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

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ABSTRACT

We describe a new species of the Palaeozoic fern genus *Botryopteris* in volcanic tuffs from the Lopingian (upper Permian) aged Junlian Formation in SW China’s Sichuan Province. The species has a large stem and stele compared to those of some other species of the genus. Xylem strands of the leaf trace and rachis are “ω”-shaped in cross section and comprise two 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 parenchymatized protostele. Several mesarch protoxylem strands, decurrent from leaf traces, 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, multicellular trichomes. *Botryopteris multifolia* sp. nov. represents the stratigraphically youngest known species of the genus and has a combination of derived evolutionary characteristics including its large stem size, parenchymatized protostele, elaborate trichome structure, roots originating from leaf traces, and the construction of xylem strand of the leaf 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 Pennsylvanian botryopterids from Euramerica. Finally, we consider the evolutionary implications of features shared between Permian members of the botryopterids and catenalean-type plants including members of the Osmundales stem group family Guaireaceae (*Shuichengella*, *Zhongmingella*, *Tiania*) and the enigmatic early ferns *Rastropteris* and *Catenopteris*.

Keywords: Botryopteridaceae, fern, anatomy, Xuanwei Formation, Lopingian, volcaniclastic tuff

1. Introduction

The Lopingian (upper Permian) sedimentary successions in southern Sichuan, western 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 occurrences of impression-compression fossil plant species (e.g., Zhao *et al*., 1980; Zhu *et 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 represent the stratigraphically youngest Palaeozoic “coal measures” wetland plant 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 preserved flora comprises sphenophytes (Wang *et al*., 2003, 2006), Osmundales (Wang *et al*., 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*., 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 floras from other areas (Wang et al., 2014b). They also provide insights into floristic change resulting from climate and environmental perturbations in the run-up to the end Permian mass extinction event (e.g., Neregato *et al*., 2016).

The genus *Botryopteris* was established by Renault (1875) and an important anatomical feature is its “ω”-shaped xylem strand in the rachis of some of the most advanced species (Galtier and Phillips, 1996). As currently characterized, the genus contains 12 species ranging stratigraphically from the Mississippian to Permian, with most known from the Pennsylvanian, largely coinciding with coal-ball type of preservation in Euramerica (Galtier and Phillips, 1996). To date, only four species of *Botryopteris* have been reported from the Permian, namely *B. tridentata* (Felix) Scott from volcaniclastic sediments from the Cisuralian of North China (Hilton et al., 2001), *B. nollii* Röβler et Galtier from the Permian of Brazil (Röβler and Galtier, 2003), and *B*. sp. 1 and sp. 2 from Cisuralian (lower Permian) aged coal balls in China (Wang et al., 2009). In the present paper, we report a new species of *Botryopteris* preserved in volcaniclastic tuffs from the Lopingian of southwestern China that has a complex organization of its foliar xylem only comparable to that known in some of the most advanced species of this genus (Fig. 1). We also use this as an opportunity to evaluate the other species of the genus from the Permian of China, to consider evolutionary trends within the genus and their relationships with other Palaeozoic fern groups.

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

3. Systematic Palaeobotany

Family Botryopteridaceae Renault

Genus *Botryopteris* Renault, 1875

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

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

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

Type locality: Junlian, Sichuan Province.

Geological horizon: Junlian Formation.

Stratigraphic age: Lopingian (upper Permian).

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

Specific diagnosis: Stem up to 17×11mm in diameter. Parenchymatized protostele about 2 mm in diameter with small parenchyma cells dispersed among the tracheids, more densely 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 thickening/pitting. Cortex consisting of parenchyma cells and divided into inner and outer cortex. Outer cortex up to 1.6 mm thick and divided into two zones; cell walls of the outer zone are thicker than those of the inner zone. Inner cortex, slightly broader than the outer 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, multicellular trichomes (up to 350 µm thick and 1 mm long). Leaf traces diverge helically (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 first reniform with adaxial protoxylem tracheids and parenchyma, becoming “ω”-shaped (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 strand is slender, up to 1.9 mm tangentially and 0.7 mm radially with much longer lateral 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 two lateral protoxylem strands. Xylem strand consists essentially of one or two rows of (80–130 µm) broad metaxylem tracheids. Primary pinnae nearly borne oppositely on the rachis. In pinna trace formation, protoxylem in one lateral xylary arm of the rachis divides and the tip crooks out and passes off as a pinna trace. Protoxylem strands of the median arm are not involved in the process of pinna trace emission. Root trace xylem originating from the lateral side of leaf traces within the stem cortex.

4. Description

4.1. Stem size and vertical changes

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

4.2. Stele

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

Protoxylem in the stem occurs as a few strands, at the margin of the stele, in exarch to commonly mesarch position (Plate I, C; Plate II, A; Plate III, A, B). Metaxylem tracheid size in this stem increases centripetally from 20~50 to 70~90 (occasionally up to 120) μm. In cross section, tracheids are nearly isodiametric and slightly elongated radially. In the outer part of the stele, tracheids are arranged tightly but in the centre of the stele, they are arranged loosely, and very small parenchyma cells (20 x 35 to 30 x 50 μm in diameter) are dispersed among the tracheids (Plate I, C, D). Parenchyma cells between tracheids are oblate (Plate I, D). According to the terminology of Schmid (1982), the stem would be called as a parenchymatized protostele. Multiseriate scalariform thickenings/pittings occur on the tracheid walls (Plate I, E).

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

4.3. Cortex

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

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).

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).

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 parenchyma cells, is round and rather large, with a diameter up to approximately 200 µm (Plate I, C). At the level where the leaf trace sepatates from the cauline stele, it is nearly reniform with its adaxial side slightly depressed showing very small tracheids and parenchyma cells (5, 6, Plate II, A; Plate III, C). The xylem strand is 750 µm wide and 400 µm thick, its two lateral arms enroll and connect with the median arm. At more distal levels the xylem strand of the leaf trace is tangentially extended, up to 0.85 mm wide, but the radial thickness is approximately 270 µm. At this level the lateral arms of the xylem strand are thinner and nearly connected with the median arm. The tip of the median arm flares laterally; the areas surrounded by the lateral and median arms are filled with small parenchyma cells

(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 (Plate III, E), the leaf trace is typically "ω"-shaped, exceeding 1 mm wide, and the two areas between the lateral and median arms are filled with a mass of sclerenchyma cells replacing the parenchyma (see also trace 5 in Plate I, C; 7–9 in Plate II A). The sclerenchyma cells are typically 20~30 μm in diameter and have cell walls that are 5~6 μm thick and poorly preserved (Plate III, E). At this stem level the median arm shows a single adaxial protoxylem area. Still more distally, the tangential width of the leaf trace increases due to enlarging of 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 notable that the median arm becomes rectangular with two protoxylem strands (arrows, Plate III, F).

Leaf traces diverge helically and the stem shows many leaf traces in each cross section (Plate I, A, B). The leaf traces are mainly distributed in the inner cortex where they number 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 are 6 new leaf traces (LT 5 to 0) that diverge from the cauline stele within a vertical distance of ca. 1.2 mm; therefore the length of the internode of the stem is about 0.2 mm.

Comparison of the successive cross sections in ascending order allowed us to interpret the phyllotaxis of this fern. On the more proximal section (on Plate II, A) there are two bulging/incipient leaf traces (numbered 3 and 4) and the older leaf traces (5 to 9) within the inner cortex. Higher up, on the section on Plate I, C, the leaf traces 7 to 9 are not visible because they have already diverged within the outer cortex; however 4 to 6 are still present in the inner cortex together with the new leaf trace 3 which separated from the stele; the younger leaf traces (2, 1 and 0) should be bulging from the stele, but leaf trace 1 has been certainly broken and displaced and thus appearing free. These two sections support a phyllotactic spiral with leaf trace (0) as the youngest. This is confirmed in the distalmost sections that are not illustrated here. This trace (0) is diverging between leaf traces 3 and 5, in the position where leaf trace 8 has been diverging within the cortex (cf. Plate II, A); these observations suggest a 3/8 phyllotaxis.

Leaf traces pass through the inner cortex at a low angle of about 10° (Plate V, A). However, in the outer cortex, the angle becomes higher. In the cross section of the stem, leaf traces are in an obliquely longitudinal section and cell wall thickenings/pitting are exposed (Plate V, B which corresponds to the departing leaf trace 8 also illustrated in Plate II, A). When entering the petiole base, the angle of the leaf trace becomes low again. Thus, in the cross section of the stem, the petiole trace is also in a cross section and tracheids are isodiametric. Like in the stem, the walls of the large tracheids of the leaf trace possess multiseriate (up to four seriate) thickenings/pitting.

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 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 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 crooked area of xylem then separates as a small C-shaped strand, quickly becoming tridentate, which corresponds to a primary pinna trace (arrows, Plate III, H; Plate IV, B). In fact, two lateral traces are detached nearly at the same level (about 0.3 cm above petiole origin), thus the primary pinnae are sub-opposite on the rachis.

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.

4.6. Trichomes

Trichomes are distributed across the entire surface of the stem (Plate I, A; arrows in Plate 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 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 some places but few in others. Seen in cross section, individual trichomes consist of nearly isodiametric cells with diameters of 20~50 μm (Plate V, C). In longitudinal section, trichome cells are longitudinally elongated, rectangular, polygonal or fusiform, with variable lengths up to 300 μm or more (Plate V, D).

4.7. Adventitious roots

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 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. In the cauline cortex, root traces extend nearly horizontally or obliquely. In cross section, roots are nearly round or elliptical, with diameters of approximately 400~500 μm. The stele 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 in color (Plate V, F). Individual cells are longitudinally elongated. When root traces have diverged from the stem, their size is nearly the same as those in stem cortex.

5. Discussion

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 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: (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 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 to mainly mesarch maturation; (4) xylem strands of the leaf traces and the petiole/rachis are “ω”-shaped in cross section, with two long lateral arms and a shorter median arm; (5) primary 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 lateral side of the departing leaf trace in the cortex.

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. nollii* is large, up to 11 mm in diameter, and has leaf traces that are obviously “ω”-shaped just 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 sclerenchyma strands. In addition, the surface of the stem of *B. nollii* is also covered by multiseriate and multicellular trichomes. Another important similarity concerns the initiation 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 the inner cortex of the stem: in the Chinese species, it is broader (2 mm or more in thickness) and contains five to seven leaf traces, while in *B. nollii*, the inner cortex is narrower, less than

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

The type species *Botryopteris forensis* Renault from the Pennsylvanian of France (Renault, 1875; Galtier and Phillips 1977) and contemporaneous specimens from North America (Mamay and Andrews, 1950; Phillips, 1961, 1974; Rothwell, 1991) have stems up to 10 mm in diameter and leaf traces that typically become "ω"-shaped just after diverging from the cauline stele as they do in the present species. However, *B. forensis* differs in its solid protostele that is up to 2.7 x 2 mm in diameter. The surface of its stem is also covered with trichomes but these are typically "equisetiform" hairs with a broad, multiseriate basal 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 those of the present species and *B. nollii* where they are not known to occur on rachises. Furthermore, the “ω”-shaped foliar xylem strand of *B. forensis* is clearly different (Fig. 4 E), being nearly round in cross section with the median arm at least as long as the lateral arms, 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 absent in other species including that documented here. Much more important is the 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 trace formation. This is different from that of *B. forensis* (Fig. 4 E) and in two other 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. respectively. In these three Euramerican species, the median arm is involved in pinna trace 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 two arms during and/or immediately following trace departure” (Galtier and Phillips, 1977, Fig. 1, 4). This “bridge” is shown in Fig. 4 D, E (asterisk). The reconstruction of the rachis xylem of *B. multifolia* showing pinna trace emission in Figure 3 must be compared to equivalent reconstructions for *B. forensis* and *B. renaultii* in Galtier and Phillips (1977, Fig. 1) in order to be understood.

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

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

5.2. Permian species diversity of Botryopteris

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

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

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

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

5.4. Evolutionary implications

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 leads us to consider the evolutionary trends among the botryopterids and the possible relationships of these plants with other contemporaneous Permian ferns. Comprehensive analysis of evolutionary trends within the genus should include consideration of both vegetative and fertile characters (Galtier and Phillips 1996), but as we only have information 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 elliptical to elaborated xylem geometries; (2) changes in the pattern of pinna trace emission; (3) changes in size and organization of the stele from solid to parenchymatized protostele and to siphonostele; (4) changes in cauline branching with rare dichotomous branching and 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 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) and to extend this with the species now known from the Permian.

The stratigraphically oldest species of *Botryopteris*, *B. antiqua* Kidston, occurred in the Tournaisian stage of the Mississippian (Figure 2). During the Pennsylvanian, the genus appears to have diversified rapidly and attained its acme, with more than ten species known 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. nollii* and *B. multifolia*; see above). Unfortunately the precise age of *B. nollii* within the Permian is unknown (Röβler and Galtier, 2003). *B. tridentata* and *B*. cf. *forensis* are important as they represent Cisuralian (lower Permian) aged occurrences of species previously known from the Pennsylvanian in Europe and North America extending their 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, 2007). *Botryopteris multifolia* represents the first definite evidence of the genus persisting into the Lopingian and represents the stratigraphically youngest species of the genus.

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

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

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

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

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*.

Features of root origin: Galtier and Phillips (1977, page 2) considered that in *Botryopteris* "…common traces divided basally into a petiolar trace and one or two lateral 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 habit differences.

In summary, the new species *B. multifolia* exhibits significant advanced features concerning its parenchymatized stele, leaf trace origin, rachis xylem with a short median arm 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. Phillips (1974) and then Galtier and Phillips (1996) suggested the occurrence of at least four phyletic lines of *Botryopteris* representing a range between the basal Mississippian (*Botryopteris antiqua* type) and the late Pennsylvanian (with *B. pseudoantiqua, B. renaultii* and *B. forensis*). We now know that *B. tridentata* (attributed by Phillips to a distinct "*ramosa* 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-forensis* line". Finally, present data suggest that the two Permian species *B. nollii* and *B. 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 *B. forensis* of which large specimens, laminate foliage and fertile parts are known. Additional information is needed before we may clarify the origin of this phyletic line from their Carboniferous ancestral stock.

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

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

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

Botryopteris multifolia displays similarity with some stratigraphically older ferns, such as *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 maturation, the configuration of leaf trace xylem changes from an initial reniform strand with 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 strand with two adaxially recurved lateral arms and a number of adaxial ridges. *B. multifolia* 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 initial reniform strand with an endarch protoxylem located always medianly on the adaxial 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* is a small bodied and perhaps epiphyllous fern without petiole mantle, petiole and rachis 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).

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; Phillips, 1974). It resembles to *B. multifolia* in its small size, protostele, cross-sectionally 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 uniseriate scalariform thickenings, a prominent decurrent parenchymatous band adaxial to the leaf traces, fewer leaf traces in cauline cortex, and slight curvature of the leaf trace. In contrast, *B. multifolia* possesses a parenchymatized protostele with multiseriate scalariform tracheidal thickenings/pittings, more leaf traces in cauline cortex, strong curvature of the leaf trace with a short but conspicuous median adaxial arm.

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

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Explanation of figures and plates

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

Figure 2. Stratigraphic distribution of species of *Botryopteris*, showing the evolutionary changes in the shape of the rachis xylem strand as seen in cross section (modified from 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 and Galtier; (7) *B. mucilaginosa* Kraentzel; (8) *B. tridentata* (Felix) Scott; (9) *B. cratis* Millay 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* Röβler et Galtier. Abbreviations: Guad. = Guadalupian; Loping. = Lopingian.

Figure 3. Reconstruction of *Botryopteris multifolia* sp. nov. rachis xylem showing pinna trace 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 by Galtier & Phillips (1977, Text-fig.1).

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

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.

Plate I. *Botryopteris multifolia* sp. nov. from the Lopingian of China. IC-inner cortex; LT-leaf trace; OC-outer cortex; P-petiole; Ra-rachis; RT-root trace; S-stele. A. Cross section of stem 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 at a basal level (peel P/Top 2) showing tissue overview with 6 leaf traces in the inner cortex (black arrows) and one in the outer cortex (white arrow). Slide: WP2-0633; Scale bar = 2 mm. C. Detail of the central part of stem of Plate I, A showing divergence of leaf traces (numbered 0 to 6), short arrows indicate protoxylem strands. The long arrow indicates the 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 μm. E. Longitudinal section through cauline stele, showing multiseriate scalariform thickening on the walls of large tracheid (arrowed). Slide: WP2-0648; Scale bar = 100 μm.

Plate II. *Botryopteris multifolia* sp. nov. from the Lopingian of China. A. Cross section of part 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 μm. C. Enlargement of the inner cortex, showing cells with dark-colored content and with tylose-like contents (arrowed). Slide: WP2-0639; Scale bar = 50 μm. 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 μm.

Plate III. *Botryopteris multifolia* sp. nov. from the Lopingian of China. A, B. Cross sections of cauline stele showing leaf trace formation. A. Protoxylem strand (arrowed) appearing at the edge of cauline stele. Slide: WP2-0640; Scale bar = 200 μm. B. Beginning of leaf trace bulging with metaxylem tracheids added to the outside of the protoxylem strand (arrowed). Slide: WP2-0642; Scale bar = 200 μm. 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 cauline stele; the lateral arms are connected with the median arm. Slide: WP2-0635; Scale bar = 200 μm. 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 = 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 a single protoxylem strand. Slide: WP2-0639; Scale bar = 200 μm. F. Cross section through a petiolar base. The median xylem arm is very short and wide and there are two protoxylem strands (arrowed). Slide: WP2-0642; Scale bar = 500 μm. G. Cross section of a free petiole showing the forked lateral arms of xylem bundle (arrowed). Slide: WP2-0643; Scale bar =

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.

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 µm. B. Departure of subopposite pinna traces (arrows) from the rachis xylem. Slide: WP2-0646; scale bar =500 µm.

Plate V. *Botryopteris multifolia* sp. nov. from the Lopingian of China. A. Longitudinal section through the stele (St) and a leaf trace (LT), showing the small angle between them. Slide: WP2-0648; Scale bar = 200 µm. 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 = 200 µm. C. Cross section through stem and rachis showing the multicellular, multiseriate trichomes. Slide: WP2-0645; Scale bar = 200 µm. D. Cross section through stem showing the dense multicellular, multiseriate trichomes. Slide: WP2-0639; Scale bar = 200 µm. E. Cross 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 µm.

Plate VI. *Shuichengella primitiva* Li from the Lopingian of China. A. Leaf trace in the inner cortex showing an adaxial median bulge with one protoxylem (black arrow) and two 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: GP_2377-3-2 (8-6), GP_2377-3-2 (7-4); Scale bar = 200 µm.