



HAL
open science

An advanced species of the fern *Botryopteris Renault* from the Permian of southwestern China

Xiao-Yuan He, Shi-Jun Wang, Jason Hilton, Jean Galtier, Hong-Guan Jiang

► **To cite this version:**

Xiao-Yuan He, Shi-Jun Wang, Jason Hilton, Jean Galtier, Hong-Guan Jiang. An advanced species of the fern *Botryopteris Renault* from the Permian of southwestern China. *Review of Palaeobotany and Palynology*, 2020, 273, pp.104136. 10.1016/j.revpalbo.2019.104136 . hal-02431756

HAL Id: hal-02431756

<https://hal.umontpellier.fr/hal-02431756v1>

Submitted on 13 Oct 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

An anatomically advanced species of the fern *Botryopteris* Renault from the Permian of southwestern China

He, Xiao-Yuan; Wang, Shi-Jun; Hilton, Jason; Galtier, Jean; Jiang, Hong-Guan

DOI:

[10.1016/j.revpalbo.2019.104136](https://doi.org/10.1016/j.revpalbo.2019.104136)

License:

Creative Commons: Attribution-NonCommercial-NoDerivs (CC BY-NC-ND)

Document Version

Peer reviewed version

Citation for published version (Harvard):

He, X-Y, Wang, S-J, Hilton, J, Galtier, J & Jiang, H-G 2020, 'An anatomically advanced species of the fern *Botryopteris* Renault from the Permian of southwestern China', *Review of Palaeobotany and Palynology*, vol. 273, 104136, pp. 1-13. <https://doi.org/10.1016/j.revpalbo.2019.104136>

[Link to publication on Research at Birmingham portal](#)

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

1 **An anatomically advanced species of the fern *Botryopteris* Renault from the**
2 **Permian of southwestern China**

3

4 Xiao-Yuan He^{a,*}, Shi-Jun Wang^b, Jason Hilton^c, Jean Galtier^d and Hong-Guan Jiang^e

5

6 *^a Institute of Deep Time Terrestrial Ecology, Yunnan University, Kunming 650091, China*

7 *^b State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese*

8 *Academy of Sciences, Beijing 100093, China*

9 *^c School of Geography, Earth and Environmental Sciences, University of Birmingham,*

10 *Edgbaston, Birmingham, B15 2TT, UK*

11 *^d CIRAD, AMAP TA 40/PS2, Boulevard de la Lironde, F-34398, Montpellier, France*

12 *^e Research Institute of Petroleum Exploration and Development, PetroChina Jilin Oilfield*

13 *Company, Songyuan 138000, China*

14

15 * Corresponding author. E-mail address hexiaoy@ynu.edu.cn (X.-Y. He)

16 **ABSTRACT**

17 We describe a new species of the Palaeozoic fern genus *Botryopteris* in volcanic tuffs from
18 the Lopingian (upper Permian) aged Junlian Formation in SW China's Sichuan Province. The
19 species has a large stem and stele compared to those of some other species of the genus.

20 Xylem strands of the leaf trace and rachis are “ ω ”-shaped in cross section and comprise two
21 long lateral arms and a single, shorter median arm. Parenchyma is distributed among the stem
22 metaxylem tracheids and is more common in the central region of the stele that comprises a
23 parenchymatized protostele. Several mesarch protoxylem strands, decurrent from leaf traces,
24 are visible in each cross section of the protostele. Root traces originate from the lateral side of
25 the leaf trace within the stem cortex. The stem surface is covered by thick, multiseriate,
26 multicellular trichomes. *Botryopteris multifolia* sp. nov. represents the stratigraphically
27 youngest known species of the genus and has a combination of derived evolutionary
28 characteristics including its large stem size, parenchymatized protostele, elaborate trichome
29 structure, roots originating from leaf traces, and the construction of xylem strand of the leaf
30 trace and rachis with distinctive pinna trace formation and emission. It is more similar in leaf
31 anatomy to the Gondwanan species *B. nollii* from the Permian of Brazil and less like late
32 Pennsylvanian botryopterids from Euramerica. Finally, we consider the evolutionary
33 implications of features shared between Permian members of the botryopterids and
34 catenalean-type plants including members of the Osmundales stem group family Guaireaceae
35 (*Shuichengella*, *Zhongmingella*, *Tiania*) and the enigmatic early ferns *Rastropteris* and
36 *Catenopteris*.

37

38 *Keywords:* Botryopteridaceae, fern, anatomy, Xuanwei Formation, Lopingian, volcanoclastic
39 tuff

40

41 **1. Introduction**

42 The Lopingian (upper Permian) sedimentary successions in southern Sichuan, western
43 Guizhou and eastern Yunnan provinces in SW China contain abundant plant fossils deposited
44 in terrestrial and paralic sedimentary facies (Wang *et al.*, 2011). These include frequent
45 occurrences of impression-compression fossil plant species (e.g., Zhao *et al.*, 1980; Zhu *et*
46 *al.*, 1984) as well as less common accounts of species preserved as permineralizations (e.g.
47 Hilton *et al.*, 2004; Neregato *et al.*, 2016; Wang *et al.*, 2017). Collectively these assemblages
48 represent the stratigraphically youngest Palaeozoic “coal measures” wetland plant
49 communities prior to their demise at the end of the Permian (Hilton and Cleal, 2007).

50 Although incompletely characterized and the focus of current research, the anatomically
51 preserved flora comprises sphenophytes (Wang *et al.*, 2003, 2006), Osmundales (Wang *et al.*,
52 2014a, b; He and Wang, 2019), Marattiales (He X *et al.*, 2013, 2019), Noeggerathiales (Wang
53 *et al.*, 2017), gigantopterids (Li and Taylor, 1998, 1999) and seed plants (Seyfullah *et al.*,
54 2010; He J. *et al.* 2013; Yang *et al.*, 2019) that represents an unique association not known
55 from other regions. These accounts suggest the regional flora to be advanced compared to
56 floras from other areas (Wang *et al.*, 2014b). They also provide insights into floristic change
57 resulting from climate and environmental perturbations in the run-up to the end Permian mass
58 extinction event (e.g., Neregato *et al.*, 2016).

59 The genus *Botryopteris* was established by Renault (1875) and an important anatomical

60 feature is its “ω”-shaped xylem strand in the rachis of some of the most advanced species
61 (Galtier and Phillips, 1996). As currently characterized, the genus contains 12 species ranging
62 stratigraphically from the Mississippian to Permian, with most known from the
63 Pennsylvanian, largely coinciding with coal-ball type of preservation in Euramerica (Galtier
64 and Phillips, 1996). To date, only four species of *Botryopteris* have been reported from the
65 Permian, namely *B. tridentata* (Felix) Scott from volcanoclastic sediments from the Cisuralian
66 of North China (Hilton et al., 2001), *B. nollii* Rößler et Galtier from the Permian of Brazil
67 (Rößler and Galtier, 2003), and *B. sp. 1* and *sp. 2* from Cisuralian (lower Permian) aged coal
68 balls in China (Wang et al., 2009). In the present paper, we report a new species of
69 *Botryopteris* preserved in volcanoclastic tuffs from the Lopingian of southwestern China that
70 has a complex organization of its foliar xylem only comparable to that known in some of the
71 most advanced species of this genus (Fig. 1). We also use this as an opportunity to evaluate
72 the other species of the genus from the Permian of China, to consider evolutionary trends
73 within the genus and their relationships with other Palaeozoic fern groups.

74

75 **2. Material and methods**

76 A single specimen preserved in volcanoclastic tuff was recovered from mine spoil at
77 Lubanshan coal mine (Figure 1), Junlian, Sichuan Province, southwestern China and
78 numbered 72012. The mine extracts coal from the Junlian Formation that contains abundant
79 fossil plants including impression-compression (Zhu *et al.*, 1984) and less commonly
80 permineralized specimens (Wang *et al.*, 2003). The fossil is permineralized by an early stage
81 diagenetic carbonate cement. Preparation was undertaken using the acetate peel method (Joy

82 *et al.*, 1956; Galtier and Phillips, 1999). The stem was initially revealed when the tuff was
83 slabbed on sections P/Bot, P/Top, L and S. Serial peeling was then undertaken on the
84 specimen in cross section on surfaces P/Bot 1 to P/Bot 3, P/Top 1 to P/top 6, L1 to L14.
85 Blocks were then re-orientated to provide longitudinal sections from S1 to S8. Peels and
86 slides were observed under light microscopy, and photography was undertaken using a Nikon
87 4500 digital camera mounted on a microscope and illuminated by transmitted light. Slides,
88 peels and the remaining parts of the rock sample are all deposited in the Museum of Institute
89 of Botany, Chinese Academy of Sciences, Beijing.

90

91 **3. Systematic Palaeobotany**

92 Family Botryopteridaceae Renault

93 Genus *Botryopteris* Renault, 1875

94 *Botryopteris multifolia* He, Wang, Hilton et Galtier sp. nov. (Fig. 3 and Plates I–V)

95 Holotype: 72012, and the Slides WP2-0633 to 0648.

96 Repository: Museum of Institute of Botany, Chinese Academy of Sciences, Beijing.

97 Type locality: Junlian, Sichuan Province.

98 Geological horizon: Junlian Formation.

99 Stratigraphic age: Lopingian (upper Permian).

100 Etymology: *Multi*-many; *folia*-leaf, specific epithet referring to the large number of leaf
101 traces visible in cross sections of the stem.

102 Specific diagnosis: Stem up to 17×11mm in diameter. Parenchymatized protosteles about

103 2 mm in diameter with small parenchyma cells dispersed among the tracheids, more densely

104 in the centre of the stele where tracheids are larger. Xylem maturation mainly mesarch to
105 exarch. Cauline metaxylem tracheids (up to 120 μm wide) exhibit multiseriate scalariform
106 thickening/pitting. Cortex consisting of parenchyma cells and divided into inner and outer
107 cortex. Outer cortex up to 1.6 mm thick and divided into two zones; cell walls of the outer
108 zone are thicker than those of the inner zone. Inner cortex, slightly broader than the outer
109 cortex, with small (less than 50 μm in diameter) thin-walled cells. Cortical cells are
110 longitudinally elongated. Surface of stem and adaxial side of petiolar bases with multiseriate,
111 multicellular trichomes (up to 350 μm thick and 1 mm long). Leaf traces diverge helically
112 ($3/8$ phyllotaxis) at very close intervals, with 6–8 leaf traces visible in each cross section of
113 the stem. Petiole size up to 4.75 mm tangentially and 3.5 mm radially. Leaf trace xylem at
114 first reniform with adaxial protoxylem tracheids and parenchyma, becoming “ ω ”-shaped
115 (about 1 mm broad tangentially) with sclerenchyma clusters of small cells (20–30 μm
116 diameter) filling the areas between the lateral and median arms. In the petiole, the xylem
117 strand is slender, up to 1.9 mm tangentially and 0.7 mm radially with much longer lateral
118 arms and short median arm. The median xylem arm initially has one protoxylem strand, then
119 it enlarges tangentially to become rectangular (0.4 mm tangentially and 0.2 mm radially) with
120 two lateral protoxylem strands. Xylem strand consists essentially of one or two rows of (80–
121 130 μm) broad metaxylem tracheids. Primary pinnae nearly borne oppositely on the rachis. In
122 pinna trace formation, protoxylem in one lateral xylary arm of the rachis divides and the tip
123 crooks out and passes off as a pinna trace. Protoxylem strands of the median arm are not
124 involved in the process of pinna trace emission. Root trace xylem originating from the lateral
125 side of leaf traces within the stem cortex.

126

127 **4. Description**

128

129 *4.1. Stem size and vertical changes*

130 A short length of ca. 17 mm of the stem is preserved; it is partially flattened due to
131 taphonomic compression (Plate I, A, B), but reveals good three-dimensional structure from
132 which its overall shape and size can be ascertained. Stem diameter increases slightly
133 acropetally (Plate I, A, B), being 13×5.4 mm at the base (measured in peel P/Bot 2) and 17
134 ×11 mm at the top (measured in the peel L9-1).

135

136 *4.2. Stele*

137 The stem has a parenchymatized protostele. At the base of the available portion of stem,
138 the stele is 1.5 mm in diameter (Plate I, B), while at the top it is ca. 2 mm in diameter (Plate I,
139 A). In cross sections of the stem, the stele is nearly round or lobed due to protruding incipient
140 to diverging leaf traces (Plate I, C). The concomitant increase of stelar and overall stem
141 diameter is suggestive of an epidogenetic development in this short section of stem.

142 Protoxylem in the stem occurs as a few strands, at the margin of the stele, in exarch to
143 commonly mesarch position (Plate I, C; Plate II, A; Plate III, A, B). Metaxylem tracheid size
144 in this stem increases centripetally from 20~50 to 70~90 (occasionally up to 120) µm. In
145 cross section, tracheids are nearly isodiametric and slightly elongated radially. In the outer
146 part of the stele, tracheids are arranged tightly but in the centre of the stele, they are arranged
147 loosely, and very small parenchyma cells (20 x 35 to 30 x 50 µm in diameter) are dispersed

148 among the tracheids (Plate I, C, D). Parenchyma cells between tracheids are oblate (Plate I,
149 D). According to the terminology of Schmid (1982), the stem would be called as a
150 parenchymatized protostele. Multiseriate scalariform thickenings/pittings occur on the
151 tracheid walls (Plate I, E).

152 The probable phloem position corresponds to a very poorly preserved, dark tissue of
153 flattened cells surrounding the stelar xylem (visible on Plate III, A, B). It is often not
154 preserved and is absent in the innermost cortex.

155

156 4.3. Cortex

157 The cortex is divided into two regions: an outer and inner cortex (OC and IC, Plate I, A,
158 B). The outer cortex is 1.1~1.6 mm thick, comprising large, tightly arranged cells with
159 diameters of 60~80 μm . It is divided into two zones (OC1, OC2, Plate II, B) with an inner
160 zone that is narrow or of variable thickness and having thin cell walls. In places, cells of the
161 inner layer of the outer cortex appear somewhat elongated tangentially. The outer zone of the
162 outer cortex is broad, and composed of cells that are mostly isodiametric with thick cell walls
163 (OC1, Plate II, B). The inner cortex is slightly broader than the outer cortex and is of variable
164 thickness due to taphonomic factors, but generally, it is partially decayed (e.g. Plate I, C)
165 from which cellular details are difficult to characterize. Cells of the inner cortex have thin
166 walls and are small, generally less than 50 μm in diameter, and are isodiametric or
167 tangentially elongated (IC, Plate II, B). Some cells possess dark colored content (Plate II, C).
168 In addition, some cells possess tylose-like structures (Plate II, C).

169 Cells of the cortex are longitudinally elongated. The length of cells in the outer cortex

170 can reach up to 350 μm or more. Cell endings are horizontal or tapering (Plate II, D, E). The
171 cells of the inner cortex are somewhat shorter, mostly less than 200 μm long (Plate II, F).

172

173 *4.4. Leaf traces*

174 Protoxylem strands appearing near the outer margin of the cauline stele are the first
175 indication of decurrent leaf traces; they are rarely exarch (Plate III, A) and commonly
176 mesarch. In an early stage of leaf trace initiation, metaxylem tracheids occur to the outside of
177 the protoxylem strand (Plate III, B) and they form an obvious bulge (Plate I, C; Plate II, A).
178 Progressive levels of the incipient leaf traces, including enlargement of the protoxylem with
179 tracheids and parenchyma mixed, are well illustrated in stages 3 and 4 of slide 12-1 (Plate II,
180 A) or 0 and 2 of slide 8-2 (Plate I, C).

181 Before separation, the bulging leaf trace (e.g. 2, Plate I, C) has a maximum tangential
182 width of 675 μm . Its single protoxylem strand, composed of small tracheids and associated
183 parenchyma cells, is round and rather large, with a diameter up to approximately 200 μm
184 (Plate I, C). At the level where the leaf trace separates from the cauline stele, it is nearly
185 reniform with its adaxial side slightly depressed showing very small tracheids and
186 parenchyma cells (5, 6, Plate II, A; Plate III, C). The xylem strand is 750 μm wide and 400
187 μm thick, its two lateral arms enroll and connect with the median arm. At more distal levels
188 the xylem strand of the leaf trace is tangentially extended, up to 0.85 mm wide, but the radial
189 thickness is approximately 270 μm . At this level the lateral arms of the xylem strand are
190 thinner and nearly connected with the median arm. The tip of the median arm flares laterally;
191 the areas surrounded by the lateral and median arms are filled with small parenchyma cells

192 (Plate III, D). Further away from the cauline stele, the leaf traces 3 and 4 (Plate I, C) show the
193 first evidence of a few sclerenchyma cells among the parenchyma. At more distal levels
194 (Plate III, E), the leaf trace is typically “ω”-shaped, exceeding 1 mm wide, and the two areas
195 between the lateral and median arms are filled with a mass of sclerenchyma cells replacing
196 the parenchyma (see also trace 5 in Plate I, C; 7–9 in Plate II A). The sclerenchyma cells are
197 typically 20~30 μm in diameter and have cell walls that are 5~6 μm thick and poorly
198 preserved (Plate III, E). At this stem level the median arm shows a single adaxial protoxylem
199 area. Still more distally, the tangential width of the leaf trace increases due to enlarging of
200 both the median and the lateral arms. As a result, the shape of the clusters of sclerenchyma
201 cells changes from nearly isodiametric to tangentially elongated (Plate III, F). It is also
202 notable that the median arm becomes rectangular with two protoxylem strands (arrows, Plate
203 III, F).

204 Leaf traces diverge helically and the stem shows many leaf traces in each cross section
205 (Plate I, A, B). The leaf traces are mainly distributed in the inner cortex where they number
206 5~7 (Plate I, B) while only 1~2 are present in the outer cortex. From the proximal level of
207 section L14-2 (Slide number 0634) to the distalmost level of L5-2 (Slide number 0644), there
208 are 6 new leaf traces (LT 5 to 0) that diverge from the cauline stele within a vertical distance
209 of ca. 1.2 mm; therefore the length of the internode of the stem is about 0.2 mm.

210 Comparison of the successive cross sections in ascending order allowed us to interpret
211 the phyllotaxis of this fern. On the more proximal section (on Plate II, A) there are two
212 bulging/incipient leaf traces (numbered 3 and 4) and the older leaf traces (5 to 9) within the
213 inner cortex. Higher up, on the section on Plate I, C, the leaf traces 7 to 9 are not visible

214 because they have already diverged within the outer cortex; however 4 to 6 are still present in
215 the inner cortex together with the new leaf trace 3 which separated from the stele; the
216 younger leaf traces (2, 1 and 0) should be bulging from the stele, but leaf trace 1 has been
217 certainly broken and displaced and thus appearing free. These two sections support a
218 phyllotactic spiral with leaf trace (0) as the youngest. This is confirmed in the distalmost
219 sections that are not illustrated here. This trace (0) is diverging between leaf traces 3 and 5, in
220 the position where leaf trace 8 has been diverging within the cortex (cf. Plate II, A); these
221 observations suggest a $3/8$ phyllotaxis.

222 Leaf traces pass through the inner cortex at a low angle of about 10° (Plate V, A).

223 However, in the outer cortex, the angle becomes higher. In the cross section of the stem, leaf
224 traces are in an obliquely longitudinal section and cell wall thickenings/pitting are exposed
225 (Plate V, B which corresponds to the departing leaf trace 8 also illustrated in Plate II, A).

226 When entering the petiole base, the angle of the leaf trace becomes low again. Thus, in the
227 cross section of the stem, the petiole trace is also in a cross section and tracheids are
228 isodiametric. Like in the stem, the walls of the large tracheids of the leaf trace possess
229 multiseriate (up to four seriate) thickenings/pitting.

230

231 *4.5. Foliar members (petiole, rachis and pinna)*

232 The free petioles or rachises (Ra, Plate I, A, B) are generally distorted and flattened. In
233 cross section, the petiole is elliptical 4.75 mm wide tangentially and 3.5 mm radially (Plate
234 III, G); the petiole xylem strand is 1.9 mm wide tangentially and 0.7 mm radially (Plate III,
235 F). The slender lateral arms of petiole trace have a long, thin and enrolled tip, consisting of

236 small tracheids. The median arm remains very short but its tangential width increases (to 0.4
237 mm wide); it is rectangular with one protoxylem strand at each adaxial tip. More distally, the
238 foliar xylem strand enlarges tangentially up to 2.2 mm (Plate III, G; Plate IV, A). The tip of
239 each lateral xylary arm arches out with a concomitant division of its protoxylem. This
240 crooked area of xylem then separates as a small C-shaped strand, quickly becoming
241 tridentate, which corresponds to a primary pinna trace (arrows, Plate III, H; Plate IV, B). In
242 fact, two lateral traces are detached nearly at the same level (about 0.3 cm above petiole
243 origin), thus the primary pinnae are sub-opposite on the rachis.

244 A reconstruction of portion of the foliar xylem of *B. multifolia* showing pinna traces
245 formation and departure (in adaxial view) is shown in Figure 3. There is no information on
246 the free primary pinnae.

247

248 4.6. *Trichomes*

249 Trichomes are distributed across the entire surface of the stem (Plate I, A; arrows in Plate
250 II, B). They are all multiseriate and multicellular but vary in size, shape and distribution. In
251 size and shape, some of them have broad bases and tapered tips, but some of them are
252 isodiametric; others are short and thin, while some others are long and thick, up to 350 μm
253 thick and nearly 1 mm long. Their distribution is uneven, with many trichomes occurring in
254 some places but few in others. Seen in cross section, individual trichomes consist of nearly
255 isodiametric cells with diameters of 20~50 μm (Plate V, C). In longitudinal section, trichome
256 cells are longitudinally elongated, rectangular, polygonal or fusiform, with variable lengths
257 up to 300 μm or more (Plate V, D).

258

259 *4.7. Adventitious roots*

260 Adventitious roots are not common. In each cross section of the stem there are only one
261 or two root traces. The root trace originates from the lateral side of the leaf trace xylem (Plate
262 V, E). Root trace production by the cauline stele has not been observed. Root traces have their
263 own cortex when they are about 250 μm away from the leaf trace from which they originate.
264 In the cauline cortex, root traces extend nearly horizontally or obliquely. In cross section,
265 roots are nearly round or elliptical, with diameters of approximately 400~500 μm . The stele
266 of the root trace is diarch with diameters of 170~250 μm . The largest metaxylem tracheids are
267 70~90 μm in diameter. The root cortex is poorly differentiated. Cell walls are thick and dark
268 in color (Plate V, F). Individual cells are longitudinally elongated. When root traces have
269 diverged from the stem, their size is nearly the same as those in stem cortex.

270

271 **5. Discussion**

272

273 *5.1. Comparisons with Botryopteris species with a “ ω ”-shaped foliar xylem strand*

274 *Botryopteris forensis*, the type species of the genus, is characterized by “ ω ”-shaped
275 xylem strands in cross sections of the leaf trace and petiole/rachis. Both this “elaborate foliar
276 xylem geometry” and the large size of rachis were interpreted as reflecting evolutionary
277 changes in one of the stratigraphically youngest species of the genus (Phillips, 1974; Galtier
278 and Phillips, 1996). This interpretation is supported by recent discoveries, in stratigraphically
279 younger Permian deposits, of *Botryopteris nollii* and the present species that also show

280 comparable “ω”-shaped foliar xylem, as illustrated in Figure 4 A–E.

281 To help with comparisons, we consider the key features of the present species as follows:

282 (1) the stem and stele are large, the stem having a diameter up to 17×11 mm and the stele up
283 to 2 mm; (2) the cauline xylem is a parenchymatized protostele with files of parenchyma cells
284 distributed among the metaxylem tracheids and, more particularly, in the central region; (3)
285 the stele is more or less circular, showing two to four peripheral protoxylem strands in exarch
286 to mainly mesarch maturation; (4) xylem strands of the leaf traces and the petiole/rachis are
287 “ω”-shaped in cross section, with two long lateral arms and a shorter median arm; (5) primary
288 pinna traces initiate and depart from the tip of the lateral arms; (6) the surface of the stem is
289 covered by thick, multiseriate, multicellular trichomes and, (7) root traces originate from the
290 lateral side of the departing leaf trace in the cortex.

291 *Botryopteris nollii* Rößler and Galtier (2003) from the Permian of Brazil shows several
292 features in common with the species from the Junlian Formation. Like the Chinese stem, *B.*
293 *nollii* is large, up to 11 mm in diameter, and has leaf traces that are obviously “ω”-shaped just
294 after they diverge from the cauline stele and with protoxylem restricted to the adaxial tips of
295 the thin foliar xylary arms. In both cases, more distally, the xylary arms enclose small adaxial
296 sclerenchyma strands. In addition, the surface of the stem of *B. nollii* is also covered by
297 multiseriate and multicellular trichomes. Another important similarity concerns the initiation
298 and departure of the primary pinna traces from the tips of the lateral arms of the rachis xylem
299 in both species (compare Fig. 4 A and B). However, there are obvious differences concerning
300 the inner cortex of the stem: in the Chinese species, it is broader (2 mm or more in thickness)
301 and contains five to seven leaf traces, while in *B. nollii*, the inner cortex is narrower, less than

302 1 mm in thickness, and contains only three to four leaf traces (Rößler and Galtier, 2003; Fig.
303 1). Trichomes in the present specimen are much shorter, about 1 mm long, whereas in *B.*
304 *nollii*, they can measure up to 5 mm (Rößler and Galtier, 2003). The cauline stele of the *B.*
305 *multifolia* specimen is up to 2 mm in diameter, which is much less than that of *B. nollii* where
306 it can reach up to 3.7 mm. In *B. nollii*, the stele is described as a solid (? to parenchymatized)
307 protostele instead of clearly parenchymatized as it is in the present species. The median arm
308 of the “ω”-shaped foliar xylem strand is shorter than the lateral strands in both species, but it
309 is not forked in *B. multifolia* while that of *B. nollii* divides into two tapering projections
310 (Rößler and Galtier, 2003; Fig. 2). This difference is illustrated on Fig. 3 A and B. In *B. nollii*,
311 the petiole or rachis is circular in cross section, up to 7.5 mm in diameter and much broader
312 than in the species from the Junlian Formation. More importantly, *B. nollii* is based on long
313 specimens consisting of spirally arranged foliar members on stems and of repetitive
314 development of shoots from foliar borne buds. This kind of epiphyllous branching is
315 unknown in *B. multifolia*. We consider that the differences mentioned above justify the
316 distinction of our specimen from *B. nollii* but confirm that the two species are closely related.

317 The type species *Botryopteris forensis* Renault from the Pennsylvanian of France
318 (Renault, 1875; Galtier and Phillips 1977) and contemporaneous specimens from North
319 America (Mamay and Andrews, 1950; Phillips, 1961, 1974; Rothwell, 1991) have stems up
320 to 10 mm in diameter and leaf traces that typically become “ω”-shaped just after diverging
321 from the cauline stele as they do in the present species. However, *B. forensis* differs in its
322 solid protostele that is up to 2.7 x 2 mm in diameter. The surface of its stem is also covered
323 with trichomes but these are typically “equisetiform” hairs with a broad, multiseriate basal

324 region, as illustrated in great detail by Galtier and Phillips (1977). These trichomes, which
325 also occur on all foliar members (and closely packed in croziers), are clearly different from
326 those of the present species and *B. nollii* where they are not known to occur on rachises.
327 Furthermore, the “ω”-shaped foliar xylem strand of *B. forensis* is clearly different (Fig. 4 E),
328 being nearly round in cross section with the median arm at least as long as the lateral arms,
329 and tangentially enlarged at its tip but not forked. In *B. forensis*, a ring of sclerenchyma
330 occurs between the inner and outer cortex of the stem and petiole (Rothwell, 1991), a feature
331 absent in other species including that documented here. Much more important is the
332 difference concerning the pattern of pinna trace formation. In both the species described here
333 and *B. nollii* (Fig. 4 A–B), the median arm of the rachis xylem is not involved in the pinna
334 trace formation. This is different from that of *B. forensis* (Fig. 4 E) and in two other
335 botryopterids with “ω”-shaped foliar xylem strand: *B. renaultii* Corsin (Fig. 4 D) and *B.*
336 *cratis* Millay and Taylor (1980) from the Pennsylvanian of France and the U.S.A.
337 respectively. In these three Euramerican species, the median arm is involved in pinna trace
338 production: “ trace formation from lateral xylem arm tip is accompanied by protoxylem
339 replacement from the median arm, and there may be a temporary xylary bridge between the
340 two arms during and/or immediately following trace departure” (Galtier and Phillips, 1977,
341 Fig. 1, 4). This “bridge” is shown in Fig. 4 D, E (asterisk). The reconstruction of the rachis
342 xylem of *B. multifolia* showing pinna trace emission in Figure 3 must be compared to
343 equivalent reconstructions for *B. forensis* and *B. renaultii* in Galtier and Phillips (1977, Fig.
344 1) in order to be understood.

345 *Botryopteris renaultii* and the smaller and slightly older *B. cratis* are certainly closely

346 related taxa; their foliar xylem is characterized by a long and very broad median arm which
347 represents another different feature with both the species documented here and *B. nollii*.
348 Furthermore, *B. cratis* is known to produce adaxial shoots detached from the median arm
349 instead of from the lateral arms as in *B. forensis* and *B. nollii*.

350 In conclusion, considering all the differences listed above, it is justified to distinguish the
351 specimen from the Julian Formation as a new species for which we erect *Botryopteris*
352 *multifolia* sp. nov. We consider *B. multifolia* to be closely related to *B. nollii*.

353

354 5.2. Permian species diversity of *Botryopteris*

355 Although initially thought to be restricted to the Carboniferous (see Galtier and Phillips
356 1996, fig. 4), four species (including the new *B. multifolia*) have now been recognized from
357 the Permian (Figure 2). This increases the anatomical diversity of the genus that comprises at
358 least 13 formally defined species from the Carboniferous and Permian. Here we discuss
359 information on previously documented Permian species of *Botryopteris*.

360 From volcanoclastic tuffs in the Taiyuan Formation, Hilton et al. (2001) documented
361 fragmentary specimens of an isolated frond member assigned to *Botryopteris tridentata*,
362 which constituted the first record of a Permian representative of this genus and its first
363 occurrence within Cathaysia. The extension of the stratigraphic range of *B. tridentata* (Figure
364 2, 8) reflects the stratigraphically younger occurrence of this species in Cathaysia when
365 compared to its late Pennsylvanian range in Euramerica. The Gondwanan species *B. nollii*
366 (Figure 2, 16) from the Permian of Brazil (Röbller and Galtier, 2003) is based on several large
367 specimens with both foliar to foliar and foliar to cauline branching. A comparison of *B.*

368 *multifolia* (15 in Figure 2) with *B. nollii* and some Euramerican taxa including *B. forensis* (13
369 in Figure 2) and *B. renaultii* (12 in Figure 2) is detailed above. From the Permian floras of
370 China, two further species of *Botryopteris* have been documented by Wang et al. (2009) who
371 illustrated rachis specimens from coal balls in the Taiyuan Formation as *Botryopteris* sp. 1
372 and sp. 2. Of these, *Botryopteris* sp. 1 (Fig. 4 C) is comparable, in the omega shape of its
373 vascular bundle, to *B. forensis* Renault (Fig. 4 E) from the Pennsylvanian of France and
374 North America. It differs slightly in its smaller size and relatively larger amount of
375 sclerenchyma between foliar xylem arms. However, further information is required to fully
376 characterize this species that is here designated, with some reservation, as *B. cf. forensis* (14
377 in Fig. 2). *Botryopteris* sp. 2 of Wang et al. (2009) broadly conforms to characters of the
378 botryopterid genus *Diodonopteris* Ma et al. (Ma et al., 2016) also from Taiyuan Formation
379 coal balls, but its rachis and foliar xylem are considerably larger than those of the monotypic
380 species *D. gracilis* (Ma et al., 2016). *Botryopteris* sp. 2 of Wang et al. (2009) does not appear
381 to belong to the genus *Botryopteris* and requires additional study in order to be adequately
382 characterized.

383

384 5.3. *The nature of the stem of Botryopteris multifolia sp. nov.*

385 As stated by Galtier and Phillips (1996), most species of *Botryopteris* are characterized
386 by the production of shoots on fronds; only two species lack epiphyllous branching, namely
387 *Botryopteris mucilaginoso* Kraentzel (Kraentzel, 1934) and *Botryopteris dichotoma* (Holmes
388 and Galtier, 1983) in which the stem is a dichotomous rhizome. Unfortunately, *Botryopteris*
389 *multifolia* sp. nov. is known only from a short (17 mm) length of its stem, and we have not

390 found evidence for foliar borne stems. In *B. multifolia*, the stem has numerous leaf traces in
391 the cortex and its leaves were densely arranged on the stem with very short internodes only
392 about 0.2 mm long. This is different from all other species of the genus in which leaves are
393 less densely arranged, e.g. in *B. forensis* the internodes can be up to 5–6 mm (Mamay and
394 Andrews, 1950). However, the acropetal increase of stem and stelar diameter is comparable
395 to that observed at the base of epiphyllous shoots of *B. antiqua* and *B. hirsuta*, as illustrated
396 by Long (1943), Galtier (1970) and Holmes (1984). Therefore, we cannot exclude the
397 possibility that the present short stem section of *B. multifolia* was a part of a detached
398 epiphyllous shoot.

399

400 *5.4. Evolutionary implications*

401 It is now established that the stratigraphic range of *Botryopteris* extends into the Permian
402 with at least four distinct species: *B. tridentata*, *B. cf. forensis*, *B. nollii* and *B. multifolia*. This
403 leads us to consider the evolutionary trends among the botryopterids and the possible
404 relationships of these plants with other contemporaneous Permian ferns. Comprehensive
405 analysis of evolutionary trends within the genus should include consideration of both
406 vegetative and fertile characters (Galtier and Phillips 1996), but as we only have information
407 on the vegetative structure of *B. multifolia*, we have restricted our discussion to vegetative
408 characters. These concern: (1) changes in foliar xylem size and configuration from simple
409 elliptical to elaborated xylem geometries; (2) changes in the pattern of pinna trace emission;
410 (3) changes in size and organization of the stele from solid to parenchymatized protostele and
411 to siphonostele; (4) changes in cauline branching with rare dichotomous branching and

412 common epiphyllous branching with shoots borne on fronds in variable position (lateral to
413 adaxial) corresponding to different habits; and (5) variation in position and origin of roots
414 that may be related to habit. This analysis leads us to discuss the proposition of distinct
415 phyletic lines within the Carboniferous botryopterids previously suggested by Phillips (1974)
416 and to extend this with the species now known from the Permian.

417 The stratigraphically oldest species of *Botryopteris*, *B. antiqua* Kidston, occurred in the
418 Tournaisian stage of the Mississippian (Figure 2). During the Pennsylvanian, the genus
419 appears to have diversified rapidly and attained its acme, with more than ten species known
420 from the Euramerican Flora (Phillips, 1974; Galtier and Phillips, 1996). By contrast, only
421 four species of *Botryopteris* are known from the Permian (*B. tridentata*, *B. cf. forensis*, *B.*
422 *nollii* and *B. multifolia*; see above). Unfortunately the precise age of *B. nollii* within the
423 Permian is unknown (Rößler and Galtier, 2003). *B. tridentata* and *B. cf. forensis* are
424 important as they represent Cisuralian (lower Permian) aged occurrences of species
425 previously known from the Pennsylvanian in Europe and North America extending their
426 temporal and spatial range, adding further support to the Euramerican origin of the
427 Carboniferous to earliest Permian Cathaysian flora (e.g., Hilton et al., 2002; Hilton and Cleal,
428 2007). *Botryopteris multifolia* represents the first definite evidence of the genus persisting
429 into the Lopingian and represents the stratigraphically youngest species of the genus.

430

431 In *Botryopteris*, the xylem strand in the rachis remains an important diagnostic feature.
432 Generally, the rachis xylem strand in *Botryopteris* changed from simple oval in older species,
433 to tridentate and then to strongly “ω”-shaped in stratigraphically younger species (Galtier and

434 Phillips, 1996). For example, the rachis xylem strand in the most ancient species,
435 *Botryopteris antiqua*, from the Tournaisian and Visean is elliptical, and there is one main
436 central protoxylem dividing to produce alternately lateral protoxylem to pinna traces. As a
437 result, depending on the more or less short distance between successive pinnae, the rachis
438 strand shows 2 or 3 poles (Galtier, 1970, plate 30, fig. 3–4). This is the case also in *B. hirsuta*
439 and *B. ramosa* (Holmes, 1984) from the early Pennsylvanian. In species of larger size like *B.*
440 *tridentata*, *B. scottii*, *B. mucilaginous* and *B. dichotoma*, the rachis xylem strand is
441 “tridentate” with three permanent protruding (tooth-like) protoxylem strands and often a
442 fourth pole near the central one (Phillips, 1974; Holmes and Galtier, 1983). During the
443 middle Pennsylvanian, in species including *B. cratis* the xylem strand is more tridentate. The
444 largest part consists of large metaxylem tracheids while the tips show the small protoxylem
445 tracheids. In the latest Pennsylvanian species *B. renaultii* and *B. forensis* (Fig. 4 D–E), bulges
446 on the adaxial side of the xylem strand are very obvious and form three long arms with nearly
447 equal lengths. In each arm, protoxylem is situated at the tip. In the Permian, the condition of
448 *B. tridentata* continues, while both *B. nollii* and *B. multifolia* have three arms on the adaxial
449 side of the xylem strand that are well developed. Furthermore, in *B. nollii* and *B. multifolia*
450 the median arm is much shorter than the lateral arms and forks (Fig. 3 and 4 A–B), unlike
451 typical Carboniferous species.

452 As discussed above, in all Carboniferous Euramerican *Botryopteris* species, the pinna
453 trace protoxylem results from division of the median/main protoxylem of the foliar xylem,
454 even in the most advanced *B. forensis* and *B. renaultii* where there is a temporary bridge
455 between median and lateral arm of the rachis (Fig. 4). The situation is different in *B.*

456 *multifolia* and *B. nollii* where the median arm is not involved in pinna trace emission (Fig. 3
457 and 4 A–B). This is suggestive of a derived condition in these Permian species.

458 The stele in *Botryopteris multifolia* consists of tracheids more loosely arranged in the
459 centre with dispersed parenchyma cells; such a parenchymatized protostele is rare in fossil
460 ferns, but resembles those of the extant *Lygodium* Sw. and *Gleichenia* Smith. (Schmid, 1982,
461 p. 870-871). This represents an evolutionarily advanced type of stele in botryopterids where
462 solid protosteles are the rule, with the only exception of the siphonostelic *B. tridentata* and
463 the questionable occurrence of a solid to parenchymatized protostele in *B. nollii*. This is
464 another important derived condition.

465 Distinct species of *Botryopteris* possess trichomes of different morphology and
466 distribution. Generally, the stratigraphically older species possess uniseriate multicellular
467 trichomes, while multiseriate multicellular trichomes appeared subsequently, such as those in
468 *B. forensis* from the Pennsylvanian and *B. nollii* as well as *B. multifolia* from the Permian. In
469 this regard, there seems to be an apparent evolutionary trend from uniseriate multicellular to
470 multiseriate multicellular trichomes within *Botryopteris*.

471 Features of root origin: Galtier and Phillips (1977, page 2) considered that in
472 *Botryopteris* "...common traces divided basally into a petiolar trace and one or two lateral
473 cauline traces associated with adventitious roots". However, roots in *B. multifolia* diverge
474 from the leaf trace in the cortex and they are not associated with the stem. This is very
475 different from other species of *Botryopteris* in which root traces diverge from the cauline
476 stele. However, it is not clear if this has evolutionary significance or if it is mainly related to
477 habit differences.

478 In summary, the new species *B. multifolia* exhibits significant advanced features
479 concerning its parenchymatized stele, leaf trace origin, rachis xylem with a short median arm
480 which is not involved in pinna trace emission. These features are essentially shared with the
481 Permian species *B. nollii*, but they are absent in the older Carboniferous *Botryopteris* species.
482 Phillips (1974) and then Galtier and Phillips (1996) suggested the occurrence of at least four
483 phyletic lines of *Botryopteris* representing a range between the basal Mississippian
484 (*Botryopteris antiqua* type) and the late Pennsylvanian (with *B. pseudoantiqua*, *B. renaultii*
485 and *B. forensis*). We now know that *B. tridentata* (attributed by Phillips to a distinct “*ramosa*
486 line”) persisted into the basalmost Permian (Asselian) of China. The occurrence of *B. cf*
487 *forensis* at the same level would support a similar extension into the Permian of the “*hirsuta-*
488 *forensis* line”. Finally, present data suggest that the two Permian species *B. nollii* and *B.*
489 *multifolia* represent a new and derived phyletic line of botryopterids. However, *B. multifolia*
490 *is* still incompletely known in comparison to *B. nollii* or advanced Carboniferous species like
491 *B. forensis* of which large specimens, laminate foliage and fertile parts are known. Additional
492 information is needed before we may clarify the origin of this phyletic line from their
493 Carboniferous ancestral stock.

494

495 5.5. Possible relationships of Permian botryopterids with other contemporaneous ferns

496 The “advanced” or “derived” foliar anatomy of *B. multifolia* and *B. nollii*, with a shorter
497 median arm that is not involved in pinna trace emission, could represent a trend towards a
498 catenalean type (adaxially concave C-shaped leaf trace) with protoxylems only on the lateral
499 tips (former lateral arms). The foliar anatomy of *B. multifolia* and *B. nollii* is somewhat

500 comparable to that of *Shuichengella primitiva* Li, a most primitive member of Guaireaceae,
501 the basal family within the Osmundales (Li, 1993; Tidwell and Ash, 1994; Wang et al.,
502 2014b). This is different from other members of the Osmundales in which the protoxylem
503 strands are distributed along the adaxial surface of the C-shaped metaxylem of the leaf trace
504 as shown in *Zhongmingella plenasioides* Wang et al. (2014b), *Tiania yunnanense* Wang et al.
505 (2014a) and *T. resinus* He et Wang (2019). In *Shuichengella primitiva*, the leaf trace was
506 described (Li, 1993) as possessing three groups of protoxylem, two of these being “located
507 adaxially near both ends of the C-shaped xylem and the third one situated in the adaxial
508 centre”. Our examination of the type material of *Shuichengella* shows that there are one or
509 two very short bulges in the median region of the C-shaped metaxylem strand of the leaf trace
510 (Plate VI). The short bulge consists of large metaxylem tracheids. At its tip there are one or
511 two protoxylem strands (arrows, Plate VI, A–B). This looks like a very short median arm
512 similar to that in *B. multifolia* and *B. nollii*. In the inner cauline cortex of *Shuichengella*
513 *primitiva* (i.e. just after its divergence from the stele), the leaf trace xylem shows only one
514 median bulge (arrow, Plate VI, A) in complement to the two protoxylem strands located near
515 both ends of the C-shaped xylem (white arrows, Plate VI, A). Higher up, in the middle and
516 outer cortex, the bulge divides into two (Plate VI, B).

517 There are also some other similarities between *S. primitiva* and *B. multifolia*, such as
518 their parenchymatized steles and roots originating from leaf traces in the cauline cortex. The
519 similarities between *S. primitiva* and *B. multifolia* as well as *B. nollii* probably represent
520 evolutionary convergence between Guaireaceae and Botryopteridaceae which are generally
521 considered as two unrelated lineages. However, this may support ancestry for the

522 Osmundales from ferns similar to or closely related to the Botryopteridaceae.

523 *Botryopteris multifolia* displays similarity with some stratigraphically older ferns, such as
524 *Rastropteris* (Galtier et al., 2001) from the early Permian of China, which is currently placed
525 within an incertae sedis group of filicalean ferns. It has a solid protostele with mesarch xylem
526 maturation, the configuration of leaf trace xylem changes from an initial reniform strand with
527 an endarch protoxylem located always medianly on the adaxial face, to a strand with three
528 adaxial ridges resembling some *Botryopteris* species, and finally to a tangentially elongated
529 strand with two adaxially recurved lateral arms and a number of adaxial ridges. *B. multifolia*
530 is similar to *Rastropteris* in possessing a protostele though parenchymatized with exarch to
531 mesarch maturation of the xylem, the configuration of leaf trace xylem changing from an
532 initial reniform strand with an endarch protoxylem located always medianly on the adaxial
533 face, to a strand with two adaxially recurved lateral arms and a short median arm at the inner
534 part of cortex. However, the differences between the two taxa are also obvious. *B. multifolia*
535 is a small bodied and perhaps epiphyllous fern without petiole mantle, petiole and rachis
536 xylem with three adaxial arms, while *Rastropteris* has a large erect stem with a petiole mantle
537 and petiole xylem with several adaxial ridges (Galtier et al., 2001).

538 *Catenopteris* is a small protostelic fern with adaxially curved, shallow, C-shaped foliar
539 xylem from the Upper Pennsylvanian of North America (Phillips and Andrews, 1966;
540 Phillips, 1974). It resembles to *B. multifolia* in its small size, protostele, cross-sectionally
541 elliptical petiole, closely spaced leaf traces and C-shaped foliar xylem with a slight median
542 adaxial ridge. However, in *Catenopteris* the stele is solid consisting of only tracheids with
543 uniseriate scalariform thickenings, a prominent decurrent parenchymatous band adaxial to the

544 leaf traces, fewer leaf traces in cauline cortex, and slight curvature of the leaf trace. In
545 contrast, *B. multifolia* possesses a parenchymatized protostele with multiseriate scalariform
546 tracheidal thickenings/pittings, more leaf traces in cauline cortex, strong curvature of the leaf
547 trace with a short but conspicuous median adaxial arm.

548 At present, the characters of botryopterids, Palaeozoic Guiariaceae, *Rastropteris* and
549 *Catenopteris* are a tantalizing mix from which additional specimens are required to further
550 assess the evolutionary and ecological implications of the shared characters.

551

552 **Acknowledgements**

553 Yi-Long Zhou is thanked for making drawings. This work was supported by the National
554 Natural Science Foundation of China (Awards No. U1702242, 41472021, 41530101), the
555 Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000)
556 and is contribution number 34 from Birmingham Institute of Forest Research.

557

558 **Literature cited**

559 Galtier, J., 1970. Recherches sur les végétaux à structure conservée du Carbonifère inférieur
560 français. Paléobiologie continentale 1, 1–221 and 54 plates.

561 Galtier, J., Phillips, T.L., 1977. Morphology and evolution of *Botryopteris* – a Carboniferous
562 age fern. Part 2. Observations on Stephanian species from Grand’Croix, France.

563 Palaeontographica B 164, 1–32.

564 Galtier J., Phillips T. L., 1996. Structure and evolutionary significance of Palaeozoic ferns.

565 In: Camus, J. M. et al., (Eds.), Pteridology in Perspective. Royal Botanic Gardens, Kew,

- 566 pp. 417–433.
- 567 Galtier J., Phillips T. L., 1999. The acetate peel technique. In: Jones T. P., Rowe N. P. (Eds.),
568 Fossil Plants and Spores: Modern Techniques. Geological Society of London, London,
569 pp. 67–71.
- 570 Galtier, J., Wang, S. J., Li C. S., Hilton, J., 2001. A new genus of filicalean fern from the
571 Permian of China. *Bot. J. Linn. Soc.* 137, 429–442.
- 572 He, J., Wang, S. J., Hilton, J., Shao, L., 2013. *Xuanweioxylon* gen. nov.: novel Permian
573 coniferophyte stems and branches with scalariform bordered pitting on secondary
574 tracheids. *Rev. Palaeobot. Palynol.* 197, 152–165.
- 575 He, X. Y., Wang, S. J., Hilton, J., Galtier, J., Li Y. J., Shao L., 2013. A unique trunk of
576 Psaroniaceae (Marattiales) – *Psaronius xuii* sp. nov., and subdivision of the genus
577 *Psaronius* Cotta. *Rev. Palaeobot. Palynol.* 197, 1–14.
- 578 He, X.Y., Wang, S.J., Wang, J., Hilton, J., 2019. The anatomically preserved tri-pinnate frond
579 *Rothwellopteris marginata* gen. et. comb. nov. from the latest Permian of South China:
580 timing the stem to crown group transition in Marattiales. *Int. J. Plant Sci.* 180, 869–881
- 581 He, X.Y., Wang, S.J., 2019. A new anatomically preserved osmundalean stem *Tiania resinus*
582 sp. nov. from the Lopingian (upper Permian) of eastern Yunnan, China. *Rev. Palaeobot.*
583 *Palynol.* 262, 52–59.
- 584 Hilton, J., Cleal, C.J., 2007. The relationship between Euramerican and Cathaysian tropical
585 floras in the Late Palaeozoic: palaeobiogeographical and palaeogeographical
586 implications. *Earth-Sci. Rev.* 85, 85–116.

- 587 Hilton, J., Wang, S.J., Galtier, J., Li C.S., 2001. An Early Permian plant assemblage from the
588 Taiyuan Formation of northern China with compression/impression and permineralized
589 preservation. *Rev. Palaeobot. Palynol.* 114, 175–189.
- 590 Hilton, J., Wang, S.J., Galtier, J., Glasspool, I.J., Stevens, L., 2004. An upper Permian
591 permineralized plant assemblage in volcanoclastic tuff from the Xuanwei Formation,
592 Guizhou Province, southern China, and its palaeofloristic significance. *Geol. Mag.* 141,
593 661–674.
- 594 Hilton, J., Wang S.J., Zhu W.Q., Tian B., Galtier, J. and Wei A.H., 2002. *Callospermarion*
595 ovules from the Early Permian of northern China: palaeofloristic and palaeogeographic
596 significance of callistophytalean seed ferns in the Cathaysian flora. *Rev. Palaeobot.*
597 *Palynol.* 120, 301–314.
- 598 Holmes, J., 1984. Morphology and evolution of *Botryopteris*, a Carboniferous age fern. Part
599 IV. Branching patterns of the European species *B. hirsuta* and *B. ramosa*. Description of
600 *B. scottii* n. sp. *Palaeontographica B* 191, 1–28.
- 601 Holmes, J., Galtier, J., 1983. Morphology and evolution of *Botryopteris*, a Carboniferous age
602 fern. Part III. *Botryopteris dichotoma*, a new Westphalian species from Belgium with
603 observations on other species. *Palaeontographica B* 186, 1–17.
- 604 Joy, K.W., Willis, A.J., Lacey, W.S., 1956. A rapid cellulose peel technique in Palaeobotany.
605 *Ann. Bot.* 20(4), 635–637.
- 606 Kraentzel, G., 1934. Étude monographique de *Botryopteris mucilaginoso* sp. nov. *Ann. Soc.*
607 *Geol. Belg.* 58, 51–76.
- 608 Li, H.Q., Taylor, D.W., 1998. *Aculeovinea yunguiensis* gen. et sp. nov. (Gigantopteridales), a

- 609 new taxon of Gigantopterid stem from the Upper Permian of Guizhou Province, China.
610 Int. J. Plant Sci. 159, 1023–1033.
- 611 Li, H.Q., Taylor, D.W., 1999. Vessel-bearing stems of *Vasovinea tianii* gen. et sp. nov.
612 (Gigantopteridales) from the Upper Permian of Guizhou Province, China. Amer. J. Bot.
613 86, 1563–1575.
- 614 Li, Z.M., 1993. The genus *Shuichengella* gen. nov. and systematic classification of the order
615 Osmundales. Rev. Palaeobot. Palynol. 77, 51–63.
- 616 Long, A.G., 1943. On the occurrence of buds on the leaves of *Botryopteris hirsute* Will. Ann.
617 Bot. (N.S.) 7, 133–146.
- 618 Ma, J., Wang, S.J., He, X.Z., He, X.Y., Ma, S.M., 2016. *Diodonopteris*, a new genus of the
619 Paleozoic leptosporangiate fern family Botryopteridaceae, from the lower Permian of
620 Shanxi Province, North China. Rev. Palaeobot. Palynol. 234, 11–24.
- 621 Mamay, S.H., Andrews H.N., 1950. A contribution to our knowledge of the anatomy of
622 *Botryopteris*. Bull. Torrey Bot. Club 77, 462–494.
- 623 Millay, M.A., Taylor, T.N., 1980. An unusual botryopterid sporangial aggregation from the
624 Middle Pennsylvanian of North America. Amer. J. Bot. 67, 758–773.
- 625 Neregato, R., D’Apolito, C., Glasspool, I.J., Wang, S.J., Feng, L., Windslow, P., Lu, J., Shao,
626 L., Hilton, J., 2016. Palynological constraints on the provenance and stratigraphic range
627 of a Lopingian (late Permian) inter-extinction floral lagerstätte from the Xuanwei
628 Formation, Guizhou Province, China. Int. J. Coal Geol. 62, 139–150.
- 629 Phillips, T.L., 1961. American species of *Botryopteris* from the Pennsylvanian. Ph.D. thesis,
630 Washington Univ., St. Louis, Missouri. 77 pp.

- 631 Phillips, T.L., 1974. Evolution of vegetative morphology in coenopterid ferns. *Ann. Missouri*
632 *Bot. Gard.* 61, 427–461.
- 633 Phillips, T.L., Andrews, H.N., 1966. *Catenopteris simplex* gen. et sp. nov., a primitive
634 pteridophyte from the Upper Pennsylvanian of Illinois. *Bull. Torrey Bot. Club.* 93, 117–
635 128.
- 636 Renault, B., 1875. Recherches sur les végétaux silicifiés d'Autun et de Saint-Étienne: Étude
637 du genre *Botryopteris*. *Ann. Sci. Nat. (Bot.)* 6e ser., 1, 220–240.
- 638 Rößler, R., Galtier, J., 2003. The first evidence of the fern *Botryopteris* from the Permian of
639 the Southern Hemisphere reflecting growth form diversity. *Rev. Palaeobot. Palynol.* 127,
640 99–124.
- 641 Rothwell, G.W., 1991. *Botryopteris forensis* (Botryopteridaceae), a trunk epiphyte of the tree
642 fern *Psaronius*. *Amer. J. Bot.* 78, 782–788.
- 643 Schmid, R., 1982. The terminology and classification of steles: historical perspective and the
644 outlines of a system. *Bot. Rev.* 48, 817–931.
- 645 Seyfullah, L.J., Hilton, J., Liang, M.M., Wang, S.J., 2010. Resolving the systematic and
646 phylogenetic position of isolated ovules: a case study from a new genus from the Upper
647 Permian of China. *Bot. J. Linn. Soc.* 164, 84–108.
- 648 Tidwell, W.D., Ash, S.A., 1994. A review of selected Triassic to Early Cretaceous ferns. *J.*
649 *Plant Res.* 107, 417–442.
- 650 Wang, H., Shao, L., Hao, L.M., Zhang, P.F., Glasspool, I.J., Wheelley, J.R., Wignall, P.B., Yi,
651 T.S., Zhang, M.Q., Hilton, J., 2011. Sedimentology and sequence stratigraphy of the
652 Lopingian (Late Permian) coal measures in southwestern China. *Int. J. Coal Geol.* 85,

- 653 168–183.
- 654 Wang, S.J., Bateman, R.M. Spencer, A.R.T., Wang, J., Shao, L., Hilton, J., 2017.
655 Anatomically preserved "strobili" and leaves from the Permian of China
656 (Dorsalistachyaceae, fam. nov.) broaden knowledge of Noeggerathiales and constrain
657 their possible taxonomic affinities. *Amer. J. Bot.* 104, 127–149.
- 658 Wang, S.J., Hilton, J., Galtier, J., He, X.Y., Shao, L.Y., 2014a. *Tiania yunnanense* gen. et sp.
659 nov., an osmundalean stem from the Upper Permian of southwestern China previously
660 placed within *Palaeosmunda*. *Rev. Palaeobot. Palynol.* 210, 37–49.
- 661 Wang, S.J., He, X.H., Hilton, J., Seyfullah, L.J., Shao, L., 2014b. Anatomy and organization
662 of *Zhongmingella* (Li) gen. et comb. nov. from the Late Permian of China and its
663 relationships with extinct Osmundalean ferns. *J. Syst. Palaeontol.* 12, 1–22.
- 664 Wang, S.J., Hilton, J., Galtier, J., Tian, B., 2006. A large anatomically preserved calamitean
665 stem from the Late Permian of southwest China with unusual growth rings, cortex
666 development and leaf traces. *Plant Syst. Evol.* 264, 229–244.
- 667 Wang, S.J., Li, S.S., Hilton, J., Galtier, J. 2003. A new species of the sphenophyte stem
668 *Arthropitys* from Late Permian volcanoclastic sediments of China. *Rev. Palaeobot.*
669 *Palynol.* 126, 65–81.
- 670 Wang, S.J., Sun, K.Q., Cui, J.Z., Ma, S.M. 2009. Fossil plants from coal balls in China.
671 Higher Education Press, Beijing. 1–222, 81 pls.
- 672 Yang, Y., He, X.Y., Hilton, J., Zhao, F.G., Chen, X.C., Wang, S.J., 2019. *Xuanweioxylon*
673 *damogouense* sp. nov., a Lopingian (late Permian) gymnosperm stem from China and its
674 systematic and palaeoecological implications. *Rev. Palaeobot. Palynol.* 269, 94–103

- 675 Zhao, X.H., Mo, Z. G., Zhang, S. Z., Yao, Z. Q., 1980. Late Permian flora from western
676 Guizhou and eastern Yunnan. In: Nanjing Institute of Geology and Palaeontology,
677 Academia Sinica (Ed.), Late Permian Coal Bearing Strata and Biota from Western
678 Guizhou and Eastern Yunnan. Science Press, Beijing, pp. 70– 122 (in Chinese).
- 679 Zhu, J.N., Hu, Y.F., Li, Z.J., 1984. Late Permian strata and fossil plants from Junlian area,
680 South Sichuan. Professional Papers of Stratigraphy and Palaeontology, 11, 133–147 (in
681 Chinese with English summary).
- 682

683 **Explanation of figures and plates**

684

685 Figure 1. A. Outline map of China showing province position with box showing border area
686 of SW Guizhou Province, NE Yunnan Province and SE Sichuan Province. B. Enlargement of
687 box area to show collection locality in black dot.

688

689 Figure 2. Stratigraphic distribution of species of *Botryopteris*, showing the evolutionary
690 changes in the shape of the rachis xylem strand as seen in cross section (modified from
691 Galtier and Phillips, 1996). (1) *B. cf. antiqua* Kidston; (2) *B. antiqua* Kidston; (3) *B. sp.*; (4)
692 *B. ramosa* (Williamson) Scott; (5) *B. hirsuta* (Williamson) Scott; (6) *B. dichotoma* Holmes
693 and Galtier; (7) *B. mucilaginoso* Kraentzel; (8) *B. tridentata* (Felix) Scott; (9) *B. cratis* Millay
694 et Taylor; (10) *B. sp.*; (11) *B. pseudoantiqua*; (12) *B. renaulii* Bertrand et Cornaille; (13) *B.*
695 *forensis* Renault; (14) *B. cf. forensis*; (15) *B. multifolia* sp. nov.; (16) *B. nollii* Rößler et
696 Galtier. Abbreviations: Guad. = Guadalupian; Loping. = Lopingian.

697

698 Figure 3. Reconstruction of *Botryopteris multifolia* sp. nov. rachis xylem showing pinna trace
699 formation and departure in the adaxial view. The median xylem arm is not involved in the
700 process, in contrast to the situation in *Botryopteris forensis* and *B. renaulii*, as reconstructed
701 by Galtier & Phillips (1977, Text-fig.1).

702

703 Figure 4. Comparison, at the same magnification, of cross sections of foliar xylem of: (A)
704 *Botryopteris multifolia* sp. nov.; (B) *B. nollii*; (C) *B. cf. forensis*; (D) *B. renaulii*; (E) *B.*

705 *forensis*. Stages in pinna trace formation and departure are shown in the right column. Xylary
706 bridge (*) occurs between median and lateral arm only in *B. renaultii* (D) and *B. forensis* (E).
707 Protoxylem as black dots on adaxial face of xylem arms. Scale bar = 1 mm. Drawings based
708 on: (A) present study; (B) Rößler & Galtier, 2003, fig. 2; (C) Wang et al. 2009, Plate 42 A;
709 (D–E) Galtier & Phillips, 1977, Fig. 4C–D and Plate 7, 46–47.

710

711 Plate I. *Botryopteris multifolia* sp. nov. from the Lopingian of China. IC-inner cortex; LT-leaf
712 trace; OC-outer cortex; P-petiole; Ra-rachis; RT-root trace; S-stele. A. Cross section of stem
713 at a distal level (peel L 8-2) showing tissue overview with 5 leaf traces (arrows) in the inner
714 cortex and one petiole base (P). Slide: WP2-0641; Scale bar = 2mm. B. Cross section of stem
715 at a basal level (peel P/Top 2) showing tissue overview with 6 leaf traces in the inner cortex
716 (black arrows) and one in the outer cortex (white arrow). Slide: WP2-0633; Scale bar = 2
717 mm. C. Detail of the central part of stem of Plate I, A showing divergence of leaf traces
718 (numbered 0 to 6), short arrows indicate protoxylem strands. The long arrow indicates the
719 taphonomic displacement of leaf trace 1. Slide: WP2-0641; Scale bar = 1 mm. D. Central part
720 of the cauline stele, showing parenchyma cells (arrowed). Slide: WP2-0642; Scale bar = 200
721 μm . E. Longitudinal section through cauline stele, showing multiseriate scalariform
722 thickening on the walls of large tracheid (arrowed). Slide: WP2-0648; Scale bar = 100 μm .

723

724 Plate II. *Botryopteris multifolia* sp. nov. from the Lopingian of China. A. Cross section of part
725 of stem at a lower level (peel L 12-1) than that of Plate I, C showing divergence of leaf traces.
726 Slide: WP2-0636; Scale bar = 1mm. B. Cross section through the cortex, showing outer zone

727 of outer cortex (OC1), inner zone of outer cortex (OC2) and inner cortex (IC). Arrows
728 indicate trichomes. Slide: WP2-0637; Scale bar = 200 μm . C. Enlargement of the inner
729 cortex, showing cells with dark-colored content and with tylose-like contents (arrowed).
730 Slide: WP2-0639; Scale bar = 50 μm . D–F. Longitudinal sections through outer zone of the
731 outer cortex (D), inner zone of the outer cortex (E) and inner cortex (F). Slide: WP2-0648;
732 Scale bar = 100 μm .

733

734 Plate III. *Botryopteris multifolia* sp. nov. from the Lopingian of China. A, B. Cross sections
735 of cauline stele showing leaf trace formation. A. Protoxylem strand (arrowed) appearing at
736 the edge of cauline stele. Slide: WP2-0640; Scale bar = 200 μm . B. Beginning of leaf trace
737 bulging with metaxylem tracheids added to the outside of the protoxylem strand (arrowed).
738 Slide: WP2-0642; Scale bar = 200 μm . C to F: cross sections of leaf traces with their adaxial
739 face down. C, D. Leaf traces in the inner cortex. C. Reniform leaf trace just departed from the
740 cauline stele; the lateral arms are connected with the median arm. Slide: WP2-0635; Scale bar
741 = 200 μm . D. Leaf trace, a little farther away from the stele, with the left lateral arm
742 connected with the median arm, while the other is now free. Slide: WP2-0639; Scale bar =
743 200 μm . E. Leaf trace farther away in the inner cortex than that in D. In each area between
744 the lateral and median arms a mass of sclerenchyma cells occurs (arrowed). Median arm with
745 a single protoxylem strand. Slide: WP2-0639; Scale bar = 200 μm . F. Cross section through a
746 petiolar base. The median xylem arm is very short and wide and there are two protoxylem
747 strands (arrowed). Slide: WP2-0642; Scale bar = 500 μm . G. Cross section of a free petiole
748 showing the forked lateral arms of xylem bundle (arrowed). Slide: WP2-0643; Scale bar =

749 500 μm . H. Cross section through a rachis: the vascular bundle has given off two traces for
750 primary pinnae (arrowed). Slide: WP2-0646; Scale bar = 500 μm .

751

752 Plate IV. *Botryopteris multifolia* sp. nov. from the Lopingian of China. A–B. Enlargements
753 showing details of figures G and H of Plate III. A. Petiolar xylem showing an advanced stage
754 in pinna trace formation from the tip of lateral arms (arrows). Slide: WP2-0643; scale bar
755 =500 μm . B. Departure of subopposite pinna traces (arrows) from the rachis xylem. Slide:
756 WP2-0646; scale bar =500 μm .

757

758 Plate V. *Botryopteris multifolia* sp. nov. from the Lopingian of China. A. Longitudinal section
759 through the stele (St) and a leaf trace (LT), showing the small angle between them. Slide:
760 WP2-0648; Scale bar = 200 μm . B. Oblique cross section through the stem, showing a leaf
761 trace in the outer cortex at a high angle to the cauline stele. Slide: WP2-0639; Scale bar = 200
762 μm . C. Cross section through stem and rachis showing the multicellular, multiseriate
763 trichomes. Slide: WP2-0645; Scale bar = 200 μm . D. Cross section through stem showing the
764 dense multicellular, multiseriate trichomes. Slide: WP2-0639; Scale bar = 200 μm . E. Cross
765 section through stem showing root trace (arrowed) diverging from a leaf trace (LT) in the
766 inner cortex. F. Root trace in cross section. Slide: WP2-0643; Scale bar = 200 μm .

767

768 Plate VI. *Shuichengella primitiva* Li from the Lopingian of China. A. Leaf trace in the inner
769 cortex showing an adaxial median bulge with one protoxylem (black arrow) and two
770 protoxylem strands (white arrows) near the lateral ends. B. Leaf trace in the middle cauline

771 cortex, showing two adaxial medianly orientated bulges (black arrows) and two protoxylem
772 strands (white arrows) near the lateral ends. Slides: GP₂₃₇₇₋₃₋₂ (8-6), GP₂₃₇₇₋₃₋₂ (7-4);
773 Scale bar = 200 μm .
774