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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 pecopteroid 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
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. sahni 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, Gigantoclea 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. 1a) and is robust, with a diameter of up to 3 cm (Fig. 1b); 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
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-taxon 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. 1a), 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. 1b–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. 1c, 1e; Fig. 2c, 2d) and anatomically they are nearly the same, comprising a narrow cortex with many small vascular bundles or meristeles within it (Fig. 1b, 1c, 1e; Fig. 2c). Epidermal cells are usually poorly preserved. Their cell walls seem to be thick and are usually preserved as a thin black homogenous layer (Fig. 1d; Fig. 2d, 2e). 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. 1d, Fig. 2d, 2e). 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. 1b–d; Fig. 2d). Sclerenchyma strands are radially elongate with radial widths of 600–700 μm and a smaller tangential width (Fig. 1d). 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. 2b, 2c) 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. 2f). 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. 1e; Fig. 2e).
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. 1e; fig. 2c). Inside
this ring, vascular bundles are arranged somewhat irregularly and not in obvious rings (fig. 3b),
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. 2c; Fig. 3b–d; fig. 4a), but some are
nearly round in cross section (fig. 3e). 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. 3c, 3d). 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. 3c, 3d with fig. 4a). Phloem and
ground tissues are poorly preserved, but many tannin cells with dark or light colored contents can be
seen (fig. 3c, 3e; fig. 4b). Tracheid walls possess scalariform thickenings (fig. 4b).

The cortex of the ultimate pinna rachis is 300–400 μm thick and lacks sclerenchymatous strands
(fig. 4e). 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. 5b; fig. 6a) or somewhat falcate (fig. 4c; fig. 5a), 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. 6b, 6c).

The midrib of the pinnule appears sturdy and is raised on the lower surface (fig. 6d; fig. 7a). 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. 6d; fig. 7a). Mesophyll is differentiated into a palisade and spongy tissue (Fig. 7b, 7c). 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. *Rothwelliopteris 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 *Rothwelliopteris* 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 *Rothwelliopteris* 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. 7d). 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. 2c and fig. 3b with fig. 7d).

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. 7e with fig. 7f).

The present species is thus also distinct from *Compsosperis* (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 Marattialean 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 *Rothwelliopteris* 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.

Acknowledgements
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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 = 100 μm. 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. 1e, 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 4d. 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. 6b).

**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 through 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.7d, 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.
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**Table 1.** Comparison of key generic features of *Rothwellopteris* gen. nov. with other Marattiales.