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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

23 microscopy.

24

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

32

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

42

43 *Keywords:* Eusporangiate fern, Marattiales, Psaroniaceae, Marattiaceae, evolution, volcaniclastic tuff,
44 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

67 vegetative and fertile fronds as well as pinnae preserved as impression-compression fossils (Tian and
68 Zhang 1980; Zhao et al. 1980; Liu et al. 2000, 2001) and permineralizations (Guo et al. 1992; Hilton
69 et al. 2004; He et al. 2006). In addition, numerous permineralized marattialean trunks with thick root
70 mantles have also been found in this region (e.g., Sze 1942, 1947; Yang 1986; Tian et al. 1992; Li et
71 al. 1995; He et al. 2008, 2010, 2013; D’Rozario et al. 2012). Here from the latest Permian of
72 Guizhou Province in SW China we report a new kind of marattialean frond preserved with both
73 morphology and anatomy that has three orders of rachises and attached vegetative pinnules. Based
74 on its preserved morphological characters, the frond is considered to be the anatomically-preserved
75 equivalent of *Pecopteris marginata* Li et al. 1974 which was erected based on
76 impression/compression fossils (Li et al. in Gu et Zhi 1974).

77

78 **Material and methods**

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

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

89 *sino-coreanum* Yabe, *Paracalamites stenocostatus* Li et al., *Annularia pingloensis* (Sze), *A. shirakii*
 90 Kawasaki, *Lobatannularia cathaysiana* Yao, *L. lingulata* (Halle). *L. multifolia* Kon'no et Asama,
 91 *Schizoneura brevifolia* Yao, *Sch. manchuriensis* Kon'no, and the noeggerathialeans *Plagiozamites*
 92 *oblongifolius* Halle, *Discinities* cf. *orientalis* Li et al. Fern and seed fern foliage includes *Chansitheca*
 93 *kidstonii* Halle, *Sphenopteris tenuis* Schenk, *Pecopteris echinata* Li et al., *P. fuyuanensis* Zhang, *P.*
 94 (*Asterotheca*) *guizhouensis* Zhang, *P. lingulata* Zhang, *P. marginata* Li et al., *P. sahnii* Hsu, *Rajahia*
 95 *guizhouensis* Zhang, *R. mirabilis* (Li et al.) Zhang, *R. rigida* (Yabe et Oishi) Zhang, *Fascipteris*
 96 (*Ptychocarpus*) *densata* Li et al., *F. hallei* (Kawasaki), *F. stena* Li et al., *Cladophlebis ozakii* Yabe et
 97 Oishi, *Cl. permica* Lee et Wang, *Cl. parapermica* Zhang, *Neuropteridium coreanicum* Koiwai, *N.*
 98 *guizhouense* Zhang, *Compsopteris imparis* Li et al., *C. contracta* Li et al., *C. punctinervis* Mo,
 99 *Gigantonoclea guizhouensis* Li et al., *G. hallei* (Asama), *G. largrelii* (Halle), *G. plumosa* Mo,
 100 *Gigantopteris dictyophylloides* Li et al., *Taeniopteris* ? *rarinervis* Zhao, *T. crassinervis* Mo,
 101 *Abrotopteris guizhouensis* (Li et al.) Mo, *Prionophyllopteris spiniformis* Mo. Cycads present in the
 102 flora are represented by *Pterophyllum eratum* Li et al. and Ginkgoales by *Rhipidopsis pani* Chow, *R.*
 103 cf. *ginkgoides* Schmalh. and *R. lobulata* Mo, while conifers include *Ullmannia* cf. *bronnii* Goeppert
 104 and *U.* sp. Permineralized fossils includes the sphenopsid *Calamostachys* sp. (Hilton et al., 2004), the
 105 marattialean ferns *Compsopteris elliptica* Chang ex Yang et Chen (Guo et al., 1992), *Eoangiopteris*
 106 sp. (Hilton et al., 2004), *Psaronius laowujiensis* He et al. (He et al., 2010), *P. panxianensis* He et al.
 107 (He et al., 2008), *P. wangii* Tian et al. (Tian et al., 1992), *P. xuii* He et al. (He et al., 2013). Filicalean
 108 ferns are rare and limited to *Anachoropteris* sp. (Hilton et al., 2004). Noeggerathialeans include
 109 pseudo-strobili of *Dorsalistachya quadrisegmentorum* Wang et Spencer (Wang et al., 2017) and
 110 associated foliage of *Plagiozamites oblongifolius* Halle (Guo et al., 1990). Seed ferns are represented

111 by *Callistophyton boysetii* (Renault) Rothwell (Seyfullah and Hilton, 2011) and ovules of
112 *Cardiocarpus huopuensis* Wang et al. (Wang et al., 2006), *Muricosperma guizhouensis* Seyfullah et
113 al. (Seyfullah et al., 2010). Anatomically preserved gigantopterids include *Gigantonoclea*
114 *guizhouensis* Li et al. (Li et al., 1994), *Aculeovinea yunguiensis* Li et Taylor (Li and Taylor, 1998),
115 *Vasovinea tianii* Li et Taylor (Li and Taylor, 1999), while conifers are represented by the wood
116 *Xuanweioxylon scalariforme* He et al. (He et al., 2013).

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

131 The specimen was prepared using the cellulose acetate peel method (Galtier and Phillips 1999),
132 as outlined by He et al. (2006, 2008, 2010, 2013) and Wang et al. (2017). The rock bearing the

133 specimen, peels and slides are deposited at the Institute of Deep Time Terrestrial Ecology, Yunnan
134 University.

135

136 **Systematic Paleobotany**

137 *Order – Marattiales Engler and Prantl, 1902*

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

139

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

143

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

146

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

150

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

152

153 *Specific diagnosis.* Vegetative frond. A tri-pinnate compound leaf. Rachis robust, main rachis up to 3
154 cm in diameter and primary pinna rachis up to 1 cm in diameter. Ultimate pinna rachis bears

155 subopposite pinnules, pinnules tongue-shaped or somewhat falcate, with length:width ratio less than
156 3:1. Lateral margin of pinnules thickened, pinnule base slightly expanding; pinnule midrib thick,
157 lateral veins forking twice and nearly perpendicular to the pinnules lateral margin. Pinnule margins
158 slightly downturned. Palisade tissue well developed, vascular bundle sheaths marked by ridges on
159 abaxial pinnule surface. Surface of the first and second order of rachis undulate. Cell walls of the
160 epidermis thick. Cortex divided into inner and outer cortex. Outer cortex further divided into inner
161 and outer zones, outer zone consisting of continuous parenchyma with uniform cell size; inner zone
162 being continuous or discontinuous sclerenchyma bands. Central part of rachis consisting of ground
163 tissue and many small vascular bundles or meristeles, arranged in poly-cycles. Abundant tannin cells
164 in ground tissue. Vascular bundles in the outmost cycle possessing a well-developed sheath with its
165 thickness greater on the pinna abaxial side than that on the adaxial side. The ultimate pinna rachis
166 possesses two cycles of vascular bundles, each consisting of four vascular bundles.

167

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

170

171 *Remarks.* *Rothwellopteris pecopteris* gen. et sp. nov. is interpreted as being the anatomically
172 preserved equivalent of the compression/impression species *Pecopteris marginata* Li et al. (1974)
173 that occurs in the Xuanwei Formation in this region. While its pinnule morphology is assignable to *P.*
174 *marginata*, the species is placed in a new genus because its main rachis and primary pinna rachis
175 have the distinctive anatomy of a marattialean fern, and deserve a more complete typification as a
176 new genus. *Rothwellopteris* fronds combine anatomical features of Marattiaceae (concentric

arrangement of meristemes) 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

199 The surface of the main rachis and primary pinna rachis is typically undulated (Fig. 1*c*, 1*e*; Fig.
200 2*c*, 2*d*) and anatomically they are nearly the same, comprising a narrow cortex with many small
201 vascular bundles or meristeles within it (Fig. 1*b*, 1*c*, 1*e*; Fig. 2*c*). Epidermal cells are usually poorly
202 preserved. Their cell walls seem to be thick and are usually preserved as a thin black homogenous
203 layer (Fig. 1*d*; Fig. 2*d*, 2*e*). The cortex comprises an outer and inner part, with the outer cortex
204 further divided into two zones of which the outermost layer consists of continuous parenchyma (Fig.
205 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
206 10 cells or 400–500 μm wide. Parenchymatous cells are nearly isodiametric in cross section with
207 diameters mainly from 40–60 μm . In the primary pinna rachis, the outer zone of the outer cortex is a
208 little narrower, 3–6 cells or 200–300 μm wide, and cells are smaller with diameters usually less than
209 50 μm . The inner zone of the outer cortex is a continuous or discontinuous sclerenchyma band. In the
210 main rachis the sclerenchyma band is mostly discontinuous and is divided into many alternating
211 sclerenchyma and parenchyma strands (Fig. 1*b–d*; Fig. 2*d*). Sclerenchyma strands are radially
212 elongate with radial widths of 600–700 μm and a smaller tangential width (Fig. 1*d*). Parenchyma
213 strands are connected with the outer zone of the outer cortex. In some parenchyma strands, the cells
214 are obviously radially elongate. Parenchyma cells of the cortex are all approximately isodiametric in
215 cross section, with diameters of 20–40 μm and thick cell walls. Secretory cavities are scattered in the
216 parenchyma and sclerenchyma, and some of them contain dark brown contents. In the primary pinna
217 rachis, the sclerenchyma band tends to be continuous (Fig. 2*b*, 2*c*) with a smaller radial width,
218 usually 300–500 μm . The inner cortex is usually poorly preserved and can be found only in some
219 places (Fig. 2*f*). Cells of the inner cortex are similar in size to those of the outer cortex but have
220 thinner cell walls. Cells of the outer and inner cortex appear elongate in longitudinal section (Fig.

221 3a).

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

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

243 are only 20–30 μm in diameter. The vascular bundle sheath is one cell thick and consists of cells
244 slightly smaller than the metaxylem tracheids. These cells possess thicker walls and are dark colored.

245
246 *Ultimate pinnae and pinnule*

247 The ultimate pinnae are all incompletely preserved with the longest one measuring 5 cm in
248 length. The width of the ultimate pinna is up to 16–18 mm. Pinnules are tongue-shaped (fig. 5*b*; fig.
249 6*a*) or somewhat falcate (fig. 4*c*; fig. 5*a*), alternate and oriented perpendicular to the ultimate pinna
250 rachis. Pinnules are up to 9 mm long and up to 3 mm wide in their middle, with blunt tips and
251 truncate and slightly expanded bases. The midrib is up to 0.3 mm wide and decurrent on the pinna.
252 The first lateral vein of the lower side at the base diverges from the decurrent part of the pinnule.
253 Lateral veins diverge from the midrib at an acute (or lower) angle and divide once, then extend to the
254 margin and divide once again. Ultimate lateral vein branches are perpendicular to the margin of the
255 pinnule (fig. 5; fig. 6*b*, 6*c*).

256 The midrib of the pinnule appears sturdy and is raised on the lower surface (fig. 6*d*; fig. 7*a*).
257 Lamina thickness varies depending on the pinnules. In some pinnules, the lamina is 350–400 μm
258 thick, while in other pinnules the lamina is only 250–300 μm thick. The lateral margin of the pinnule
259 is thicker and bends or is even involute toward the lower surface (fig. 6*d*; fig. 7*a*). Mesophyll is
260 differentiated into a palisade and spongy tissue (Fig. 7*b*, 7*c*). Palisade tissue is well developed and its
261 cells have a length reaching half of the thickness of the lamina with many of them possessing black
262 or dark brown contents. The vascular bundle of the lateral veins is located within the spongy tissue
263 and has a diameter of 110–130 μm . Vascular bundle sheaths consists of 1–2 layers of nearly round
264 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 Tadelaceae 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

287 leaf of the specimen described here. *P. marginata* has a broad rachis and its primary pinna rachis is
288 up to 6–7 mm wide. The margin of the pinnule has a narrow thickened band, and the base of the
289 pinnule is slightly expanded. In *P. marginata* the pinnule midrib is thick, lateral veins fork twice and
290 are perpendicular to the lateral margin of the pinnule. *Rothwellopteris pecopteroides* also has a thick
291 rachis (rachis is up to 30 mm wide and the second order of rachis is up to 10 mm wide) and the size
292 of ultimate pinna and pinnules of the present frond are similar to those of the type specimen of *P.*
293 *marginata*. The base of the pinnules of *Rothwellopteris* are also slightly expanded and the lateral
294 margin bends or is involute toward the lower surface, and there is a thickened band at the margin of
295 the pinnule. In the new genus, the midrib is also prominent and lateral veins mostly forked twice and
296 are perpendicular to the lateral margin of the pinnule. Differences between the present frond and the
297 type specimen of *P. marginata* is that the new frond is tri-pinnately compound leaf, while the type
298 specimen of *P. marginata* is a bi-pinnately compound leaf, but this may be the result of
299 fragmentation and incomplete preservation in the type specimen of *P. marginata*. Furthermore, the
300 present frond and the type specimen of *P. marginata* were both collected from the same locality and
301 same stratigraphic interval making it additionally probable that they belong to the same species, with
302 the *Rothwellopteris* specimen being a permineralized example of *P. marginata*. The discovery of the
303 new frond specimen establishes that *P. marginata* is a tri-pinnately compound leaf, and not a
304 bi-pinnately compound leaf.

306 *Comparison with permineralized fossil and living Marattiales*

307 The discovery of the present frond is important as it presents an opportunity to study the
308 anatomy of a Cathaysian species of *Pecopteris* for the first time. The rachis of the tri-pinnate frond

309 from the Xuanwei Formation has numerous anatomical features that allow it to be placed within the
310 Marattiales including (1) the presence of abundant vascular bundles that are roughly arranged in
311 concentric rings, (2) individual vascular bundles being short, band-like and bend internally, (3)
312 protoxylem distributed along the innermost side of the vascular bundle, and (4) abundant tannin cells
313 dispersed throughout the tissues (Ogura 1972b).

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

323 *Compsopteris elliptica* was established by Yang and Chen (1979) for impression-compression
324 fossils of mono-pinnate compound marattialean leaves from the Longtan Formation in Guangdong
325 Province that they considered to most likely represent the frond of a seed fern. Anatomical
326 preservation of *C. elliptica* was later identified by Guo et al. (1992) who also assigned a
327 permineralized rachis from the same Formation to *Compsopteris* sp., considering both to represent
328 marattialean fronds. While *Stewartiopteris* and *Stipitopteris* each possess only 1–2 tangentially
329 elongate vascular bundles, both *C. elliptica* and *C. sp.* possess more bundles, at least 4–5 in *C.*
330 *elliptica* and many more in *C. sp.* (Guo et al. 1992), as does the present frond (Table 1). However, the

331 rachises of *C. elliptica* and *C. sp.* are obviously ventral-dorsal in cross section and vascular bundles
332 are arranged in regular rings which are depressed at the ventral side (or upper side) and consists of
333 short vascular bundles, while at the dorsal side (or lower side) the rings consists of much longer
334 vascular bundles (fig. 7d). Unlike *C. elliptica* and *C. sp.*, rachises of the present frond are not
335 ventral-dorsal in cross section and are not depressed at the ventral side and the vascular bundles of
336 the present frond are all short or small throughout the frond (compare fig. 2c and fig. 3b with fig. 7d).
337 Further differences include *C. elliptica* and *C. sp.* having large cells containing dark colored contents
338 within the outer zone of cortex, and the thickness of the vascular bundle sheath is large and cells are
339 arranged more tightly at the inner side than at the outer side where the thickness of vascular bundle
340 sheath is small and cells are arranged loosely. In the present frond, large cells with dark colored
341 contents within the outer zone of the cortex are absent, and the thickness of vascular bundle sheath is
342 large and consists of thicker-walled cells at the outer side, but the thickness of the vascular bundle
343 sheath is small and consists of thinner-walled cells at the inner side (compare fig. 7e with fig. 7f).
344 The present species is thus also distinct from *Compsopteris* (Table 1).

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

353 *Angiopteris* is bi-pinnate) and pinnules are large and their base is contracted and petioled (Stidd
354 1971).

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

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

368 It is known that up to now most of marattialean fronds with *Pecopteris*-type pinnules were
369 produced by the *Psaronius* Cotta plant, a marattialean tree fern that was common during the
370 Pennsylvanian and Permian periods and possessed petioles and rachises assignable to either
371 *Stewartiopteris* or *Stipitopteris* (e.g., Stidd 1971). The discovery of the present frond enriches the
372 diversity of the petiole and rachis of marattialean plants with *Pecopteris*-type pinnules.

373 *Rothwellopteris* in demonstrating the first anatomical preservation of a pecopterid marattialean frond
374 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 pectopterid pinnules.

The co-existence of *Rothwellopteris pectopteroides*, *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. pectopteroides*, *C. elliptica* and *C.* sp. each possess multiple vascular bundles, they are each different from each other. The vascular bundles of *R. pectopteroides* 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

- 401 Bateman RM, J Hilton 2009 Palaeobotanical systematics for the phylogenetic age: applying
402 organ-species, form-species and phylogenetic species concepts in a framework of reconstructed
403 fossil and extant whole-plants. *Taxon* 58:1254–1280.
- 404 DiMichele WA, TL Phillips 1977 Monocyclic *Psaronius* from the Lower Pennsylvanian of the
405 Illinois Basin. *Can J Bot* 55:2514–2524.
- 406 D’Rozario A, B Sun, J Galtier, SJ Wang, WY Guo, YF Yao, CS Li 2011 Studies on the Late Permian
407 permineralized tree fern *Psaronius housuoensis* sp. nov. from Yunnan Province, southwest China.
408 *Rev Palaeobot Palynol* 163:247–263.
- 409 Galtier J, TL Phillips 1999 The acetate peel technique. Pages 67–71 in TP Jones, NP Rowe, (Eds)
410 Fossil plants and spores: modern techniques. London: Special Publication of the Geological
411 Society.
- 412 Guo YT, BL Tian DX Han 1990 The anatomical study of *Plagiozamites oblongifolius* and the
413 systematic position of *Plagiozamites*. *Acta Bot Sin* 30:799–804 (in Chinese with English
414 abstract).
- 415 Guo YT, BL Tian, DX Han 1992 Anatomical study of the rachis of *Compsopteris elliptica* and the
416 systematic position of *Compsopteris*. *Acta Bot Sin* 34:630–633 (in Chinese).
- 417 He J, SJ Wang, J Hilton, L Shao 2013. *Xuanweioxylon* gen. nov.: novel Permian coniferophyte stems

418 and branches with scalariform bordered pitting on secondary tracheids. Rev Palaeobot
 419 Palynol 197:152–165.

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

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

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

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

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

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

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

- 440 Herbst R 1999 Studies on Psaroniaceae. IV. Two species of *Psaronius* from Araguaina, State of
441 Tocantins, Brazil. *Facena* 15:9–17.
- 442 Hill CR, RH Wagner, AA El-Khayal 1985 *Qasimia* gen. nov., an early *Marattia*-like fern from the
443 Permian of Saudi Arabia. *Scripta Geol* 79:1–50.
- 444 Hilton J, SJ Wang, J Galtier, I Glasspool, L Stevens 2004 A Late Permian permineralized plant
445 assemblage in volcanoclastic tuff from the Xuanwei Formation, Guizhou Province, China, and its
446 palaeofloristic significance. *Geol Mag* 141:661–674.
- 447 Li HQ, BL Tian, EL Taylor, TN Taylor 1994 Foliage anatomy of *Gigantonoclea guizhouensis* Gu et
448 Zhi (Gigantopteridales) from the Upper Permian of Guizhou Province, China. *Amer J Bot* 81:
449 678–689.
- 450 Li HQ, DW Taylor 1998 *Aculeovinea yunguiensis* gen. et sp. nov., a new taxon of gigantopterid axis
451 from the Upper Permian of Guizhou province, China. *Inter J Plant Sci* 159:1023–1033.
- 452 Li HQ, DW Taylor 1999 Vessel-bearing stems of *Vasovinea tianii* gen. et sp. nov. (Gigantopteridales)
453 from the Upper Permian of Guizhou province, China. *Amer J Bot* 86:1563–1575.
- 454 Li XX (Ed.) 1995 Fossil floras of China through the geological ages. Guangdong Sci Tech Press, pp
455 695, pls 144. Guangzhou, China. (English edition)
- 456 Liu ZH, J Hilton, CS Li 2000 Review of the origin, evolution and phylogeny of Marattiales. *Chinese*
457 *Bull Bot* 17:39–52.
- 458 Mickle JE 1984 Taxonomy of specimens of the Pennsylvanian-age marattialean fern *Psaronius* from
459 Ohio and Illinois. *Ill State Mus Sci Pap* 19:1–64.
- 460 Millay MA 1997 A review of permineralized Euramerican Carboniferous tree ferns. *Rev Palaeobot*
461 *Palynol* 95:191–209.

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

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

465 Morgan J, T Delevoryas 1952b *Stewartiopteris singularis*: a new psaroniaceous fern rachis. Am J Bot
 466 39:479–484.

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

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

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

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

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

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

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

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

- 484 Stidd BM 1971 Morphology and anatomy of the frond of *Psaronius*. *Palaeontogr Abt B* 134:87–123.
- 485 Sze HC 1942 Über ein neues Exemplar von *Psaronius* aus dem Omeishan Basalt in Weining
486 (Kueichou) mit besonderer Berücksichtigung des Alters des Basaltes in Südwest China. *Bull*
487 *Geol Soc China* 22:105–131.
- 488 Sze HC 1947 On the structures of *Psaronius sinensis* from the Omeishan Basalt Series in
489 southwestern China. *Geol J Amer* 55:160–167.
- 490 Taylor TN, Taylor EL, Krings M 2009 The biology and evolution of fossil plants (2nd edition).
491 Elsevier, Amsterdam, Netherlands.
- 492 Tian BL, YJ Li, YT Guo 1992 On the study of *Psaronius wangii* (sp. nov.) from Xuanwei Formation
493 of Pan Xian, Guizhou. pp 74–78, 3 pls in ZL Li (Ed.), *Collected works for memory of the 100th*
494 *anniversary of the Birthday of Dr. Wang Zhu-Quan*. Coal Industry Press, Beijing, (in Chinese).
- 495 Tian BL, Zhang LW 1980. Fossil atlas of Wangjiazhai mine region in Suicheng, Guizhou. Coal Ind
496 Press, Beijing (In Chinese).
- 497 Wang SJ, J Hilton, MM Liang, L Stevens 2006 Permineralized seed plants from the Upper Permian
498 of southern China: a new species of *Cardiocarpus*. *Int J Plant Sci* 167:1247–1257.
- 499 Wang SJ, RM Bateman, ART Spencer, J Wang, LY Shao, J Hilton 2017 Anatomically preserved
500 “strobili” and leaves from the Permian of China (Dorsalistachyaceae fam. nov.) broaden
501 knowledge of Noeggerathiales and constrain their possible taxonomic affinities. *Amer J Bot* 104:
502 127–149.
- 503 Xiang N, SM Ma, BL Tian, SJ Wang, MS Zhang 2008 New species of the isolated psaroniaceous
504 rachis from the Early Permian in China. *J Integra Plant Biol* 50:119–127.
- 505 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 μ m. 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

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

533

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

539

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

548

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

550 from fig. 6b).

551

552 **Fig. 6.** *a*, Paradermal section through an ultimate pinna, showing tongue-shaped pinnules. Scale bar
553 = 5 mm. Slide YH-0223. *b*, Paradermal section through two slightly falcate pinnules, showing the
554 venation. Scale bar = 1 mm. Slide YH-0222. *c*, Paradermal section through the lower lobe of a
555 pinnule, showing lateral veins. Scale bar = 0.5 mm. Slide YH-0225. *d*, Cross section through a
556 pinnule, showing midrib (Mr) and thickened lateral margin (arrow). Scale bar = 0.5 mm. Slide
557 YH-0230.

558

559 **Fig. 7.** *a*, Cross section through a pinnule showing thick midrib, U-shaped vascular bundle,
560 thickened lateral margin (arrows) and possible hydathodes. Scale bar = 0.5 mm. Slide YH-0230. *b–c*,
561 Part of a cross section through a pinnule, showing palisade tissue, spongy tissue and veins. Scale bars
562 = 0.5 mm. Slides YH-0230, YH-0228. *d*, Cross section of *Compsopteris elliptica* rachis showing
563 tangentially elongate vascular bundles near the dorsal surface. Scale bar = 1 mm. Slide WP2-0193. *e*,
564 Enlargement of specimen in Fig. 7*d*, showing large cells with brown content (arrows) in the outer
565 zone of the outer cortex (OZ); note the thick inner vascular bundle sheath (1), thin outer vascular
566 bundle sheath (2), xylem strand (XS). Scale bar = 200 µm. *f*, Cross section of a second order rachis
567 of *Rothwellopteris pecopteroides*, with no large cells with brown content in outer zone (OZ) of the
568 outer cortex. The inner vascular bundle sheath (1) is thin and the outer vascular bundle sheath (2) is
569 slightly thicker. Scale bar = 200 µm. Slide YH-0229.

570

571

572

	<i>Rothwellopteris</i>	<i>Compsopteris elliptica</i>	<i>Compsopteris</i> sp.	<i>Stewartiopteris</i>	<i>Stipitopteris</i>	<i>Angiopteris</i>
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	<i>Narrow attachment</i>	Unknown	Broad attachment	Broad attachment	<i>Narrow attachment</i>

573

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

575

576