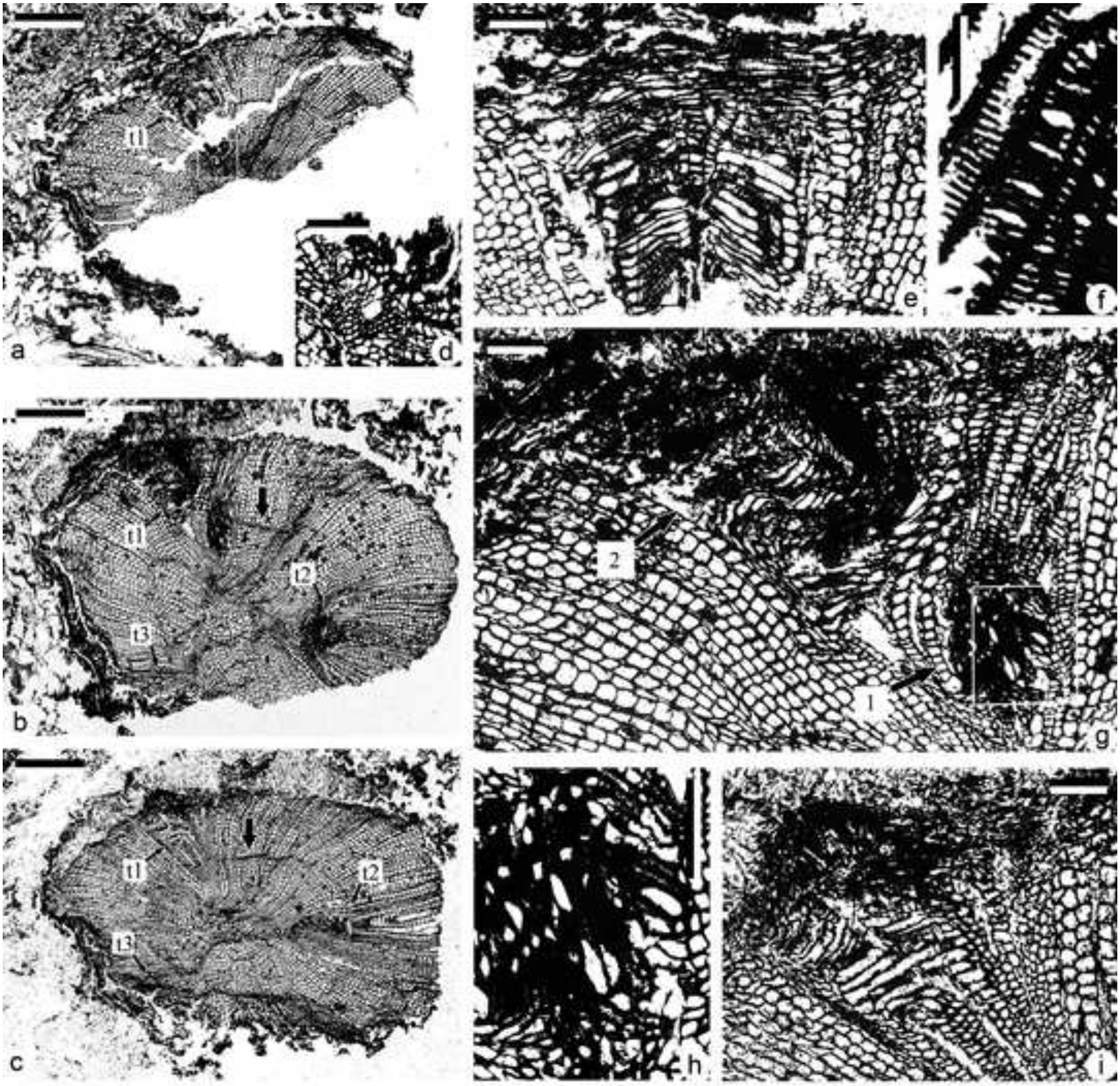

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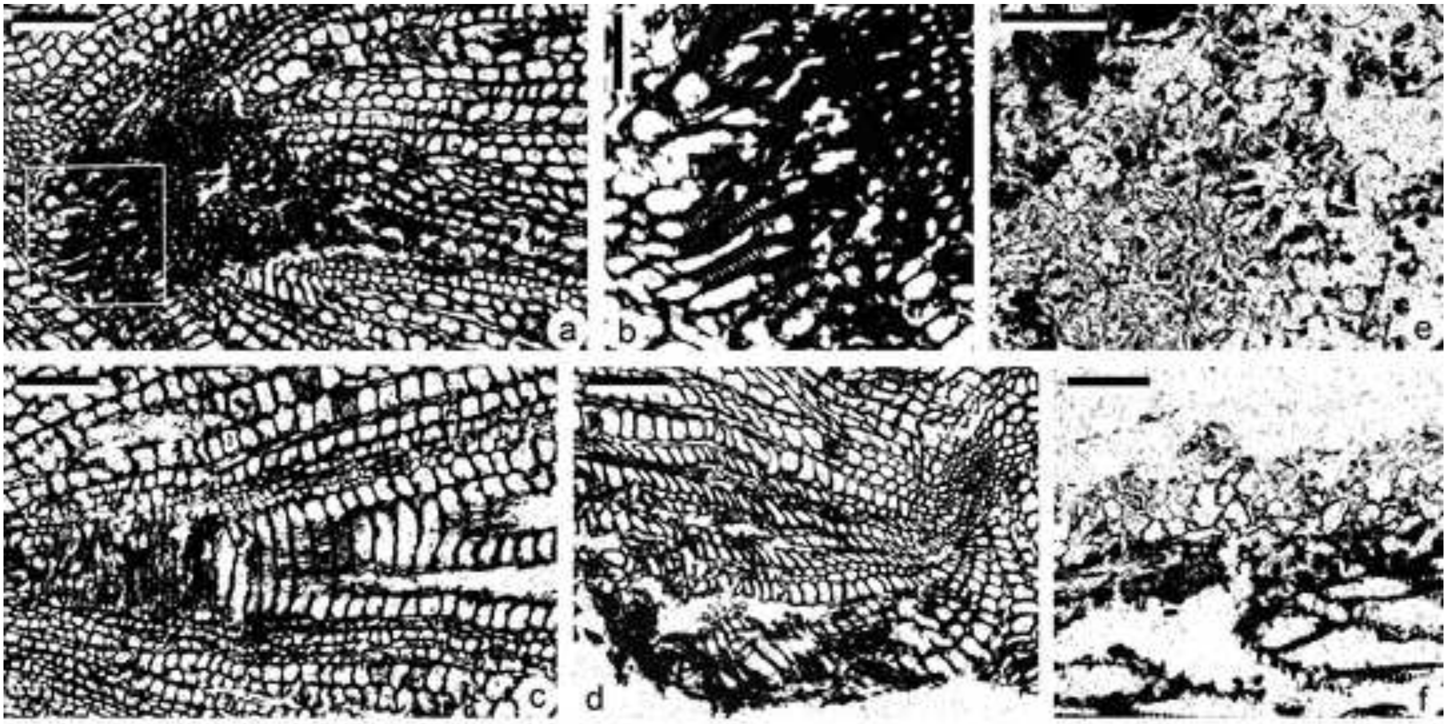

Sup fig 1