

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-02431756

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.

UNIVERSITY^{OF} BIRMINGHAM University of Birmingham Research at Birmingham

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

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 <i>Botryopteris</i> 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 (XY. He)

16 ABSTRACT

We describe a new species of the Palaeozoic fern genus Botryopteris in volcanic tuffs from 1718 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 "\u00f6"-shaped in cross section and comprise two 21 long lateral arms and a single, shorter median arm. Parenchyma is distributed among the stem metaxylem tracheids and is more common in the central region of the stele that comprises a 22 parenchymatized protostele. Several mesarch protoxylem strands, decurrent from leaf traces, 23 24 are visible in each cross section of the protostele. Root traces originate from the lateral side of the leaf trace within the stem cortex. The stem surface is covered by thick, multiseriate, 25 multicellular trichomes. Botryopteris multifolia sp. nov. represents the stratigraphically 26 27 youngest known species of the genus and has a combination of derived evolutionary characteristics including its large stem size, parenchymatized protostele, elaborate trichome 28 structure, roots originating from leaf traces, and the construction of xylem strand of the leaf 29 30 trace and rachis with distinctive pinna trace formation and emission. It is more similar in leaf anatomy to the Gondwanan species B. nollii from the Permian of Brazil and less like late 31 32 Pennsylvanian botryopterids from Euramerica. Finally, we consider the evolutionary implications of features shared between Permian members of the botryopterids and 33 34 catenalean-type plants including members of the Osmundales stem group family Guaireaceae (Shuichengella, Zhongmingella, Tiania) and the enigmatic early ferns Rastropteris and 35 36 Catenopteris.

2

37

Keywords: Botryopteridaceae, fern, anatomy, Xuanwei Formation, Lopingian, volcaniclastic
 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 in terrestrial and paralic sedimentary facies (Wang et al., 2011). These include frequent 44 occurrences of impression-compression fossil plant species (e.g., Zhao et al., 1980; Zhu et 45 46 al., 1984) as well as less common accounts of species preserved as permineralizations (e.g. Hilton et al., 2004; Neregato et al., 2016; Wang et al., 2017). Collectively these assemblages 47 represent the stratigraphically youngest Palaeozoic "coal measures" wetland plant 48 49 communities prior to their demise at the end of the Permian (Hilton and Cleal, 2007). Although incompletely characterized and the focus of current research, the anatomically 50 preserved flora comprises sphenophytes (Wang et al., 2003, 2006), Osmundales (Wang et al., 51 52 2014a, b; He and Wang, 2019), Marattiales (He X et al., 2013, 2019), Noeggerathiales (Wang et al., 2017), gigantopterids (Li and Taylor, 1998, 1999) and seed plants (Seyfullah et al., 53 54 2010; He J. et al. 2013; Yang et al., 2019) that represents an unique association not known from other regions. These accounts suggest the regional flora to be advanced compared to 55 floras from other areas (Wang et al., 2014b). They also provide insights into floristic change 56 resulting from climate and environmental perturbations in the run-up to the end Permian mass 57 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 volcaniclastic sediments from the Cisuralian
66	of North China (Hilton et al., 2001), B. nollii Röβler 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 volcaniclastic 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.

75 **2. Material and methods**

A single specimen preserved in volcaniclastic tuff was recovered from mine spoil at Lubanshan coal mine (Figure 1), Junlian, Sichuan Province, southwestern China and numbered 72012. The mine extracts coal from the Junlian Formation that contains abundant fossil plants including impression-compression (Zhu *et al.*, 1984) and less commonly permineralized specimens (Wang *et al.*, 2003). The fossil is permineralized by an early stage 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 protostele 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 exarch. Cauline metaxylem tracheids (up to 120 µm wide) exhibit multiseriate scalariform 105 106 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 longitudinally elongated. Surface of stem and adaxial side of petiolar bases with multiseriate, 110 multicellular trichomes (up to 350 µm thick and 1 mm long). Leaf traces diverge helically 111 112 (3/8 phyllotaxis) at very close intervals, with 6–8 leaf traces visible in each cross section of the stem. Petiole size up to 4.75 mm tangentially and 3.5 mm radially. Leaf trace xylem at 113 114 first reniform with adaxial protoxylem tracheids and parenchyma, becoming "\u00fc"-shaped 115 (about 1 mm broad tangentially) with sclerenchyma clusters of small cells (20-30 µm diameter) filling the areas between the lateral and median arms. In the petiole, the xylem 116 strand is slender, up to 1.9 mm tangentially and 0.7 mm radially with much longer lateral 117 118 arms and short median arm. The median xylem arm initially has one protoxylem strand, then it enlarges tangentially to become rectangular (0.4 mm tangentially and 0.2 mm radially) with 119 two lateral protoxylem strands. Xylem strand consists essentially of one or two rows of (80-120 130 µm) broad metaxylem tracheids. Primary pinnae nearly borne oppositely on the rachis. In 121 pinna trace formation, protoxylem in one lateral xylary arm of the rachis divides and the tip 122 crooks out and passes off as a pinna trace. Protoxylem strands of the median arm are not 123 124 involved in the process of pinna trace emission. Root trace xylem originating from the lateral side of leaf traces within the stem cortex. 125

4. Description

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	\times 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) μ m. 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 μ m 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 μ m. 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 μ m 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

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

173 *4.4. Leaf traces*

Protoxylem strands appearing near the outer margin of the cauline stele are the first indication of decurrent leaf traces; they are rarely exarch (Plate III, A) and commonly mesarch. In an early stage of leaf trace initiation, metaxylem tracheids occur to the outside of the protoxylem strand (Plate III, B) and they form an obvious bulge (Plate I, C; Plate II, A). Progressive levels of the incipient leaf traces, including enlargement of the protoxylem with tracheids and parenchyma mixed, are well illustrated in stages 3 and 4 of slide 12-1 (Plate II, 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 width of 675 µm. Its single protoxylem strand, composed of small tracheids and associated 182 parenchyma cells, is round and rather large, with a diameter up to approximately 200 µm 183 (Plate I, C). At the level where the leaf trace sepatates from the cauline stele, it is nearly 184 reniform with its adaxial side slightly depressed showing very small tracheids and 185 parenchyma cells (5, 6, Plate II, A; Plate III, C). The xylem strand is 750 µm wide and 400 186 µm thick, its two lateral arms enroll and connect with the median arm. At more distal levels 187 the xylem strand of the leaf trace is tangentially extended, up to 0.85 mm wide, but the radial 188 thickness is approximately 270 µm. At this level the lateral arms of the xylem strand are 189 thinner and nearly connected with the median arm. The tip of the median arm flares laterally; 190 the areas surrounded by the lateral and median arms are filled with small parenchyma cells 191

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

Leaf traces diverge helically and the stem shows many leaf traces in each cross section 204 (Plate I, A, B). The leaf traces are mainly distributed in the inner cortex where they number 205 206 5~7 (Plate I, B) while only 1~2 are present in the outer cortex. From the proximal level of section L14-2 (Slide number 0634) to the distalmost level of L5-2 (Slide number 0644), there 207 are 6 new leaf traces (LT 5 to 0) that diverge from the cauline stele within a vertical distance 208 of ca. 1.2 mm; therefore the length of the internode of the stem is about 0.2 mm. 209 Comparison of the successive cross sections in ascending order allowed us to interpret 210 the phyllotaxis of this fern. On the more proximal section (on Plate II, A) there are two 211 bulging/incipient leaf traces (numbered 3 and 4) and the older leaf traces (5 to 9) within the 212

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)*

The free petioles or rachises (Ra, Plate I, A, B) are generally distorted and flattened. In cross section, the petiole is elliptical 4.75 mm wide tangentially and 3.5 mm radially (Plate III, G); the petiole xylem strand is 1.9 mm wide tangentially and 0.7 mm radially (Plate III, 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 mm wide); it is rectangular with one protoxylem strand at each adaxial tip. More distally, the 237 238 foliar xylem strand enlarges tangentially up to 2.2 mm (Plate III, G; Plate IV, A). The tip of each lateral xylary arm arches out with a concomitant division of its protoxylem. This 239 crooked area of xylem then separates as a small C-shaped strand, quickly becoming 240 tridentate, which corresponds to a primary pinna trace (arrows, Plate III, H; Plate IV, B). In 241 fact, two lateral traces are detached nearly at the same level (about 0.3 cm above petiole 242 origin), thus the primary pinnae are sub-opposite on the rachis. 243

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

247

248 *4.6. Trichomes*

Trichomes are distributed across the entire surface of the stem (Plate I, A; arrows in Plate 249 250 II, B). They are all multiseriate and multicellular but vary in size, shape and distribution. In size and shape, some of them have broad bases and tapered tips, but some of them are 251252 isodiametric; others are short and thin, while some others are long and thick, up to 350 µm thick and nearly 1 mm long. Their distribution is uneven, with many trichomes occurring in 253some places but few in others. Seen in cross section, individual trichomes consist of nearly 254 isodiametric cells with diameters of 20~50 µm (Plate V, C). In longitudinal section, trichome 255256 cells are longitudinally elongated, rectangular, polygonal or fusiform, with variable lengths up to 300 µm or more (Plate V, D). 257

259 4.7. Adventitious roots

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

Botryopteris forensis, the type species of the genus, is characterized by "ω"-shaped
xylem strands in cross sections of the leaf trace and petiole/rachis. Both this "elaborate foliar
xylem geometry" and the large size of rachis were interpreted as reflecting evolutionary
changes in one of the stratigraphically youngest species of the genus (Phillips, 1974; Galtier
and Phillips, 1996). This interpretation is supported by recent discoveries, in stratigraphically
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.

To help with comparisons, we consider the key features of the present species as follows: 281 282 (1) the stem and stele are large, the stem having a diameter up to 17×11 mm and the stele up to 2 mm; (2) the cauline xylem is a parenchymatized protostele with files of parenchyma cells 283 284 distributed among the metaxylem tracheids and, more particularly, in the central region; (3) the stele is more or less circular, showing two to four peripheral protoxylem strands in exarch 285 to mainly mesarch maturation; (4) xylem strands of the leaf traces and the petiole/rachis are 286 " ω "-shaped in cross section, with two long lateral arms and a shorter median arm; (5) primary 287 288 pinna traces initiate and depart from the tip of the lateral arms; (6) the surface of the stem is covered by thick, multiseriate, multicellular trichomes and, (7) root traces originate from the 289 lateral side of the departing leaf trace in the cortex. 290

291 Botryopteris nollii Rößler and Galtier (2003) from the Permian of Brazil shows several features in common with the species from the Junlian Formation. Like the Chinese stem, B. 292 nollii is large, up to 11 mm in diameter, and has leaf traces that are obviously "\u00f6"-shaped just 293 294 after they diverge from the cauline stele and with protoxylem restricted to the adaxial tips of the thin foliar xylary arms. In both cases, more distally, the xylary arms enclose small adaxial 295 sclerenchyma strands. In addition, the surface of the stem of *B. nollii* is also covered by 296 multiseriate and multicellular trichomes. Another important similarity concerns the initiation 297 298 and departure of the primary pinna traces from the tips of the lateral arms of the rachis xylem in both species (compare Fig. 4 A and B). However, there are obvious differences concerning 299 the inner cortex of the stem: in the Chinese species, it is broader (2 mm or more in thickness) 300 and contains five to seven leaf traces, while in B. nollii, the inner cortex is narrower, less than 301

302	1 mm in thickness, and contains only three to four leaf traces (Röβler and Galtier, 2003; Fig.
303	1). Trichomes in the present specimen are much shorter, about 1 mm long, whereas in B .
304	<i>nollii</i> , they can measure up to 5 mm (Rö β ler and Galtier, 2003). The cauline stele of the <i>B</i> .
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 <i>B. nollii</i> , 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 <i>B. multifolia</i> while that of <i>B. nollii</i> divides into two tapering projections
310	(Rößler and Galtier, 2003; Fig. 2). This difference is illustrated on Fig. 3 A and B. In <i>B. nollii</i> ,
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 <i>B. multifolia</i> . We consider that the differences mentioned above justify the
316	distinction of our specimen from <i>B. nollii</i> 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 also occur on all foliar members (and closely packed in croziers), are clearly different from 325 326 those of the present species and *B. nollii* where they are not known to occur on rachises. Furthermore, the "\u00f6" shaped foliar xylem strand of *B. forensis* is clearly different (Fig. 4 E), 327 328 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 occurs between the inner and outer cortex of the stem and petiole (Rothwell, 1991), a feature 330 absent in other species including that documented here. Much more important is the 331 332 difference concerning the pattern of pinna trace formation. In both the species described here and B. nollii (Fig. 4 A-B), the median arm of the rachis xylem is not involved in the pinna 333 trace formation. This is different from that of *B. forensis* (Fig. 4 E) and in two other 334 335 botryopterids with "ω"-shaped foliar xylem strand: *B. renaultii* Corsin (Fig. 4 D) and *B.* cratis Millay and Taylor (1980) from the Pennsylvanian of France and the U.S.A. 336 respectively. In these three Euramerican species, the median arm is involved in pinna trace 337 338 production: "trace formation from lateral xylem arm tip is accompanied by protoxylem replacement from the median arm, and there may be a temporary xylary bridge between the 339 two arms during and/or immediately following trace departure" (Galtier and Phillips, 1977, 340 Fig. 1, 4). This "bridge" is shown in Fig. 4 D, E (asterisk). The reconstruction of the rachis 341 xylem of B. multifolia showing pinna trace emission in Figure 3 must be compared to 342 equivalent reconstructions for B. forensis and B. renaultii in Galtier and Phillips (1977, Fig. 343 344 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 <i>B. forensis</i> and <i>B. nollii</i> .
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. nolli.
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 <i>B. multifolia</i>) 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 volcaniclastic 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 <i>B. tridentata</i> (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 (Rößler 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 <i>B. renaultii</i> (12 in Figure 2) is detailed above. From the Permian floras of
370	China, two further species of <i>Botryopteris</i> 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 <i>B. forensis</i> 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.

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

As stated by Galtier and Phillips (1996), most species of *Botryopteris* are characterized by the production of shoots on fronds; only two species lack epiphyllous branching, namely *Botryopteris mucilaginosa* Kraentzel (Kraentzel, 1934) and *Botryopteris dichotoma* (Holmes and Galtier, 1983) in which the stem is a dichotomous rhizome. Unfortunately, *Botryopteris 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 <i>B. forensis</i> 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 <i>B. antiqua</i> and <i>B. hirsuta</i> , 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 <i>B. multifolia</i> was a part of a detached
398	epiphyllous shoot.

400 5.4. Evolutionary implications

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

412 common epiphyllous branching with shoots borne on fronds in variable position (lateral to adaxial) corresponding to different habits; and (5) variation in position and origin of roots 413 414 that may be related to habit. This analysis leads us to discuss the proposition of distinct phyletic lines within the Carboniferous botryopterids previously suggested by Phillips (1974) 415 416 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 Tournaisian stage of the Mississippian (Figure 2). During the Pennsylvanian, the genus 418 appears to have diversified rapidly and attained its acme, with more than ten species known 419 420 from the Euramerican Flora (Phillips, 1974; Galtier and Phillips, 1996). By contrast, only four species of Botryopteris are known from the Permian (B. tridentata, B. cf. forensis, B. 421 nollii and B. multifolia; see above). Unfortunately the precise age of B. nollii within the 422 423 Permian is unknown (Rößler and Galtier, 2003). B. tridentata and B. cf. forensis are important as they represent Cisuralian (lower Permian) aged occurrences of species 424 previously known from the Pennsylvanian in Europe and North America extending their 425 426 temporal and spatial range, adding further support to the Euramerican origin of the Carboniferous to earliest Permian Cathaysian flora (e.g., Hilton et al., 2002; Hilton and Cleal, 427 2007). Botryopteris multifolia represents the first definite evidence of the genus persisting 428 into the Lopingian and represents the stratigraphically youngest species of the genus. 429 430

In *Botryopteris*, the xylem strand in the rachis remains an important diagnostic feature.
Generally, the rachis xylem strand in *Botryopteris* changed from simple oval in older species,
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 <i>B. hirsuta</i>
439	and <i>B. ramosa</i> (Holmes, 1984) from the early Pennsylvanian. In species of larger size like <i>B</i> .
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*. The stele in *Botryopteris multifolia* consists of tracheids more loosely arranged in the centre with dispersed parenchyma cells; such a parenchymatized protostele is rare in fossil ferns, but resembles those of the extant *Lygodium* Sw. and *Gleichenia* Smith. (Schmid, 1982, p. 870-871). This represents an evolutionarily advanced type of stele in botryopterids where solid protosteles are the rule, with the only exception of the siphonostelic *B. tridentata* and the questionable occurrence of a solid to parenchymatized protostele in *B. nollii*. This is another important derived condition.

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

from the leaf trace in the cortex and they are not associated with the stem. This is very

different from other species of *Botryopteris* in which root traces diverge from the cauline

stele. However, it is not clear if this has evolutionary significance or if it is mainly related to

477 habit differences.

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

494

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

The "advanced" or "derived" foliar anatomy of *B. multifolia* and *B. nollii*, with a shorter median arm that is not involved in pinna trace emission, could represent a trend towards a catenalean type (adaxially concave C-shaped leaf trace) with protoxylems only on the lateral 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 <i>B. multifolia</i> and <i>B. nollii</i> . In the inner cauline cortex of <i>Shuichengella</i>
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

519 similarities between *S. primitiva* and *B. multifolia* as well as *B. nollii* probably represent

their parenchymatized steles and roots originating from leaf traces in the cauline cortex. The

- 520 evolutionary convergence between Guaireaceae and Botryopteridaceae which are generally
- 521 considered as two unrelated lineages. However, this may support ancestry for the

518

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

Botryopteris multifolia displays similarity with some stratigraphically older ferns, such as 523 524 Rastropteris (Galtier et al., 2001) from the early Permian of China, which is currently placed within an incertae sedis group of filicalean ferns. It has a solid protostele with mesarch xylem 525 526 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 adaxial ridges resembling some Botryopteris species, and finally to a tangentially elongated 528 strand with two adaxially recurved lateral arms and a number of adaxial ridges. B. multifolia 529 530 is similar to *Rastropteris* in possessing a protostele though parenchymatized with exarch to mesarch maturation of the xylem, the configuration of leaf trace xylem changing from an 531 initial reniform strand with an endarch protoxylem located always medianly on the adaxial 532 533 face, to a strand with two adaxially recurved lateral arms and a short median arm at the inner part of cortex. However, the differences between the two taxa are also obvious. B. multifolia 534is a small bodied and perhaps epiphyllous fern without petiole mantle, petiole and rachis 535 536 xylem with three adaxial arms, while *Rastropteris* has a large erect stem with a petiole mantle and petiole xylem with several adaxial ridges (Galtier et al., 2001). 537 538 Catenopteris is a small protostelic fern with adaxially curved, shallow, C-shaped foliar xylem from the Upper Pennsylvanian of North America (Phillips and Andrews, 1966; 539 Phillips, 1974). It resembles to B. multifolia in its small size, protostele, cross-sectionally 540

- elliptical petiole, closely spaced leaf traces and C-shaped foliar xylem with a slight median
- 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 <i>Botryopteris</i> – 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.

- Galtier J., Phillips T. L., 1999. The acetate peel technique. In: Jones T. P., Rowe N. P. (Eds.),
 Fossil Plants and Spores: Modern Techniques. Geological Society of London, London,
 pp. 67–71.
- Galtier, J., Wang, S. J., Li C. S., Hilton, J., 2001. A new genus of filicalean fern from the
 Permian of China. Bot. J. Linn. Soc. 137, 429–442.
- 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
- tracheids. Rev. Palaeobot. Palynol. 197, 152–165.
- 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.

- 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:
- timing the stem to crown group transition in Marattiales. Int. J. Plant Sci. 180, 869–881
- He, X.Y., Wang, S.J., 2019. A new anatomically preserved osmundalean stem *Tiania resinus*
- sp. nov. from the Lopingian (upper Permian) of eastern Yunnan, China. Rev. Palaeobot.
- 583 Palynol. 262, 52–59.
- Hilton, J., Cleal, C.J., 2007. The relationship between Euramerican and Cathaysian tropical
- floras in the Late Palaeozoic: palaeobiogeographical and palaeogeographical
- 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 volcaniclastic 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 <i>Botryopteris</i> , 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 mucilaginosa 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

- new taxon of Gigantopterid stem from the Upper Permian of Guizhou Province, China.
- 610 Int. J. Plant Sci. 159, 1023–1033.
- 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.
- Li, Z.M., 1993. The genus *Shuichengella* gen. nov. and systematic classification of the order
 Osmundales. Rev. Palaeobot. Palynol. 77, 51–63.
- Long, A.G., 1943. On the occurrence of buds on the leaves of *Botryopteris hirsute* Will. Ann.
- 617 Bot. (N.S.) 7, 133–146.
- Ma, J., Wang, S.J., He, X.Z., He, X.Y., Ma, S.M., 2016. Diodonopteris, a new genus of the
- Paleozoic leptosporangiate fern family Botryopteridaceae, from the lower Permian of
 Shanxi Province, North China. Rev. Palaeobot. Palynol. 234, 11–24.
- 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
- 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,
- 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.

- 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**.

- Renault, B., 1875. Recherches sur les végétaux silicifiés d'Autun et de Saint-Étienne: Étude
 du genre *Botryopteris*. Ann. Sci. Nat. (Bot.) 6e ser., 1, 220–240.
- 638 Röβler, R., Galtier, J., 2003. The first evidence of the fern *Botryopteris* from the Permian of
- the Southern Hemisphere reflecting growth form diversity. Rev. Palaeobot. Palynol. 127,
 99–124.
- Rothwell, G.W., 1991. *Botryopteris forensis* (Botryopteridaceae), a trunk epiphyte of the tree
 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.

- Tidwell, W.D., Ash, S.A., 1994. A review of selected Triassic to Early Cretaceous ferns. J.
 Plant Res. 107, 417–442.
- Wang, H., Shao, L., Hao, L.M., Zhang, P.F., Glasspool, I.J., Wheeley, J.R., Wignall, P.B., Yi,
- T.S., Zhang, M.Q., Hilton, J., 2011. Sedimentology and sequence stratigraphy of the
- 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 volcaniclastic 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).

Explanation of figures and plates

684

685

of SW Guizhou Province, NE Yunnan Province and SE Sichuan Province. B. Enlargement of 686 687 box area to show collection locality in black dot. 688 Figure 2. Stratigraphic distribution of species of *Botryopteris*, showing the evolutionary 689 changes in the shape of the rachis xylem strand as seen in cross section (modified from 690 691 Galtier and Phillips, 1996). (1) B. cf. antiqua Kidston; (2) B. antiqua Kidston; (3) B. sp.; (4) B. ramosa (Williamson) Scott; (5) B. hirsuta (Williamson) Scott; (6) B. dichotoma Holmes 692 and Galtier; (7) B. mucilaginosa Kraentzel; (8) B. tridentata (Felix) Scott; (9) B. cratis Millay 693 694 et Taylor; (10) B. sp.; (11) B. pseudoantiqua; (12) B. renaultii Bertrand et Cornaille; (13) B. forensis Renault; (14) B. cf. forensis; (15) B. multifolia sp. nov.; (16) B. nollii Rößler et 695 Galtier. Abbreviations: Guad. = Guadalupian; Loping. = Lopingian. 696 697 Figure 3. Reconstruction of Botryopteris multifolia sp. nov. rachis xylem showing pinna trace 698 699 formation and departure in the adaxial view. The median xylem arm is not involved in the process, in contrast to the situation in Botryopteris forensis and B. renaulti, as reconstructed 700 by Galtier & Phillips (1977, Text-fig.1). 701 702 703 Figure 4. Comparison, at the same magnification, of cross sections of foliar xylem of: (A)

Figure 1. A. Outline map of China showing province position with box showing border area

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

710

726

Plate I. Botryopteris multifolia sp. nov. from the Lopingian of China. IC-inner cortex; LT-leaf 711 trace; OC-outer cortex; P-petiole; Ra-rachis; RT-root trace; S-stele. A. Cross section of stem 712 713 at a distal level (peel L 8-2) showing tissue overview with 5 leaf traces (arrows) in the inner cortex and one petiole base (P). Slide: WP2-0641; Scale bar = 2mm. B. Cross section of stem 714 715 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 = 2mm. C. Detail of the central part of stem of Plate I, A showing divergence of leaf traces 717 (numbered 0 to 6), short arrows indicate protoxylem strands. The long arrow indicates the 718 719 taphonomic displacement of leaf trace 1. Slide: WP2-0641; Scale bar = 1 mm. D. Central part of the cauline stele, showing parenchyma cells (arrowed). Slide: WP2-0642; Scale bar = 200 720 721 µm. E. Longitudinal section through cauline stele, showing multiseriate scalariform thickening on the walls of large tracheid (arrowed). Slide: WP2-0648; Scale bar = $100 \mu m$. 722 723 Plate II. Botryopteris multifolia sp. nov. from the Lopingian of China. A. Cross section of part 724 725 of stem at a lower level (peel L 12-1) than that of Plate I, C showing divergence of leaf traces.

Slide: WP2-0636; Scale bar = 1mm. B. Cross section through the cortex, showing outer zone

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

733

Plate III. Botryopteris multifolia sp. nov. from the Lopingian of China. A, B. Cross sections 734 735 of cauline stele showing leaf trace formation. A. Protoxylem strand (arrowed) appearing at the edge of cauline stele. Slide: WP2-0640; Scale bar = $200 \mu m$. B. Beginning of leaf trace 736 bulging with metaxylem tracheids added to the outside of the protoxylem strand (arrowed). 737 738 Slide: WP2-0642; Scale bar = $200 \mu m$. C to F: cross sections of leaf traces with their adaxial face down. C, D. Leaf traces in the inner cortex. C. Reniform leaf trace just departed from the 739 cauline stele; the lateral arms are connected with the median arm. Slide: WP2-0635; Scale bar 740741 $= 200 \,\mu\text{m}$. D. Leaf trace, a little farther away from the stele, with the left lateral arm connected with the median arm, while the other is now free. Slide: WP2-0639; Scale bar = 742 743 200 µm. E. Leaf trace farther away in the inner cortex than that in D. In each area between the lateral and median arms a mass of sclerenchyma cells occurs (arrowed). Median arm with 744 a single protoxylem strand. Slide: WP2-0639; Scale bar = $200 \mu m$. F. Cross section through a 745petiolar base. The median xylem arm is very short and wide and there are two protoxylem 746strands (arrowed). Slide: WP2-0642; Scale bar = $500 \mu m$. G. Cross section of a free petiole 747 showing the forked lateral arms of xylem bundle (arrowed). Slide: WP2-0643; Scale bar = 748

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

751

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

757

Plate V. Botryopteris multifolia sp. nov. from the Lopingian of China. A. Longitudinal section 758 through the stele (St) and a leaf trace (LT), showing the small angle between them. Slide: 759 760 WP2-0648; Scale bar = 200 μ m. B. Oblique cross section through the stem, showing a leaf trace in the outer cortex at a high angle to the cauline stele. Slide: WP2-0639; Scale bar = 200761 μm. C. Cross section through stem and rachis showing the multicellular, multiseriate 762 763 trichomes. Slide: WP2-0645; Scale bar = $200 \mu m$. D. Cross section through stem showing the dense multicellular, multiseriate trichomes. Slide: WP2-0639; Scale bar = $200 \mu m$. E. Cross 764 765 section through stem showing root trace (arrowed) diverging from a leaf trace (LT) in the inner cortex. F. Root trace in cross section. Slide: WP2-0643; Scale bar = $200 \mu m$. 766 767 Plate VI. Shuichengella primitiva Li from the Lopingian of China. A. Leaf trace in the inner 768cortex showing an adaxial median bulge with one protoxylem (black arrow) and two 769

protoxylem strands (white arrows) near the lateral ends. B. Leaf trace in the middle cauline

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