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ANATOMICALLY PRESERVED MARATTIALEAN PLANTS FROM THE UPPER PERMIAN OF SOUTHWESTERN CHINA: THE TRUNK OF *PSARONIUS LAOWUJIENSIS* SP. NOV.

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A marattialean trunk of *Psaronius laowujiensis* sp. nov. is described from the Upper Permian of the Xuanwei Formation, Panxian County, Guizhou Province, South China. The specimen most likely represents the lower part of the trunk, because the preserved thickness of the root mantel is somewhat larger than the diameter of the stem. Meristeles of the stem are arranged in approximately five tangential stelar cycles but not in radial files. Inner meristeles are in small number, ~12–13, and loosely arranged. Leaf traces diverge helically and are organized in a 2/5 phyllotaxy. The leaf base vascular configuration consists of three strands that include a large U-shaped, centrifugal strand, a small centripetal strand, and an inverted Ω-shaped internal strand. A vascular bundle sheath one or two cell layers thick surrounds each meristele. Within the centripetal concavity of each peripheral cauline bundle there are anchor-shaped sclerenchymatous strands. Ground tissue appears to consist of aerenchymatous parenchyma, in which secretory cavities are dispersed. Bound roots mostly possess seven to nine protoxylem poles. The vascular bundle sheath is one or two cell layers thick. The inner cortex consists of aerenchymatous parenchyma. A detailed comparison of the present specimen with known species of *Psaronius* from the Permian of South China is made. Our specimen is similar to *Psaronius wangii* in many aspects, but the two can be clearly distinguished by the structure of the ground tissue of the stem and the leaf base vascular configuration, which leads to the erection of a new species, *P. laowujiensis*, for this specimen. Certain important characters in species from the Permian of South China are discussed. The tree- or anchor-shaped sclerenchymatous configuration within the centripetal concavity of the peripheral cauline bundles is unique to species from the South China Permian. The permanent vascular bundle sheath surrounding the meristeles of the stem and the stele of the root is another remarkable feature of those species. The analogous tissue, termed "inner cortex" by certain authors, is also present in some *Psaronius* from the Euramerican and North China floras, but in those cases it is thinner walled and not as remarkable as the vascular bundle sheath in the species from South China. The leaf base vascular configuration of the species from the Permian in South China is more diverse than those from other places.

Keywords: Marattiales, *Psaronius*, anatomy, Permian, South China.

Introduction

Psaronius is a fossil genus of anatomically preserved stems that probably originated from a marattialean fern of the late Paleozoic, although it is sometimes also used as a genus of whole plants (Morgan 1959). The genus was established by Cotta (1832, pp. 27–36), and since that time it has been widely reported from the Carboniferous (Pennsylvanian) into the Permian of North America, South America, Europe, Southeast Asia, and China (Corda 1845; Dawson 1871; Brongniart 1872; Williamson 1876; Lesquereux 1880; Zeiller 1890; Stenzel 1906; Hirmer 1927; Blickle 1940; Sze 1942, 1947; Dolianti 1948; Morgan 1959; Andrews et al. 1970; Ogura 1972; Gu and Zhi 1974; DiMichele and Phillips 1977; Rothwell and Blickle 1982; Mickle 1984; Herbst 1985, 1986, 1999; Ma 1985; Yang 1986; Li 1987; Tian et al. 1992; Yao et al. 1994; He et al. 2008).

A number of species of *Psaronius* have been reported from the Upper Permian of South China, including Jiangsu, Sichuan, Yunnan, and Guizhou provinces (He et al. 2008). These species demonstrate several features not found in those from other regions and stratigraphic intervals. These features include the vascular bundle sheath surrounding the meristeles and leaf traces of the stem, configuration of the sclerenchymatous strand in the periphery of the stem, and the vascular configuration of the leaf base in certain species, such as *Psaronius octogonus* (Yao et al. 1994), *Psaronius panxianensis* (He et al. 2008), and *Psaronius wangii* (Tian et al. 1992). These features increase the diversity of the anatomical aspects and probably demonstrate some evolutionary trends of the genus.

In this article, we describe a new species, *Psaronius laowujiensis* sp. nov., from the Upper Permian Xuanwei Formation,

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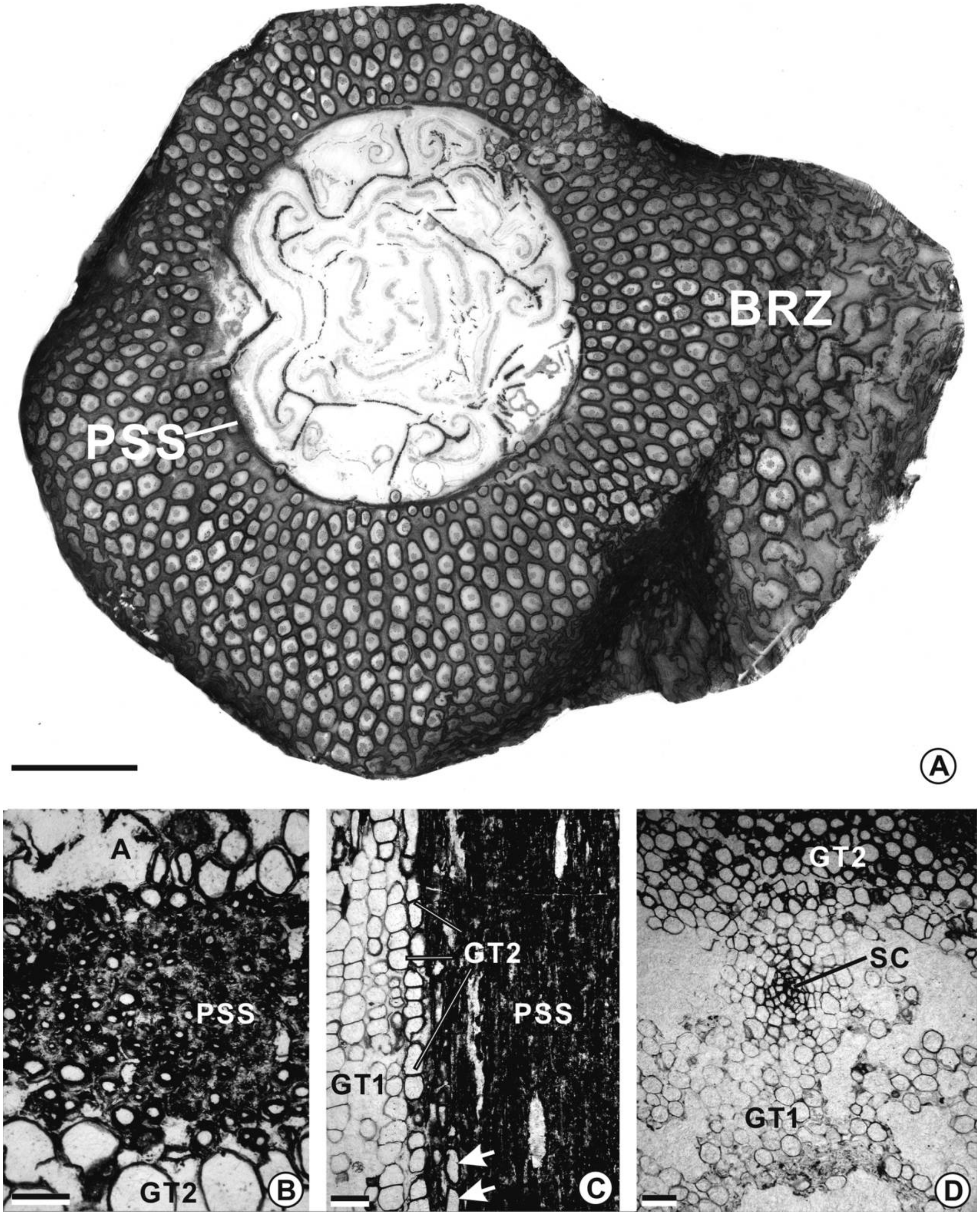


Fig. 1 *A*, Transverse section through trunk of *Psaronius laowujiensis* sp. nov., showing the gross shape of the stem, the peripheral sclerenchymatous sheath (*PSS*), and the bound-root zone (*BRZ*). Peel LWJ2007-2A. Scale bar = 20 mm. *B*, *C*, Cross section and longitudinal section, respectively, through the peripheral part of the stem, showing the area (*A*) between the peripheral sclerenchymatous sheath and the bound-root zone, thinner-walled (*GT1*) and thicker-walled (*GT2*) ground tissue, and thicker-walled cells in the peripheral sclerenchymatous sheath (arrows in C). Slides WP2L-0034 (*B*), WP2L-0033 (*C*). Scale bars = 100 μm (*B*) and 200 μm (*C*). *D*, Cross section through the peripheral part of the stem, showing thinner-walled (*GT1*) and thicker-walled (*GT2*) ground tissue and a secretory cavity (*SC*). Slide WP2L-0034. Scale bar = 200 μm.

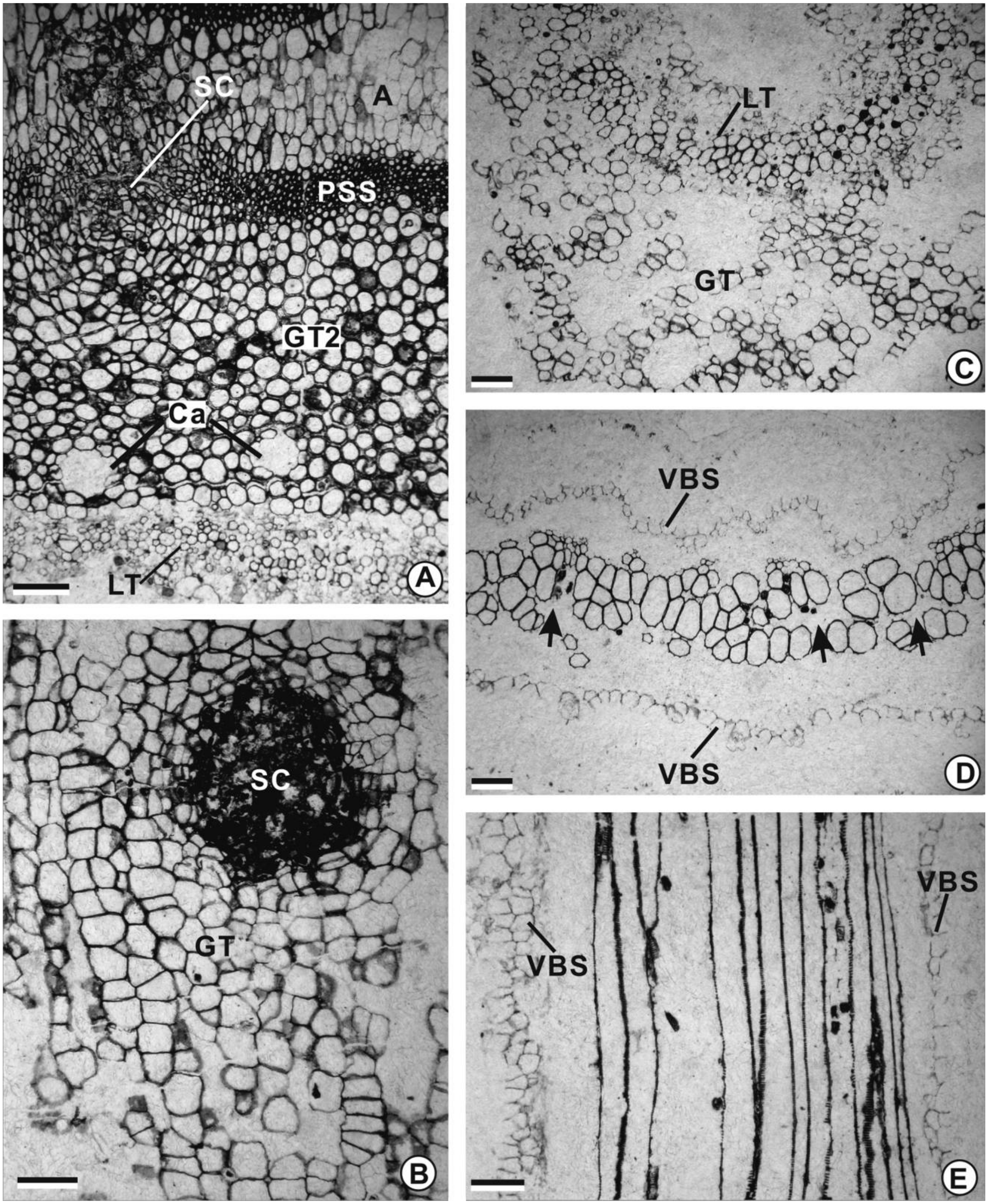


Fig. 2 *A*, Cross section through the peripheral part of the stem, showing the area (*A*) between the peripheral sclerenchymatous sheath (*PSS*) and the bound-root zone, a secretory cavity (*SC*), and air cavities (*Ca*) within the thicker-walled ground tissue (*GT2*). Slide WP2-0022. Scale bar = 200 μm. *B*, Tangential section through the peripheral part of the stem, showing a large secretory cavity (*SC*) with black content in ground tissue (*GT*). Slide WP2L-0034. Scale bar = 200 μm. *C*, Cross section of the stem, showing aerenchymatous parenchyma (*GT*) around the leaf trace (*LT*). Slide WP2L-0034. Scale bar = 100 μm. *D*, Part of an inner meristele in cross section, showing the vascular bundle sheath (*VBS*). Arrows indicate

Panxian County, Guizhou Province, South China. This species shows a new, changing pattern of the leaf trace configuration. In addition, some important characters specific to species of *Psaronius* from the Permian of South China are summarized and compared with those of *Psaronius* species from other locations.

Material and Methods

The species investigated in this study consists of a trunk (numbered LWJ2007-2), preserved in volcaniclastic tuffs and permineralized with calcium carbonate, from the Upper Permian Xuanwei Formation in the Laowuji coal mine, Panxian County, western Guizhou Province. Specimens were collected within mine spoil, so the precise horizon within the Xuanwei Formation is unknown.

Geologic information on the Xuanwei Formation, including plant compression/impression assemblages, has been published by Yao et al. (1980) and Zhao et al. (1980). Fragmentary plant fossils preserved in volcaniclastic tuffs from the Xuanwei Formation at the Shanjiaoshu and Huopu coal mines have been preliminarily studied by Hilton et al. (2004) and Wang et al. (2006). Further work on this assemblage is in progress.

The permineralized trunk was cut with a rock saw to reveal morphological and anatomical aspects in transverse and longitudinal sections. Cut faces were prepared by the acetate peel technique (Galtier and Phillips 1999); 5% HCl was used to etch the mineral matrix. Peels were mounted on glass slides with Canada balsam. Large peels were photographed under reflected light with a Nikon 4500 digital camera. Glass slides were photographed with a Nikon transmitted-light microscope equipped with a Nikon 4500 digital camera. Images were adjusted with Adobe Photoshop (ver. 7), and plates were constructed with Corel-draw (ver. 12). Specimens with peels and the slides made from them are deposited in the Palaeobotanical Department of the National Herbarium of China, Institute of Botany, the Chinese Academy of Sciences.

Systematic Palaeobotany

Order—Marattiales

Family—Psaroniaceae Stenzel

*Genus—*Psaronius *Cotta 1832*

*Type Species—*Psaronius helmintholithus *Cotta 1832*

*Species—*Psaronius laowujiensis *sp. nov.*

Derivation of specific name. From Laowuji, the locality where the specimen was collected.

Specific diagnosis. Stem nearly round. Peripheral sclerenchymatous sheath continuous, 0.35–0.75 mm thick, consisting of sclerenchymatous cells. Sclerenchymatous tissues in the stem mainly present in stelar cycle 1 and between cycles 1 and 2. Anchor-shaped sclerenchymatous strand located at the centripetal side of the peripheral cauline bundles. Two anchor-shaped sclerenchymatous strands on each side of a leaf trace connected to each other by their handle- or arc-shaped parts, forming a large, wide, U-shaped sclerenchymatous strand. The polycyclic dictyostele consists of at least five concentric stelar cycles. Inner meristeles sparse, ~12 in number, arranged irregularly in a radial pattern and two to five tracheid layers thick. Peripheral cauline bundles and leaf traces or leaf bases occurring alternately; leaf traces diverging into spirals. Inner meristeles, peripheral cauline bundles, and leaf traces differ in thickness and size of tracheids. Vascular bundle sheath one or two cell layers thick. Vascular configuration in leaf base consisting of a large, U-shaped centrifugal strand, a small centripetal strand, and an inverted Ω-shaped internal strand. Ground tissue consisting of aerenchymatous parenchyma. Secretory cavities distributed in ground tissue near the peripheral sclerenchymatous sheath. Bound roots arranged randomly, with sizes ranging from 2 to 5 (mostly 3–4) mm. Stele usually possessing seven to nine protoxylem poles. Vascular bundle sheath one or two cell layers thick. Inner cortex consisting of aerenchymatous parenchyma and some secretory cells with dark content near the vascular bundle sheath. Sclerenchymatous rings usually five to eight cell layers thick, within which elliptical gum sacs are dispersed.

Holotype. LWJ2007-2 and peels and slides made from it.

Type locality. Laowuji coal mine, Panxian County, western Guizhou Province, China.

Geological horizon. Xuanwei Formation.

Description of the Specimen

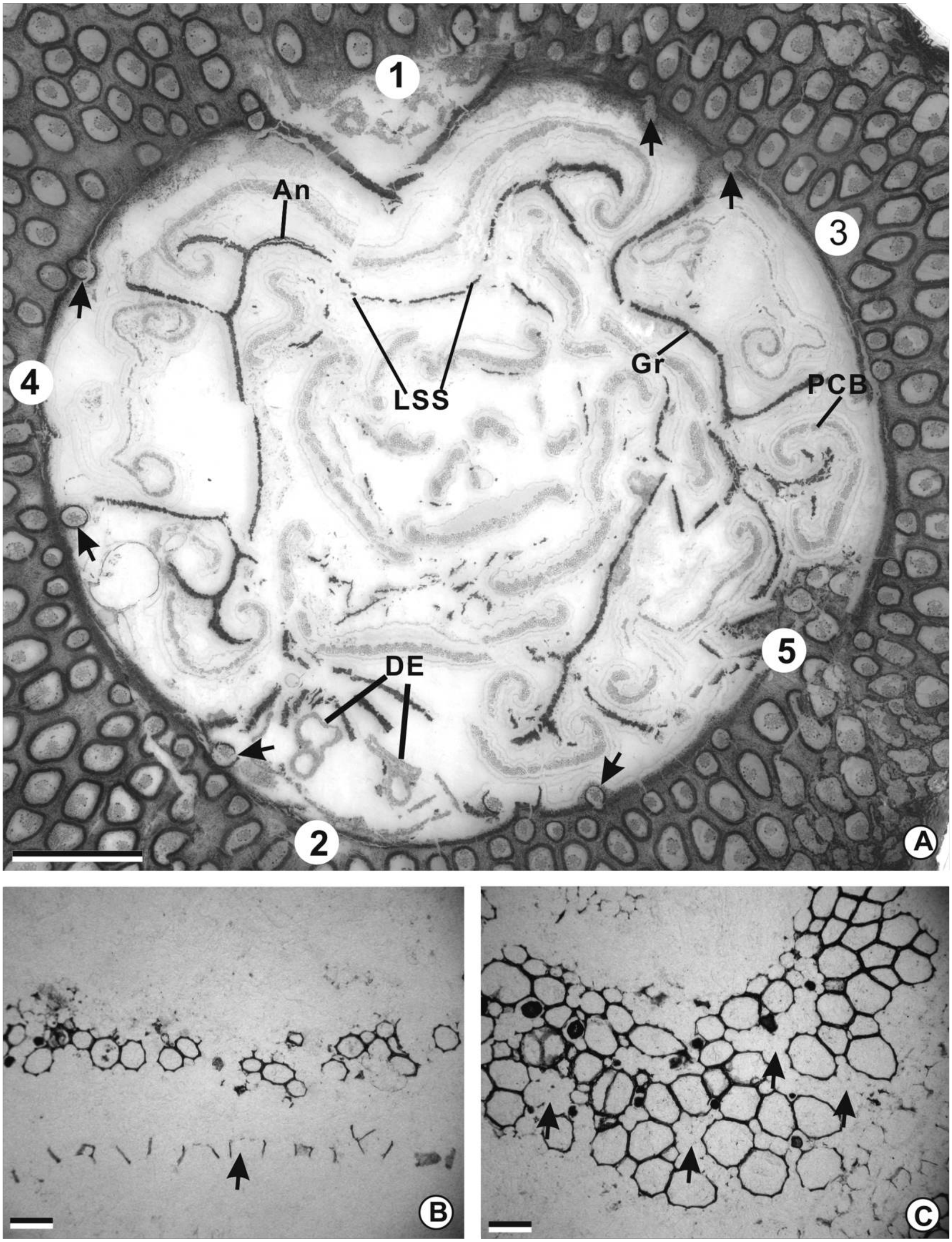
General Features

Just one specimen, numbered LWJ2007-2, is described in this article. It is a trunk with a preserved length of 17 cm and a transverse size of 14.8 cm × 12.3 cm, including the complete stem and the incompletely preserved root mantle (fig. 1*A*). The stem is nearly round in cross section, with a diameter of 6 cm × 6.5 cm (figs. 1*A*, 3*A*). Except for the ground tissue in the stem and most of the cortex of roots that collapsed and left vacuous spaces, the tissues of the specimen are well preserved.

Peripheral Sclerenchymatous Sheath

The stem is surrounded by a continuous peripheral sclerenchymatous sheath, usually with a thickness varying from 350 to 750 μm. It consists of fiber cells and occasionally thicker-walled parenchymatous cells. Fiber cells are nearly isodiametric in transverse section, 25–55 (mostly 40–45) μm in diameter, densely arranged (fig. 1*B*), and elongate in longitudinal section, with a length of more than 500 μm (fig. 1*C*). However,

xylem parenchyma. Slide WP2L-0034. Scale bar = 200 μm. *E*, Part of an inner meristele in longitudinal section, showing the vascular bundle sheath. Slide WP2L-0033. Scale bar = 200 μm.


1
An
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PCB
3
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5
2
A
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C

at the leaf base, both the thickness of the sclerenchymatous sheath and the diameter of fiber cells decrease; these are finally replaced by parenchymatous cells (fig. 2*A*; fig. 4*E*, 4*F*; fig. 5*A*, 5*C*). The cell walls are bilayered, with the outer, primary one having a uniform thickness of 3–4 μm, densely constructed, and yellow in transmitted light, while the secondary one is usually loosely constructed, variable in thickness (5–13 μm), and dark brown in transmitted light. The margin of the peripheral sclerenchymatous sheath is uneven because of the invasion of the ground tissue of the stem.

Ground Tissue

Little ground tissue is preserved, so the areas between individual meristeles are mostly void. However, remains of ground tissue can occasionally be found near the inner side of the peripheral sclerenchymatous sheath (fig. 1*C*, 1*D*; fig. 2*A*) and in leaf bases (fig. 2*C*). The ground tissue consists of isodiametric parenchymatous cells with a diameter of 50–120 (mostly 70–100) μm. Tannin cells are present but scarce. Parenchymatous cells near the peripheral sclerenchymatous sheath are either thicker walled and densely arranged (figs. 1*D*, 2*A*) or thinner walled and loosely arranged, with well-developed intercellular spaces (fig. 1*D*). Air cavities are present in both thicker- and thinner-walled ground tissue (figs. 1*D*, 2*A*). Secretory cavities sizes ranging from 250 to 1000 μm, sometimes with black content, can be seen in this zone (fig. 1*D*; fig. 2*A*, 2*B*). In other places, ground tissue is typically thin walled and aerenchymatous (fig. 2*C*). In longitudinal section, cells of the ground tissue are slightly horizontally elongate in shape (figs. 1*C*, 2*B*).

Sclerenchymatous Tissue in the Stem

Sclerenchymatous tissues in the stem are typically organized in continuous strands. They are mainly distributed between stelar cycles 1 and 2, where they either surround leaf traces or extend into the concavities of the peripheral cauline bundles. Sclerenchymatous strands are rarely present in the leaf trace and between inner stelar cycles. They possess slightly uneven sides, consist of fiber cells, and are narrower than the peripheral sclerenchymatous sheath.

The sclerenchymatous strand located in the concavities of the peripheral cauline bundles has an anchor-shaped configuration (fig. 3*A*). It consists of an arc-shaped part extending along the centripetal side of the peripheral cauline bundle and a handle-shaped part extending inward from the middle point of the arc. Two anchor-shaped sclerenchymatous strands on each side of a leaf trace tend to be connected with each other by their handle- or arc-shaped parts, forming a large, wide, U-shaped sclerenchymatous strand (fig. 3*A*). The leaf traces are enclosed by sclerenchymatous strands from the centripetal and lateral sides and by the peripheral sclerenchymatous sheath from the centrifugal side, forming various configurations, depending on their level. When the leaf trace is at a lower level on the trunk, the sclerenchyma configuration is nearly rectangular (i.e., leaf traces 3 and 4 in fig. 3*A*), while at a higher level, where the leaf trace enters the leaf base, the sclerenchymatous configuration is roughly pentagonal or rhomboid (e.g., leaf trace 1 in fig. 3*A*).

Stele

The stem has a polycyclic dictyostele that consists of five concentric stelar cycles (numbered from 1 to 5 inward). Adjacent cycles are separated by empty areas that mark the position of ground tissue.

Cycle 1, the outermost cycle, consists of alternately arranged peripheral cauline bundles and leaf traces (fig. 3*A*). The peripheral cauline bundles are often C- or bluntly V-shaped, with their edges conspicuously incurved centripetally (e.g., *PCB* in fig. 3*A*). Leaf traces possess different vascular configurations, depending on the their level. Inner meristeles are sparse, ~12 in number, and arranged irregularly in the radial direction. They are often band shaped and slightly wavy, with their edges more or less incurved centripetally or centrifugally. The length of the meristeles is variable, and occasionally very short ones can be seen at the center of the stele. Meristeles consist of xylem strands and the vascular bundle sheath. Phloem is typically absent because of bad preservation. Xylem maturation is endarch. Protoxylem is located in irregularly spaced groups, usually in low and tangentially elongate protrusions, of four to nine tracheids, and protoxylem tracheids are 20–40 μm in diameter. Tracheids of the metaxylem are mostly isodiametric, sometimes slightly radially elongate in shape, and 50–250 (mostly 100–150) μm in diameter in cross section. Xylem strands of inner meristeles, peripheral cauline bundles, and leaf traces differ in thickness and in the size of tracheids. Generally, the thickness of the xylem strands of inner meristeles is uniform or slightly variable, usually 600–750 μm or two to five cell layers thick; tracheids are larger and can be more than 200 μm (usually 80–150 μm) in diameter. The xylem strand of the peripheral cauline bundles is slightly thinner, and the tracheids are also a little smaller. The xylem strands of leaf traces as a whole are even thinner, and the tracheids are even smaller. At the main part of the leaf trace, the xylem strand is 100–150 μm or two or three cell layers thick, and the tracheids are 25–60 μm in diameter (fig. 3*B*), while at the inrolled edges, the xylem strand is 350–400 μm or four to six cell layers thick, and the tracheids are up to 200 μm in diameter (fig. 3*C*). Nearly isodiametric or radially elongate and polygonal parenchyma cells are small, usually 30–50 μm in transverse diameter, and are dispersed between the metaxylem tracheids. Some parenchyma have dark, amorphous contents

Fig. 3 *A*, Transverse section of the stem, showing leaf traces (*1–5*); anchor-shaped sclerenchymatous strands (*An*) in the centripetal concavity of peripheral cauline bundles (*PCB*); groove-shaped sclerenchymatous strands surrounding the leaf trace (*Gr*); large U-shaped sclerenchymatous strands (*LSS*); two C-shaped strands (*DE*) derived from the strongly inrolled edges of the leaf trace; roots in the stem (arrows). Peel LWJ2007-2A. Scale bar = 10 mm. *B*, *C*, Parts of a leaf trace. Slide WP2L-0034. Scale bar = 100 μm. *B*, Middle part, with very thin xylem strand and very small tracheids; arrow indicates vascular bundle sheath. *C*, Inrolled edge, with thicker xylem strand and larger tracheids; arrows indicate xylem parenchyma.

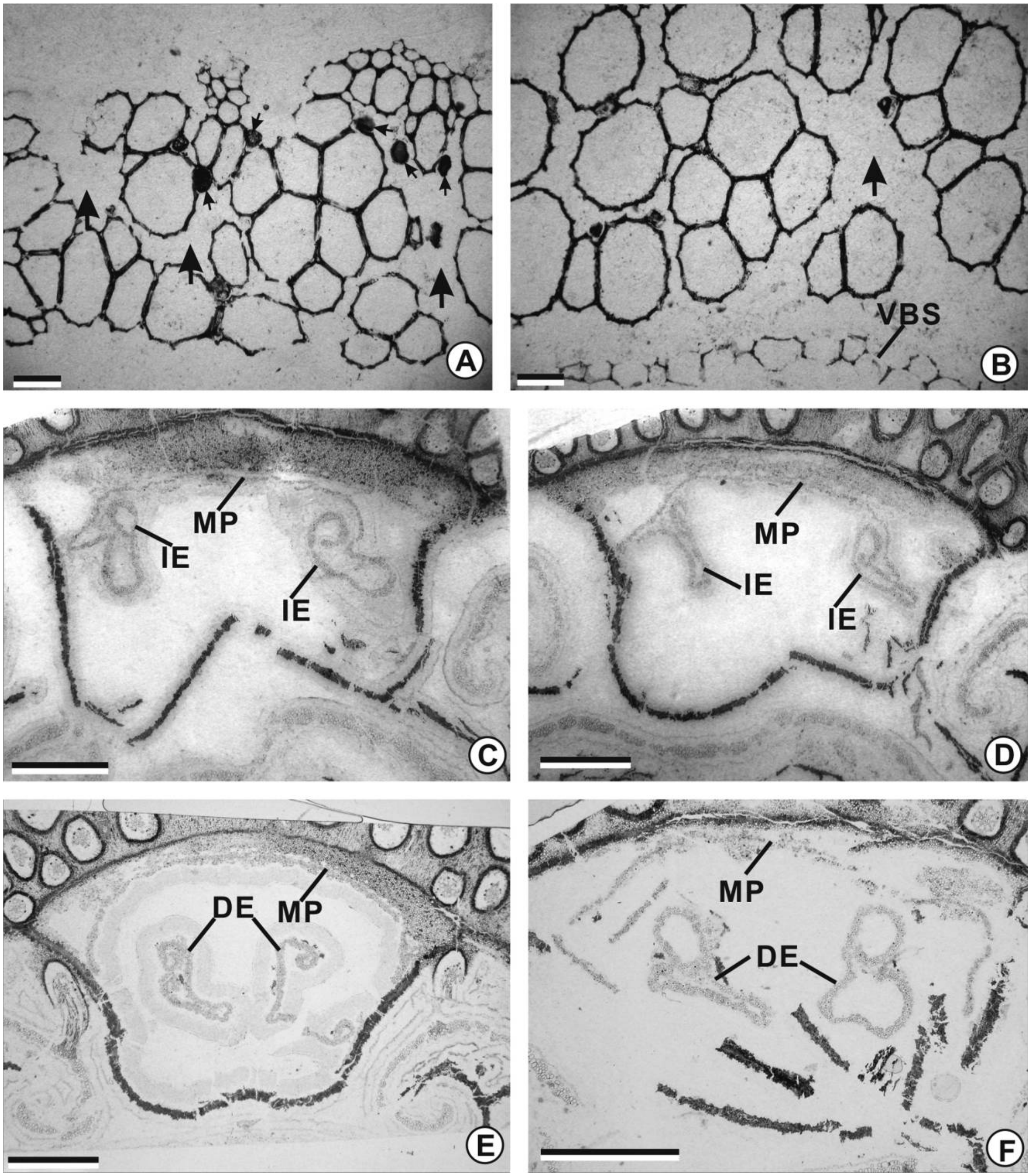


Fig. 4 *A*, Part of a peripheral cauline bundle with a much thicker xylem strand and much larger tracheids, compared to those in fig. 3*B*, 3*C*; large arrows indicate xylem parenchyma, and small ones indicate tannin cells. Slide WP2L-0034. Scale bar = 100 μm. *B*, Part of an inner meristele with an even thicker xylem strand and even larger tracheids; arrow indicates xylem parenchyma; *VBS* = vascular bundle sheath. Slide: WP2L-0034. Scale bar = 100 μm. *C–F*, Acropetal serial cross sections of the stem, showing the change in the leaf trace configuration at different levels (see text for detailed explanations). Scale bars = 5 mm. *C*, Peel LWJ2007-2C/BOT. *D*, Peel LWJ2007-2B/BOT/4. *E*, Slide WP2-0022. *F*, Slide WP2-0034. *DE* = small C-shaped strands with their convex sides opposite each other that are missing from the main part (*MP*) of the leaf trace; *IE* = inrolled edges of the leaf trace.

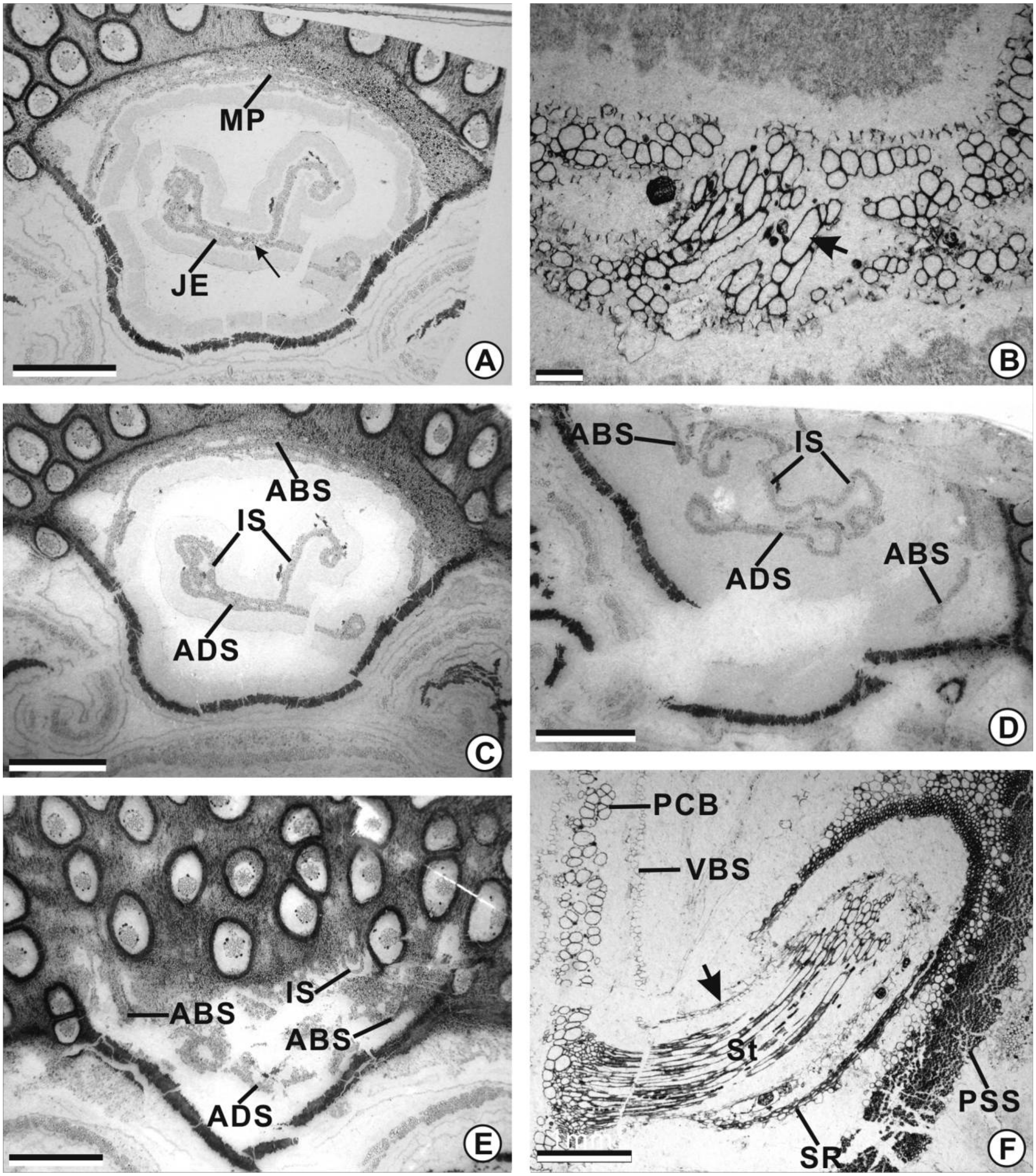


Fig. 5 *A*, *C–E*, Acropetal serial cross sections of the stem, showing the change in the leaf trace configuration at different levels (see text for detailed explanations). Scale bars = 5 mm. *A*, Arrow indicates the joint enlarged in *B*. Slide WP2-0023. *B*. Enlargement of the joint (arrow in *A*). Scale bar = 200 μm. *C*, Peel LWJ2007-2-B/BOT. *D*, Peel LWJ2007-2 D/BOT. *E*, Leaf trace in its highest level; peel LWJ2007-2A. *ABS* = centrifugal strand; *ADS* = centripetal strand; *IS* = inverted Ω-shaped internal strand; *JE* = compound strand joined by two small C-shaped strands missing from the main part of the leaf trace (*MP*). *F*, Cross section of the part of a peripheral cauline bundle (*PCB*), showing a root diverging from its centrifugal side; note that the vascular bundle sheath of the root (arrow) is connected to that of the stem (*VBS*). *PSS* = peripheral sclerenchymatous sheath; *SR* = sclerenchymatous ring; *St* = stele. Slide WP2-0022. Scale bar = 2 mm.

(fig. 3*C*; fig. 4*A*, 4*B*). These xylem parenchymatous cells are usually collapsed because of their very thin walls, so metaxylem at times appears loosely constructed. The vascular bundle sheath is one or two cell layers thick. Cells in this zone are nearly isodiametric in cross section, with a diameter of 25–110 (mostly 50–80) μm, and compactly arranged, without intercellular spaces (figs. 3*B*, 4*B*). Some outer and inner tangential walls are collapsed, but the radial walls are always well preserved (fig. 3*B*). The wall is 3–5 μm thick and light brown or yellow in transmitted light. In longitudinal section, the cells of this zone are also nearly isodiametric in outline (fig. 2*B*). Between the vascular bundle sheath and the xylem strand, there are often empty areas that appear to be in the position of the otherwise missing phloem.

Phyllotaxy and Change in Vascular Configuration of the Leaf Trace

The stem possesses five orthostichies. In each transverse section there are five leaf traces displaying different vascular configurations; thus, they are organized in a spiral and are arranged in a 2/5 phyllotaxy (fig. 3*A*). In the section shown in figure 3*A*, leaf trace 1 represents the vascular configuration at the highest, most developed level among these five leaf traces. Leaf trace 5 is formed latest; it represents the vascular configuration at the lowest level among them. We made serial peels to reveal the changes in vascular configuration of the leaf trace. At the lower level of the leaf trace, its vascular configuration is C-shaped, with two edges strongly inrolled (fig. 4*C*, 4*D*; fig. 6*A*). In the higher level, two edges of the C-shaped leaf trace are separated from the main part of the leaf trace, forming two small, hook-shaped strands (fig. 4*E*, 4*F*; fig. 6*B*, 6*C*). When these two strands join with each other (arrows in fig. 5*A*, 5*B*; fig. 6*D*), they become compound. At an even higher level or in a leaf base, the compound strand divides and forms two new strands: the inverted Ω-shaped internal strand (*IS* in fig. 5*C*–5*E*; fig. 6*E*, 6*F*) and the centripetal strand (*ADS* in fig. 5*C*–5*E*; fig. 6*E*, 6*F*). Thus, in the leaf base, the vascular configuration consists of three strands: the large C-shaped centrifugal strand (*ABS* in fig. 5*C*–5*E*; fig. 6*E*, 6*F*) that is derived from the main part of the C-shaped leaf trace in the lower level, the small centripetal strand (*ADS*), and the inverted Ω-shaped internal strand (*IS*).

Area between the Bound-Root Zone and Stem

The area between the bound-root zone and the peripheral sclerenchymatous sheath is very narrow, at most five cells thick, and consists of isodiametric parenchyma cells. No air cavities, tannin cells, or gum canals were found in this zone.

Roots

In the stem, the root traces diverge singly from the centrifugal side near the edge of the peripheral cauline bundles. The vascular bundle sheath and probably the sclerenchymatous ring of the root trace are derived from the vascular bundle sheath of the peripheral cauline bundles (fig. 5*F*; fig. 7*A*, 7*B*).

Only the bound-root zone of the root mantle is present, with a greatest preserved thickness of nearly 6 cm. Bound roots are mostly arranged randomly, although some appear roughly arranged in radial files. Individual roots are more or less radially elongate and oval or irregular in outline, ranging in size from 2 to 5 (mostly 3–4) mm. Dense tissue made up of parenchyma cells fills the space between bound roots (fig. 7*C*–7*E*; fig. 8*D*). The cells of the interstitial tissue are more or less radially elongate, with rectangular, subtriangular, elliptical, and polygonal shapes in cross section. Individual bound roots consist of polyarch and exarch actinostele innermost and the vascular bundle sheath, inner cortex, and scler-

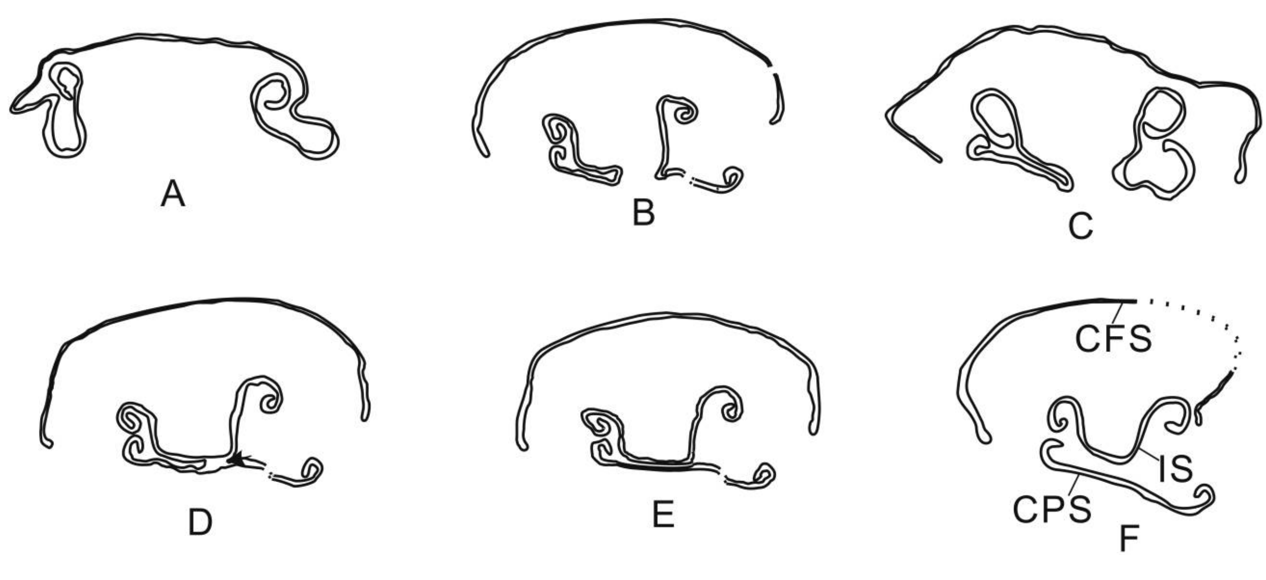


Fig. 6 Diagram showing the change in leaf trace configuration at different levels (see text for detailed explanations). *A* is drawn from fig. 4*C*; *B* is drawn from fig. 4*E*; *C* is drawn from fig. 4*F*; *D* is drawn from fig. 5*A*; *E* is drawn from fig. 5*C*; and *F* is drawn from fig. 5*D*. *CFS* = centrifugal strand; *CPS* = centripetal strand; *IS* = inverted Ω-shaped internal strand.

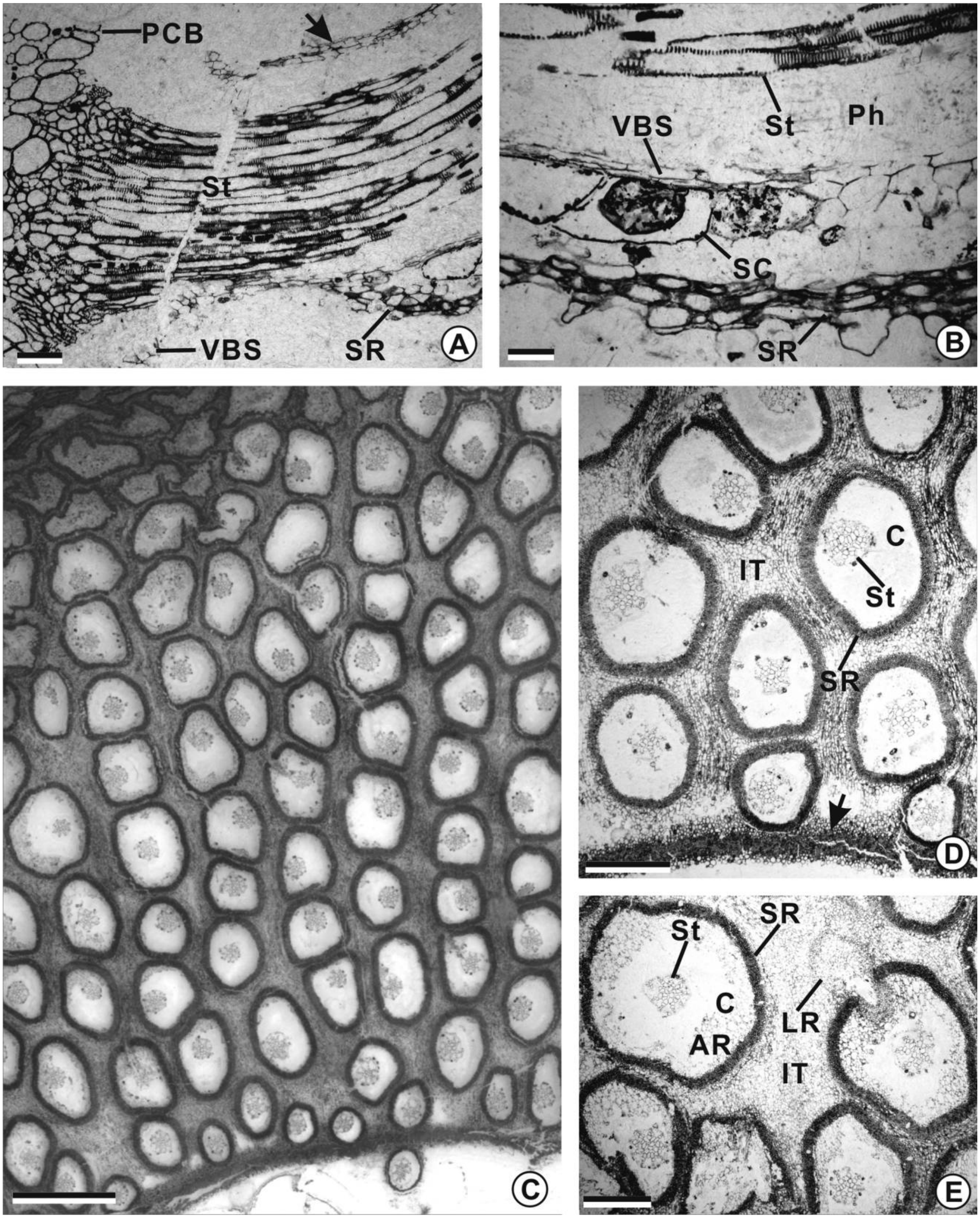
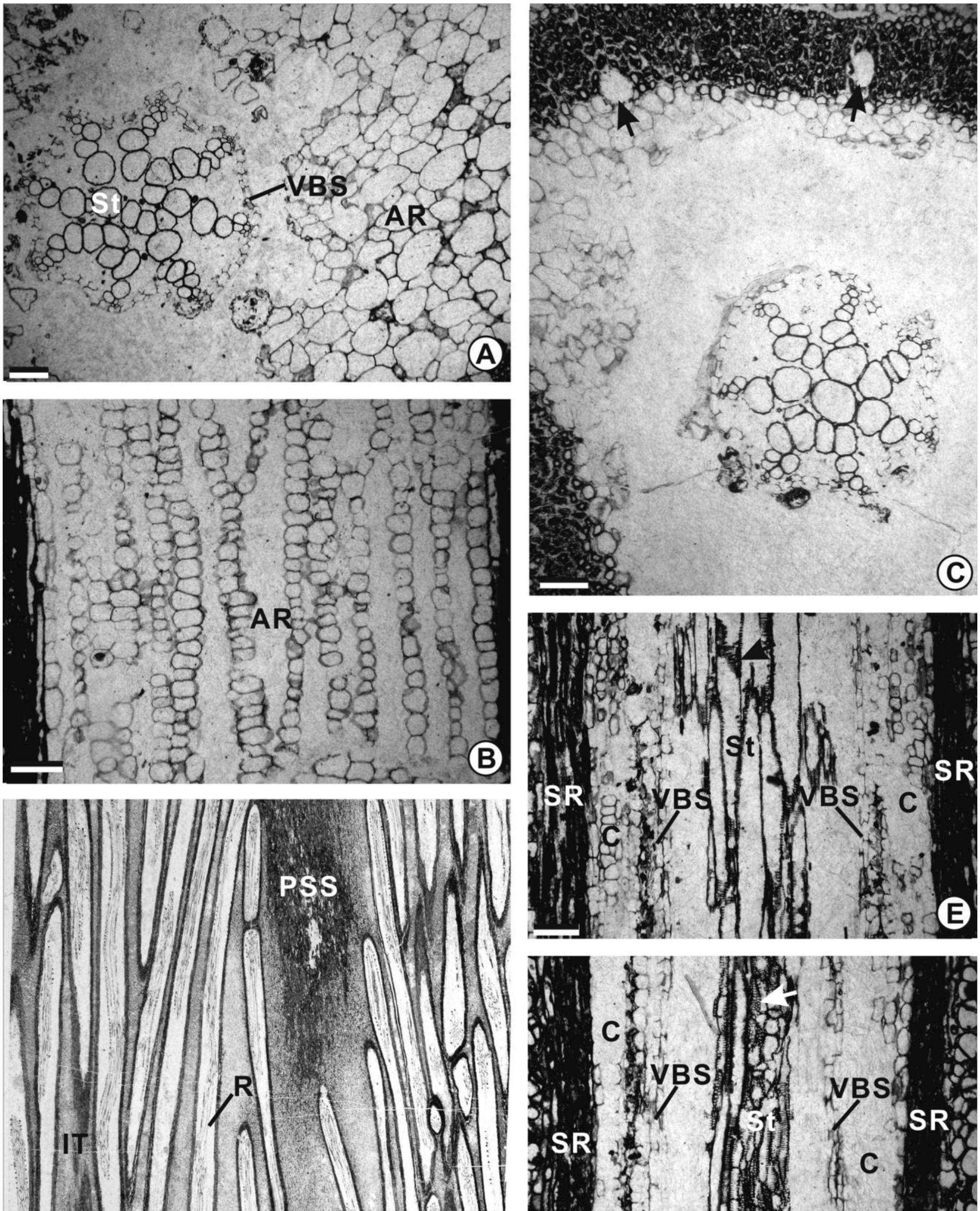


Fig. 7 *A*, *B*, Enlargements of fig. *5F*. *PCB* = peripheral cauline bundle; *Ph* = phloem; *SC* = secretory cell; *SR* = sclerenchymatous ring; *St* = stele; *VBS* = vascular bundle sheath. Scale bars = 200 μm. *C*, Cross section of the inner part of the bound-root zone, showing the arrangement and shape of roots. Peel LWJ2007-2. Scale bar = 5 mm. *D*, Enlargement of *C*. *C* = cortex; *IT* = interstitial tissue. Scale bar = 2 mm. *E*, Cross section through several roots in the outer part of the bound-root zone. *AR* = aerenchymatous parenchyma; *LR* = lateral root. Scale bar = 2 mm.



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enchymatous ring outermost. The stele possesses seven to 10 (mostly seven to nine) protoxylem poles (fig. 8*A*, 8*B*). The heptarch roots are few and account for 9% of the total. The octarch and ennearch roots are much more abundant and account for 46% and 45%, respectively, of the total. The tracheids of the metaxylem are 50–160 μm in diameter, with scalariform (or occasionally reticulate) thickenings on longitudinal walls. Phloem is typically absent because of poor preservation. Enclosing the stele is the vascular bundle sheath, usually consisting of one or two layers of cells that are usually rectangular in outline, with a tangential dimension of 50–90 μm and a radial dimension of 25–35 μm (fig. 8*A*, 8*C*). The anticlinal walls are slightly thickened. In some roots, the inner cortex is well preserved and consists of aerenchymatous parenchyma in which the cells are arranged in chains that surround large air spaces (fig. 8*A*). The parenchymatous cells are isodiametric in cross section, with a diameter of 60–130 μm. In longitudinal section, the parenchymatous cells are isodiametric or slightly flattened and arranged in vertical files (fig. 8*B*). Individual secretory cells with dark content are sparsely distributed in the inner cortex, especially near the vascular bundle sheath, and are nearly round, elliptical, or sometimes irregular in shape, with a size of 70–150 μm. Sclerenchymatous rings are 200–400 (usually 250–350) μm or five to eight (usually six or seven) cell layers thick. The cells of the sclerenchymatous ring in the inner part of the bound-root zone are 25–50 μm in diameter, while those in the outer part of the bound-root zone are a little larger, usually 45–65 μm. Gum sacs can be seen in the sclerenchymatous rings, and they are generally elliptical, with a size of 100–200 μm (fig. 8*C*).

Comparison

Our specimen, with its unique sclerenchymatous configuration between stelar cycles 1 and 2, is conspicuously different from the species of *Psaronius* from Euramerica, South America, and other sites of Cathaysian flora, except South China. Thus, it is mainly compared with some species from the Permian of South China.

Psaronius panxianensis (He et al. 2008) is a species comprehensively described on the basis of well-preserved specimens from the same locality as our specimen. The stem consists of six cycles of meristele, one more than the five of our specimen; it was therefore deduced that the specimen of *P. panxianensis* was probably located at a position higher in the trunk, thus representing a higher level than our specimen. There are conspicuous differences between *P. panxianensis* and our specimen in several aspects, although they resemble each other in sclerenchymatous configuration between stelar cycles 1 and 2 and the vascular configuration of the leaf base. The first difference is in the sclerenchymatous tissue. *Psaronius panxianensis* possesses robust peripheral sclerenchymatous sheaths 0.6–1.0 mm thick. In the stem, besides the anchor- or tree-shaped sclerenchymatous strand in the centripetal concavity of each peripheral cauline bundle, there is also a sclerenchymatous strand, continuous or discontinuous, associated with each leaf trace, i.e., extending along the inner side of the leaf trace (see figs. 21–25 in He et al. 2008). In our specimen, however, the peripheral sclerenchymatous sheaths are slender, usually 0.35–0.75 mm thick. Sclerenchymatous strands associated with the leaf trace are usually absent or very weakly developed (fig. 4*E*, 4*F*; fig. 5*A*–5*D*).

The second difference is in the construction of the ground tissue of the stem and the area between the peripheral sclerenchymatous sheath and the bound-root zone. In *P. panxianensis*, no secretory cavities with black content exist in the ground tissue, and the area between the peripheral sclerenchymatous sheath and the bound-root zone typically consists of thin-walled parenchymatous cells containing some air cavities and gum sacs with dark content; the latter are also present in the ground tissue of the leaf base. In the ground tissue of our specimen, however, there are secretory cavities with black content (fig.1*C*; fig. 2*A*, 2*B*) but no air cavities or gum sacs in the area between the peripheral sclerenchymatous sheath and the bound-root zone. There are also no gum sacs in the ground tissue of the leaf base.

The third difference is in the vascular tissue. In *P. panxianensis*, xylem strands of inner meristeles are robust and relatively contiguously organized, three to eight cell layers or 0.7–1.4 mm thick; the vascular bundle sheath is two or three (occasionally four or five) cell layers thick. In our specimen, xylem strands of inner meristeles are thinner, two to five cell layers or 0.6–0.75 mm thick and loosely constructed, resulting in abundant thin-walled parenchymatous xylem cells; the vascular bundle sheath is one or two cell layers thick. In addition, the changes in the vascular configuration in the leaf trace from its lowest level to the leaf base differ conspicuously between *P. panxianensis* and our specimen (cf. our fig. 6 and fig. 20 in He et al. 2008), although the vascular configuration in the leaf base is the same in both species.

Another species, *Psaronius wangii*, was erected on the basis of well-preserved specimens from the same locality as our specimen and was described in detail by Tian et al. (1992), which means that it is possible to make a detailed comparison between it and our specimen. The species is similar to our specimen in certain aspects, such as the thickness of xylem strands of inner meristeles, the size of the tracheids, the thick-

Fig. 8 *A*, Cross section of a bound root with an octoarch stele (*St*), a one- or two-cell-layers-thick vascular bundle sheath (*VBS*), and chainlike aerenchymatous parenchyma (*AR*) in cortex. Slide WP2-0025. *B*, Longitudinal section through the cortex of a bound root, showing chainlike aerenchymatous parenchyma. Slide WP2L-0033. *C*, Cross section of a bound root with a heptarch stele, showing gum sacs in sclerenchymatous ring (arrows). Slide WP2L-0034. *D*, Obliquely longitudinal section through the bound-root zone and the peripheral sclerenchymatous sheath (*PSS*), showing interstitial tissue (*IT*) and roots (*R*). Slide WP2L-0035. *E*, Longitudinal section of a bound root, showing a metaxylem tracheid with scalariform thickenings (arrow), vascular bundle sheath (*VBS*), cortex (*C*), and sclerenchymatous ring (*SR*). Slide WP2L-0033. *F*, Longitudinal section of another root, showing some metaxylem tracheids with reticulated thickenings (arrow). Slide WP2L-0035. Scale bars = 200 μm (*A*–*C*, *E*, *F*), 10 mm (*D*).

ness of the vascular bundle sheath, the construction of the peripheral sclerenchymatous sheath, the size of bound roots, the number of protoxylem poles of each bound root, and the thickness of the sclerenchymatous ring of bound roots. However, the two species are conspicuously different in the construction of the ground tissue and metaxylem of the stem, the arrangement of inner meristeles, and the vascular configuration in the leaf base. In our specimen, tannin cells are scarce in the ground tissue of the stem and the leaf base; protoxylem of the vascular bundles of the stem usually occurs in low and tangentially elongate protrusions; the xylem strands of meristeles are loosely constructed for the abundant xylem parenchymatous cells, and most of tracheids have an isodiametric transverse outline; inner meristeles of the stem are arranged irregularly, or not in apparent radial alignment; and the leaf base possesses a vascular configuration consisting of a large, U-shaped centrifugal strand and a C-shaped centripetal strand, with an inverted Ω-shaped one between them. In *P. wangii*, there are abundant tannin cells in the ground tissue of the stem and the leaf base; the protoxylem of the vascular bundles of the stem is usually in conspicuously pointed protrusions; the metaxylem of meristeles and that of the leaf traces are constructed so as to be contiguous, and tracheids usually have a polygonal, rhomboid, or triangular transverse outline; inner meristeles in the stem are arranged in an apparently radial alignment; and the leaf base possesses a vascular configuration consisting of a large, U-shaped centrifugal strand and two smaller C-shaped strands. Furthermore, the secretory cavities dispersed in the ground tissue near the peripheral sclerenchymatous sheath in our specimen are not found in *P. wangii*.

Still another species, *Psaronius jiangsuensis*, was erected on the basis of specimens from the late Early Permian in Jiangsu Province. The specimens are mostly well preserved, but the ground tissue has nearly all disappeared, leaving voids. The species is similar to our specimen in the sclerenchymatous tissue of the stem and the thickness of the vascular bundle sheath. The species differs from our specimen mainly in the phyllotaxy of the stem and the vascular configuration of the leaf base. In *P. jiangsuensis*, Yao et al. (1994) noted that the stem possesses a 2/7 helical phyllotaxy; however, from our observation of the illustration of the species (pl. 2, fig. 2 in Yao et al. 1994), we think that the stem possesses six orthostichies and that the leaf traces diverge in whorls, with three leaf traces in each whorl. Moreover, the leaf base of *P. jiangsuensis* possesses a simple C-shaped vascular configuration (text fig. 1 and pl. 2, figs. 1–2 in Yao et al. 1994). In our specimen, however, the stem possesses a 2/5 helical phyllotaxy, and the leaf base has a more complex vascular configuration consisting of three vascular bundles (see fig. *5A*–*5D*; fig. *6E*, *6F*). Furthermore, there is a minor difference in the bound roots. In *P. jiangsuensis*, the bound roots have 9–12 (commonly 11–12) protoxylem poles, somewhat more than the seven to nine of our specimen.

Psaronius octogonus was erected on the basis of a single specimen of trunk from the same locality as *P. jiangsuensis* (Yao et al. 1994). It has the same sclerenchymatous configuration between stelar cycles 1 and 2 and vascular configuration in the leaf base as our specimen does, although there are minor differences between them (cf. our fig. *6F* and fig. *46C* in He et al. 2008). The species has a dictyostele consisting of eight stelar cycles and eight orthostichies. Inner meristeles are arranged regularly in a radial alignment. Whorls diverge and consist of four leaf traces. Thus, the specimen of *P. octogonus* probably represents a location on the trunk higher than that of our specimen. Because no serial cross sections of the stem of *P. octogonus* are available, it is unknown whether a change in the vascular configuration from a leaf trace with a simple C shape at the lowest level to more complexity in the leaf base occurred in this species. Also, some other features in *P. octogonus*, such as the construction of ground tissue in the stem, the thickness of the vascular bundle sheath and meristeles, the shape and size of the tracheids of inner meristeles, and the thickness of the peripheral sclerenchymatous sheath, are unknown, which makes it difficult to compare *P. octogonus* in detail with our specimen.

Psaronius hexagonus was reported on the basis of a single specimen from the Permian in Sichuan Province of southern China. The specimen possesses the same sclerenchymatous configuration between stelar cycles 1 and 2 as our specimen, but in many other aspects the two specimens are conspicuously different. *Psaronius hexagonus* possesses nine stelar cycles and six orthostichies. Inner meristeles are arranged in regular radial rows and display a hexagonal organization (Gu and Zhi 1974; Li and Cui 1995). Leaf traces diverge in a whorled phyllotaxy, and in each whorl there are three leaf traces. The vascular configuration of the leaf base is a simple C shape. Bound roots are small, 2–3 mm in diameter, and the stele usually has five, sometimes six to eight, protoxylem poles. More information, such as the construction of the ground tissue, the thickness of inner meristeles, the shape and size of tracheids, and the thickness of vascular bundle sheaths, is not available.

The main features of our specimen and the five other species from the Permian in South China are summarized in table 1. From the observations above, our specimen is conspicuously different from other known species from the Permian of South China and even more different from the species from Euramerican and Gondwanan floras and other places where Cathaysian flora occurred (see “Discussion”). It represents a new species of *Psaronius*, for which the specific name *Psaronius laowujiensis* sp. nov. is suggested.

Discussion

Eight species of *Psaronius* have been reported from the Permian in South China: *P. hexagonus*, *P. jiangsuensis*, *P. laowujiensis* sp. nov., *P.* cf. *magnificus*, *P. octogonus*, *P. panxianensis*, *P. sinensis*, and *P. wangii*. Among these species, the gross morphology and detailed histology of *P. sinensis* is poorly known because of the poor preservation of the specimens (Sze 1942, 1947). Detailed histology of *P. hexagonus*, *P.* cf. *magnificus*, and *P. octogonus* is unknown because no information has been offered, although their gross morphology is clearly displayed in illustrations (pl. 112, fig. 4 in Gu and Zhi 1974; pl. 1, fig. 1 in Yao et al. 1994; pls. 42, 43 in Li and Cui 1995). These species have certain features different from those of species from places other than South China.

Table 1

Main Characters of Select Species of *Psaronius* from the Permian in South China

Characters	*P. hexagonus*	*P. jiangsuensis*	*P. laowujiensis* sp. nov.	*P. octogonus*	*P. panxianensis*	*P. wangii*
Size of stem (cm)	9.5	5 × 5.5	5.8 × 6.5	14.5	7.4 × 4.5	5.8 × 6.5 to 7 × 6
No. stelar cycles	9	5–6	4–5	~8	6–7	5–7
No. orthostichies	6	6	5	8	7	5 or 7
Phyllotaxy	Whorls	Whorls	2/5 spirals	Whorls	2/7 spirals	Spirals
No. IM	Probably >45	~30	12	Probably >50	31–34	21–27
Arrangement of IM	In radial assignment	Roughly in radial assignment	Not in radial assignment	In radial assignment	Roughly in radial assignment	In radial assignment
Thickness of IM (cell layers)	Unknown	3–8	2–5 (.6–.75 mm)	Unknown	3–8 (.7–1.4 mm)	4–5 (.55–.7 mm)
Size of tracheids of IM (μm)	Unknown	Unknown	Mostly 100–150	Unknown	80–250	Mostly 100–150
Thickness of VBS (cell layers)	Unknown	Probably 1–2	1–2	Unknown	Mostly 2–3	1–2
Size of cells of GT (μm)	Unknown	Unknown	50–120	Unknown	30–100	40–100
Tannin cells in GT of stem	Unknown	Scarce	Scarce	Unknown	Small amount	Abundant
Gum sacs	Unknown	Scarce; in SR of roots	Common; in SR of roots	Unknown	Scarce; in LB	Scarce; in SR of roots
Thickness of PSS (mm)	Unknown	Unknown	.35–.75	Unknown	.6–1.0	.4–.6
Air cavities in PSS	Unknown	Scarce	Scarce	Unknown	Common	Scarce
Thickness of root mantel (cm)	>4.2	>6	>6	8	>4.5	4–6
Size of roots (mm)	2–3	3.0 × 5.0	2.0–5.0	Unknown	.7–2.0	2.0–3.5
No. PP in roots	5 (sometimes 6–8)	Mostly 11–12	7–9 (mostly 8–9)	Unknown	4–11 (typically 7)	6–8 (mostly 7)
Thickness of SR of roots (mm)	Unknown	.22–.5	.2–.4 (5–8 cells)	Unknown	.28–.5 (8–11 cells)	.25–.4 (6–14 cells)

Note. GT = ground tissue; IM = inner meristeles; LB = leaf base; PP = protoxylem poles; PSS = peripheral sclerenchymatous sheath; SR = sclerenchymatous ring; VBS = vascular bundle sheath.

Vascular Bundle Sheath/Inner Cortex

When studying the structure of the phloem in a stem of *Psaronius* sp. from North America, Smoot (1984) identified the peripheral sclerenchymatous sheath as the outer cortex, the ground tissue between meristeles as the middle cortex, and a thin zone of parenchymatous cells surrounding each meristele as the inner cortex. The cells of the inner cortex in *Psaronius* sp. were thinner walled than those of the middle cortex or ground tissue. The inner cortex is probably also present in other species from the Euramerican flora, but it appears to have been overlooked by other authors. In some species from the Early Permian of North China, there is also an inner cortex similar to that in species from North America (Wang et al. 2009). In stems of the species from the Permian in South China, the inner cortex is somewhat different; the cells are usually thicker walled, especially their radial walls, and in most cases were well preserved even when the ground tissue had tended to collapse or disappear. Because of its close association with the meristeles of the stem, He et al. (2008) termed it the "vascular bundle sheath," a term also employed in this article. Tian et al. (1992) and Yao et al. (1994) identified this tissue as phloem, although the sieve cells of the phloem are typically vertically elongate (fig. 58 in Morgan 1959; figs. 3, 6–9 in Smoot 1984) and not nearly as isodiametric as those in species from the Permian of South China. The vascular bundle sheath looks somewhat like the endodermis (figs. 2*D*, 3*B*), but the latter is usually only a single cell layer thick and does not exist in mature stems and roots of Marattiales (Morgan 1959; Ogura 1972). The somewhat thick-walled and closely associated vascular bundle sheath likely serves a protective role in the life of psaroniaceous plants from the Permian of South China.

Moreover, in roots of the new species and other species from this time, around the stele there is also a zone of cells similar to the vascular bundle sheath in the stem. In a previous paper on *P. panxianensis*, the tissue was termed "endodermis" (fig. 39 in He et al. 2008), but in this article the term "vascular bundle sheath" is employed because the tissue is derived from the vascular bundle sheath of the stem (fig. 5*F*). Different from those in the stem, the cells of the vascular bundle sheath in roots are typically much more flattened in cross section and radial longitudinal section (cf. fig. 2*D*, 2*E* and fig. 8*A*, 8*C*, 8*E*, 8*F*). As is true for the stem, the vascular bundle sheaths of the roots are also usually better preserved than the cortex (fig. 8*C*).

Sclerenchymatous Configurations between Stelar Cycles 1 and 2

According to the information available at present, in all species—except *P. sinensis*, for which information is not available—the sclerenchymatous strands between stelar cycles 1 and 2 tend to extend into the centripetal concavity of the peripheral cauline bundles and there form a tree- or anchor-shaped configuration (see fig. 46*C*, 46*D* in He et al. 2008). This tree- or anchor-shaped sclerenchymatous strand is well preserved, even in poorly preserved specimens. On the basis of this character, it is very easy to distinguish these *Psaronius* species from those from places other than South China. However, in species from the Euramerican and Gondwanan floras and other locations of the Cathaysian flora, the sclerenchymatous strands between stelar cycles 1 and 2 do not extend (fig. 46*A*, 46*B* in He et al. 2008) or extend just a very short distance into the centripetal concavity of the peripheral cauline bundles (fig. 9). Thus, the sclerenchymatous configuration between stelar cycles 1 and 2 could be taken as one of the diagnostic features of *Psaronius* species from the Permian of South China.

Vascular Configuration in the Leaf Base

Until now, there were three types of leaf base vascular configuration in the known species of *Psaronius* from the Permian of South China. The first type is present in *P. hexagonus* and *P. jiangsuensis* and consists of a single vascular bundle with a C or horseshoe shape. The second type is represented by *P. wangii* and consists of three vascular bundles, i.e., a large, U-shaped centrifugal vascular bundle and two C-shaped centripetal ones with their convex sides opposite each other. The third type, seen in *P. panxianensis*, *P. octogonus*, and *P. laowujiensis* sp. nov., also consists of three vascular bundles: a large, U-shaped centrifugal one, a small centripetal one, and an internal bar- or inverted Ω-shaped one. It is interesting that although both *P. panxianensis* and *P. laowujiensis* sp. nov. have the same type of the vascular configuration in their leaf bases, their developmental process is clearly different (cf. our fig. 6 and fig. 20 in He et al. 2008). For lack of serial cross sections, the developmental process of the vascular configuration in the leaf base of *P. octogonus* is unknown. In a comparison of the leaf base vascular configurations of *P. wangii* and *P. laowujiensis* sp. nov., it is noted that the former is analogous to the vascular configuration of the leaf trace that will become a leaf base in a higher level in the latter. In other words, the leaf base configuration of *P. wangii* is actually equal to an earlier developmental stage of that of *P. laowujiensis* sp. nov.

In the Euramerican flora, there are two types of leaf base vascular configurations in *Psaronius* species: the stewartiopterid type, where there is only a single C-, U-, or V-shaped vascular

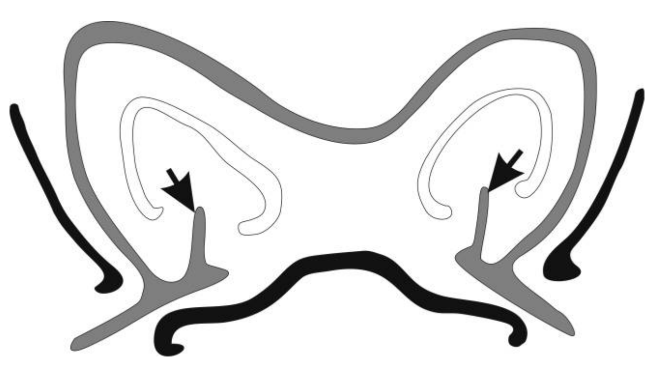

Fig. 9 Diagram of *Psaronius chasei*(?), showing that the sclerenchymatous strand between stelar cycles 1 and 2 extends a very short distance into the centripetal concavity (arrows) of the peripheral cauline bundle (drawn from fig. 49 in Morgan 1959). Black indicates inner meristele and leaf trace; white indicates peripheral cauline bundle; gray indicates the sclerenchymatous strand.

bundle in the leaf base, and the stipitopterid type, where the vascular configuration in the leaf base consists of an outer O-shaped strand and an internal bar- or W-shaped strand. These two types of leaf base vascular configuration can occur concurrently in the same species or in the same stem and can change from the stewartiopterid into the stipitopterid type, although sometimes there is only one type in a stem (Stidd 1971).

In the Gondwanan flora of South America, there are two or three types of leaf base vascular configuration. One is the stewartiopterid type, present in *Psaronius arrojadoi* (Pelourde; (Herbst 1985) and *Psaronius* sp. (Herbst 1999); another, consisting of several vascular bundles (Herbst 1999), is present in *Psaronius sinuosus* Herbst. The leaf base vascular configuration of *Psaronius brasiliensis* is not clear. According to Morgan (1959), the leaf base vascular configuration of this species consists of a large horseshoe-shaped bundle accompanied by some smaller ones in its centripetal concavity. This would represent a third type of leaf base vascular configuration. However, Herbst (1999) considered these so-called small vascular bundles to be sclerenchymatous strands. If this is the case, then they represent a stewartiopterid-type leaf base vascular configuration.

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