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The anatomically preserved tri-pinnate frond *Rothwellopteris pecopteroides* gen. et sp. nov. from the latest Permian of South China: timing the stem to crown group transition in Marattiales

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Premise of research. Fern fronds are common in Late Paleozoic and Mesozoic strata. Large, tri- or multi- pinnate fronds are mainly preserved as impression-compressions while anatomically preserved specimens are typically smaller and comprise dispersed petioles, rachides, ultimate pinna or pinnules. Here we describe a large, anatomically preserved tri-pinnate frond from the latest Permian of SW China that provides the first detailed histological information on a Cathaysian marattialean with pinnule morphology of the cosmopolitan Carboniferous-Permian pecopteriod type, but with different frond anatomy.

Methodology. Specimens were prepared by the cellulose acetate peel technique and studied by light microscopy.

Pivotal results. The tri-pinnate frond has a main rachis and primary pinnae rachis with many (> 70) small vascular bundles arranged in cycles, and abundant tanniferous cells. Pinnules are small and their bases are entirely attached to the ultimate rachis. Abundant vascular bundles in its rachises are distinct from previously recognized marattialean genera justifying to the establishment of *Rothwellopteris pecopteroides* gen. et sp. nov. Comparison of pinnule morphology with compression/impression fossils demonstrates the specimen to be an anatomically preserved equivalent of *Pecopteris marginata* Li et al. 1974.

Conclusions. *R. pecopteroides* displays a novel combination of marattialean characters from the extinct Paleozoic family Psaroniaceae and the extant family Marattiaceae. Its frond morphology resembles Psaroniaceae including *Psaronius*, but differs from extant Marattiaceae that are mono-pinnate, palmate or as in *Angiopteris* bi-pinnate, and have large pinnules with contracted bases. By contrast, its anatomy with abundant vascular bundles is similar to Marattiaceae, especially *Angiopteris*, but is distinct from members of the Psaroniaceae in which the rachis possesses one or two tangentially elongate vascular bundles. *P. marginata* shows that by the latest Permian Marattiales had already evolved frond anatomy typical of extant genera, demonstrating that the stem group to crown group transition commenced prior to the Triassic.

Keywords: Eusporangiate fern, Marattiales, Psaroniaceae, Marattiaceae, evolution, volcaniclastic tuff, Xuanwei Formation, stem group, crown group

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Introduction

Marattiales are a clade of living eusporangiate ferns that have an extensive fossil record going back into the early Pennsylvanian approximately 320 million years ago (e.g., DiMichele and Phillips, 1977; Liu et al. 2000; Rothwell et al. 2018). During the late Paleozoic, marattialean ferns were widely distributed in the Euramerican (Morgan 1959; Mickle 1984; Millay 1997; Taylor et al. 2009), Gondwanan (Herbst 1986, 1987, 1992, 1999) and Cathaysian floras (Ogura 1972a; Hill et al. 1985; Gu et Zhi 1974; Li et al. 1995). In these floras fronds and pinnae are relatively commonly, with most preserved as impression/compression fossils that can be identified and classified based on the morphological characters including pinnule shape, size and venation. By contrast, anatomically preserved (permineralized) marattialean leaves mainly represent isolated rachises or terminal pinna that are identified and classified based on the vasculature of rachides (Morgan and Delevoryas 1952a, b; Stidd 1971). In exceptional cases, morphological features of marattialean leaves can also be observed in permineralized specimens, such as *Compsopteris ellipticum* Chang ex Yang et Chen (see Guo et al. 1992). Such fossils, preserved with morphological and anatomical characters, are key to associate impression/compression taxa with permineralized fossils in order to reveal the relationships between them. This is important to the development of whole-plant concepts from fragmentary fossil assemblages (e.g., Rothwell 1999; Bateman and Hilton 2009).

In the late Paleozoic Cathaysian flora, marattialean ferns flourished until the late Permian in eastern Yunnan and western Guizhou provinces in SW China where they constitute an important component in latest Permian floras (Zhao et al. 1980). From this region Marattiales are abundant as vegetative and fertile fronds as well as pinnae preserved as impression-compression fossils (Tian and Zhang 1980; Zhao et al. 1980; Liu et al. 2000, 2001) and permineralizations (Guo et al. 1992; Hilton et al. 2004; He et al. 2006). In addition, numerous permineralized marattialean trunks with thick root mantles have also been found in this region (e.g., Sze 1942, 1947; Yang 1986; Tian et al. 1992; Li et al. 1995; He et al. 2008, 2010, 2013; D'Rozario et al. 2012). Here from the latest Permian of Guizhou Province in SW China we report a new kind of marattialean frond preserved with both morphology and anatomy that has three orders of rachises and attached vegetative pinnules. Based on its preserved morphological characters, the frond is considered to be the anatomically-preserved equivalent of *Pecopteris marginata* Li et al. 1974 which was erected based on impression/compression fossils (Li et al. in Gu et Zhi 1974).

Material and methods

The permineralized marattialean frond reported in this paper was found embedded in a large rock block (number YNUPB11001) collected from mine spoil from the Xuanwei Formation (Lopingian Epoch, late Permian period) in Panxian mining district of western Guizhou Province, SW China. The rock is a volcanic tuff that is white-grey colored but on its surface has weathered to a yellow-grey color.

A diverse fossil plant assemblage has been previously been reported from the Xuanwei Formation in the Panxian mining district including impression/compression and permineralized specimens. Impression/compression fossils were primarily described by Zhao et al. (1980). The assemblage includes the lycopsids *Lepidodendron acutangulum* (Halle), *L. lepidophloides* Yao, *Stigmaria ficoides* (Sternb.), the sphenopsids *Sphenophyllum koboense* Kobatake, *Sph.*

sino-coreanum Yabe, *Paracalamites stenocostatus* Li et al., *Annularia pingloensis* (Sze), *A. shirakii* Kawasaki, *Lobatannularia cathaysiana* Yao, *L. lingulata* (Halle). *L. multifolia* Kon'no et Asama, *Schizoneura brevifolia* Yao, *Sch. manchuriensis* Kon'no, and the noeggerathialeans *Plagiozamites oblongifolius* Halle, *Discinites* cf. *orientalis* Li et al. Fern and seed fern foliage includes *Chansitheca kidstonii* Halle, *Sphenopteris tenuis* Schenk, *Pecopteris echinata* Li et al., *P. fuyuanensis* Zhang, *P.* (*Asterotheca*) *guizhouensis* Zhang, *P. lingulata* Zhang, *P. marginata* Li et al., *P. sahnii* Hsu, *Rajahia guizhouensis* Zhang, *R. mirabilis* (Li et al.) Zhang, *R. rigida* (Yabe et Oishi) Zhang, *Fascipteris* (*Ptychocarpus*) *densata* Li et al., *F. hallei* (Kawasaki), *F. stena* Li et al., *Cladophlebis ozakii* Yabe et Oishi, *Cl. permica* Lee et Wang, *Cl. parapermica* Zhang, *Neuropteridium coreanicum* Koiwai, *N. guizhouense* Zhang, *Compsopteris imparis* Li et al., *C. contracta* Li et al., *C. punctinervis* Mo, *Gigantonoclea guizhouensis* Li et al., *G. hallei* (Asama), *G. largrelii* (Halle), *G. plumosa* Mo, *Gigantopteris dictyophylloides* Li et al., *Taeniopteris* ? *rarinervis* Zhao, *T. crassinervis* Mo, *Abrotopteris guizhouensis* (Li et al.) Mo, *Prionophyllopteris spiniformis* Mo. Cycads present in the flora are represented by *Pterophyllum eratum* Li et al. and Ginkgoales by *Rhipidopsis pani* Chow, *R.* cf. *ginkgoides* Schmalh. and *R. lobulata* Mo, while conifers include *Ullmannia* cf. *bronnii* Goeppert and *U.* sp. Permineralized fossils includes the sphenopsid *Calamostachys* sp. (Hilton et al., 2004), the marattialean ferns *Compsopteris elliptica* Chang ex Yang et Chen (Guo et al., 1992), *Eoangiopteris* sp. (Hilton et al., 2004), *Psaronius laowujiensis* He et al. (He et al., 2010), *P. panxianensis* He et al. (He et al., 2008), *P. wangii* Tian et al. (Tian et al., 1992), *P. xuii* He et al. (He et al., 2013). Filicalean ferns are rare and limited to *Anachoropteris* sp. (Hilton et al., 2004). Noeggerathialeans include pseudo-strobili of *Dorsalistachya quadrisegmentorum* Wang et Spencer (Wang et al., 2017) and associated foliage of *Plagiozamites oblongifolius* Halle (Guo et al., 1990). Seed ferns are represented by *Callistophyton boysetii* (Renault) Rothwell (Seyfullah and Hilton, 2011) and ovules of *Cardiocarpus huopuensis* Wang et al. (Wang et al., 2006), *Muricosperma guizhouensis* Seyfullah et al. (Seyfullah et al., 2010). Anatomically preserved gigantopterids include *Gigantonoclea guizhouensis* Li et al. (Li et al., 1994), *Aculeovinea yunguiensis* Li et Taylor (Li and Taylor, 1998), *Vasovinea tianii* Li et Taylor (Li and Taylor, 1999), while conifers are represented by the wood *Xuanweioxylon scalariforme* He et al. (He et al., 2013).

In the tuff the fossil is permineralized by calcium carbonate, with preservation occurring before significant decay occurred (Neregato et al. 2016). The frond is large and consists of three orders of branches. We follow Stidd's definition and name the three orders of branches as frond, primary pinna and ultimate pinna respectively (Stidd, 1971). Frond consists of a rachis (main rachis) and lateral appendages, i.e. primary pinnae; primary pinna consists of a rachis (primary pinna rachis) and lateral appendages, i.e. ultimate pinnae; ultimate pinna consists of a rachis (ultimate pinna rachis) and pinnules. Main rachis is partly exposed on the surface of the rock (Fig. 1*a*) and is robust, with a diameter of up to 3 cm (Fig. 1*b*); primary pinna rachis has a diameter of more than 1 cm, with both the main rachis and primary pinna rachis having many small vascular bundles; the ultimate pinna rachis has 4–5 vascular bundles and bears vegetative pinnules. The large size and attached nature of the different orders of branching in the fossil infers that it was not subjected to significant taphonomic transportation and fragmentation prior to its preservation as is typical of other permineralized fossil plant assemblages from tuffaceous sediments in the Xuanwei Formation (e.g., Hilton et al. 2004; Neregato et al. 2016; Wang et al. 2017).

The specimen was prepared using the cellulose acetate peel method (Galtier and Phillips 1999), as outlined by He et al. (2006, 2008, 2010, 2013) and Wang et al. (2017). The rock bearing the specimen, peels and slides are deposited at the Institute of Deep Time Terrestrial Ecology, Yunnan University.

Systematic Paleobotany

Order – Marattiales Engler and Prantl, 1902

Genus – Rothwellopteris *gen. nov.* XY He, SJ Wang, J Wang and J Hilton

Generic diagnosis. Vegetative frond tri-pinnate, pinnules broadly attached, parallel sided, lingulate with rounded tips, veins twice forked. Main rachis and primary pinna rachis possessing numerous small vascular bundles arranged in layers or concentric cycles. Protoxylem endarch.

Etymology. The new genus is named in honor of the paleobotanical achievements of Gar W. Rothwell.

Remarks. The new genus is distinguished from all other genera by its combination of *Pecopteris* pinnule morphology with a tri-pinnate frond with its main rachis and primary pinna rachis having many (> 70) small vascular bundles arranged in cycles.

Species – Rothwellopteris pecopteroides *sp. nov.* He XY, Wang SJ, Wang J and Hilton J

Specific diagnosis. Vegetative frond. A tri-pinnate compound leaf. Rachis robust, main rachis up to 3 cm in diameter and primary pinna rachis up to 1 cm in diameter. Ultimate pinna rachis bears subopposite pinnules, pinnules tongue-shaped or somewhat falcate, with length:width ratio less than 3:1. Lateral margin of pinnules thickened, pinnule base slightly expanding; pinnule midrib thick, lateral veins forking twice and nearly perpendicular to the pinnules lateral margin. Pinnule margins slightly downturned. Palisade tissue well developed, vascular bundle sheaths marked by ridges on abaxial pinnule surface. Surface of the first and second order of rachis undulate. Cell walls of the epidermis thick. Cortex divided into inner and outer cortex. Outer cortex further divided into inner and outer zones, outer zone consisting of continuous parenchyma with uniform cell size; inner zone being continuous or discontinuous sclerenchyma bands. Central part of rachis consisting of ground tissue and many small vascular bundles or meristeles, arranged in poly-cycles. Abundant tannin cells in ground tissue. Vascular bundles in the outmost cycle possessing a well-developed sheath with its thickness greater on the pinna abaxial side than that on the adaxial side. The ultimate pinna rachis possesses two cycles of vascular bundles, each consisting of four vascular bundles.

Etymology. The new species is named after the distinctive pecopteroid-shape of the attached pinnules.

Remarks. *Rothwellopteris pecopteris* gen. et sp. nov. is interpreted as being the anatomically preserved equivalent of the compression/impression species *Pecopteris marginata* Li et al. (1974) that occurs in the Xuanwei Formation in this region. While its pinnule morphology is assignable to *P. marginata*, the species is placed in a new genus because its main rachis and primary pinna rachis have the distinctive anatomy of a marattialean fern, and deserve a more complete typification as a new genus. *Rothwellopteris* fronds combine anatomical features of Marattiaceae (concentric arrangement of meristeles) and the Psaroniaceae (petiolar fiber sheath, some tangentially elongate vascular bundles, pinnule anatomy). We have not retained the species name from the impression/compression fossil species *Pecopteris marginata* to avoid confusion and to keep the fossil-taxa separate; we consider the different species reflect an association between different preservational media of what may be the same biological species.

Holotype. YNUPB11001

Depository. Institute of Deep Time Terrestrial Ecology, Yunnan University.

Locality. Panxian Mine District, Guizhou Province.

Stratigraphy and age. Xuanwei Formation, Lopingian Epoch, Permian Period.

Description

The frond is a tri-pinnated compound leaf with a preserved length for the first order rachis (main rachis) up to 30 cm (Fig. 1*a*), but is apically and distally incomplete thus preserving only the middle part of the frond. The diameter of the main rachis is nearly the same at both ends (Fig. 1*b*–*c*) with no obvious tapering, inferring its entire length pre-fragmentation to have been much longer, thus constituting a large frond.

Rachis anatomy

The surface of the main rachis and primary pinna rachis is typically undulated (Fig. 1*c*, 1*e*; Fig. 2*c*, 2*d*) and anatomically they are nearly the same, comprising a narrow cortex with many small vascular bundles or meristeles within it (Fig. 1*b*, 1*c*, 1*e*; Fig. 2*c*). Epidermal cells are usually poorly preserved. Their cell walls seem to be thick and are usually preserved as a thin black homogenous layer (Fig. 1*d*; Fig. 2*d*, 2*e*). The cortex comprises an outer and inner part, with the outer cortex further divided into two zones of which the outermost layer consists of continuous parenchyma (Fig. 1*d*, Fig. 2*d*, 2*e*). In the main rachis, the outer zone of the outer cortex has a larger radial width, up to 10 cells or 400–500 μm wide. Parenchymatous cells are nearly isodiametric in cross section with diameters mainly from 40–60 μm. In the primary pinna rachis, the outer zone of the outer cortex is a little narrower, 3–6 cells or 200–300 μm wide, and cells are smaller with diameters usually less than 50 μm. The inner zone of the outer cortex is a continuous or discontinuous sclerenchyma band. In the main rachis the sclerenchyma band is mostly discontinuous and is divided into many alternating sclerenchyma and parenchyma strands (Fig. 1*b*–*d*; Fig. 2*d*). Sclerenchyma strands are radially elongate with radial widths of 600–700 μm and a smaller tangential width (Fig. 1*d*). Parenchyma strands are connected with the outer zone of the outer cortex. In some parenchyma strands, the cells are obviously radially elongate. Parenchyma cells of the cortex are all approximately isodiametric in cross section, with diameters of 20–40 μm and thick cell walls. Secretory cavities are scattered in the parenchyma and sclerenchyma, and some of them contain dark brown contents. In the primary pinna rachis, the sclerenchyma band tends to be continuous (Fig. 2*b*, 2*c*) with a smaller radial width, usually 300–500 μm. The inner cortex is usually poorly preserved and can be found only in some places (Fig. 2*f*). Cells of the inner cortex are similar in size to those of the outer cortex but have thinner cell walls. Cells of the outer and inner cortex appear elongate in longitudinal section (Fig.

3*a*).

There are many small vascular bundles (or meristeles) in the mid part of the main and second order rachis. The outermost vascular bundles are arranged in a regular ring (fig. 1*e*; fig. 2*c*). Inside this ring, vascular bundles are arranged somewhat irregularly and not in obvious rings (fig. 3*b*), probably due to taphonomic disturbance. The number of vascular bundles is more than 70. Most of vascular bundles are band-like and centripetally arced (fig. 2*c*; Fig. 3*b*–*d*; fig. 4*a*), but some are nearly round in cross section (fig. 3*e*). The well preserved vascular bundles consist of a xylem strand and sheath. The xylem strand is 1–2 tracheids thick and protoxylem is endarch, located along the inner side of the strand (fig. 3*c*, 3*d*). Metaxylem tracheids of the main rachis are mainly polygonal in cross section and with diameters mostly more than 40–50 μm, while those of the primary pinna rachis are smaller, and typically 30–40 μm in diameter. The vascular bundles of the outermost ring are different from those of the inner rings; cells of the vascular bundle sheath of the former possess thicker walls that are dark brown or black colored, while cell walls of the vascular bundle sheath in the inner rings are thinner and are light colored (compare fig. 3*c*, 3*d* with fig. 4*a*). Phloem and ground tissues are poorly preserved, but many tannin cells with dark or light colored contents can be seen (fig. 3*c*, 3*e*; fig. 4*b*). Tracheid walls possess scalariform thickenings (fig. 4*b*).

The cortex of the ultimate pinna rachis is 300–400 μm thick and lacks sclerenchymatous strands (fig. 4*e*). It can be roughly divided into two zones. Cells of the outer zone are smaller, 20–30 μm in diameter and with thick walls, while cells of the inner zone are larger, up to 40–60 μm in diameter and have thinner walls. There are two rings of vascular bundles in the middle part of the ultimate pinna, with each ring consisting of four vascular bundles among which the one located at the dorsal side is longer than the others. Xylem strands are thin, 1–2 tracheids thick, and metaxylem tracheids are only 20–30 μm in diameter. The vascular bundle sheath is one cell thick and consists of cells slightly smaller than the metaxylem tracheids. These cells possess thicker walls and are dark colored.

Ultimate pinnae and pinnule

The ultimate pinnae are all incompletely preserved with the longest one measuring 5 cm in length. The width of the ultimate pinna is up to 16–18 mm. Pinnules are tongue-shaped (fig. 5*b*; fig. 6*a*) or somewhat falcate (fig. 4*c*; fig. 5*a*), alternate and oriented perpendicular to the ultimate pinna rachis. Pinnules are up to 9 mm long and up to 3 mm wide in their middle, with blunt tips and truncate and slightly expanded bases. The midrib is up to 0.3 mm wide and decurrent on the pinna. The first lateral vein of the lower side at the base diverges from the decurrent part of the pinnule. Lateral veins diverge from the midrib at an acute (or lower) angle and divide once, then extend to the margin and divide once again. Ultimate lateral vein branches are perpendicular to the margin of the pinnule (fig. 5; fig. 6*b*, 6*c*).

The midrib of the pinnule appears sturdy and is raised on the lower surface (fig. 6*d*; fig. 7*a*). Lamina thickness varies depending on the pinnules. In some pinnules, the lamina is 350–400 μm thick, while in other pinnules the lamina is only 250–300 μm thick. The lateral margin of the pinnule is thicker and bends or is even involute toward the lower surface (fig. 6*d*; fig. 7*a*). Mesophyll is differentiated into a palisade and spongy tissue (Fig. 7*b*, 7*c*). Palisade tissue is well developed and its cells have a length reaching half of the thickness of the lamina with many of them possessing black or dark brown contents. The vascular bundle of the lateral veins is located within the spongy tissue and has a diameter of 110–130 μm. Vascular bundle sheaths consists of 1–2 layers of nearly round cells. On the lower and upper surface of the vascular bundle sheath there is a strand of cells which connect the epidermis and the vascular bundle sheath. The strand which connects the upper epidermis and the vascular bundle sheath is slender and consists of small, thick-walled cells, while the strand connecting the lower epidermis and the vascular bundle sheath is shorter, thicker, and consists of large thin-walled cells. The vascular bundle sheath appears circular in section and defines a ridge on the abaxial (lower) pinnule surface (Fig. 6d).

Discussion

Comparisons with impression-compression species

The frond from the Xuanwei Formation is preserved revealing both its morphology and anatomy from which information on its pinnule outline and venation enables comparisons with impression-compression species. In outline pinnules are tongue-shaped or falcate with a blunt tip and a truncate and slightly expanded base. These features conform to the circumscription of the genus *Pecopteris* Brongniart, a genus for specimens preserved as impression/compression fossils. Although most species of *Pecopteris* belong to members of the Marattiales, other species have also been assigned to the Zygopteridales, "filicales" including the Tedelaceae or seed plant (e.g., Stewart and Rothwell, 1993). To date, 10 species of *Pecopteris* have been reported from the Xuanwei Formation in western Guizhou and eastern Yunnan provinces, namely: *P*. *arcuata* Halle, *P*. *echinata* Gu et Zhi, *P*. *elegantula* Zhang, *P*. *fuyuanensis* Zhang, *P*. (*Asterotheca*) *guizhouensis* Zhang, *P*. *lingulata* Zhang, *P*. *longifolioides* Zhang, *P*. *marginata* Gu et Zhi, *P*. *qingyunensis* Zhang and *P*. *sahnii* Hsu (Li et al., 1974; Zhao et al., 1980; Tian et Zhang, 1980). Among these species, the present frond is comparable to *Pecopteris marginata* Li et al. (1974) in its pinnule outline and venation pattern. However, the type specimen of *P*. *marginata* is a bipinnately compound leaf which is distinct from the tri-pinnate leaf of the specimen described here. *P*. *marginata* has a broad rachis and its primary pinna rachis is up to 6–7 mm wide. The margin of the pinnule has a narrow thickened band, and the base of the pinnule is slightly expanded. In *P. marginata* the pinnule midrib is thick, lateral veins fork twice and are perpendicular to the lateral margin of the pinnule. *Rothwellopteris pecopteroides* also has a thick rachis (rachis is up to 30 mm wide and the second order of rachis is up to 10 mm wide) and the size of ultimate pinna and pinnules of the present frond are similar to those of the type specimen of *P*. *marginata*. The base of the pinnules of *Rothwellopteris* are also slightly expanded and the lateral margin bends or is involute toward the lower surface, and there is a thickened band at the margin of the pinnule. In the new genus, the midrib is also prominent and lateral veins mostly forked twice and are perpendicular to the lateral margin of the pinnule. Differences between the present frond and the type specimen of *P*. *marginata* is that the new frond is tri-pinnately compound leaf, while the type specimen of *P*. *marginata* is a bi-pinnately compound leaf, but this may be the result of fragmentation and incomplete preservation in the type specimen of *P. marginata*. Furthermore, the present frond and the type specimen of *P*. *marginata* were both collected from the same locality and same stratigraphic interval making it additionally probable that they belong to the same species, with the *Rothwellopteris* specimen being a permineralized example of *P*. *marginata*. The discovery of the new frond specimen establishes that *P*. *marginata* is a tri-pinnately compound leaf, and not a bi-pinnately compound leaf.

Comparison with permineralized fossil and living Marattiales

The discovery of the present frond is important as it presents an opportunity to study the anatomy of a Cathaysian species of *Pecopteris* for the first time. The rachis of the tri-pinnate frond from the Xuanwei Formation has numerous anatomical features that allow it to be placed within the Marattiales including (1) the presence of abundant vascular bundles that are roughly arranged in concentric rings, (2) individual vascular bundles being short, band-like and bend internally, (3) protoxylem distributed along the innermost side of the vascular bundle, and (4) abundant tannin cells dispersed throughout the tissues (Ogura 1972b).

Existing Paleozoic records of anatomically preserved vegetative marattialean fronds have mainly been found from in the Euramerican and Cathaysian floras. Those from the Euramerican flora occur in the Pennsylvanian and Cisuralian (lower Permian) from which petioles and rachises are placed in the genera *Stewartiopteris* Morgan and Delevoryas and *Stipitopteris* Grand'Eury (Morgan and Delevoryas 1952a, b; Stidd 1971; Table 1). Those from Cathaysia occur in the Cisuralian and Lopingian (upper Permian) where anatomically preserved petioles or rachises are also assigned to *Stewartiopteris* and *Stipitopteris* (Xiang et al. 2008). However, the rachises of the present frond possess abundant small vascular bundles, which clearly distinguish it from both of these genera that have only one or two long and continuous vascular bundles (Table 1).

Compsopteris elliptica was established by Yang and Chen (1979) for impression-compression fossils of mono-pinnate compound marattialean leaves from the Longtan Formation in Guangdong Province that they considered to most likely represent the frond of a seed fern. Anatomical preservation of *C. elliptica* was later identified by Guo et al. (1992) who also assigned a permineralized rachis from the same Formation to *Compsopteris* sp., considering both to represent marattialean fronds. While *Stewartiopteris* and *Stipitopteris* each possess only 1–2 tangentially elongate vascular bundles, both *C. elliptica* and *C.* sp. possess more bundles, at least 4–5 in *C. elliptica* and many more in *C.* sp. (Guo et al. 1992), as does the present frond (Table 1). However, the rachises of *C. elliptica* and *C*. sp. are obviously ventral-dorsal in cross section and vascular bundles are arranged in regular rings which are depressed at the ventral side (or upper side) and consists of short vascular bundles, while at the dorsal side (or lower side) the rings consists of much longer vascular bundles (fig. 7*d*). Unlike *C. elliptica* and *C*. sp., rachises of the present frond are not ventral-dorsal in cross section and are not depressed at the ventral side and the vascular bundles of the present frond are all short or small throughout the frond (compare fig. 2*c* and fig. 3*b* with fig. 7*d*). Further differences include *C. elliptica* and *C*. sp. having large cells containing dark colored contents within the outer zone of cortex, and the thickness of the vascular bundle sheath is large and cells are arranged more tightly at the inner side than at the outer side where the thickness of vascular bundle sheath is small and cells are arranged loosely. In the present frond, large cells with dark colored contents within the outer zone of the cortex are absent, and the thickness of vascular bundle sheath is large and consists of thicker-walled cells at the outer side, but the thickness of the vascular bundle sheath is small and consists of thinner-walled cells at the inner side (compare fig. 7*e* with fig. 7*f*). The present species is thus also distinct from *Compsopteris* (Table 1).

In certain living marattialean plants, the petiole or main rachis also possess abundant short or small vascular bundles that are arranged in concentric rings, for example, up to 4–5 rings in *Angiopteris* (Stidd 1971; Ogura 1972b). In this regard, the anatomy of the present frond is more comparable to living crown group members of the Marattiales within the family Marattiaceae rather than to extinct members of the Marrattialean stem group placed in the family Psaroniaceae (Rothwell et al. 2018). Obvious differences between the present frond and extant marattialean plants occur in terms of their morphology (Table 1). The *Rothwellopteris* frond is tri-pinnate with small pinnules that are basally truncate, while fronds in Marattiaceae are mostly mono-pinnate or palmate (only

Angiopteris is bi-pinnate) and pinnules are large and their base is contracted and petioled (Stidd 1971).

As well as being distinct from Paleozoic members of the Marattiales within the Psaroniaceae based on its anatomy, the new frond is also distinct from living Marattiales based on its frond morphology, leading us to establish the genus *Rothwellopteris* gen. nov. based on its unique combination of characters. We consider *Rothwellopteris pecopteroides* to represent the permineralized equivalent of the compression/impression fossil species *Pecopteris marginatus*. New anatomical information allows moving *P. marginata* from the genus *Pecopteris* that is restricted to compression/impression specimens, and recognizes its distinct anatomy that has features of both the Marattiaceae and Psaroniaceae.

We consider that *Rothwellopteris* represents an intermediate between the Paleozoic Psaroniaceae and the stratigraphically younger Marrattiaceae (see Rothwell et al. 2018), constituting a stem group member of the lineage leading to Marratiaceae. *Rothwellopteris* demonstrates that by the end of the Permian period the ancestral Psaroniaceae had started to diversify and that the stem to crown group transition within Marattiales was already underway.

It is known that up to now most of marattialean fronds with *Pecopteris*-type pinnules were produced by the *Psaronius* Cotta plant, a marattialean tree fern that was common during the Pennsylvanian and Permian periods and possessed petioles and rachises assignable to either *Stewartiopteris* or *Stipitopteris* (e.g., Stidd 1971). The discovery of the present frond enriches the diversity of the petiole and rachis of marattialean plants with *Pecopteris*-type pinnules. *Rothwellopteris* in demonstrating the first anatomical preservation of a pecopterid marattialean frond from China shows that at least some Cathaysian species were distinct from those from Euramerica, and presumably were not produced by the *Psaronius* plant. However, to date no whole-plant species of Cathaysian marattialean fern has been reconstructed from stems or fertile foliage to further assess the organization of the Cathaysian members of the Psaroniaceae with pectoperid pinnules.

The co-existence of *Rothwellopteris pecopteroides*, *Compsopteris elliptica* and *Compsopteris* sp. in the Lopingian (upper Permian) flora of eastern Yunnan and western Guizhou shows that the type of petiole and rachis which possess multiple vascular bundles typical of living marattialean plants had diverged from the ancestral marattialean Psaroniaceae by this stratigraphic interval of time. Although the rachis of *R. pecopteroides*, *C. elliptica* and *C*. sp. each possess multiple vascular bundles, they are each different from each other. The vascular bundles of *R. pecopteroides* are smaller and more numerous, being closer to living marattialean plants than the other species, but in terms of its morphology, it has tri-pinnate compound leaves and its pinnules are small and have a truncated base, characters that may be interpreted as more primitive. Although also different from the frond of *Rothwellopteris*, *C. elliptica* and *C*. sp. also appear more primitive than living marattialean plants in the anatomy of the rachis because it can have long vascular bundles. However, in other regards, the morphology of *C. elliptica* and *C*. sp. are closer to living marattialean plants than *Rothwellopteris* because it has a mono-pinnate compound leaf, its pinnules are large and their base is contracted and petioled. What is now required to further assess the systematic and phylogenetic relationships of *Rothwellopteris* is the development of a whole-plant concept, associating fertile organs and trunks to the same plant species. Such research is currently in progress.

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Literature Cited

Bateman RM, J Hilton 2009 Palaeobotanical systematics for the phylogenetic age: applying organ-species, form-species and phylogenetic species concepts in a framework of reconstructed fossil and extant whole-plants. Taxon 58:1254–1280.

DiMichele WA, TL Phillips 1977 Monocyclic *Psaronius* from the Lower Pennsylvanian of the Illinois Basin. Can J Bot 55:2514–2524.

D'Rozario A, B Sun, J Galtier, SJ Wang, WY Guo, YF Yao, CS Li 2011 Studies on the Late Permian permineralized tree fern *Psaronius housuoensis* sp. nov. from Yunnan Province, southwest China. Rev Palaeobot Palynol 163:247–263.

Galtier J, TL Phillips 1999 The acetate peel technique. Pages 67–71 *in* TP Jones, NP Rowe, (Eds) Fossil plants and spores: modern techniques. London: Special Publication of the Geological Society.

Guo YT, BL Tian DX Han 1990 The anatomical study of *Plagiozamites oblongifolius* and the systematic position of *Plagiozamites*. Acta Bot Sin 30:799–804 (in Chinese with English abstract).

Guo YT, BL Tian, DX Han 1992 Anatomical study of the rachis of *Compsopteris elliptic*a and the systematic position of *Compsopteris*. Acta Bot Sin 34:630–633 (in Chinese).

He J, SJ Wang, J Hilton, L Shao 2013. *Xuanweioxylon* gen. nov.: novel Permian coniferophyte stems and branches with scalariform bordered pitting on secondary tracheids. Rev Palaeobot Palynol 197:152–165.

He XY, SJ Wang, J Hilton, YL Zhou 2006 A new species of the marattialean fern *Scolecopteris* (Zenker) Millay from the uppermost Permian of Guizhou Province, southwestern China. Bot J Linn Soc 151:279–288**.**

He XY, SJ Wang, J Hilton, BL Tian, YL Zhou 2008 Anatomically preserved marattialean plants from the Upper Permian of southwestern China: the trunk of *Psaronius panxianensis* sp. nov. Pl Syst Evol 272:155–180.

He XY, JH Jin, SJ Wang, XP Fu, N Li, Y Li 2010 Anatomically preserved marattialean plants from the Upper Permian of southwestern China: the trunk of *Psaronius laowujiensis* sp. nov. Inter J Plant Sci 171:662–678.

He XY, SJ Wang, J Hilton, J Galtier, YJ Li, L Shao 2013 A unique trunk of Psaroniaceae (Marattiales)—*Psaronius xuii* sp. nov., and subdivision of the genus *Psaronius* Cotta. Rev Palaeobot Palynol 197:1–14.

Herbst R 1986 Studies on Psaroniaceae. I. The family Psaroniaceae (Marattiales) and a redescription of *Tietea singularis* Solms-Laubach; from the Permian of Brazil. Actas IV Congr Argentino Paleontol y Bioestratigrafia 1:163–171.

Herbst R 1987 Studies on Psaroniaceae. II. *Tuvichapteris solmsi* nov. gen. et sp. from the Permian of Paraguay and Uruguay. Actas IV Congr Latinoamer Paleont, Santa Cruz de la Sierra, Anais Bolivia 1: 267–282.

Herbst R 1992 Studies on Psaroniaceae. III, *Tietea derbyi* n.sp., from the Permian of Brazil. Cour Forsch Senck 147:155–161.

Herbst R 1999 Studies on Psaroniaceae. IV. Two species of *Psaronius* from Araguaina, State of Tocantins, Brazil. Facena 15:9–17.

Hill CR, RH Wagner, AA El-Khayal 1985 *Qasimia* gen. nov., an early *Marattia*-like fern from the Permian of Saudi Arabia. Scripta Geol 79:1–50.

Hilton J, SJ Wang, J Galtier, I Glasspool, L Stevens 2004 A Late Permian permineralized plant assemblage in volcaniclastic tuff from the Xuanwei Formation, Guizhou Province, China, and its palaeofloristic significance. Geol Mag 141:661–674.

Li HQ, BL Tian, EL Taylor, TN Taylor 1994 Foliage anatomy of *Gigantonoclea guizhouensis* Gu et Zhi (Gigantopteridales) from the Upper Permian of Guizhou Province, China. Amer J Bot 81: 678–689.

Li HQ, DW Taylor 1998 *Aculeovinea yunguiensis* gen. et sp. nov., a new taxon of gigantopterid axis from the Upper Permian of Guizhou province, China. Inter J Plant Sci 159:1023–1033.

Li HQ, DW Taylor 1999 Vessel-bearing stems of *Vasovinea tianii* gen. et sp. nov. (Gigantopteridales) from the Upper Permian of Guizhou province, China. Amer J Bot 86:1563-1575.

Li XX (Ed.) 1995 Fossil floras of China through the geological ages. Guangdong Sci Tech Press, pp 695, pls 144. Guangzhou, China. (English edition)

Liu ZH, J Hilton, CS Li 2000 Review of the origin, evolution and phylogeny of Marattiales. Chinese Bull Bot 17:39–52.

Mickle JE 1984 Taxonomy of specimens of the Pennsylvanian-age marattialean fern *Psaronius* from Ohio and Illinois. Ill State Mus Sci Pap 19:1–64.

Millay MA 1997 A review of permineralized Euramerican Carboniferous tree ferns. Rev Palaeobot Palynol 95:191–209.

Morgan J 1959 The morphology and anatomy of American species of the genus *Psaronius*. Ill. Biol Monogr 27:1–108.

Morgan J, T Delevoryas 1952a An anatomical study of *Stipitopteris*. Amer J Bot 39:474–478.

Morgan J, T Delevoryas 1952b *Stewartiopteris singularis*: a new psaroniaceous fern rachis. Am J Bot 39:479–484.

Neregato R, C D'Apolito, I Glasspool, SJ Wang, L Feng, P Windslow, J Lu, L Shao, J Hilton 2016 Palynological constraints on the provenance and stratigraphic range of a Lopingian (late Permian) inter-extinction floral lagerstätte from the Xuanwei Formation, Guizhou Province, China. Int J Coal Geol 62:139–150.

Ogura Y 1972a *Psaronius* from Linggiu, Johore, Malaya. Geol Paleontol SE Asia 10:117–124.

Ogura Y 1972b Comparative anatomy of vegetative organs of the pteridophytes (2nd edition). Gebruder borntraeger, Berlin.

Rothwell GW 1999 Fossils and ferns in the resolution of land plant phylogeny. Bot Rev 65:188–218.

Rothwell GW, MA Millay, RA Stockey 2018 Resolving the overall pattern of marattialean fern phylogeny. Amer J Bot 105:1304–1314.

Seyfullah LJ, J Hilton, MM Liang, SJ Wang 2010 Resolving the systematic and phylogenetic position of isolated ovules: a case study from a new genus from the Upper Permian of China. Bot J Linn Soc 164:84–108.

Seyfullah LJ, J Hilton 2011 Callistophytalean pteridosperms from the Permian floras of China. Palaeontology 54:287–302.

Stewart WN, GW Rothwell 1993 Paleobotany and the evolution of plants (2nd edition) Cambridge Univ Press, New York. 521 p.

Stidd BM 1971 Morphology and anatomy of the frond of *Psaronius*. Palaeontogr Abt B 134:87–123.

Sze HC 1942 Über ein neues Exemplar von *Psaronius* aus dem Omeishan Basalt in Weining (Kueichou) mit besonderer Berücksichtigung des Alters des Basaltes in Südwest China. Bull Geol Soc China 22:105–131.

Sze HC 1947 On the structures of *Psaronius sinensis* from the Omeishan Basalt Series in southwestern China. Geol J Amer 55:160–167.

Taylor TN, Taylor EL, Krings M 2009 The biology and evolution of fossil plants (2nd edition). Elsevier, Amsterdam, Netherlands.

Tian BL, YJ Li, YT Guo 1992 On the study of *Psaronius wangii* (sp. nov.) from Xuanwei Formation of Pan Xian, Guizhou. pp 74–78, 3 pls *in* ZL Li (Ed.), Collected works for memory of the 100th anniversary of the Birthday of Dr. Wang Zhu-Quan. Coal Industry Press, Beijing, (in Chinese).

Tian BL, Zhang LW 1980. Fossil atlas of Wangjiazhai mine region in Suicheng, Guizhou. Coal Ind Press, Beijing (In Chinese).

Wang SJ, J Hilton, MM Liang, L Stevens 2006 Permineralized seed plants from the Upper Permian of southern China: a new species of *Cardiocarpus*. Int J Plant Sci 167:1247–1257.

Wang SJ, RM Bateman, ART Spencer, J Wang, LY Shao, J Hilton 2017 Anatomically preserved “strobili” and leaves from the Permian of China (Dorsalistachyaceae fam. nov.) broaden knowledge of Noeggerathiales and constrain their possible taxonomic affinities. Amer J Bot 104: 127–149.

Xiang N, SM Ma, BL Tian, SJ Wang, MS Zhang 2008 New species of the isolated psaroniaceous rachis from the Early Permian in China. J Integra Plant Biol 50:119–127.

Yang ZC 1986 A new species of the genus *Psaronius* Cotta from Yunnan Province, China. Geol

China 21:30 (in Chinese).

Yang GX, F Chen 1979 Palaeobotany. Pages 104–139 *in* HF Hou et al. (Eds). The coal-bearing strata and fossils of Late Permian from Guangdong. Geol Publ House, Beijing (in Chinese).

Zhao XH, ZG Mo, SZ Zhang, ZQ Yao 1980 Late Permian flora from western Guizhou and eastern Yunnan. pp 70–122 *in* Nanjing Inst Geol Palaeont, Acad Sinica (Eds.), Late Permian coal bearing strata and biota from western Guizhou and eastern Yunnan. Science Press, Beijing, pp 1-277 (in Chinese).

Figure captions

Fig. 1. *a*, Main rachis, partly exposed on the surface of the rock. Scale bar = 2 cm. *b*–c, Cross section of the two ends of the main rachis with a second order of rachis (SOR) diverging from the upper side of the main rachis (MR) in *c*. Scale bars = 0.5 cm. Slides YH-0220, YH-0221. *d*, Detail of the cross section of the main rachis showing the outer cortex that consists of an outer continuous parenchyma zone (OZ) and an inner discontinuous sclerenchyma zone (IZ). Scale bar = 100 µm. Slide YH-0220. *e*, Cross section of a primary pinna rachis. Arrow indicates an ultimate pinna with two pinnules diverging from the upper side of the second order of rachis. The area in the box is enlarged in fig. 3*b*. Scale bar = 0.5 cm. Slide YH-0224. *f,* Cross section of a primary pinna rachis (SOR) to which ultimate pinnae (UP) are attached. Scale bar = 0.5 cm. Slide YH-0229

Fig. 2. *a*, Primary pinna rachis in tangentially longitudinal section (at 1) and the cross sections of two ends (at 2 and 3). Scale bar = 5 mm. Slide YH-0230. *b*, Part of a cross section through a primary

pinna rachis (SOR) and longitudinal section of an ultimate rachis (UR). Scale bar = 5 mm. Slide YH-0226. *c*, Cross section through a primary pinna rachis. Note outermost ring of vascular bundles (arrows) and vascular bundles in the mid region (VB). Scale bar = 2 mm. Slide YH-0229. *d–f,* Cross section through cortex of primary pinna rachis; epidermis (E), outer zone (OZ) and inner zone (IZ) of the outer cortex, inner cortex (IC). Scale bars for *d*, *f* = 200 µm, *e* = 100µm. Slide YH-0230.

Fig. 3. *a*, Longitudinal section of the cortex of a primary pinna rachis; epidermis (E), outer zone (OZ) and inner zone (IZ) of outer cortex. Scale bar = 200 µm. Slides YH-0230. *b*, Enlargement of boxed area from fig. 1*e*, showing many small vascular bundles in the mid region of the primary pinna rachis. Scale bar = 1 mm. Slide YH-0224. *c*–e, Individual vascular bundles of the mid region of rachis. Scale bars = 100 µm. Slide YH-0221.

Fig. 4. *a*, Cross section of a primary pinna rachis showing cortex and vascular bundles of the outermost ring. Scale bar = 1 mm. Slide YH-0224. *b*, Oblique section of vascular bundle of a primary pinna rachis showing scalariform thickenings on the tracheid walls. Scale bar = 100 µm. Slide YH-0226. *c*. Paradermal section through an ultimate pinna, showing the slightly falcate pinnules. Scale bar = 2 mm. Slide YH-0222. *d*, Cross section through an ultimate pinna rachis and an attached pinnule. Scale bar = 1 mm. Slide YH-0228. *e*, Enlargement of the ultimate pinna rachis from fig 4*d*. Scale bar = 0.5 mm. *f*, Oblique cross section of the pinnule lamina showing palisade tissue and vein sheath. Scale bar = 100 µm. Slide YH-0230.

Fig. 5. Paradermal section through adjacent pinnules, showing pinnule outline and venation (drawn

from fig. 6*b*).

Fig. 6. *a*, Paradermal section through an ultimate pinna, showing tongue-shaped pinnules. Scale bar = 5 mm. Slide YH-0223. *b*, Paradermal section through two slightly falcate pinnules, showing the venation. Scale bar = 1 mm. Slide YH-0222. *c*, Paradermal section through the lower lobe of a pinnule, showing lateral veins. Scale bar = 0.5 mm. Slide YH-0225. *d*, Cross section though a pinnule, showing midrib (Mr) and thickened lateral margin (arrow). Scale bar = 0.5 mm. Slide YH-0230.

Fig. 7. *a,* Cross section through a pinnule showing thick midrib, U-shaped vascular bundle, thickened lateral margin (arrows) and possible hydathodes. Scale bar = 0.5 mm. Slide YH-0230. *b–c*, Part of a cross section through a pinnule, showing palisade tissue, spongy tissue and veins. Scale bars = 0.5 mm. Slides YH-0230, YH-0228. *d*, Cross section of *Compsopteris elliptica* rachis showing tangentially elongate vascular bundles near the dorsal surface. Scale bar = 1 mm. Slide WP2-0193. *e*, Enlargement of specimen in Fig.7*d*, showing large cells with brown content (arrows) in the outer zone of the outer cortex (OZ); note the thick inner vascular bundle sheath (1), thin outer vascular bundle sheath (2), xylem strand (XS). Scale bar = 200 μm. *f*, Cross section of a second order rachis of *Rothwellopteris pecopteroides*, with no large cells with brown content in outer zone (OZ) of the outer cortex. The inner vascular bundle sheath (1) is thin and the outer vascular bundle sheath (2) is slightly thicker. Scale bar = 200 μm. Slide YH-0229.

	Rothwellopteris	***Compsopteris elliptica***	***Compsopteris* sp.**	***Stewartiopteris***	***Stipitopteris***	***Angiopteris***
Number of vascular bundles	Numerous	Numerous	Numerous	One	Two	Numerous
Frond morphology	Tri-pinnate	Mono-pinnate	Unknown	At least tri-pinnate	At least tri-pinnate	Bi-pinnate
Pinnule	Broad attachment	*Narrow attachment*	Unknown	Broad attachment	Broad attachment	*Narrow attachment*

Table 1. Comparison of key generic features of *Rothwellopteris* gen. nov. with other Marattiales.