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

4
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21 ABSTRACT

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

37

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

39

40 **1. Introduction**

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

43 preserved as impression/compressions (Tian and Zhang 1980; Zhao et al. 1980; Liu et al. 2000,
44 2001) and permineralizations (Sze 1942, 1947; Yang 1986; Tian et al. 1992; Tian and Wang, 1995;
45 Hilton et al. 2004; He et al. 2006, 2008, 2010, 2013; D’Rozario et al. 2011). Rarely, specimens
46 preserve both morphology and anatomy with these including the frond leaves *Compsopteris elliptica*,
47 *Compsopteris* sp. (Guo et al., 1992) and *Rothwellopteris pecopteroides* (He et al., 2019). The
48 combination of morphological and anatomical information in these species reveals they have a
49 mosaic of characters shared with members of the Paleozoic family Psaroniaceae and the
50 stratigraphically younger family Marattiaceae. He et al. (2019) interpreted *Rothwellopteris* to be a
51 member of the evolutionary stem-group lineage leading to the Marattiaceae. However, the available
52 fossil materials of *C. elliptica* and *R. pecopteroides* are not especially well-preserved and put limits
53 on the comprehensive characterization of the species. *C. elliptica* is represented by two fragmented,
54 monopinnate compound leaves in which only one or two incomplete pinnules are preserved, and
55 anatomical features of the pinnules are presently unknown (Guo et al., 1992). *Compsopteris* sp. is
56 less well-known and based on a simple description of one illustrated peel that appears to be distinct
57 from the closely related species *C. elliptica* (Guo et al., 1992). *Rothwellopteris pecopteroides* is
58 based on a large tripinnate leaf embedded within the rock matrix, and its pinnule morphology
59 (including shape, size and venation pattern) is revealed by cut sections parallel to the surface of the
60 pinnule. Its rachises are deformed in varying degrees making the organization of the vascular bundles
61 enigmatic, and the ground tissue is poorly preserved (He et al., 2019). In all cases other parts of the
62 parent plants are unknown preventing a more detailed understanding of their evolutionary and
63 ecological significance.

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

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

71

72 **2. Materials and methods**

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

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

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

90

91 **3. Geological information**

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

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

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

113 Stratigraphically, the Xuanwei Formation extends from the Wujiapingian to Changshingian
114 stages of the Permian (Zhao et al., 1980; Shao et al., 1998, Wang et al., 2011). The tuff from
115 Sanjiaoshu has not been dated by biostratigraphic or radiometric methods. It is lithologically similar
116 to the tuff from the Xuanwei Formation at the nearby Huopu mine (Wang et al. 2011; Neregato et al.,
117 2016) that was dated biostratigraphically to the Wujiapingian stage of the Lopingian using
118 palynomorphs (Neregato et al., 2016). While the Sanjiaoshu tuff was also probably deposited during
119 the Wujiapingian, we prefer to consider it to be of Wuchiapingian to Changshingian age based on the
120 age range of the Xuanwei Formation (Shao et al., 1998; Wang et al., 2011). Radiometric dating of the
121 fossil plant bearing tuffs from this part of south China are now needed to make more precise age
122 determinations for their fossil plants.

123

124 **4. Systematic Paleobotany**

125 *Order:* MARATTIALES Engler and Prantl, 1902

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

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

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

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

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

142 *Holotype*: YNUPB1105

143 *Paratype*: YNUPB1106

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

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

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

149 *Stratigraphic horizon*: Xuanwei Formation

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

152

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

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

169 Penultimate pinna rachises are round in cross section but are sometimes transversely elliptical
170 due to compression from the vertical pressure of strata loading. Two cross sections of the penultimate
171 pinna rachis were prepared from specimen YNUPB1105 of which one is 6 mm wide and about 4.2
172 mm high (Plate III, 1) and the other is 6.5 mm wide and only 3.3 mm high (Plate III, 2). The
173 penultimate pinna rachis of specimen YNUPB1106 is round in cross section and slightly larger, up to
174 8.5 mm in diameter (Plate IV, 1 and 2; Plate V, 1). The surface of the penultimate rachis is smooth
175 and lacks wrinkles and trichomes. In cross sections, rachis tissue consists of epidermis, sub-

176 epidermal cortex, ground tissue and the polycyclic vascular system. In YNUPB1106, the epidermis
177 consists of a single layer of small, nearly round cells with diameters of about 15 μm . The cortex is
178 approx. 300 μm thick and divided into outer and inner parts (Plate V, 2). The outer cortex is slightly
179 thicker than the inner cortex and consists of isodiametric parenchyma cells with diameters from 30–
180 40 μm . The inner cortex consists of sclerenchyma cells with diameters of 15–30 μm . Ground tissue
181 consists of parenchyma cells and secretory ducts. Parenchyma cells are isodiametric with diameters
182 of 36–60 μm . In specimen YNUPB1105, the cortex is approx. 200 μm thick and its inner cortex
183 differs from specimen YNUPB1106 in lacking a uniform zone of sclerenchyma cells and having
184 sclerenchyma intermingling with parenchyma cells. Parenchyma cells of the ground tissue are
185 isodiametric, elongated or polygonal (Plate V, 2 and 3). Secretory ducts in the two specimens are
186 numerous and dispersed in the ground tissue, and consist of 6–8 slightly tangentially elongated
187 parenchyma cells surrounding a central cavity with the diameter of 70–120 μm . Cavities are empty
188 or filled with yellow or brown contents (Plate V, 3; Plate VI, 1).

189 Viewed in cross sections the polycyclic vascular system of the penultimate pinna rachis consists
190 of numerous vascular bundles of different lengths. The smaller diameter YNUPB1105 rachis has 40–
191 60 bundles arranged in five cycles with a high proportion of laterally elongate bundles (Fig. 1A;
192 Plate III, 1 and 2). In the larger diameter YNUPB1106 rachis, there are up to 110 bundles arranged in
193 six cycles with a higher proportion of short bundles (Fig. 1B; Plate IV, 1 and 2; Plate V, 1). In
194 general, both specimens have long bundles located on the abaxial side and arranged in one radial
195 row, while shorter bundles are located on the adaxial side and are arranged in two radial rows. The
196 smallest bundles are mostly located at the center and lateral sides of the rachis (Fig. 1; Plate III, 1
197 and 2; Plate IV, 1 and 2; Plate V, 1).

198 Individual vascular bundles comprise a xylem strand and sheath. Phloem is probably located
199 between the xylem strand and the sheath but is poorly preserved and represented by a gap between
200 these tissues. The xylem strand is band-like with its ends more or less centripetally arced and is
201 narrow with its radial thickness mostly of 2–3 tracheids. The bundle sheath has a radial thickness of
202 2–3 cells with thicker cell walls on the outer side than on the inner side (Plate V, 3; Plate VI, 1).

203 Viewed in longitudinal sections, cells of the outer cortex are rectangular or polygonal and 57–
204 140 µm long. Cells of the inner cortex are fusiform and up to 550 µm long. Parenchyma cells of the
205 ground tissue are also rectangular or polygonal and up to 200 µm long. Cells of the bundle sheath are
206 also longitudinally elongated, but their shape is not clear because of their thick cell walls. Tracheids
207 possess scalariform thickenings on their lateral walls (Plate VI, 2; Plate VII, 1).

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

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

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

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

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

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

254 The morphology of the present specimens is most similar to *Pecopteris andersonii* Halle (1927)
255 and *Pecopteris heteropinna* Li et al. (1974). Pinnules of *Pecopteris andersonii* are falcate and have a
256 length:width ratio of 2–2.5:1. Pinnules are arranged tightly and have a decurrent midrib that tapers
257 toward the tip. The first lateral vein of the lower side diverges at the base from the decurrent part of
258 the midrib and immediately forks and then forks again. *P. andersonii* differs in having ultimate
259 pinnae that are lanceolate and attached to the ventral side of the rachis. The pinnule bases are
260 decurrent and the margins of a pair of basal pinnules on the ultimate pinna have incisions (Li et al.,
261 1974). *P. heteropinna* is similar to *R. sanjiaoshuensis* by having ultimate pinnae that are linear and
262 more than 12 cm long, with falcate pinnules, a thick midrib, and lateral veins that fork once or twice.
263 *P. heteropinna* differs by having pinnules of different lengths and by their attachment to the ventral

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

266

267 **5. Discussion**

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

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

286 vascular bundles surrounded by a sheath of sclerenchyma cells. In *Compsopteris*, cells of the outer
287 side of the bundle sheath have thinner walls than those of the inner side, while in *Rothwellopteris*,
288 cells of inner side of the bundle sheath have thinner walls than those of the outer side (He et al.,
289 2019). A vascular bundle sheath is absent from extant marattialean and the late Carboniferous and
290 early Permian marattialean frond rachises *Stewartiopteris* and *Stipitopteris* from the Euramerican and
291 Cathaysian floras (Stidd, 1971; He et al., 2019; Wang et al., 2021). In marattialean stems from the
292 upper Permian of southwestern China, cauline bundles and the vascular bundles of leaf traces and
293 petiolar bases possess a sheath. In most species, such as *Psaronius panxianensis* He et al. (2008), *P.*
294 *laowujiensis* He et al. (2010), *P. housuoensis* (D’Rozario et al., 2011) and *P. wangii* Tian et al.
295 (1992), the sheath consists of thin-walled parenchyma cells, which is different from the bundle
296 sheath of *Compsopteris* and *Rothwellopteris* which consists of thick-walled, sclerenchyma cells.
297 Only *Psaronius xuii* He et al. (2013) has cauline bundles and vascular bundles of its leaf traces and
298 petiolar base that possess a sheath comprised of thick-walled sclerenchyma cells. However, the thick-
299 walled cells of the bundle sheath of *P. xuii* are isodiametric in longitudinal section and unlike those
300 of *Compsopteris* and *Rothwellopteris* that are longitudinally elongated.

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

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

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

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

339 Esau (1977) considered features indicative of xeromorphy to include thick cuticles, coriaceous
340 pinnules, inrolled margins, well-developed palisade mesophyll, hypodermis, sunken stomata
341 organized in grooves, and the presence of papillae and hairs. Arens (1999) evaluated the ecological
342 implications of sun exposure on frond anatomy in the tree fern *Cyathea caracasana* (Dicksoniaceae)
343 and concluded that compared to shade leaves, sun leaves are thicker, have thicker palisade
344 mesophyll, longer palisade cells, tighter mesophyll cell packing, and have thicker cuticles and
345 epidermis. In *Rothwellopteris pecopteroides* pinnules are coriaceous and rigid with thick laminae
346 (250–400 μm), have more-or-less inrolled margins, well-developed palisade mesophyll and a
347 hypodermis. These features suggest that *R. pecopteroides* was adapted for xeromorphy and/or was a
348 sun leaf. The rachis of *R. pecopteroides* is usually covered by a thin, black, homogenous layer that
349 He et al. (2019) considered to be a poorly preserved epidermis. However, we now consider that this
350 feature more likely represents an imperfectly preserved thick cuticle. In contrast, no cuticle was
351 found covering the epidermis of the rachis in *Rothwellopteris sanjiaoshuensis*. In this species

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

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

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

381

382 **6. Concluding remarks**

383 To more fully understand the transition from the Psaroniaceae stem- to Marattiaceae crown-group
384 within Marattiales (Rothwell et al., 2018, He et al., 2019), it remains essential to reconstruct
385 additional whole plant fossil species that lie outside the circumscription of the *Psaronius blicklei*
386 Group of He et al. (2013). The most comprehensive analysis of fossil Marattiales (Rothwell et al.,
387 2018) lacked representatives of the *Psaronius panxianensis* Group of He et al. (2013) including
388 *Rothwellopteris* that was established subsequently (He et al., 2019). Although a distinct possibility, it
389 remains uncertain if *Rothwellopteris* and *Compsopteris* from the late Permian of China represent the
390 fronds of plants with trunks conforming to the characterization of the *Psaronius panxianensis* Group;
391 if so, these plants would likely justify the establishment of a new family of advanced Paleozoic
392 Marattiales transitional between the Psaroniaceae and Marattiaceae. Similarly, other organs of the
393 advanced Paleozoic marattialean trunk genera *Tietea* and *Tuvichapteris* from the late Permian of
394 South America are unknown; these plants may also belong to a distinct family that lies between the
395 Psaroniaceae and Marattiaceae. As presently characterized these late Permian plants present

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

407

408 **Declaration of Competing Interest**

409 None.

410

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418

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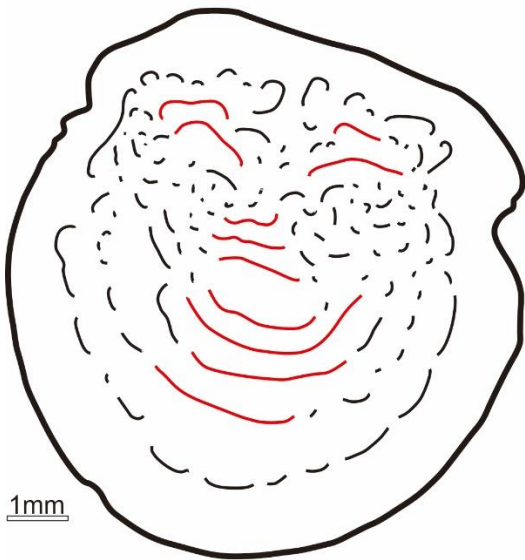
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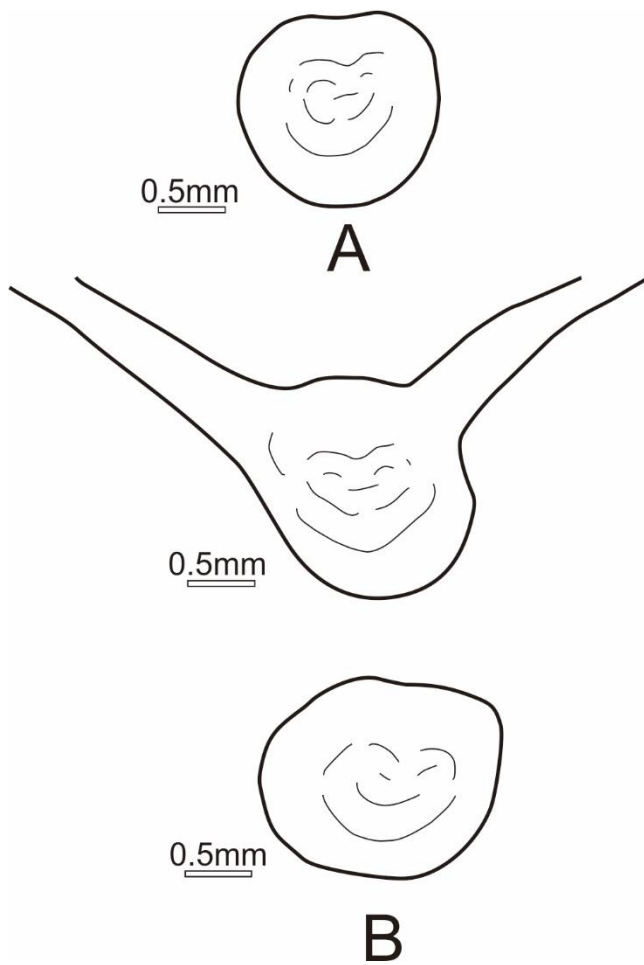
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A



B



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546 **Fig. 2.** Line drawings of the cross sections of ultimate pinna rachis of *Rothwellopteris pecopteroides*

547 (A) and *R. sanjiaoshuensis* sp. nov. (B) showing the tricyclic vascular system. A is drawn from Fig.

548 4e of He et al. (2019) and B from Plate VII, 3 and 4.

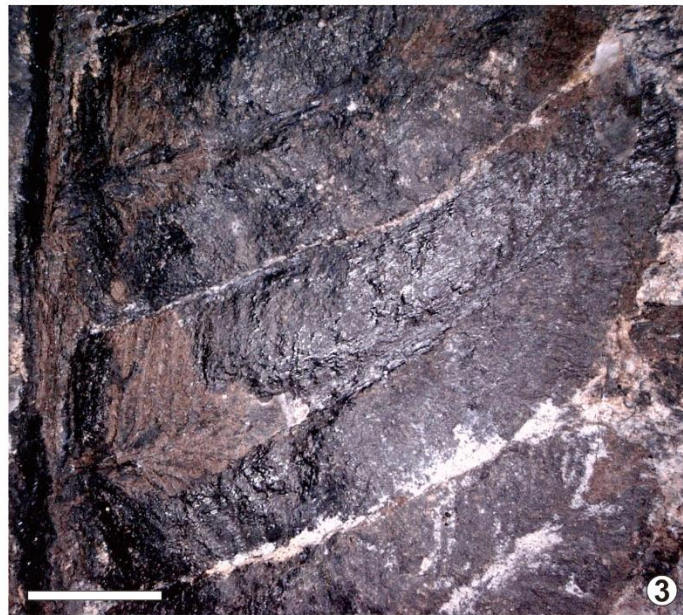
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551 **Plate I.** *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou, China.

552 (1–3). Morphology of specimen YNUPB1105 (holotype). (1). Gross morphology. Arrow indicates

553 the penultimate pinna rachis. Scale bar = 2 cm. (2). Two ultimate pinnae. Scale bar = 1 cm. (3).

554 Pinnules, showing the venation. Scale bar = 0.2 cm.

555



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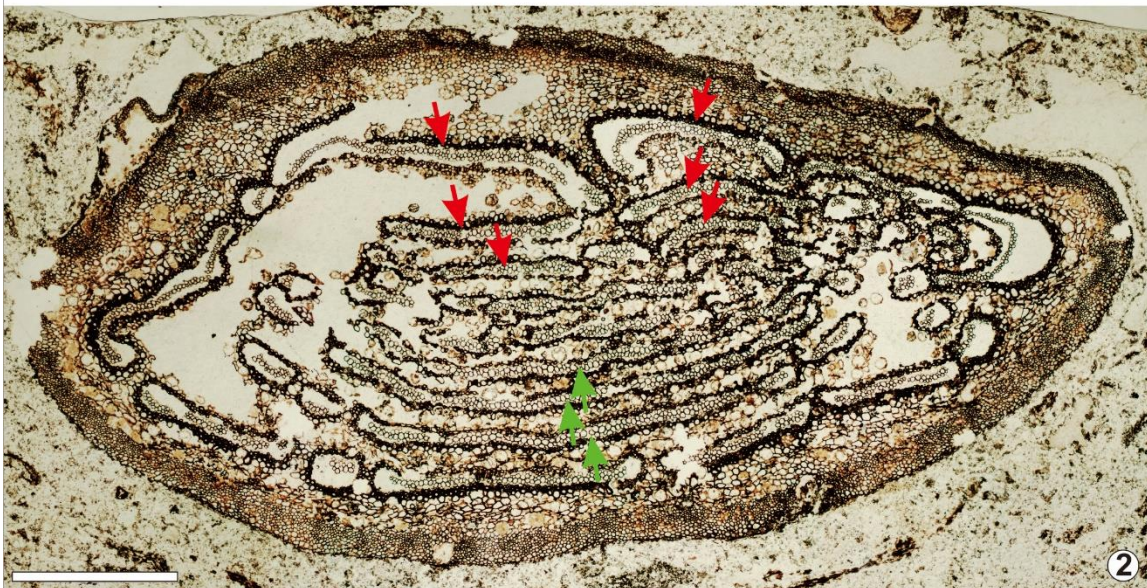
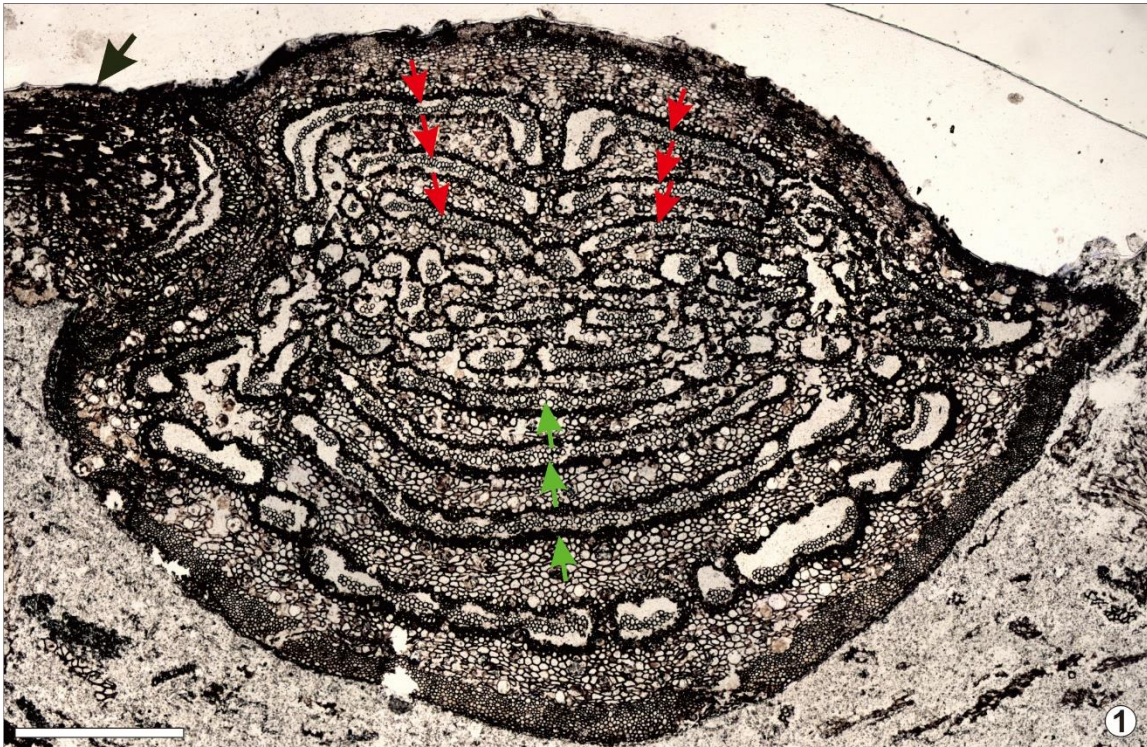
557 **Plate II.** *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou,

558 China. (1–3). Morphology of specimen YNUPB1106 (paratype). (1). Gross morphology. Arrows

559 indicate the penultimate pinna rachises. Scale bar = 2 cm. (2). Two ultimate pinnae. Scale bar = 1

560 cm. (3). Part of an ultimate pinna, showing the venation of pinnules. Scale bar = 0.5 cm.

561



562

563 **Plate III.** *Rothwellopteris sanjiaoshuensis* sp. nov. from the upper Permian in western Guizhou,

564 China. (1–2). General view of cross sections of the penultimate pinna rachis of specimen

565 YNUPB1105 showing the polycyclic vascular system. Red arrows indicate shorter bundles arranged

566 in two radial rows at ventral side of the rachis; green arrows indicate longer bundles arranged in one

567 radial row at the dorsal side of the rachis; black arrow indicates a departing ultimate pinna rachis.

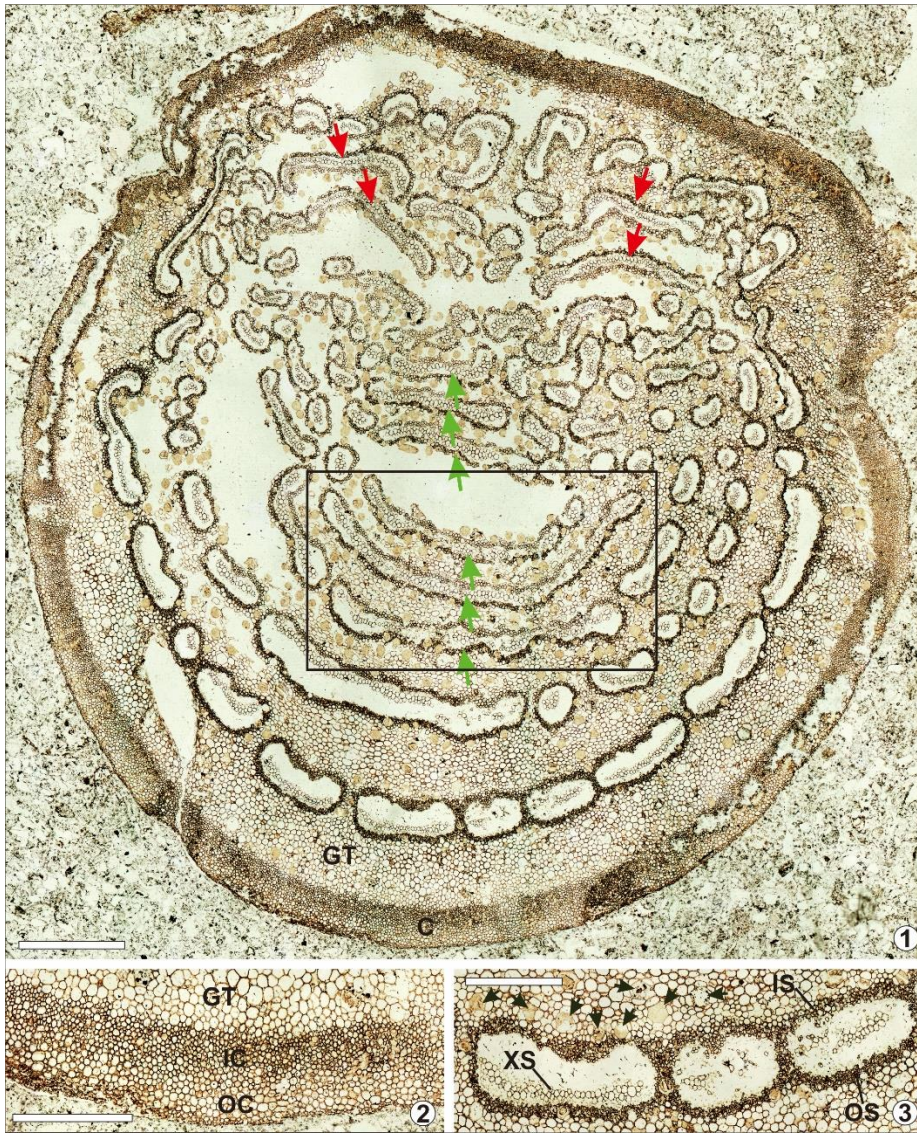
568 Slides: YH-0738 and YH-0730; Scale bars = 1 mm.



569

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

575



576

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

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



586

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

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

596



597

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

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