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Exploring the stem to crown group transition in Marattiales: a new species of frond from the late Permian of China with features of the Psaroniaceae and Marattiaceae

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ABSTRACT

A new species of the Marattialean fern frond *Rothwellopteris* is proposed for specimens preserving both morphology and anatomy from the Wuchiapingian-Changshingian (late Permian) aged Xuanwei Formation of South China. Fronds are at least bipinnate and bear falcate, pecopteroid pinnules with a thin lamina. The penultimate pinna rachis has a polycyclic vascular system with endarch primary xylem and longer vascular bundles located abaxially in a single radial row, and shorter vascular bundles adaxially arranged in two radial rows, with a vascular bundle sheath of sclerenchyma cells. Ground tissue comprises parenchyma cells and numerous secretory ducts. Features of the new species suggest that it was adapted for mesomorphy, while the previously recognized species *Rothwellopteris pecopteroides* was adapted for xeromorphy or was a sun-leaf. Like *R. pecopteroides*, the new species displays a mosaic of morphological and anatomical features characteristic of both the Paleozoic family Psaroniaceae and the extant family Marattiaceae; we interpret it to be a member of the evolutionary stem-group from which stratigraphically younger Marattiaceae evolved. Our findings show that the stem- to crown-group transition within Marattiales commenced before the end of the Permian and that a greater diversity of transitional forms can now be recognized from the late Permian and include the genera *Compsopteris, Rothwellopteris*, *Tietea* and *Tuvichapteris*.

Keywords: Marattiales, Psaroniaceae, Marattiaceae, frond, Xuanwei Formation, xeromorphy

1. Introduction

Marattiales are an important element in the late Permian Cathaysian Flora in eastern Yunnan and western Guizhou provinces, Southwest China. Their fossils are abundant in floral assemblages

preserved as impression/compressions (Tian and Zhang 1980; Zhao et al. 1980; Liu et al. 2000, 2001) and permineralizations (Sze 1942, 1947; Yang 1986; Tian et al. 1992; Tian and Wang, 1995; Hilton et al. 2004; He et al. 2006, 2008, 2010, 2013; D'Rozario et al. 2011). Rarely, specimens preserve both morphology and anatomy with these including the frond leaves *Compsopteris elliptica, Compsopteris* sp. (Guo et al., 1992) and *Rothwellopteris pecopteroides* (He et al., 2019). The combination of morphological and anatomical information in these species reveals they have a mosaic of characters shared with members of the Paleozoic family Psaroniaceae and the stratigraphically younger family Marattiaceae. He et al. (2019) interpreted *Rothwellopteris* to be a member of the evolutionary stem-group lineage leading to the Marattiaceae. However, the available fossil materials of *C. elliptica* and *R. pecopteroides* are not especially well-preserved and put limits on the comprehensive characterization of the species. *C. elliptica* is represented by two fragmented, monopinnate compound leaves in which only one or two incomplete pinnules are preserved, and anatomical features of the pinnules are presently unknown (Guo et al., 1992). *Compsopteris* sp. is less well-known and based on a simple description of one illustrated peel that appears to be distinct from the closely related species *C. elliptica* (Guo et al., 1992). *Rothwellopteris pecopteroides* is based on a large tripinnate leaf embedded within the rock matrix, and its pinnule morphology (including shape, size and venation pattern) is revealed by cut sections parallel to the surface of the pinnule. Its rachises are deformed in varying degrees making the organization of the vascular bundles enigmatic, and the ground tissue is poorly preserved (He et al., 2019). In all cases other parts of the parent plants are unknown preventing a more detailed understanding of their evolutionary and ecological significance.

Here we report a kind of marattialean frond with well-preserved morphological and anatomical

features from the late Permian of western Guizhou Province, Southwest China. It occurs in tuffaceous sediment from the Xuanwei Formation that was deposited under paralic depositional settings (Wang et al., 2011). The Xuanwei Formation contains an abundant flora rich in marattialean ferns (Zhao et al., 1980; He et al., 2019). The frond described here resembles the stratigraphically contemporaneous species *Rothwellopteris pecopteroides* also from the Xuanwei Formation but detailed comparisons reveal it constitutes a new species of the genus.

2. Materials and methods

This investigation is based on two specimens (YNUPB1105 and YNUPB1106) collected from mine spoil from the Sanjiaoshu coal mine, Panxian mining district in Guizhou Province, southwest China. Both specimens are bipinnate compound leaves. However, as they are not attached to the parent plant, it is not known if they were bi-pinnate in life or if they represent the distal portions of larger, tripinnate compound leaves. In the following account we opt to use the terms of penultimate pinna and ultimate pinna to describe them. In specimen YNUPB1105 the preserved length of the rachis is about 5.5 cm and only one penultimate pinna is preserved with 3–4 ultimate pinnae attached to each side of the rachis (Plate I, 1). In specimen YNUPB1106, two penultimate pinnae are preserved. Each of these penultimate pinnae is partly exposed on the surface of the rock but is mostly embedded within the matrix. From the exposed parts of the two penultimate pinnae, five and three ultimate pinnae can be seen attached to the penultimate pinna rachises respectively (Plate II, 1).

Both specimens are embedded in grey-white to grey-brown volcanic tuff that preserves morphology and anatomy of the fossil plants. Cellular details are permineralized in calcium carbonate. Specimens were prepared using the cellulose acetate peel method (Joy et al., 1956; Galtier

and Phillips, 1999), etching cut faces for 20–30 seconds in 10% HCL. Individual peels were mounted on glass slides with coverslips using Canada balsam. The rocks bearing the specimens, peels and slides are deposited at Yunnan University, Kunming, China.

3. Geological information

Sanjiaoshu mine extracts coal from the Lopingian (late Permian) aged Xuanwei Formation (Hilton et al., 2004; Wang et al., 2011). Mining brings sediments from the Xuenwei Formation surrounding the worked coal seams to the surface; mining does not encounter other geological formations so we are confident with the source of the materials being from the Xuanwei Formation. We have not been able to access the underground workings to sample the geological succession or to provide sedimentary context for the ex-situ samples. The specimens are permineralized by calcium carbonate that occurred early during diagenesis prior to significant decay having occurred. Compression/impression and permineralized fossil plant assemblages from the Xuanwei Formation have recently been summarized by He et al. (2019); this information will not be repeated here.

The two tuff samples documented here contain large, delicate fossil plants that have not been fragmented by taphonomic processes. The individual fossils go right to the edge of the rocks that contain them and were broken by the mining processes rather than by geological processes such as transportation in sedimentary systems. We consider it likely that the two specimens were preserved intact and in-situ, probably by an ash-fall obrution event similar to that known from the early Permian tuff at Wuda in North China (Opluštil et al., 2020). This is different from the previously recognized tuff samples from the Sanjiaoshu Mine (Hilton et al., 2004) that contained permineralized fossils plants broken up and size sorted by taphonomic processes and they were probably deposited as pyroclastic flows or re-worked as epiclastic deposits such as lahars. The volcanic tuff from nearby

Huopu coal mine (Neregato et al., 2016; Wang et al., 2017) in the Xuanwei Formation also contains highly fragmented and size sorted fossil plants; it may also have been deposited as pyroclastic flows or lahars (Neregato et al., 2016).

Stratigraphically, the Xuanwei Formation extends from the Wujiapingian to Changshingian stages of the Permian (Zhao et al., 1980; Shao et al., 1998, Wang et al., 2011). The tuff from Sanjiaoshu has not been dated by biostratigraphic or radiometric methods. It is lithologically similar to the tuff from the Xuanwei Formation at the nearby Huopu mine (Wang et al. 2011; Neregato et al., 2016) that was dated biostratigraphically to the Wujiapingian stage of the Lopingian using palynomorphs (Neregato et al., 2016). While the Sanjiaoshu tuff was also probably deposited during the Wujiapingian, we prefer to consider it to be of Wuchiapingian to Changshingian age based on the age range of the Xuanwei Formation (Shao et al., 1998; Wang et al., 2011). Radiometric dating of the fossil plant bearing tuffs from this part of south China are now needed to make more precise age determinations for their fossil plants.

4. Systematic Paleobotany

Order: MARATTIALES Engler and Prantl, 1902

Genus: **Rothwellopteris** X. Y. He et al., 2019

Type species: Rothwellopteris pecopteroides X. Y. He et al., 2019

Rothwellopteris sanjiaoshuensis X. Y. He, S. J. Wang et J. Hilton sp. nov. (Figs 1–2; Plates I–VII)

Diagnosis: Pinnules somewhat falcate, with parallel margins and rounded apex and their bases not expanding. Midrib position low and broad on abaxial side of pinnule. Lamina of pinnule

uniformly thin, lateral margins without thickened band and not bending toward the abaxial surface. Lateral veins produced at an acute angle, branching once or twice before reaching pinnule margin at the angle of 60–70°. Vascular bundle sheaths of midrib plane convex or semi-circular in cross section with adaxial side flat and thin and abaxial side convex and thicker. Surface of penultimate rachis a continuous curve without wrinkles and trichomes. Epidermis uniseriate over thin sclerified cortex with ground tissue consisting of isodiametric parenchyma cells and secretory ducts. Polycyclic vascular system of penultimate rachis ventral-dorsal with longer vascular bundles located on abaxial side, arranged radially in a single row, with shorter vascular bundles located on adaxial side and arranged radially in two rows. Bundle sheaths consisting of sclerenchyma cells with those of outer side with thicker walls and those of inner side with thinner walls.

Holotype: YNUPB1105

Paratype: YNUPB1106

Etymology: The specific name *sanjiaoshuensis* refers to the locality from where the present specimens were collected.

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

Age: Wuchiapingian to Changhsingian stages of the Lopingian, Permian (Zhao et al., 1980; Shao et al., 1998; Wang et al., 2011).

Stratigraphic horizon: Xuanwei Formation

Repository: Institute of Palaeontology, Yunnan Key Laboratory for Palaeobiology, MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University.

Description: The width of the *Rothwellopteris sanjiaoshuensis* penultimate pinna rachis on the

surface of the rock is about 5 mm in specimen YNUPB1105 and 7 mm in specimen YNUPB1106. Both specimens have smooth surfaces. Ultimate pinnae are linear, tightly arranged and attached to the penultimate pinna rachis at the angle of 70–80° (Plate I, 1; Plate II, 1). Tips of all ultimate pinnae are not preserved, with the longest preserved about 9 cm long with 22 pairs of pinnules in YNUPB1105 and about 9.5 cm long with 24 pairs of pinnules in YNUPB1106. The ultimate pinna rachis is less than 1 mm wide in YNUPB1105 and about 1.5 mm in YNUPB1106. Ultimate pinna rachises have smooth surfaces. Pinnules are alternate, tightly arranged and oriented nearly perpendicular to the ultimate pinna rachis with the tips of the pinnules aligning to a position on the pinna forward of the pinnule base (Plate I, 2; Plate II, 2). Pinnules are somewhat falcate, 10–12 mm long and 3–4 mm wide, with rounded tips and truncate bases. Midribs are robust but taper toward to the tips and are slightly decurrent on the pinna (Plate I, 3; Plate II, 3). The first lateral vein of the lower pinnule base diverges from the decurrent part of the midrib and immediately forks once and then the two resultant veins fork again. The other lateral veins fork once or twice. There are typically more than 40 veins per cm at the pinnule margin. Ultimate lateral vein branches meet the margin of the pinnule at an angle of 60 to 70° (Plate I, 3; Plate II, 3).

Penultimate pinna rachises are round in cross section but are sometimes transversely elliptical due to compression from the vertical pressure of strata loading. Two cross sections of the penultimate pinna rachis were prepared from specimen YNUPB1105 of which one is 6 mm wide and about 4.2 mm high (Plate III, 1) and the other is 6.5 mm wide and only 3.3 mm high (Plate III, 2). The penultimate pinna rachis of specimen YNUPB1106 is round in cross section and slightly larger, up to 8.5 mm in diameter (Plate IV, 1 and 2; Plate V, 1). The surface of the penultimate rachis is smooth and lacks wrinkles and trichomes. In cross sections, rachis tissue consists of epidermis, sub-

epidermal cortex, ground tissue and the polycyclic vascular system. In YNUPB1106, the epidermis consists of a single layer of small, nearly round cells with diameters of about 15 μm. The cortex is approx. 300 μm thick and divided into outer and inner parts (Plate V, 2). The outer cortex is slightly thicker than the inner cortex and consists of isodiametric parenchyma cells with diameters from 30–40 μm. The inner cortex consists of sclerenchyma cells with diameters of 15–30 μm. Ground tissue consists of parenchyma cells and secretory ducts. Parenchyma cells are isodiametric with diameters of 36–60 μm. In specimen YNUPB1105, the cortex is approx. 200 μm thick and its inner cortex differs from specimen YNUPB1106 in lacking a uniform zone of sclerenchyma cells and having sclerenchyma intermingling with parenchyma cells. Parenchyma cells of the ground tissue are isodiametric, elongated or polygonal (Plate V, 2 and 3). Secretory ducts in the two specimens are numerous and dispersed in the ground tissue, and consist of 6–8 slightly tangentially elongated parenchyma cells surrounding a central cavity with the diameter of 70–120 μm. Cavities are empty or filled with yellow or brown contents (Plate V, 3; Plate VI, 1).

Viewed in cross sections the polycyclic vascular system of the penultimate pinna rachis consists of numerous vascular bundles of different lengths. The smaller diameter YNUPB1105 rachis has 40–60 bundles arranged in five cycles with a high proportion of laterally elongate bundles (Fig. 1A; Plate III, 1 and 2). In the larger diameter YNUPB1106 rachis, there are up to 110 bundles arranged in six cycles with a higher proportion of short bundles (Fig. 1B; Plate IV, 1 and 2; Plate V, 1). In general, both specimens have long bundles located on the abaxial side and arranged in one radial row, while shorter bundles are located on the adaxial side and are arranged in two radial rows. The smallest bundles are mostly located at the center and lateral sides of the rachis (Fig. 1; Plate III, 1 and 2; Plate IV, 1 and 2; Plate V, 1).

Individual vascular bundles comprise a xylem strand and sheath. Phloem is probably located between the xylem strand and the sheath but is poorly preserved and represented by a gap between these tissues. The xylem strand is band-like with its ends more or less centripetally arced and is narrow with its radial thickness mostly of 2–3 tracheids. The bundle sheath has a radial thickness of 2–3 cells with thicker cell walls on the outer side than on the inner side (Plate V, 3; Plate VI, 1).

Viewed in longitudinal sections, cells of the outer cortex are rectangular or polygonal and 57–140 μm long. Cells of the inner cortex are fusiform and up to 550 μm long. Parenchyma cells of the ground tissue are also rectangular or polygonal and up to 200 μm long. Cells of the bundle sheath are also longitudinally elongated, but their shape is not clear because of their thick cell walls. Tracheids possess scalariform thickenings on their lateral walls (Plate VI, 2; Plate VII, 1).

Ultimate pinna rachises are attached near the adaxial side of the penultimate pinna rachis (Plate III, 1; Plate IV, 2) and are nearly round or elliptical in the cross section with diameters of approx. 1.5 mm (Plate VII, 2 − 4). The surface is smooth and lacks wrinkles or trichomes. In cross sections the cortex is 110–130 μm thick and consists of isodiametric parenchyma cells with diameters of 20–30 μm. Parenchyma cells of the ground tissue are isodiametric with diameters of 30–50 μm. Secretory ducts are 50–70 μm in diameter. The ultimate pinna rachis of *Rothwellopteris sanjiaoshuensis* has a tricyclic vascular system. The outer two cycles consist of three or four bundles and the central cycle consists of only a single bundle. In the outermost cycle, the longest bundle is C-shaped and located at the abaxial side of the rachis; the shorter bundle is located at the adaxial side and is concave at its mid part. The xylem strand and sheath are thin with a radial thickness of 1–2 cells.

Pinnules are attached near the adaxial side of the ultimate pinna rachis (Fig. 2B; Plate VII, 3). In cross sections, the pinnule midrib is wide, approx. 0.6–0.7 mm, and low relative to lamina

attachment. The lamina is uniformly thin and approx. 130 μm thick (Plate VII, 5 and 6). The midrib has a small C-shaped xylem strand which is surrounded by a semicircular or planoconvex sheath. The adaxial side of the sheath is flat and thin, 2–3 cells thick, and the abaxial side is convex and thick, up to 3–5 cells thick. In cross section cells of the sheath are isodiametric and larger on the abaxial side with diameters of 20–25 μm but smaller on the adaxial side with diameters of 10–15 μm. The palisade tissue of the lamina is weakly developed. Vascular bundles of the lateral veins are located within the spongy tissue. The lower pinnule surface is smooth without ridges marking the position of veins (Plate VII, 6).

Comparison: The present specimens possess pecopteroid-type vegetative pinnules, a polycyclic vascular system comprising many long and short bundles or meristeles, and endarch primary xylem. These characters are consistent with the generic diagnosis of the at least tripinnate compound frond *Rothwellopteris* He et al. (2019) also from the Xuanwei Formation. The present specimens are preserved as bipinnate compound leaves, but they could be terminal parts of a larger, at least tripinnate compound leaf. We have assigned the present specimens to the genus *Rothwellopteris* based on these characteristics.

The genus *Rothwellopteris* is based on the species *R. pecopteroides* He et al. (2019) that was interpreted to be the permineralized equivalent of the compression/impression species *Pecopteris marginata* Li et al. (1974). The present specimens and *R. pecopteroides* both have linear ultimate pinnae, falcate pinnules, and pinnule midribs that are slightly decurrent on the ultimate pinna rachis. In both species the first lateral vein of the lower side at the pinnule base diverge from the decurrent part of the midrib and immediately forks, with the resulting branch veins forking again. Other lateral veins of the pinnule fork once or twice and terminate nearly perpendicular to the margin of the

pinnule (Li et al., 1974; He et al., 2019). However, the pinnule morphology of *R. sanjiaoshuensis* differs by lacking the lingulate pinnules characteristic of *R. pecopteroides.* In addition, the pinnule base does not expand and it lacks the thickened band at the pinnule margin characteristic of *P. marginata* (Li et al., 1974; He et al., 2019). Anatomically, the present specimens are also distinct from *R. pecopteroides* because the surface of the penultimate pinna rachis is smooth and lacks wrinkles and trichomes that characterize that species. Furthermore, in *R. sanjiaoshuensis* the midrib on the abaxial pinnule surface is low with a planoconvex sheath, the pinnule lamina is uniformly thin, and the pinnule margin is not thickened or curved toward the abaxial surface. In *R. pecopteroides* the surface of the penultimate pinna rachis is undulate, the midrib and lateral veins are raised on the abaxial surface, the lamina is thick, and the lateral margin is thickened and bends toward the abaxial surface of the pinnule (He et al., 2019). These differences lead us to assign the present specimens to a new species of *Rothwellopteris* for which we erect *R. sanjiaoshuensis* sp. nov.

The morphology of the present specimens is most similar to *Pecopteris andersonii* Halle (1927) and *Pecopteris heteropinna* Li et al. (1974). Pinnules of *Pecopteris andersonii* are falcate and have a length:width ratio of 2–2.5:1. Pinnules are arranged tightly and have a decurrent midrib that tapers toward the tip. The first lateral vein of the lower side diverges at the base from the decurrent part of the midrib and immediately forks and then forks again. *P. andersonii* differs in having ultimate pinnae that are lanceolate and attached to the ventral side of the rachis. The pinnule bases are decurrent and the margins of a pair of basal pinnules on the ultimate pinna have incisions (Li et al., 1974). *P. heteropinna* is similar to *R. sanjiaoshuensis* by having ultimate pinnae that are linear and more than 12 cm long, with falcate pinnules, a thick midrib, and lateral veins that fork once or twice. *P. heteropinna* differs by having pinnules of different lengths and by their attachment to the ventral

side of the rachis (Li et al., 1974). Pinnules of *R. sanjiaoshuensis* are attached near the ventral side of the rachis and have nearly the same length to one another.

5. Discussion

Four species of late Permian marattialean frond rachis with a polycyclic vascular system are now known; *Compsopteris elliptica* (Guo et al., 1992), *C*. sp. (Guo et al., 1992; He et al., 2019), *R. pecopteroides* (He et al., 2019) and *R. sanjiaoshuensis* sp. nov. When comparing the anatomical features of *R. pecopteroides* with species of *Compsopteris*, He et al. (2019) considered that the polycyclic vascular system of *R. pecopteroides* lacks dorsiventral symmetry and consists of short bundles, while the vascular system of *Compsopteris* is dorsiventral and consists of longer bundles at the abaxial side and shorter bundles at the adaxial side. In *R. sanjiaoshuensis* sp. nov., the polycyclic vascular system of the penultimate pinna rachis in specimen YNUPB1105 has a small diameter and a higher ratio of longer bundles to shorter bundles, with longer bundles positioned abaxially and shorter bundles adaxially to give a ventral-dorsal organization. In specimen YNUPB1106, the polycyclic vascular system of the penultimate pinna has a larger diameter and a lower ratio of longer to shorter bundles and is slightly ventral-dorsal organized. Because the penultimate pinna rachis of *R. pecopteroides* has a larger diameter (up to 10 mm) than that of the present specimens (up to 8.5 mm), it may be expected that its vascular system mainly consists of shorter bundles and a weakly ventral-dorsal organization. In contrast, the vascular systems of the much smaller ultimate pinna rachises of *R. pecopteroides* and *R. sanjiaoshuensis* are obviously ventral-dorsal with the longer bundles positioned abaxially and shorter bundles adaxially (Fig. 2; Plate VII, 2–4).

In each of the four species of late Permian marattialean frond rachis the vascular system has

vascular bundles surrounded by a sheath of sclerenchyma cells. In *Compsopteris,* cells of the outer side of the bundle sheath have thinner walls than those of the inner side, while in *Rothwellopteris,* cells of inner side of the bundle sheath have thinner walls than those of the outer side (He et al., 2019). A vascular bundle sheath is absent from extant marattialeans and the late Carboniferous and early Permian marattialean frond rachises *Stewartiopteris* and *Stipitopteris* from the Euramerican and Cathaysian floras (Stidd, 1971; He et al., 2019; Wang et al., 2021). In marattialean stems from the upper Permian of southwestern China, cauline bundles and the vascular bundles of leaf traces and petiolar bases possess a sheath. In most species, such as *Psaronius panxianensis* He et al. (2008), *P. laowujiensis* He et al. (2010), *P. housuoensis* (D'Rozario et al., 2011) and *P. wangii* Tian et al. (1992), the sheath consists of thin-walled parenchyma cells, which is different from the bundle sheath of *Compsopteris* and *Rothwellopteris* which consists of thick-walled, sclerenchyma cells. Only *Psaronius xuii* He et al. (2013) has cauline bundles and vascular bundles of its leaf traces and petiolar base that possess a sheath comprised of thick-walled sclerenchyma cells. However, the thick-walled cells of the bundle sheath of *P. xuii* are isodiametric in longitudinal section and unlike those of *Compsopteris* and *Rothwellopteris* that are longitudinally elongated.

The frond rachis, leaf trace and petiolar base in stems of the basally divergent marattialean family Psaroniaceae from the Pennsylvanian and early Permian in the Euramerican and Cathaysian floras possess only one (stewartiopterid-type) or two (stipitopterid-type) vascular bundles (Morgan and Delevoryas, 1952a, b; Taylor et al., 2009; Wang et al., 2009), while those of the living Marattiaceae possess multiple bundles (e.g. Rothwell et al., 2018; He et al., 2019). The leaf trace and petiolar base of some marattialean stems from the upper Permian of the Gondwanan flora in South America also possess multiple bundles, such as *Psaronius sinuosus* Herbst (1999), *Tietea* (Solms-

Laubach) Herbst (1986) and *Tuvichapteris* Herbst (1987). Up to now, the reported late Permian marattialean stems from southwestern China all belong to Psaroniaceae. Their leaf trace and petiolar base mostly possess three bundles, including *Psaronius wangii* Tian et al. (1992), *P. panxianensis* He et al. (2008), *P. laowujiensis* He et al. (2010) and *P. housuoensis* (D'Rozario et al., 2011) while only *Psaronius xuii* He et al. (2013) possesses a single bundle in its leaf trace and petiolar base. No marattialean stems possessing leaf trace and petiolar base with multiple bundles have been found from the upper Permian of southwestern China. Therefore, the stems of the *Rothwellopteris* and *Compsopteris* plants possessing leaf trace and petiolar bases with multiple bundles, like those of *Tietea* and *Tuvichapteris*, have probably not yet been discovered. However, the polycyclic vascular system of the pinna rachis in *Compsopteris* and *Rothwellopteris* may have been derived from a leaf trace and petiolar base with one or three bundles by repeated divisions in the rachis that produce multiple bundles. Fossil Marattiales with stems preserved in organic attachment to fronds and/or the development of conceptual whole-plant templates (Bateman and Hilton, 2009) for these plants are now required to address the origin of the polycyclic vascular system in these intriguing late Permian marattialeans.

Stidd (1971) summarized the differences in the frond morphology of Psaroniaceae and Marattiaceae. Fronds of Psaroniaceae are at least tripinnate and pinnules are small and basally truncate, while fronds of Marattiaceae are mostly monopinnate or palmate (only *Angiopteris* is bipinnate) and pinnules are large with their bases contracted and petioled. Anatomically, frond rachises of Psaroniaceae possess typically one (*Stewartiopteris*) or two (*Stipitopteris*) vascular bundles (Morgan and Delevoryas, 1952a, 1952b; Stidd, 1971), while those of Marattiaceae possess more vascular bundles arranged in concentric rings (Stidd, 1971). Fronds of *Compsopteris* are

monopinnate, pinnules are large with their bases contracted and petioled, and frond rachises possess several or more vascular bundles (Guo et al., 1992). Its features are therefore consistent with those of the Marattiaceae. However, *Rothwellopteris* has a mosaic of features including having at least tripinnate fronds bearing small pinnules with truncate bases characteristic of the Psaroniaceae, combined with many vascular bundles in the frond rachises (He et al., 2019; this paper) which are characteristic of the Marattiaceae. This mosaic of characters in *Rothwellopteris* may enrich our understanding of the transition from stem-group Psaroniaceae to crown-group Marattiaceae in Marattiales, showing that vascular bundles in the front rachises evolved into the Marattiaceae configuration before frond and pinnule morphology did.

Esau (1977) considered features indicative of xeromorphy to include thick cuticles, coriaceous pinnules, inrolled margins, well-developed palisade mesophyll, hypodermis, sunken stomata organized in grooves, and the presence of papillae and hairs. Arens (1999) evaluated the ecological implications of sun exposure on frond anatomy in the tree fern *Cyathea caracasana* (Dicksoniaceae) and concluded that compared to shade leaves, sun leaves are thicker, have thicker palisade mesophyll, longer palisade cells, tighter mesophyll cell packing, and have thicker cuticles and epidermis. In *Rothwellopteris pecopteroides* pinnules are coriaceous and rigid with thick laminae (250–400 μm), have more-or-less inrolled margins, well-developed palisade mesophyll and a hypodermis. These features suggest that *R. pecopteroides* was adapted for xeromorphy and/or was a sun leaf. The rachis of *R. pecopteroides* is usually covered by a thin, black, homogenous layer that He et al. (2019) considered to be a poorly preserved epidermis. However, we now consider that this feature more likely represents an imperfectly preserved thick cuticle. In contrast, no cuticle was found covering the epidermis of the rachis in *Rothwellopteris sanjiaoshuensis*. In this species

pinnules are not coriaceous, have a thin lamina (up to 130 µm), the lateral margins are not inrolled, the palisade mesophyll is weakly-developed and a hypodermis is absent. These features are more consistent with mesomorphic fronds and are distinct from the xeromorphic or sun-leaf morphology of *R. pecopteroides*. Although we recognize *R. pecopteroides* and *R. sanjiaoshuensis* as distinct species, they could possibly represent different frond leaves of the same parent plant that adapted to different environmental conditions. Such speculation requires a further development of whole-plant concepts to further evaluate. Likewise, it is not possible to determine if *R. pecopteroides* fronds are from a xeromorphic plant or a sun leaf from a non-xeromorphic plant, because the other parts of the parent plant are not known. Furthermore, as both species of *Rothwellopteris* were collected ex-situ from mine spoil, geological features from the sedimentary succession containing the fossil plants are not known, preventing additional palaeoecological interpretations being made.

The fossil record of Marattiales provides good evidence on the timing of their origin during the Carboniferous (Rothwell et al., 2018) and for timing the commencement of the transition from the stem group family Psaroniaceae to the crown group family Marattiaceae (He et al., 2019). In the present paper we show that key structural features of the Marattiaceae had evolved by the end of the Permian period and that more taxa support the stem- to crown- group transition before the end of the Paleozoic. This is in problematic agreement with recent molecular evidence that dates the origin of the most recent common ancestor of the crown-group Marattiaceae to the late Triassic (236–201 Ma; Lehtonen et al., 2020) or the Triassic-Jurassic Boundary (c. 201 Ma; Smith et al., 2010). Lehtonen et al. (2017) used fossil evidence to date the family transition to the middle to late Triassic (242–214 Ma), while Hill, Wagner and El-Khayal (1985) described convincing Marattiaceae fertile foliage from the Permian of Saudi Arabia. It is reassuring that these molecular analyses do not dramatically

overestimate the date of the origin for this group in relation to its known fossil record as has happened in other lineages including the angiosperms (Coiro et al., 2019; Budd and Mann, 2020). In this regard recognition of the significantly reduced rate of molecular evolution in Marattiales is key to choosing appropriate molecular dating methods for the group for which established molecular clock programs remain problematic (Lehtonen et al., 2020). The group is well-represented in the fossil record overall (e.g., Rothwell et al., 2018), and we find it unlikely that older fossils of Marattiales were present but not preserved due to inadequacies of the fossil record.

6. Concluding remarks

To more fully understand the transition from the Psaroniaceae stem- to Marattiaceae crown-group within Marattiales (Rothwell et al., 2018, He et al., 2019), it remains essential to reconstruct additional whole plant fossil species that lie outside the circumscription of the *Psaronius blicklei* Group of He et al. (2013). The most comprehensive analysis of fossil Marattiales (Rothwell et al., 2018) lacked representatives of the *Psaronius panxianensis* Group of He et al. (2013) including *Rothwellopteris* that was established subsequently (He et al., 2019). Although a distinct possibility, it remains uncertain if *Rothwellopteris* and *Compsopteris* from the late Permian of China represent the fronds of plants with trunks conforming to the characterization of the *Psaronius panxianensis* Group; if so, these plants would likely justify the establishment of a new family of advanced Paleozoic Marattiales transitional between the Psaroniaceae and Marattiaceae. Similarly, other organs of the advanced Paleozoic marattialean trunk genera *Tietea* and *Tuvichapteris* from the late Permian of South America are unknown; these plants may also belong to a distinct family that lies between the Psaroniaceae and Marattiaceae. As presently characterized these late Permian plants present

tantalizing glimpses into the morphology and anatomy of advanced members of the Marattiales at the end of the Paleozoic, but none are sufficiently known to include them in a meaningful evolutionary cladistic analysis. We consider that such work would make a more significant contribution to understanding the timing and nature of the transition from the Marattiales stem- to crown-group than undertaking further molecular dating investigations on gene sequences from living species alone. However, few researchers have the expertise to undertake this kind of labor- and time intensive palaeobotanical study, and it requires extensive fieldwork to search for high quality anatomically preserved specimens suitable to be reconstructed (Bateman and Hilton, 2009). Jean Galtier has taught several generations of palaeobotanists, including ourselves, these skills and with great respect, we thank him for passing on his skills and knowledge so this important area of palaeobotanical research can advance.

Declaration of Competing Interest

None.

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Figures and Plate Captions

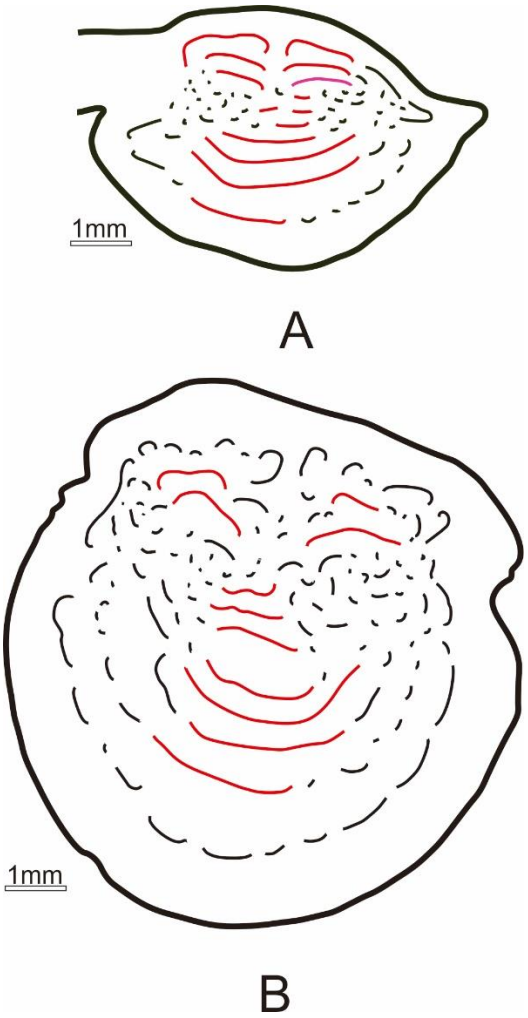

Fig. 1. Line drawings of the cross sections of penultimate pinna rachis of *Rothwellopteris sanjiaoshuensis* sp. nov. showing the polycyclic vascular system. Note the arrangement of the longer and shorter bundles (in red). A is drawn from Plate III, 1 and B is drawn from Plate V, 1.

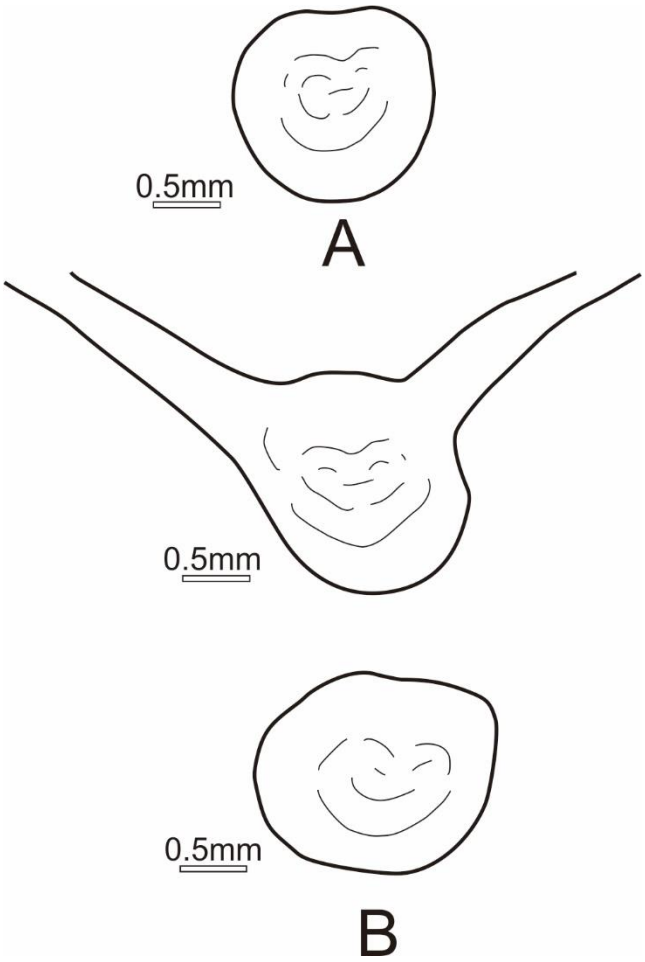

Fig. 2. Line drawings of the cross sections of ultimate pinna rachis of *Rothwellopteris pecopteroides* (A) and *R. sanjiaoshuensis* sp. nov. (B) showing the tricyclic vascular system. A is drawn from Fig. 4e of He et al. (2019) and B from Plate VII, 3 and 4.

Plate I. *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou, China. (1–3). Morphology of specimen YNUPB1105 (holotype). (1). Gross morphology. Arrow indicates the penultimate pinna rachis. Scale bar = 2 cm. (2). Two ultimate pinnae. Scale bar = 1 cm. (3). Pinnules, showing the venation. Scale bar = 0.2 cm.

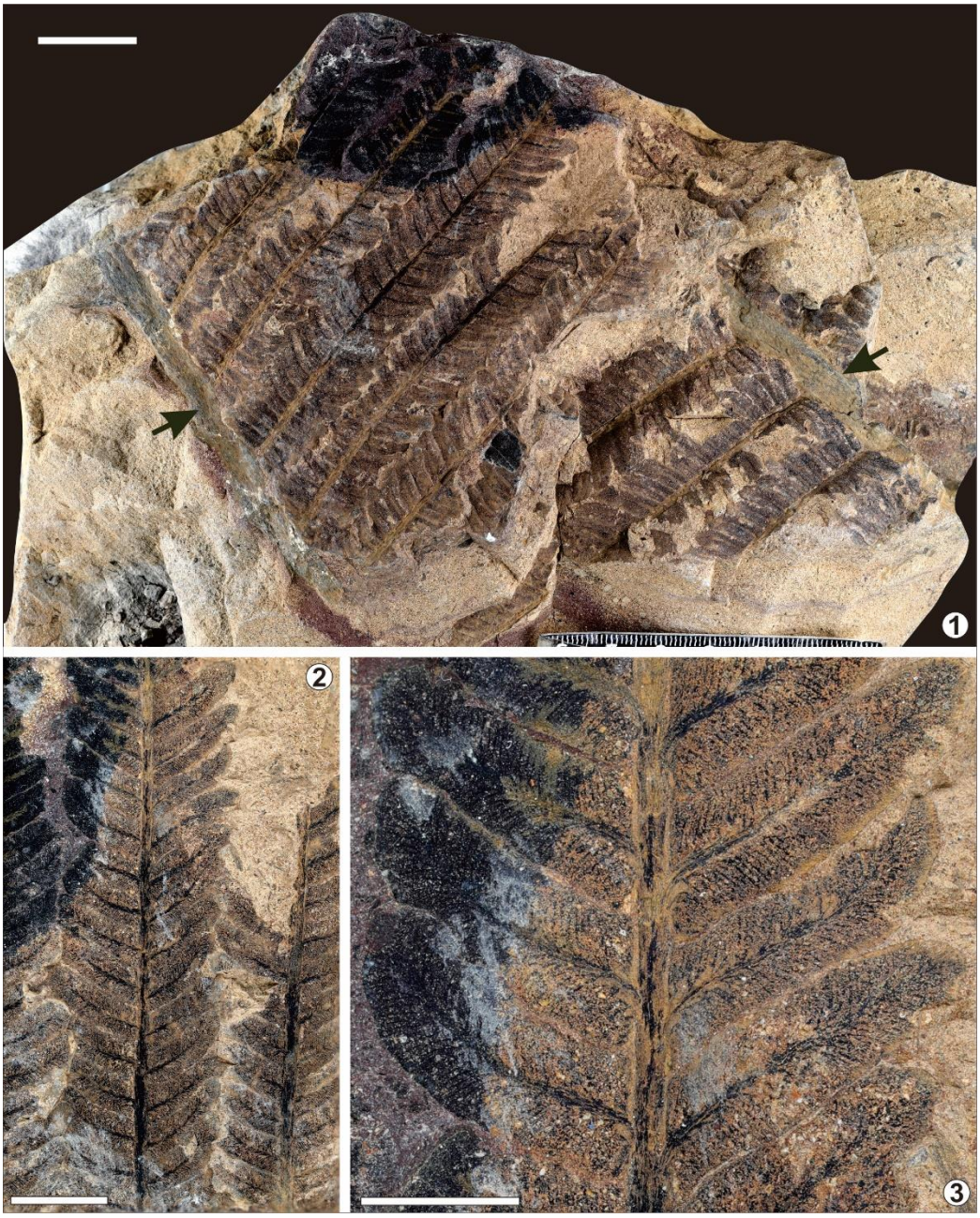

Plate II. *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou, China. (1–3). Morphology of specimen YNUPB1106 (paratype). (1). Gross morphology. Arrows indicate the penultimate pinna rachises. Scale bar = 2 cm. (2). Two ultimate pinnae. Scale bar = 1 cm. (3). Part of an ultimate pinna, showing the venation of pinnules. Scale bar = 0.5 cm.

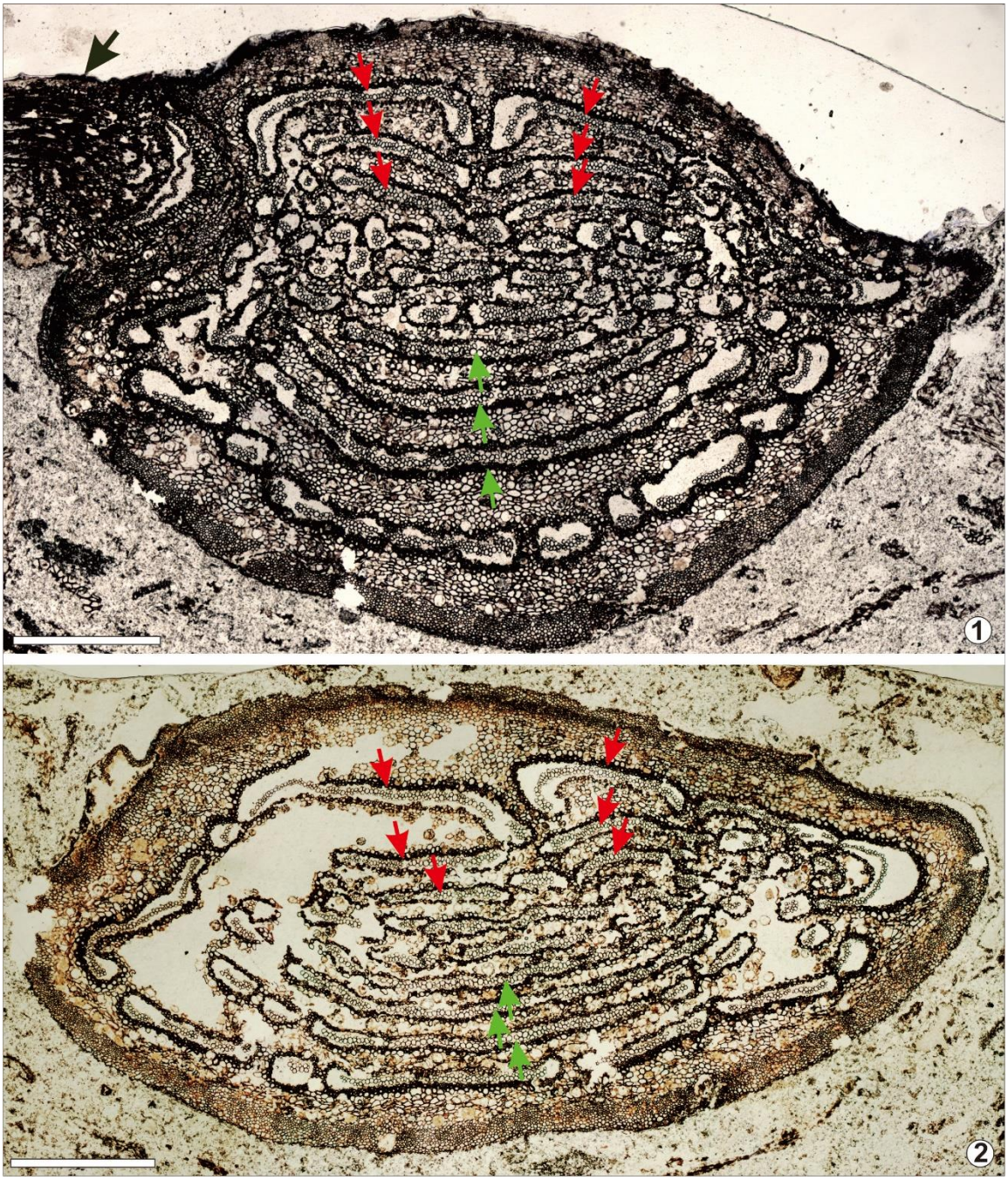

Plate III. *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou, China. (1–2). General view of cross sections of the penultimate pinna rachis of specimen YNUPB1105 showing the polycyclic vascular system. Red arrows indicate shorter bundles arranged in two radial rows at ventral side of the rachis; green arrows indicate longer bundles arranged in one radial row at the dorsal side of the rachis; black arrow indicates a departing ultimate pinna rachis. Slides: YH-0738 and YH-0730; Scale bars = 1 mm.

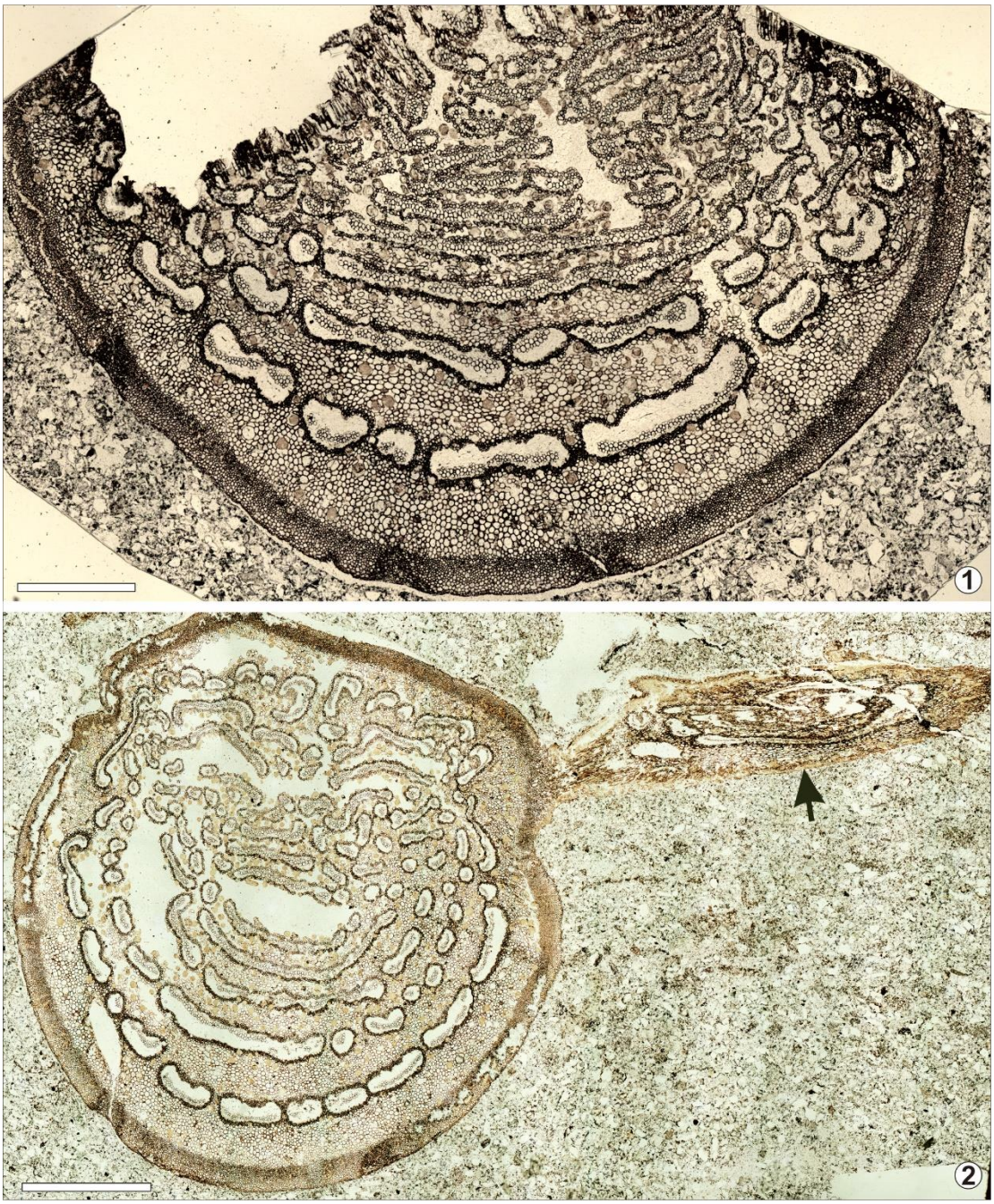

Plate IV. *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou, China. (1–2). Gross morphology from cross sections of the penultimate pinna rachis of specimen YNUPB1106 showing the polycyclic vascular system. (1). Incompletely preserved specimen in cross section. Slide: YH-0737; Scale bar = 1 mm. (2). Completely preserved cross section showing an attached ultimate pinna rachis (arrowed). Slide: YH-0733; Scale bar = 2 mm.

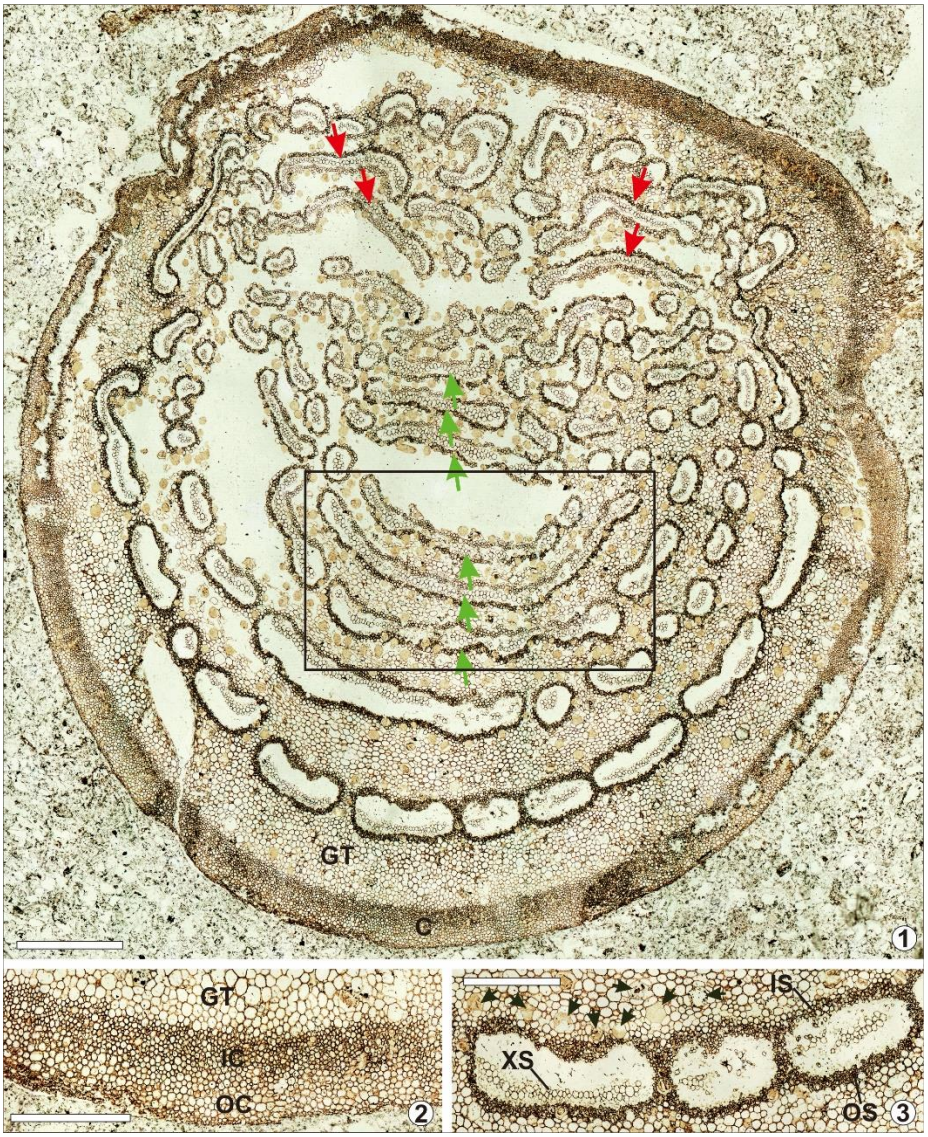

Plate V. *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou, China. (1). Enlargement from Plate IV, 2 showing the cross section of the penultimate pinna rachis. Red arrows indicate shorter bundles arranged in two radial rows at the ventral side of the rachis; green arrows indicate longer bundles arranged in one radial row at the dorsal side of the rachis. The area in the box is enlarged in Plate VI, 1. C − cortex; GT − ground tissue. Scale bar = 1 mm. (2). Enlargement from (1) showing a part of the ground tissue (GT) and cortex comprising inner cortex (IC) and outer cortex (OC). Scale bar = 0.5 mm. (3). Enlargement from (1) showing three vascular bundles from the outmost cycle and secretory ducts (arrowed) in the ground tissue. XS − xylem

strand; IS − inner bundle sheath; OS − outer bundle sheath. Scale bar = 0.5 mm.

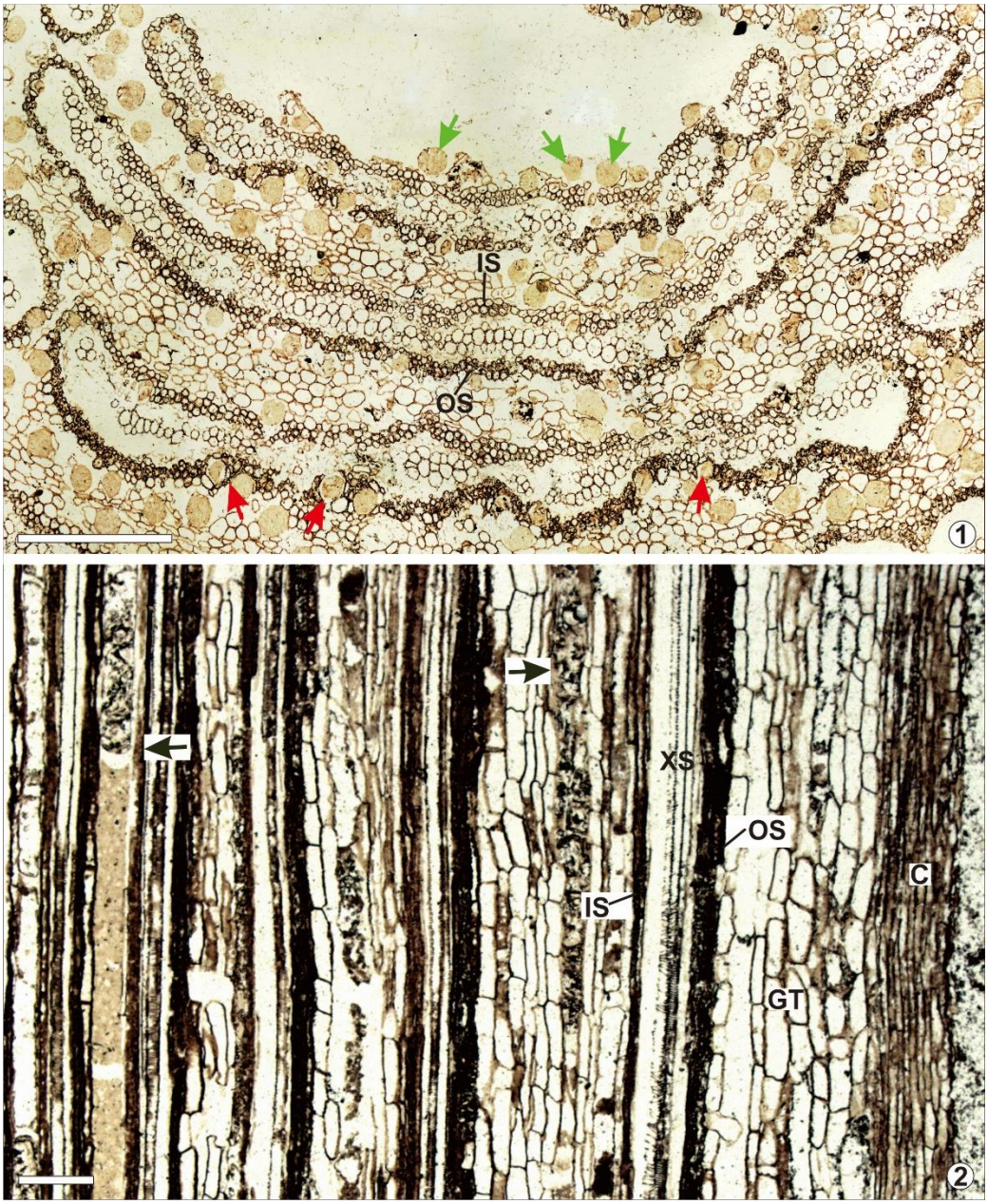

Plate VI. *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou, China. (1). Enlargement of the boxed area from Plate V, 1 showing the structure of vascular bundles and ground tissue. Note that cells of the outer bundle sheath (OS) have thicker walls than those of the inner bundle sheath (IS). Secretory ducts with yellowish brown content are dispersed among the parenchyma cells and in the bundle sheath (red arrows). Some secretory ducts are broken and only their yellowish-brown content remains (green arrows). Scale bar = 0.5 mm. (2). Longitudinal section

of the penultimate pinna rachis of specimen YNUPB1106 showing cortex (C), ground tissue (GT), outer bundle sheath (OS), inner bundle sheath (IS), xylem strand (XS) and secretory ducts (arrows). Slide: YH-0740; Scale bar = 200 μm.

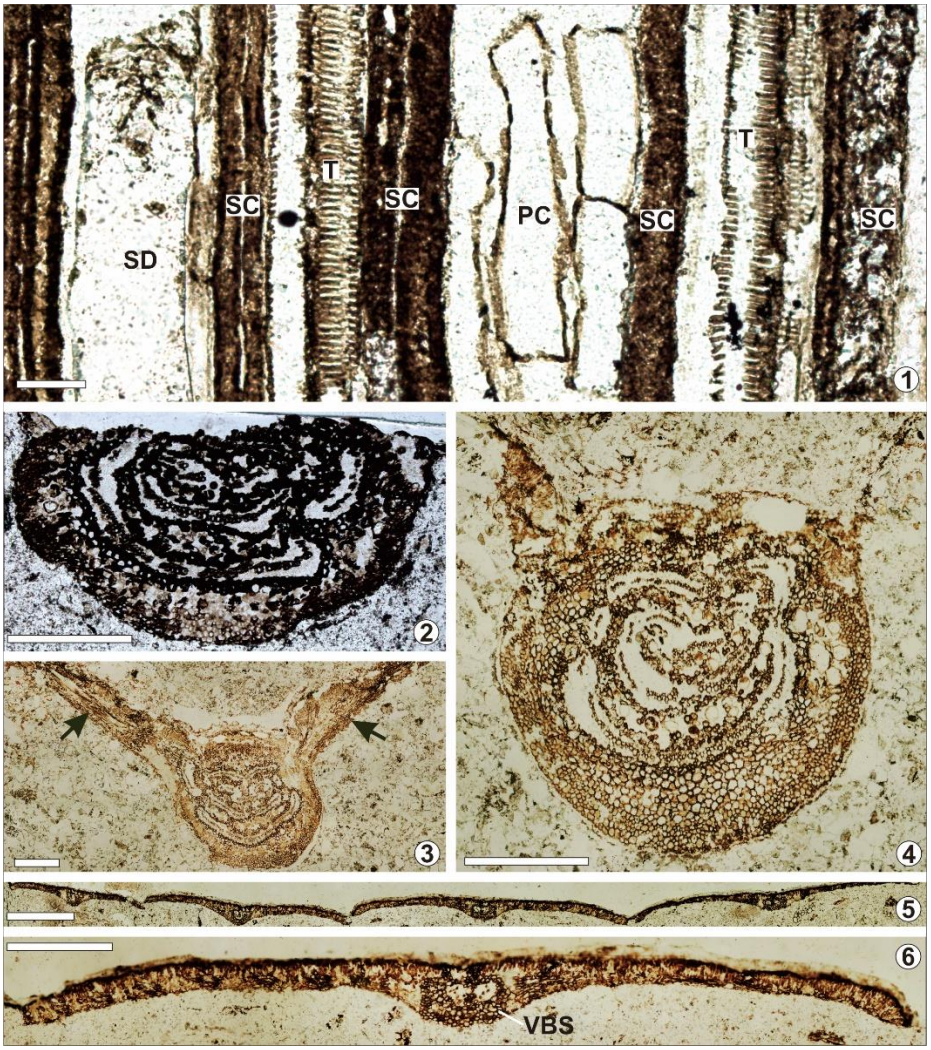

Plate VII. *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou, China. (1). Longitudinal section of the penultimate pinna rachis of specimen YNUPB1106, showing parenchyma cells (PC) and secretory duct (SD) of the ground tissue, vertically elongated sclerenchyma cells (SC) of the bundle sheath, and tracheids of the xylem strand with scalariform thickenings (T). Slide: YH-0740; Scale bar = 50 μm. (2). Cross section of the ultimate rachis of the

specimen YNUPB1105. Slide: YH-0739; Scale bar = 0.5 mm. (3–4). Cross sections of the ultimate rachis of the specimen YNUPB1106. Arrows indicate pinnules. Slide: YH-0734; Scale bars = 0.5 mm. (5). Cross section of four pinnules. Slide: YH-0732; Scale bar =1 mm. (6). Cross section of a pinnule from (5) showing the low and broad midrib on the abaxial side of the pinnule and the plane convex or semi-circular bundle sheath (VBS). Scale bar = 0.5 mm.