Research paper

**Diodonopteris**, a new genus of the Paleozoic leptosporangiate fern family Botryopteridaceae, from the lower Permian of Shanxi Province, North China

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**A B S T R A C T**

Anatomically preserved botryopterid specimens from Cisuralian (early Permian) aged coal balls in Shanxi Province, North China are investigated. Stems are relatively small, branch dichotomously, and possess a haplostele with metaxylen tracheids showing uniseriate scalariform thicknesses. Protoxylem groups are associated with the forming of the petiolar trace, and a parenchyma plate appears in the process of separating petiolar traces. The cortex consists of three parts, with inner and middle parenchymatous zones and an outer sclerenchymatous zone. Stems are radially organized and bear helically arranged petioles. Petioles extend from the stems in various orientations while adventitious roots extend through the cauline cortex perpendicular or oblique to the stem. Associated rachides are D-shaped in cross section and the xylem is slightly to conspicuously adaxially curved with 1 protoxylem ridge at each lateral margin. Differences with previously known genera of Botryopteridaceae lead to creation of new genus, Diodonopteris gracilis Ma et al. gen. nov. et sp. nov. that demonstrates features that overlap to some extent with those of previously known genera within Botryopteridaceae. The habit and growth forms of *D. gracilis* are considered. *D. gracilis* represents by far the best known plant of Botryopteridaceae recognized from the Cathaysian Flora.

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1. Introduction

Botryopteridaceae are a group of early leptosporangiate ferns that represented an important component of wetland vegetation during the Carboniferous and Permian. Members of the family are characterized by their more or less adaxially curved xylem configuration in their rachides and petioles. This is distinct from other contemporaneous early leptosporangiate ferns in which the rachides and petiole xylem strands are typically abaxially curved as seen in members of the Anachoropteridaceae, Kaplanopteridaceae, Psalixochlaenaceae and Sermayaceae (Tomescu et al., 2006; Taylor et al., 2009; Galtier and Phillips, 2014).

Botryopteridaceae are mainly based on anatomically preserved specimens and as presently characterized include three genera, namely *Botryopteris* Renault, *Rhabdoxylon* Holden and *Catenopteris* Phillips et Andrews (Andrews et al., 1970; Taylor et al., 2009). Recently, however, a fourth genus, *Sonapteris* Plenica et al. (2005), based on three-dimensionally compressed fertile specimen was also included within this family. *Botryopteris* is the type genus of the family and is the most commonly occurring within it (Taylor et al., 2009). Among the three genera based on anatomically preserved specimens, *Botryopteris* was established in 1875 by Renault with Botryopteris forensis from France as the type species (Renault, 1875). *Rhabdoxylon*, with three species of which *Rhabdoxylon dichotomum* is the type species, was established in 1960 by Holden, while *Catenopteris* was established in 1966 by Phillips and Andrews and includes the single species *Catenopteris simplex*.


There are totally 10 species of *Botryopteris* that have been identified on the basis of cauline and rachis anatomies (Rößler and Galtier, 2003). *Rhabdoxylon* is a small plant, the conspicuous character of it is a simple stem anatomy comprising a circular protostele with isotomous dichotomous branching. There is only one protoxylem strand on the adaxial side of the metaxylem of petiolar trace, petiole and rachis (Holden, 1960). *Rhabdoxylon* is rare in comparison to *Botryopteris* which is recorded from vegetative and fertile specimens.

*Catenopteris* has adaxially curved and slightly C-shaped xylem strands in its petiolar traces and petioles. No clearly defined protoxylem groups are present in the cauline stele. The cauline metaxylem tracheid walls have uniseriate scalariform thickenings (Phillips and Andrews, 1966).

The majority of previous studies on Botryopteridaceae have been undertaken on fossil specimens from the Euramerican Flora. Besides, a single species, *B. nollii* Rößler et Galtier, was well documented from the South American Gondwana Flora (Rößler and Galtier, 2003). Early leptosporangiate ferns in the Cathaysian Flora are less well known than those from the Euramerican and the Gondwana Floras. From the Cathaysian Flora only some isolated stems and rachides have been reported to date. Hilton et al. (2001) reported isolated rachides of *Botryopteris* that were identified as *B. tridentata*. These specimens occur within tuffaceous sediments of the Taiyuan Formation of Yangshuling mine in Hebei Province, North China, and are of Cisuralian (early Permian) age. From coal balls occurring in the No. 7 coal seam of the Xishan Coalfield in Shanxi Province, North China, Wang et al. (2009) illustrated and described isolated rachides of *Botryopteris* sp. 1 and B. sp. 2, *Anachropteris* cf. *clavata* Graham and *Etapteris* cf. *scottii* Bertrand, and Ma et al. (2016) reported the first stems of the early leptosporangiate ferns in the Cathaysian Flora, i.e.*Rhabdoxylon taiyuanense* Ma et al. Furthermore, several pinnae of *Anachropteris* sp. were described from an Upper Permian permineralized plant assemblage in volcanioclastic tuff from the Xuanwei Formation, Guizhou Province, southern China (Hilton et al., 2004). However, early leptosporangiate taxa are very rare and have only been described from fragmentary specimens in China and as such little is known about the relationship between stems, rachides and fertile parts, and habits of these plants within the Cathaysian Flora. As Botryopteridaceae from Euramerica and Gondwana are mainly Carboniferous in age and only a few are of Permian age (Barthel, 1976; Rößler and Galtier, 2003), finding botryopterid ferns in the Permian Cathaysian Flora will be of great significance and will present a unique opportunity to understand the floral composition and taxonomic diversity within various ecological and stratigraphic contexts.

2. Locality information

Specimens occur in coal balls collected from an outcrop of the No. 7 coal seam, located near Xiedao village, Xishan Coalfield, about 15 km west of Taiyuan City, Shanxi Province, North China (Fig. 1). Coal balls from this locality preserve a diverse wetland fossil plant community and occur in the upper part of the Taiyuan Formation (Fig. 2) (Wang, 1989; Tian et al., 1996; Wang et al., 2009). The coal seam bearing the coal balls was deposited during the Asselian–Sakmarian stages of the Cisuralian (early Permian) based on fusulinid biostratigraphy (Tian et al., 1996; Wang et al., 2009).

3. Materials and methods

The specimens occur in coal ball 72001 which was cut with a rock saw lubricated by water using a 30 cm diameter and 2 mm thick blade. The coal ball was cut into six parts with cut surfaces labeled.
from A to J. The initial cuts revealed numerous fossils of Botryopteridaceae, including stems with attached petioles and petiolar bases as well as isolated petioles, rachides and sporangia. As the specimens share similar features with each other and are found in close association, they are here described as a single species. Five stems bearing lateral petioles and roots are present and numbered S1–S5 of which S4 and S5 were revealed in longitudinal and oblique longitudinal sections, while S1, S2 and S3 were revealed in cross and oblique cross sections. Individual blocks were re-oriented and specimens were cut again to reveal the fossils in transverse and longitudinal sections where possible.

Serial acetate peels were made according to the method of Joy et al. (1956) and Galtier and Phillips (1999). Cut surfaces were successively ground on a glass plate using No180 and No600 carborundum grit with ground surfaces then being etched using 5% dilute hydrochloric acid for approximately 5 s to remove calcite. Peels were then pulled off the specimen surface and mounted on glass slides using Canada Balsam and a cover slip.

To enable reconstruction of the specimens, line drawings of individual peels were made using a camera lucida, and peels and slides were studied under reflected and transmitted light using a Motic stereoscope and an Olympus BH2 transmitted light microscope. Photographs were made using a Nikon 4500 digital camera mounted on microscope eye pieces. Plates and line drawings were processed using Corel Draw v.16.0 and Adobe Photoshop CS 6.0 to edit images (adjusting brightness, contrast, tone, cropping).

The remaining parts of the coal ball and all prepared peels and slides are deposited in National Museum of Plant History of China (NMPHC), Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing, China.

4. Systematics

Family: Botryopteridaceae Renault, 1883
Genus: Diodonopteris Ma et al. gen. nov.
Type species: Diodonopteris gracilis Ma et al. gen. nov. et sp. nov.

Generic diagnosis:
Ferns with isotonic dichotomous branching and protostelic stems bearing helically arranged fronds and diarch adventitious roots. Cortex of the stem divided into the sclerenchymatous outer part and parenchymatous inner part. Metaxytem tracheid walls of the stem possessing uniseriate scalariform thickenings. Tracheid diameter of the petiolar trace and petiole conspicuously smaller than that of the stem. Xylem strand of the rachis with two protoxylem groups on the adaxial side.

Etymology: Diodon (Greek) — two teeth, referring to the two teeth-like protoxylem groups on the adaxial side of rachis xylem; opteris — fern.

Remark: According to Stidd’s definition (Stidd, 1971), the petiole is the axial portion of the frond extending from the stem to the first lateral appendage, i.e. primary pinna. The main or principal rachis is the axial portion of the frond extending from the first lateral appendage to the distal end of the frond and bearing successive lateral appendage, i.e. primary pinna. The pinna rachis is the central axis of a pinna and may be of primary, secondary, or tertiary order. In the present specimens, the term rachis or rachides are used because it is difficult to tell the order of them due to their isolated preservative condition.

Diodonopteris gracilis Ma et al. gen. nov. et sp. nov. (Fig. 3 and Plates I to V)

Holotype: Stem 1 (S1) which exhibits well-preserved stem, cauline branching and petioles (Fig. 3; Plate I, Plate II, 6, 7; Plate III, 4, 6; Plate IV, 4). Surface numbers: 72001 A, 72001 B, 72001 D, 72001 F, 72001 H, 72001 J; Peel numbers: 72001A/1 to 6, 72001A-1/1 to 44, 72001F/1 to 43, 72001H/1 to 36, 72001J/1 to 46. Slide numbers: WP11–0353, WP11–0357, WP11–0360, WP11–0363, WP11–0366, WP11–0371, WP11–0372, WP11–0374, WP11–0376 to WP11–0380, WP11–0382 to WP11–0384.

Paratype: Stem 2 (S2) which exhibits well-preserved stem and petioles (Plate II, 1, 2; Plate III, 1–3, 7–8, Plate IV, 5). Surface numbers: 72001 F, 72001 H, 72001 J; Peel numbers: 72001F/30 to 43, 72001H/44 to H/1, 72001J/1 to 43. Slide numbers: WP11–0366, WP11–0371, WP11–0381, WP11–0385 to WP11–0390.

Repository: All preparations are from the same specimen (Coal ball 72001) and are stored in the National Museum of Plant History of China (NMPHC), Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing.

Type locality: Xishan Coalfield in Shanxi Province, North China.

Geological horizon: No. 7 coal seam, the upper part of the Taiyuan Formation.

Age: Asselian–early Sakmarian; Cisuralian (early Permian).

Etymology: Specific epithet refers to the feature of diminutive stems. Gracilis — Latin word, means “slender”.

Specific diagnosis:

Stem slender with the diameter usually less than 2 mm and with isotonic dichotomous branching. Haplostele with tracheid diameter decreasing outward. A single protoxylem strand located at c. 1/3 diameter of the stele and associated with petiolar trace formation. A plate of parenchymatous cells present between the incipient petiolar trace and the cauline stele. Uniseriate scalariform thickenings present on cauline tracheid walls. Inner cortex consisting of tangentially elongated and contiguously arranged parenchymatous cells; middle cortex of larger, isodiametric and more or less loosely arranged parenchymatous cells;
Plate I. *Diodonopteris gracilis* gen. nov. et sp. nov. Coal ball 72001, Stem S1 – Holotype. Cross sections of Stem S1 at different levels. All scale bars = 200 μm.

1. Basal part of the stem showing a petiolar trace (PT) is diverging from the cauline stele (St) and an adventitious root trace (RT). Slide WP11–0380.
2. Stem with equal dichotomous branching to produce daughter Stems 1 (S1–1) and 2 (S1–2). Slide WP11–0363.
3. Level higher than that shown in 2, showing the daughter Stem 1 (S1–1). Note a diverging petiolar trace (PT). Slide WP11–0384.
4–6. Levels of daughter Stem 1 (S1–1) higher than that shown in 3, showing different stages of an obliquely upward extending petiolar base (P).
4. Petiolar base (P) separating from the stem (left), but the both shares the cortex. Slide WP11–0372.
5. The level higher than 4, showing a petiole (P) separating from the stem (left). Slide WP11–0374.
6. The level even higher than 5, showing the petiole (P) has formed completely; arrows indicate the epidermis. Slide WP11–0374.
outer cortex of sclerenchymatous cells. Xylem of petiolar trace and petiole usually with one protoxylem group adaxially. Petioles round with the diameter up to 1 mm. Metaxylem tracheids of petiolar traces and petioles conspicuously smaller than those of the stem. Adventitious roots diverging from the periphery of cauline stele or abaxial side of the incipient petiolar trace and sparse. Rachis D-shaped, up to 500 μm in maximum width. Xylem of rachis slightly to conspicuously adaxially curved with 1 protoxylem group at each lateral margin.
5. Description

5.1. Gross morphology

Stems have only been found incomplete with preserved lengths of 45 mm for S1 (as reconstructed in Fig. 3), 22 mm for S2, 10 mm for S3, 6 mm for S4 and 12 mm for S5. Individual stems are slender with diameters up to 1.7 mm and branch by equal dichotomy. They vary in size and shape to some extent in cross section (Plate I, 1–6; Plate II, 1–3; Plate III, 1–9). For example, in cross section the basal part of S1 is oval in shape and 1.6 × 1.1 mm in size (Plate I, 1), whereas just below the level of dichotomous branching it is larger and 2.25 × 1.25 mm (Plate I, 2), and above the level of dichotomy the resultant daughter stems are smaller with one (S1–1) being 0.9 × 1.45 mm and the other (S1–2) 1.1 × 1.5 mm (see Fig. 3). The size of S1–1 slightly increases to about 1.5 mm at a higher level and is nearly round in cross section (Fig. 3; Plate I, 4–6). In addition, stems appear to have partial taphonomically making cross sections ovate rather than round (Plate I, 1, 3; Plate III, 1–3, 7–9).

5.2. Stem morphology

Stems dichotomize equally as seen in S1 (Plate I, 2) and S5 (Plate II, 5) and petioles diverge from the stem helically. On S1, four petioles and petiole bases (p1 to p4 in Fig. 3) occur below the level of dichotomous branching and a further four (p5 to p8 in Fig. 3) are attached to the daughter branch S1–1 that has a preserved length of about 2.3 cm. Based on serial sections of S1, it is estimated that internodes between petioles are about 4–5 mm long and in S4 internode length is about 4 mm.

5.3. Stem anatomy

Stems are haplostelic and the xylem cylinder is round or oval in cross section and varies from 160 to 300 μm or more in diameter. Generally stems with a larger diameter have larger xylem cylinders and the ratio of stem diameter to xylem diameter ranges from 4:1 to 6:1 but is mostly between 5:1 and 5.5:1. No protoxylem is present in the internodal region of the xylem cylinder but is visible when petiolar traces start to arise (Plate II, 6, 7). Tracheids are usually polygonal in cross section and the largest tracheids occupy the center of the xylem cylinder where they are up to 50 × 70 μm thick, decreasing to 20–30 μm toward the margin. Tracheids possess uni-seriate scalariform thickenings on longitudinal tracheid walls (Plate IV, 1–3).

Phloem consists of 2–3 layers of small and thin-walled cells that are round or tangentially elongated and typically 15 × 20 μm in diameter, and in longitudinal section they are longitudinally elongated (Plate IV, 1). On the external surface of the phloem a more or less conspicuous dark line is present that represents a thin endodermis (Plate II, 6, 7).

Cortex is differentiated into three zones except apically where the cortex is nearly uniform. Inner cortex consists of 2 to 4 layers of tangentially elongated and contiguously arranged parenchymatous cells with the size of 15–20 × 20–30 μm in cross section (Plate I, 5, 6). Middle cortex consists of 5 to 8 layers of larger, isodiametric and more or less loosely arranged parenchymatous cells with the diameter of up to 60–70 μm in cross section. Outer cortex is as wide as the inner plus middle cortex and consists of sclerenchymatous cells with the similar shape and size as those of the middle cortex in cross section. In most of the specimens, the cell walls of the outer cortex are 5–10 μm thick and dark in color. In contrast, in smaller stems that represent distal parts or young stems, they are thinner and typically 3–5 μm thick and light colored (Plate I, 1, 3). In longitudinal section, cells of the inner, middle and outer cortex are all elongated with the length of 80–300 μm (typically from 110 to 240 μm) for the inner and middle cortex and up to 500 μm for the outer cortex (Plate II, 5; Plate IV, 1).

In some well-preserved specimens, epidermis covers the outer cortex as a single layer of small cells. In larger or more mature stems, the epidermal cells are round, elliptical or irregular in shape with size varying from 15 to 20 × 20–30 μm in diameter; these cells are not particularly distinct from the underlying ground tissue (Plate I, 6). In smaller or younger stems, or apically on the stem, epidermal cells are tangentially elongated and nearly rectangular, and are 20–25 × 35–40 μm in size in cross section (Plate II, 1). Trichomes have not been observed on most of the stem but occur apically on S2 where poorly preserved trichomes are present (Plate II, 1).

5.4. Petiolar traces and petioles

Petiolar traces are derived from a group of small tracheids, 7–8 μm in diameter, that represent protoxylem elements (Plate II, 6) and occur at about one-third diameter of stem xylem cylinder. At higher levels in the stem, the outline of the xylem cylinder becomes oval to elliptical and a 4–5 cell thick parenchymatous plate appears (Plate II, 7). The parenchymatous plate consists of small, thin-walled cells with diameters of 15–20 μm and extends across the stele and through the protoxylem strand, and separates from the stem stele with the smaller division being the petiolar trace (Plate II, 7). Petiolar traces diverge at a very narrow angle that is consistently <10° from the xylem cylinder (Plate IV, 3), so that a typical cross section of the stele displays a nearly cross section of the petiolar trace. After the petiolar trace leaves the stele, no protoxylem strand exists in the xylem cylinder of the stem until the initiation of the next successive petiolar trace.

In the cross section of the stem cortex, petiolar traces have a round or slightly tangentially elongated monarch xylem strand that is up to 150 μm in diameter. The largest metaxylem tracheids of the petiolar trace are typically smaller than those of the stem and are 25–40 μm in diameter (Plate I, 4–6; Plate II, 2). Metaxylem tracheids of the petiolar trace possess uniseriate scalariform thickening on the longitudinal walls (Plate IV, 3).

Petioles extend from the surface of stems outward in different ways. Some extend obliquely upward such as petioles 1 and 8 in S1 (see Figs. 3 and 6; Plate I, 4–6), while others extend horizontally with their distal parts bending laterally (Fig. 5; Plate III, 7–9), and some extend...
Plate III. *Diodonopteris gracilis* gen. nov. et sp. nov. Coal ball 72001. All scale bars = 500 μm.

1–3. Stem S2 – Paratype. Acropetal successive cross sections of Stem 2 (S2) showing a petiole (P) with its distal end bending downward. Slide WP11–0389.
1. The lower level showing the distal (P) and proximal portions of petiole, which means that the petiole bends downward.
2. The middle level showing that the distal portion is nearly connected with the proximal portion of petiole.
3. The upper level showing that the distal portion is connected with the proximal portion of petiole.
4–6. Stem S1 – Holotype. Acropetal successive cross sections of daughter branch 1 (S1–1) of Stem 1 (S1) showing a petiole (P) with its distal end bending downward.
4. The lower level showing the distal portion of petiole (P). Slide WP11–0378.
5. The middle level showing the distal portion of petiole (P) is connected with the proximal portion of petiole by the cortex. Slide WP11–0377.
6. The upper level showing the distal portion is connected with the proximal portion of petiole by the vascular strand (VS). Slide WP11–0377.
7–8. Stem S2 – Paratype. Acropetal successive cross sections of Stem 2 (S2) showing a horizontally extending petiole (arrows). Slide WP11–0381.
9. Stem S1 – Holotype. A horizontally extending petiole (P) of Stem 1 (S1) with its distal portion bending laterally. Slide WP11–0382.
Plate IV. *Diodonopteris gracilis* gen. nov. et sp. nov. Coal ball 72001.

1–3. Longitudinal radial section of Stem 5 (S5), Slide WP11-0392.
1. From right to left showing cauline stele (St), phloem (Ph), inner cortex (IC), middle cortex (MC) and outer cortex (OC). Scale bar = 50 μm.
2. Enlargement of 1 showing scalariform thickenings on cauline metaxylem tracheid walls. Scale bar = 30 μm.
3. Petiolar trace (PT) is diverging from the cauline stele (St) at a narrow angle. Scale bar = 50 μm.

4. Stem S1 – Holotype. Cross section of Stem 1 showing inner cortex (IC) and an adventitious root trace (RT) with its own cortex (C) located at the boundary of cauline outer cortex (OC) and middle cortex (MC). Slide WP11-0353, scale bar = 100 μm.

5. Stem S2 – Paratype. Enlargement of Plate II, 2 showing detail of a bifurcating adventitious root trace. Arrows indicate two branches of the root. Slide WP11-0388, scale bar = 100 μm.
horizontally for certain distance and then distally turn down (Fig. 4; Plate III, 1–3, 4–6). Petioles are thickest basally and decrease in size distally with petiole size smaller than the size of the parent stem. For example, petiole 8 of S1 is 1 mm in diameter at its base and the stem is 1.5 mm in diameter; petiole 4 is 0.8 mm in diameter at its base and the stem is 1.5 mm in diameter, while in S4, the stem is 0.7 mm and the petiole is 0.3 mm in diameter at its base. Usually petiole diameter varies from 1/2 to 3/5 of the stem’s diameter. Well-preserved petioles are up to 7 mm long (Fig. 4; Plate III, 7, 8). Petioles have a round or oval xylem strand that is up to 200 μm in diameter, with 1–2 protoxylem bundles on its adaxial surface. The largest metaxylem tracheids of the petiole are also smaller than those of the stem (Plate I, 5, 6; Plate III, 4). Within the
petiole the cortex is uniform or poorly differentiated into a narrow inner cortex of small parenchymatous cells and a wide outer cortex of large sclerenchymatous cells (Plate I, 5; Plate III, 1, 4).

5.5. Adventitious roots

Root traces depart from the stem stele or the abaxial side of the initiating petiolar trace. Then root traces extend outward through the cortex of the stem in a course nearly perpendicular to the surface of the stem (Plate I, 1; Plate II, 2, 4) or in an oblique course (Plate IV, 4). Root traces are not so frequently observed and only one (Plate I, 1, 4) or rarely two or more (Plate II, 2) occur in a single cross section of the stem. Root traces are round in cross section, increasing in diameter from 200 to 300 μm outward and have a diarch protostele (Plate IV, 4). Individual root traces have their own cortex when they extend through the cortex of the stem. The outer cortex consists of small, thick-walled cells and occupies about 3/4 of the entire cortical thickness of the root trace. The inner cortex consists of thin-walled parenchymatous cells. Because of the presence of thick-walled cells in outer cortex, the roots are in dark color as a whole. In rare cases, the bifurcating roots can be seen (Plate IV, 5).

5.6. Associated rachides

In the same coal ball there are many isolated rachides (= foliar member of Phillips, 1970) in close proximity to the stems. The size and shape in cross section of the rachides varies and they probably represent different orders of rachides. They are often more or less D-shaped in cross section, and up to 500 μm in maximum width (Plate V, 1–5). The central metaxylem in some rachides is 2–3 cells deep and slightly adaxially curved (Plate V, 5), while in others the metaxylem is 1–2 cells deep and conspicuously adaxially curved into a shallow C shape (Plate V, 1–4). In both cases, there is 1 minute adaxial protoxylem ridge at each lateral margin of the metaxylem and they are more or less involute (Plate V, 2–4). The largest metaxylem tracheids can be up to 60 × 80 μm and bear reticulate thickenings on the longitudinal walls. Proxoxylem tracheids are 10–15 μm in diameter. Phloem is approximately 3 cells thick and surrounds the xylem (Plate V, 1, 4, 5), but in some cases it is not preserved and replaced by a cavity (Plate V, 2, 3). The cortex is somewhat different from that of the petioles and is poorly differentiated. The outer zone consists of small and thick-walled cells with the diameter of 15–25 μm in diameter. This zone is 1–2 cells thick, but its thickness increases toward the lateral margins (Plate V, 5) and even extend into short wings in some specimens. The middle zone consists of 2–3 layers of large and thin-walled cells with the diameter of 40–50 μm. The inner zone comprises 1–2 layers of cells that are conspicuously tangentially elongated (Plate V, 5).

6. Discussion

6.1. Comparison

The present stems are small and simply constructed with a haplostele and a cylindrical petiolar xylem that is round or slightly tangentially elongated in cross section, with a single adaxial protoxylem pole. The associated rachides possess more or less adaxially curved xylem. These features bear resemblance to the Botryopteridaceae (Phillips, 1974; Taylor et al., 2009) (Table 1).

As presently characterized, the Botryopteridaceae comprise three genera that are distinguished primarily on the xylem configuration of

<table>
<thead>
<tr>
<th>Stem</th>
<th>Forked or not Cortex</th>
<th>Petiole size</th>
<th>Rachis</th>
<th>Epiphyllous shoots</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Botryopteris</td>
<td>Mostly not</td>
<td>Smaller than or same as that of petiole</td>
<td>Xylem is mostly o-shaped with 3 p.x.</td>
<td>Mostly have</td>
<td>Roßler and Galtier (2003)</td>
</tr>
<tr>
<td>Didonopteris</td>
<td>Thick-walled outer part and thin-walled inner part</td>
<td>Larger than that of petiole</td>
<td>Xylem is slightly to conspicuously C-shaped with 2 p.x.</td>
<td>Unknown</td>
<td>This paper</td>
</tr>
<tr>
<td>Rhabdoxylon</td>
<td>Yes</td>
<td>Xylem is round or tangentially elliptical with 1 p.x.</td>
<td>Xylem is round or tangentially elliptical with 1 p.x.</td>
<td>No</td>
<td>Holmes (1979)</td>
</tr>
<tr>
<td>Catenopteris</td>
<td>Uniformly thin-walled</td>
<td>Same as that of petiole</td>
<td>Xylem is round or tangentially elliptical with 1 p.x.</td>
<td>Unknown</td>
<td>Phillips and Andrews (1966)</td>
</tr>
</tbody>
</table>

Note: Simple — uniseriate scalariform thickenings; complicated — multiseriate scalariform thickenings, reticulate and/or multiseriate bordered pits; p.x. — protoxylem.
the rachis and/or petiole in cross section (Phillips and Andrews, 1966; Phillips, 1974). In Rhabdadox- lon, the xylem of the rachis and petiole is similar, i.e. round or slightly elliptical with a single adaxial protaxylem group (Holden, 1960; Dennis, 1968; Holmes, 1979). In Catenopteris Phillips et Andrews, rachides are unknown and the xylem of the petiole is adaxially curved shallow C-shaped with smaller (presumably protoxylem) tracheids present on the concave surface (Phillips and Andrews, 1966). The xylem configuration of the rachis, petiolar trace and petioles in Botryopteris Renault is diverse. In Botryopteris antiqua Kidston, the oldest (Visean) and presumably most primitive species within the genus, the xylem of the petiolar trace is tangentially elliptical with two mesarch protoxylem groups, while in the petiole and rachis 1 or 2 endarch protoxylem groups are situated at the adaxial surface of the tangentially elliptical xylem (Phillips, 1970, 1974). In Bashkirian (Westphalian A) aged species, including Botryopteris hirsuta (Williamson) Scott, Botryopteris ramosa (Williamson) Scott, Botryopteris scottii Holmes, Botryopteris dichotoma Holmes et Galtier and Botryopteris mucilaginosa Kraenzel, the xylem of petiolar trace, petiole and rachis is usually tangentially elliptical with 1 (petiolar trace and petiole) or 3 (rachis) adaxial protaxylem groups (Phillips, 1970, 1974; Holmes and Galtier, 1983; Holmes, 1984). In even younger (later than Westphalian A) species of the genus, including B. tridentata (Felix) Gothan, Botryopteris cratis Millay et Taylor, Botryopteris renaultii Bertrand et Cornaille, B. forensis Renault and B. nollii Rößler et Galtier, the metaxylogy of rachis is elaborated to three adaxially directed xylem arms that are α-shaped and terminated with protoxylem groups (Galtier and Phillips, 1977; Millay and Taylor, 1980; Rothwell and Good, 2000; Rößler and Galtier, 2003). The petiolar trace of B. tridentata is slightly adaxially curved with 2 protaxylem groups at its concave side (Rothwell and Good, 2000). The xylem configuration of petiolar trace and petiole is unknown in B. cratis and B. renaultii (Galtier and Phillips, 1977; Millay and Taylor, 1980). In B. forensis and B. nollii, petiolar trace and petiole possess also α-shaped xylem configuration, same as that in the rachis.

Apart from the xylem configuration of the rachis and/or petiole, other characters are also of taxonomic significance in recognition of genera within the Botryopteridaceae. Stems of Rhabdadoxylon are isodichotomously branching and the cortex is uniformly parenchymatous (Holden, 1960; Dennis, 1968; Holmes, 1979; Ma et al., 2016). The stems of Catenopteris share the uniformly parenchymatous cortex with Rhabdadoxylon but do not dichotomize. In this genus clearly defined protoxylem groups are absent in the cauline stele, and uniseriate scalariform thickenings occur on the metaxylogy tracheid walls. Furthermore, a lens of parenchyma is present adaxial to the incipient petiolar trace (Phillips and Andrews, 1966). However, stems of Botryopteris are mostly unforked, except Botryopteris dichotoma and B. mucilaginosa. The cortex is usually differentiated into a thick-walled outer part and a parenchymatous inner part. Pitting on metaxylogy tracheid walls is more complicated than in Rhabdadoxylon and Catenopteris, and includes multiseriate scalariform thickenings, reticulate and multiseriate bordered pits.

The present specimens cannot be assigned to any of the existing genera within the Botryopteridaceae. In the present specimens the xylem configuration of the rachis and the petiole, the diagnostic character to recognize genera of the Botryopteridaceae, substantially differs from that in Botryopteris, Rhabdadoxylon and Catenopteris, and is more or less adaxially curved with one protoxylem group at each lateral margin. In Botryopteris it is usually α-shaped with 4 protoxylem groups, while in Rhabdadoxylon it is round or slightly elliptical with only 1 protoxylem group (Holmes, 1979). Although the rachis of Catenopteris is unknown, the xylem configuration of its petiole (shallow C-shaped) is very different from that of the present specimens (round or slightly elliptical). The stems and petioles of the present specimens also differ from existing genera and from Botryopteris by (1) their isodichotomously branching, (2) having simple uniseriate scalariform thickenings on cauline metaxylogy tracheids, (3) the presence of a plate of parenchyma adaxial to the incipient petiolar trace, and (4) the conspicuously smaller tracheid size of petiolar trace and petiole compared to the tracheids of the cauline stele. The cortex of the stem of both Rhabdadoxylon and Catenopteris is uniformly parenchymatous, which is quite different from that of the present specimens, which is conspicuously differentiated into a sclerenchymatous outer cortex and a parenchymatous inner and middle cortex. Furthermore, no clearly defined protoxylem groups can be seen in the cauline stele of Catenopteris (Phillips and Andrews, 1966), while it is well developed in the present stems. These differences lead to the creation of a new genus, Diodonopteris Ma et al. gen. nov. The new genus is defined by the characters that rachis xylem typically with two protoxylem groups, well differentiated cortex, simple uniseriate scalariform thickenings on cauline metaxylogy tracheids, and the conspicuously smaller tracheid size of petiolar trace and petiole compared to the tracheids of the cauline stele.

6.2. Botryopterid plants in the Cathaysian Flora

To date, five species of Botryopteridaceae including Diodonopteris gracilis gen. nov. et sp. nov. have been reported from the Permian of China. Wang et al. (2009) documented Botryopteris sp.1 and B. sp. 2 and Ma et al. (2016) described a new species of Rhabdadoxylon, R. tayuanense, from coal balls in the Taiyuan Formation in Shanxi Province, with these taxa co-occurring with D. gracilis. In addition Hilton et al. (2001) documented B. tridentata from volcaniclastic sediments from the Taiyuan Formation in Hebei Province. Each of the other Chinese species are only either represented by isolated rachides, i.e. B. tridentata, Botryopteris sp.1 and B. sp. 2, that are typically ~2 mm in diameter being considerably larger than the ~0.5 mm rachides of D. gracilis, or by stems with petioles, i.e. R. tayuanense Ma et al. The present paper represents the first account of botryopterid plant fossils with stems, petioles and also rachides preserved from the Permian of China, offering new insight into the diversity, structure and habit of these plants in the Cathaysian Flora.

6.3. The habit of Diodonopteris gracilis gen. nov. et sp. nov.

Holmes (1989) summarized the relationship between megaphyll branching and growth pattern in Paleozoic leptosporangiate ferns and concluded that most taxa were probably creeping or scrambling plants. By contrast, Rothwell (1991) reconstructed B. forensis as an epiphyte on the trunk of Psaronius, while Rößler and Galtier (2003) considered that the small and simple structure of Botryopteris may have been supported by other plants and was a herbaceous plant. Dichotomous branches always show an equal development of the cauline system and may have had semi-erect or erect growth habit (Rößler and Galtier, 2003). According to the morphology of stems and the arrangement of the petioles and roots in Botryopteris, Holmes and Galtier (1983) suggest that
B. dichotoma was semi-erect, and Holmes (1979) predicted that *Rhododendron americanum* may have been an erect plant as it has closely-packed leaves.

From the morphology of *Diodonopteris gracilis* we deduce that it probably has a semi-upright growth habit. Firstly, although the outer cortex consists of well-developed sclerenchyma, which could have offered mechanical support, it would have been difficult to grow upright because of its very thin stem. We postulate that it needed support of other plants living alongside. Secondly, the adventitious roots of *D. gracilis* only occur occasionally and some of them extend obliquely down through the cortex of the stem. Plants with a rhizome or creeping stems usually possess abundant adventitious roots which mostly extend in a course vertical to the surface of the stem or rhizome such as in *rhi-
zone of Botryopteris antiqua* (Phillips, 1970). Thirdly, some petioles in *D. gracilis* bend downward in their distal parts and resemble a hook (to right in Fig. 6). These “hook-shaped” petioles may have functioned as a clasp to grasp surrounding vegetation. In the same coal ball in which *D. gracilis* exist, several isolated rachides and petioles have been found surrounding, sticking to or even clasping the stems of a cordaitean plant *Shanxioxylon sinense* Wang et al. (Wang et al., 2003; see Plate V, 6, 7).

The structure and organization of frond branching and foliar-borne buds show considerable variation in relation to different growth habits. Rothwell (1991) concluded that *Botryopteris* was epiphyllous based on its growth among the root mantles of *Psaronius* tree ferns, while other studies have suggested creeping or scrambling (Holmes, 1989) or semi-erect growth habits (Holmes and Galtier, 1983; Holmes, 1989). Rößler and Galtier (2003) proposed that this kind of fern may have been supported by the other elements of the vegetation and grew as a kind of herbaceous plant.

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