Article

A New Fern-like Plant *Xinhangia spina* Gen. et sp. Nov. from the Upper Devonian of China

Jiang-Nan Yang and De-Ming Wang *

Key Laboratory of Orogenic Belts and Crustal Evolution, Department of Geology, Peking University, Beijing 100871, China

*Correspondence: dmwang@pku.edu.cn

Simple Summary: In 2019, Late Devonian Xinhang forest was reported from Anhui Province, China. It represents the earliest forest in Asia and China, and was regarded as monospecific with numerous small trees of the lycopsid. Recently, we found some other plants from the forest and now erect a new fern-like plant named *Xinhangia*. It is small with height of tens of centimeters, and usually has two orders of branches in alternate and sometimes triseriate pattern. Spines densely occur on the main axes and primary branches. Its leaf-like organs are very simple and dichotomize into recurved tips. Fertile organs are similar to the “leaves” but terminated in elongate and paired sporangia. Both the “leaves” and fertile organs are alternately arranged on secondary branches. In anatomy, the primary xylem is “8”-shaped and is surrounded by secondary xylem. With simple characters, *Xinhangia* represents a morphologically primitive plant and is of uncertain affinity at class or order level. As a component of Xinhang forest, *Xinhangia* will help understand the growth habit and habitat of fern-like plants, as well as the structure and ecology of ancient forests in the future.

Abstract: Palaeozoic fern-like plants show great diversity in their morphology and/or anatomy. Within this group, a novel taxon, *Xinhangia spina* gen. et sp. nov., is now reported from the Upper Devonian (Famennian) Wutong Formation of Anhui Province, China. The primary and secondary branches are borne alternately and sometimes in a triseriate pattern. Spines are evident on the main axes or stems and on the primary branches. Vegetative ultimate appendages with recurved tips are alternate, usually dichotomous 1–2 times, and sometimes as an aphlebia located at the base of primary or secondary branches. Fertile ultimate appendages are alternate, usually dichotomous 1–2 times, and terminate in elongated and paired sporangia. The stele has a clepsydroid-like primary xylem with each end bearing a protoxylem strand. The secondary xylem surrounding the primary xylem illustrates uniseriate rays. With rare divisions in both the vegetative and fertile ultimate appendages, *Xinhangia* represents a morphologically primitive plant. It is of uncertain affinity at the class or order level. The stelar architecture suggests that the clepsydroid stele may not be emphasized in discussing the relationship among fern-like plants such as rhacophyllaleans.

Keywords: fern-like plants; triseriate branching; Late Devonian; stele; *Xinhangia*; Wutong Formation

1. Introduction

Ferns with megaphylls (laminate leaves containing multiple veins) bearing sporangia originated in the Carboniferous and have evolved until now, while fern-like plants (as probable fern precursors), without foliar-borne sporangia, usually existed in the Middle Devonian–Carboniferous [1–5]. The fern-like plants include the iridopteridaleans, pseudosporochnaleans, nonpseudosporochnaleans, rhacophyllaleans and stauroporidaleans. Generally, they have sporangia-terminating branches, lack megaphylls and are anatomically characterized by a permanent protoxylem located near the periphery of mesarch primary xylem segments. In fern-like plants, the composition of rhacophyllaleans (Rhacophytales) is controversial and the relationship among the members remains unclear [2,3,6].
Here, we report a new fern-like plant, *Xinhangia spina* gen. et sp. nov. from the Upper Devonian in China. On the basis of its fertile and vegetative morphology and associated anatomy, *Xinhangia* is compared with other fern-like plants and its affinity is discussed. The anatomical features of the rhacophytaleans are reconsidered.

2. Materials and Methods

Specimens were collected from the lowermost part of Leigutai Member (Wutong Formation), in the Yongchuan clay mine near Jianchuan village, Xinhang Town, Guangde City, Anhui Province, China (referring to Figure 1A in [7]). The Yongchuan mine is still under excavation and has a 60-hectare excavated area at present. Wang et al. [7] have briefly described the strata near Xinhang Town, which mainly includes the Leigutai Member and underlying Guanshan Member of the Upper Devonian Wutong Formation. The dominant species of the Xinhang Forest, arborescent *Guangdedendron micrum* [7,8], is widely distributed in the rock layers of the Leigutai Member at the Yongchuan mine. The stratum containing this new plant is ca. 4 m thick and mainly constituted of yellow or grey sandstone, siltstone and mudstone.

More than 100 specimens were collected for a detailed study. Steel needles were used to expose the morphology of the plant under a light microscope (LM). The permineralized axes were embedded, sectioned and ground to show the anatomy, and some of them were macerated with hydrofluoric acid (HF). The anatomy was observed under an LM through reflected light. Some tracheids were observed with a scanning electron microscope (SEM). By extensive observation under the microscope, no *in situ* spores were found from any of the sporangia. The photographs were taken with a digital camera and the LM. All the figures were prepared using Adobe Photoshop CC 2018 and Adobe Illustrator CC 2018 software. All the specimens illustrated in this paper are housed at the Department of Geology, Peking University, Beijing, China.

3. Systematics Palaeontology

- **Class and Order:** Incertae sedis
- **Genus:** *Xinhangia* Yang et Wang gen. nov.
- **Type species:** *Xinhangia spina* Yang et Wang gen. et sp. nov.
- **Generic diagnosis:** Main axes dichotomous. Primary and secondary branches borne alternately and sometimes in triseriate pattern. Vegetative or fertile ultimate appendages arranged alternately on secondary branch. Vegetative ultimate appendages with recurved tips usually dichotomizing 1–2 times. Fertile ultimate appendages usually dichotomizing 1–2 times to terminate in elongated and paired sporangia. Primary xylem mesarch, clepsydroid-shaped with two protoxylem poles, and surrounded by secondary xylem. Tracheid wall with scalariform thickenings or circular to elliptical bordered pits.
- **Etymology:** The generic name derived from Xinhang Town, indicating the locality where the new plant was collected.
- *Xinhangia spina* Yang et Wang gen. et sp. nov. (Figure 1A–K, Figure 2a,b, Figure 3A–I, Figure 4A–M, Figure 5A–M, Figure 6a–h, Figure 7A–T and Figure 8A–P).
- **Specific diagnosis:** As in the generic diagnosis. Main axes 1.8–6.0 mm wide and up to 111 mm long, with primary branches arranged at 45–70°. Primary branches 0.7–3.0 mm wide and up to 65 mm long; secondary branches 0.3–1.0 mm wide and up to 50 mm long; tertiary branches 0.2–0.4 mm wide and up to 7 mm long. Sometimes a dichotomous aphlebia inserted at the base of primary and secondary branches. Spines on main axes and primary axes, 1–3 mm long. Basal axes within fertile ultimate appendages 0.2–0.4 mm wide. Sporangia 0.3–0.5 mm wide and 0.9–1.5 mm long. In main axes, xylem column 2 mm in diameter. Primary xylem 220–360 µm by 720–870 µm in transverse section. Tracheids in protoxylem, metaxytem and secondary xylem 10–25 µm, 30–51 µm, 32–73 µm in diameter, respectively.
- **Etymology:** The specific name referring to the occurrence of spines.
appendages 0.2–0.4 mm wide. Sporangia 0.3–0.5 mm wide and 0.9–1.5 mm long. In main axes, xylem column 2 mm in diameter. Primary xylem 220–360 μm by 720–870 μm in transverse section. Tracheids in protoxylem, metaxylem and secondary xylem 10–25 μm, 30–51 μm, 32–73 μm in diameter, respectively.

• Etymology: The specific name referring to the occurrence of spines.

Figure 1. Morphology of Xinhangia spina gen. et sp. nov. from Guangde City, Anhui Province, China. (A,B) Part and counterpart of dichotomous main axis bearing one primary branch (arrow). (C) Enlargement
of (A) (rectangle area) showing the spines on the main axis. (D) Enlargement of (B) (arrow) showing primary branch bearing two alternate secondary branches. (E) Main axis with dense spines and two alternate and spiny primary branches. (F) Main axis (arrow 4) with a pair (arrow 2, 3) and a single (arrow 6) primary branch in a triseriate pattern. Arrow 1 indicates single sporangial cluster enlarged in Figure 5A. (G, H) Two stages of dégagement showing two primary branches bearing fertile secondary branches alternately. (I) Enlargement of F (arrow 5) showing basal position of the pair of primary branches. (J) Enlargement of F (arrow 7) showing dichotomous aphlebia at base of primary branch. (K) Enlargement of (G) (right) showing attachment of paired and a single primary branch. Arrow indicates branch scar.

Figure 2. Morphology of Xinhangia spina gen. et sp. nov. from Guangde City, Anhui Province, China. (a,b) Line drawing of Figure 1F,H, respectively, ma, main axis; pb, primary branch; sb, secondary branch; tb, tertiary branch; vua, vegetative ultimate appendage; ap: aphlebia; fo, fertile organ; fo ?: assumed fertile organ.
Figure 3. Morphology of *Xinhangia spina* gen. et sp. nov. from Guangde City, Anhui Province, China. (A) Secondary branch bearing vegetative ultimate appendages (arrows) in alternate arrangement. (B, C) Primary branch with secondary branch bearing vegetative ultimate appendages alternately. Arrow 1 in B indicates a dichotomized vegetative ultimate appendage. Arrow 2 in B and arrow 2 in (C) indicate aphlebia at the base of secondary branch. Arrow 1 in C indicates secondary branch. (D–F) Primary branch bearing secondary branches alternately. Arrows 1–4 in (D) and arrow in (F) indicate secondary branches. Arrows 1 and 2 in (E) indicate dichotomized vegetative ultimate appendages. (G) Enlargement of (D) (arrow 1) showing secondary branch bearing vegetative ultimate appendages alternately (arrows 2–8) and one aphlebia at base (arrow 1). (H) Enlargement of (F) (arrow) showing secondary branch bearing vegetative ultimate appendages alternately. (I) Upper portion of secondary branch bearing vegetative ultimate appendages alternately.
Figure 4. Morphology of *Xinhangia spina* gen. et sp. nov. from Guangde City, Anhui Province, China. (A) Fertile primary branch alternately bearing four secondary branches with one fertile organ connected (arrow). (B) Fertile secondary branches bearing fertile organs. Dispersed fertile organs in matrix. (C,D) Relatively complete fertile secondary branch near a main axis, bearing fertile organs alternately. (E–M) Secondary branches bearing fertile organs alternately. (G–I) Represent enlargement from Figure 1G (left arrow) and 1H (arrows 1, 2), respectively. All the sporangia indicated by arrows are enlarged in Figure 5.
Figure 5. Morphology of *Xinhangia spina* gen. et sp. nov. from Guangde City, Anhui Province, China. (A) One single sporangial cluster bearing two pairs of elongate sporangia enlarged from Figure 1F (arrow 1). (B) Enlargement of Figure 4A (arrow) showing one fertile organ arranged on secondary branch.
(C) Two clusters of sporangia enlarged from Figure 4B (arrow). (D,G) Fertile secondary branches bearing fertile organs enlarged from the rectangle areas in Figure 4C and 4D, respectively. (E) Enlargement of (D) (left arrow) showing one fertile organ with one pair of sporangia. (F) Enlargement of (D) (right arrow) showing dichotomous fertile organ with terminal sporangial cluster. (H) Enlargement of (G) (arrow) showing one fertile organ consisting of two pairs of sporangia. (I,J,O,P) Dichotomous fertile organ consisting of two major clusters bearing two to four pairs of sporangia. Enlarged from Figure 4E (arrows 1, 2), 4I (arrow 2), 4L (arrow), respectively. (K–N,Q–S) Single cluster of sporangia consisting of one to four pairs. Enlarged from Figure 4E (arrow 3), 4G (arrow), 4H (arrow), 4I (arrow 1), 4J (arrow), 4M (arrows 1, 2), respectively. (T–W) Serial dégagement of one cluster of fertile organs showing that the cluster consists of four sporangia.

Figure 6. Morphology of *Xinhangia spina* gen. et sp. nov. from Guangde City, Anhui Province, China. (a–h) Line drawing of part of fertile branches and fertile organs in Figure 5 showing terminal sporangial pairs. (a–g) correspond to Figure 5D,G,A,C,I,K, respectively, and (h) corresponds to the serial dégagement of Figure 5T–W, where blue dotted lines and red lines indicate removed and newly exposed parts, respectively. pb, primary branch; sb, secondary branch.
Figure 7. Anatomy of Xinhangia spina gen. et sp. nov. from Guangde City, Anhui Province, China. 
(A) Two axes before transverse sectioning. (B–D) Serial sections of the left axis in (A), showing 
clepsydroid-shaped primary xylem surrounded by secondary xylem (a13, a14', a17'). (E–L) Serial 
sections of the right axis in A, showing clepsydroid-shaped primary xylem surrounded by secondary 
oxylem (b3, b4, b5, b6', b7, b8', b9, b9'). (M–Q) Close-up views of primary xylem of (B,D,G,K,L), 
respectively, showing two prominent protoxylem poles (arrows) and primary xylem tracheids. (R–T) 
Close-up views of secondary xylem of (F,J,L), respectively, showing radial files of secondary xylem 
tracheids and rays. Arrows indicate rays.
Figure 8. Anatomy of *Xinhangia spina* gen. et sp. nov. from Guangde City, Anhui Province, China. 
(A) Specimen from which axis in (C) was obtained (left arrow), and right arrow indicating a spiny axis. 
(B) Specimen from which axis in (D) was obtained (arrow). 
(C, D) Overview of SEM of two axes
from (A,B) representing longitudinal and tangential sections, respectively. (E–J) Enlargement of the white, blue, red and yellow rectangle areas in (C) and the white and yellow rectangle areas in (D), respectively, showing xylem tracheids and ray cells. Rectangles in (F–J) are enlarged in (K–P). (K,L) Enlargement of rectangle areas in (F,G), showing scalariform thickenings and ray cell walls. (M) Enlargement of rectangle area in (H), showing scalariform thickenings. (N) Enlargement of the white rectangle area in (I), showing transverse view of ray cells. (O) Enlargement of the red rectangle area in (I), showing bordered pits. (P) Enlargement of rectangle area in (J), showing transverse view of ray cells and bordered pits.

4. Description

The description of *Xinhangia* involves its morphology (Figures 1–6) and anatomy (Figures 7 and 8). The measurements of the morphology and anatomy are given in Table 1.

Table 1. Measurements of morphology and anatomy of *Xinhangia spina*.

| Morphological Organs         | Length (mm) | Diameter (mm) |
|------------------------------|-------------|---------------|
| main axes up to 111          | up to 65    | 0.7–3.0       |
| primary branches up to 65    | up to 50    | 0.3–1.0       |
| secondary branches up to 7   | up to 50    | 0.2–0.4       |
| axes within fertile organ    | up to 7     | 0.2–0.4       |
| sporangia                    | 0.9–1.5     | 0.3–0.5       |

| Anatomical Structures        | Length (mm) | Diameter (mm) |
|------------------------------|-------------|---------------|
| primary xylem 720–870        | 220–360     |               |
| protoxylem tracheids         | -           | 10–25         |
| metaxytem tracheids          | -           | 30–51         |
| secondary xylem tracheids    | -           | 32–73         |

4.1. Main Axes and Primary Branches

The main axes or stems have an upright habit and are covered by dense spines of 1–3 mm in length (Figures 1A–F and 2a). One main axis is dichotomous, up to 6 mm in diameter and 11 cm in length (Figure 1A,B). The main axes sometimes present a slightly zigzag shape, bending at the position where the primary branches occur (Figure 1F). No roots are found on the main axes.

The primary branches are straight in most cases (Figures 1F–H and 3B,D) and slightly zigzag in some instances (Figures 3E and 4A). They are arranged on the main axes in alternate (Figure 1E) or triseriate (Figures 1F and 2a) branching patterns at 45–70°. The paired primary branches (Figure 1F, arrows 2, 3) and a single primary branch (Figure 1F, arrow 6) constitute a triseriate pattern. A presumed aphlebia is dichotomous and inserted at the base of a primary branch (Figure 1J). The primary branches are 0.7–3.0 mm in diameter and up to 6.5 cm long. Compared to those on the main axes, the spines on the primary branches are sparse and short. No ultimate appendages are visible on the primary branches.

4.2. Vegetative Secondary Branches and Vegetative Ultimate Appendages

The secondary branches are alternately arranged on the primary ones at 50–90° (Figures 1F and 3D,F). They lack spines and measure 0.4–0.7 mm in diameter and up to 5 cm long. A single dichotomous aphlebia is located at the base of some of the secondary branches (Figure 3B, arrow 2; Figure 3C, arrow 2; Figure 3G, arrow 1). The aphlebiae are similar in shape to the vegetative ultimate appendages but appear a little larger. The upper portion of a secondary branch is preserved, tapered and appears distally recurved (Figure 3I).
The vegetative ultimate appendages occur alternately on the secondary branches and bear recurved tips (Figure 3). Most of these appendages dichotomize once to form a ‘Y’ shape (Figure 3A, arrows 1, 3; Figure 3B, arrow 1; Figure 3E, arrows 1, 2; Figure 3G, arrows 2, 3, 5). Some appendages dichotomize twice (Figure 3A, arrow 2; Figure 3G, arrow 4) or thrice (Figure 3G, arrows 6–8), or not (Figure 3H,I).

4.3. Fertile Branches

Most of the fertile secondary branches occur alternately on the primary branches at 50–90° (Figures 1H and 4A). However, as exemplified by one specimen (Figures 1G,H,K and 2b), three fertile secondary branches alternate on the lower part of the primary branch; a pair of fertile secondary branches and a single branch occur oppositely or sub-oppositely on the upper part of the primary branch. In this example, these fertile secondary branches appear to form a triseriate branching pattern. The fertile secondary branches (e.g., Figure 4E,I) are quite similar to the vegetative ones (e.g., Figure 3A,B); their only difference lies in the separate occurrence of fertile and vegetative ultimate appendages. A complete secondary branch shows alternate fertile ultimate appendages (fertile organs) and terminates in one fertile organ (Figures 5D and 6a). No aphlebiae are found inserted at the base of the secondary branches.

Tertiary branches were discovered only in one specimen (Figure 1H). They are alternately arranged and bear fertile organs (Figure 2b, tb), resembling fertile secondary branches (e.g., Figure 4G–I) in shape and size.

4.4. Fertile Organs

Fertile organs are inserted mostly on the secondary branches (Figure 4) and rarely on the tertiary ones (Figure 2b). A fertile organ consists of two parts, i.e., the terminal sporangia and a basal axis. The sporangia with pointed tips are elongate in shape and borne in pairs (Figures 5 and 6). They range 0.3–0.5 mm wide and 0.9–1.5 mm long. The smooth basal axes within the fertile organs measure 0.2–0.4 mm in diameter and usually dichotomize but sometimes do not. In the distal area of the secondary branches, such axes lack dichotomy and terminate in one pair of sporangia (Figure 5E,N). In most of the examples, the basal axes dichotomize once or twice to produce two or four pairs of terminal sporangia (Figure 5H,O,P,T and Figure 6g). Occasionally, the basal axes dichotomize thrice to form possibly eight pairs of sporangia (Figure 5J and Figure 6e). As to one fertile organ with twice dichotomizing, the serial dégagement shows two pairs of terminal sporangia in three dimensions (Figure 5T–W and Figure 6h).

4.5. Anatomy

Two limonitized axes containing only the xylem, ca. 2 mm in diameter, were embedded and transversely sectioned into 18 and 15 slices, respectively (Figure 7A). Of these, 11 slices are selected to show the relatively complete structure (Figure 7B–L). The stele has a primary xylem surrounded by a radial secondary xylem. Though these two axes were preserved as isolates without an organic connection with the morphological parts, we believe that they belong to Xinhangia, with a high probability, because of the close relationship of the preservation and correspondence between the two-poled pattern in the anatomy and the alternate branching pattern in the morphology. For the limonitized axis observed by SEM (Figure 8A, left arrow), a spiny axis was preserved beside it (Figure 8A, right arrow), indicating the close relationship among the axes in Figure 8A. Considering the tissues outside the xylem and the diameter of the main axes and branches, it is assumed that these limonitized axes represent the main axes.

The primary xylem, 720–870 µm by 220–360 µm in the transverse section, is mesarch in maturation and has a clepsydroid shape in the cross-section (Figure 7M–Q). At each end of the primary xylem, there is a prominent protoxylem pole (Figure 7M–Q, arrows), which may have been originally filled with parenchymal cells. The smallest tracheids surrounding the protoxylem poles indicate the protoxylem and measure 10–25 µm in diameter. The bigger
tracheids between and surrounding the protoxylem represent metaxylem and 30–51 µm in diameter.

The tracheids of the secondary xylem are arranged in radial files (Figure 7R–T) and are 32–73 µm in diameter. In the transverse sections, the rays can be recognized between the rows of the secondary xylem tracheids (Figure 7R–T, arrows). With SEM, the uniseriate rays appear to occur between every row of the secondary xylem tracheids (Figure 8D, J,N,P). A single ray is one to six cells in height (Figure 8C,E,H,K). The secondary wall of the secondary xylem tracheids may possess scalariform thickenings (Figure 8L,M). In the tangential section (Figure 8D), circular to elliptical bordered pits are visible in the walls of the secondary xylem tracheids (Figure 8J,O,P).

5. Comparisons

Table 2 indicates comparisons among *Xinhangia*, other fern-like plants and related groups. The comparisons involve the vegetative branching pattern, basal aphlebiae, fertile organs (fertile ultimate appendages) and stelar architecture.
| Taxon (Reference) | Vegetative Branch | Fertile Organ | Anatomy |
|------------------|------------------|--------------|---------|
|                  | Primary          | Secondary    | Tertiary | Arrangement Branching Pattern | Sporangia | Stelar Structure | Secondary Xylem |
| **Xinhangia**    | alternate triseriate | alternate triseriate | alternate | present | alternate dichotomous 1–2 times | terminal, paired, elongate | clepsydroid | present |
| Iridopteridales [9,10] | whorled | absent | whorled | 3-D dichotomous | terminal, paired, elongate | actinostele | usually absent |
| Pseudosporochnales [9–11] | digitate | absent | usually irregular | mostly 3-D dichotomous | terminal, paired, elongate | dissected | usually absent |
| Metacladophyton [12] | whorled | decussate opposite | absent | present | alternate 3-D dichotomous about 6 times | terminal, single, elongate | protostele dissected | present |
| Denglongia [13,14] | whorled | absent | subopposite | 3-D dichotomous many times | actingostele | separate | absent |
| Rhacophyton [15–17] | quadriseriate, helical | quadriseriate | alternate | present | paired at secondary branch base | terminal on pinnate segments, elongate | actinostele | clepsydroid | present |
| Ellesmeris [18] | quadriseriate, alternate | alternate subopposite | absent | present | paired at branch base or alternate on branch | terminal, paired, elongate | clepsydroid | absent |
| Eocladoxylon [19] | alternate | present | alternate | terminal on dichotomous 2–3 times | unknown | unknown | unknown |
| Melvillipteris [6] | quadriseriate | alternate | absent | present | alternate 3-D dichotomous up to 5 times | terminal, elongate | unknown | unknown |
| Protopteridiphyton [20] | helical in two ranks | quadriseriate | quadriseriate | absent | 3-D dichotomous about 6 times | terminal, paired, elongate | ? actinostele | absent |
| Stauropteridales [2,21] | quadriseriate, trichotomous | present | few (single or paired) sporangia terminal on aphlebia-like branch or on branch node | actinostele | absent |
| Shougangia [4] | helical | irregularly helical | alternate (sub)–opposite | absent | terminal on tertiary branch with pinnules | terminal, paired, elongate | ? actinostele | present |
| Aneurophytales [2,22] | helical or decussate | absent | terminal on pinnate divisions of a dichotomous branching system | actinostele | present |

* modified from Table 2 in [4]; 3-D, three dimensionally; ? actinostele, possible actinostele.
5.1. Iridopteridales, Pseudosporochnales and Nonpseudosporochnaleans

Middle Devonian–Early Carboniferous Iridopteridales and Pseudosporochnales are assigned to the Cladoxylopsida [9]. Alternatively, the Pseudosporochnales and nonpseudosporochnaleans, as an informal group, are placed in this class [10]. The recent phylogenetic analysis regards that the cladoxylopsids sensu lato refer to the iridopteridaleans and cladoxylopsids sensu stricto, which include the pseudosporochnaleans and nonpseudosporochnaleans [23]. In general, the iridopteridaleans refer to plants such as Anapaulia [24], Arachnoxylon [25], Asteropteris [26], Compsocradus [27], Ibyka [28], Iridopteris [29], Keraphyton [30] and, possibly, Metacladophyton [12,31], the pseudosporochnaleans to Calamophyton [32], Lorophyton [33], Pseudosporochnus [11] and Wattieza [34], and the nonpseudosporochnaleans to the taxa such as Cladoxylon [35], Panxia [36,37], Pietzschia [1,38], Polyxylon [10] and, possibly, Denglongia [13,14].

Xinhangia and most cladoxylopsids s.l. share similar fertile organs (three-dimensional dichotomous branches, terminated by elongate and paired sporangia) and mesarch primary xylem. However, Xinhangia is characterized by a triseriate branching pattern and clepsydroid stele, which are absent in the cladoxylopsids s.l.

Whorled organs (the branches and ultimate appendages) and actinostele (a protostele with the primary xylem ribs arranged radially and more or less connected in the stelar center) occur in all the iridopteridaleans but not in Xinhangia. The digitate branching and dissected stele characterizing the pseudosporochnaleans are absent in Xinhangia. Furthermore, the iridopteridaleans and pseudosporochnaleans usually have no secondary xylem. Dissected stele typifies (most) nonpseudosporochnaleans but is not recorded in Xinhangia.

Among the nonpseudosporochnaleans, Panxia [36,37] is known for its morphology. As with Xinhangia, Panxia has alternate branches and simple vegetative ultimate appendages with distal recurving. Nevertheless, its discoidal sporangia with stalks are borne laterally and closely. Metacladophyton [12,31] is treated as a nonpseudosporochnalean [23]. It morphologically differs from Xinhangia mainly in the whorled and decussate branches. Denglongia [13,14] is placed in the cladoxylopsids s.s., but is not allied with the nonpseudosporochnaleans or nonpseudosporochnaleans [23]. It shows clear differences with Xinhangia in the whorled branches, complex and unique fertile organs with alternate segments and actinostele.

5.2. Rhacophyton with (Possibly) Related Plants

Late Devonian (Famennian) Rhacophyton is characterized by quadriseriate (alternate pairs of) branches with basal aplebia and a clepsydroid-shaped primary xylem surrounded by a secondary xylem [15–17,39]. Rhacophyton is assigned to the Rhacophytales, relating to plants such as Ellesmeris, Eocladoxylon, Melvillipteris and Protopteridophyton [2,3,6], which have quadriseriate branching and/or the clepsydroid stele preserved.

As in Xinhangia, Eocladoxylon [19], Melvillipteris [6] and Protopteridophyton [20] show elongate and sometimes paired sporangia terminating in three-dimensionally dichotomous axes; Ellesmeris [18], Eocladoxylon, Melvillipteris and Rhacophyton possess basal aplebiae; Ellesmeris, Eocladoxylon and Rhacophyton demonstrate clepsydroid xylem. However, all of these plants lack triseriate branching and some present quadriseriate branching; Rhacophyton has fertile organs paired at the branch base, and such arrangement occurs sometimes in Eocladoxylon; the fertile organs of Rhacophyton are very complex and unique, with pinnate segments, and those of Protopteridophyton are quadriseriate in arrangement and also complex.

5.3. Stauropteridales

Late Devonian–Carboniferous Stauropteridales [2] is characterized by quadriseriate branching, usually single sporangium terminating branches and actinostele usually with four primary xylem ribs and without secondary xylem. Such morphological and anatomical features are lacking in Xinhangia. Among the members, Multifurcatus has trichotomous branches, basal aplebiae and a single sporangium at the node of the branches [39]. Its
trichotomous branches appear to form alternate pairs. In contrast, *Xinghangia* possesses triseriate branches and terminal sporangia in pairs.

5.4. *Shougangia*

Late Devonian (Fammenian) *Shougangia* is unknown for affinity at the class level. As a derived fern-like plant, it possesses helical branches, laminate vegetative leaves, very complex fertile organs, which terminate in branches with pinnules and dichotomize up to 10 times, and dissected stele [4,5]. These traits show clear differences from *Xinghangia*, although both genera have terminal and elongate sporangia in pairs.

5.5. *Aneurophytales*

Middle to Late Devonian (Late Eifelian to Frasnian) *Aneurophytales* is considered the most primitive progynnosperm [2,22], which is characterized by: (1) three-dimensional branching systems with laterals helically or decussately arranged, (2) a primary xylem stele consisting of three or more ribs with protoxylem strands occurring near the tips and along the midplanes of the ribs, (3) elongate sporangia terminally inserted on the ultimate pinnate fertile appendages [2]. *Xinghangia* exhibits an alternate and sometimes a triseriate branching pattern, which differs from the *Aneurophytales*. The clepsydroid-shaped primary xylem and protoxylem strands occurring around the two poles in *Xinghangia* distinguish it from the order. Furthermore, the *Aneurophytales* shows more complicated style in their fertile appendages, while the fertile organs of *Xinghangia* are simpler, by contrast.

6. Discussion

*Xinghangia* and most fern-like plants share fertile organs with three-dimensionally dichotomous axes terminated by elongate and paired sporangia and mesarch primary xylem with a permanent protoxylem (strand near the periphery of the xylem). Nevertheless, this taxon cannot be placed in the Iridopteridales, with whorled organs and actinostele, or in the Pseudosporochnales, with digitate branching and dissected stele, or in the nonpseudosporochnaleans with dissected stele. It cannot be assigned to the Rhacophytales and Stauropteridales, which typically have a quadriseriate branching pattern. It also cannot be classified into *Aneurophytales*, for their helical or decussate branching pattern, multiple ribs in the stele and the complex fertile appendages. Thus, *Xinghangia* is now treated as a fern-like genus of an uncertain affinity at the class or order level.

*Rhacophyton* *ceratangium* and *Ellesmeris sphenopteroides* possess both quadriseriate branching and clepsydroid xylem. Specifically, in *R. ceratangium*, the common bases of each pair of primary branches are alternately attached to the main axis or stem [17,39]; in *E. sphenopteroides*, the common bases of the paired primary branches have the same arrangement, and the secondary branches are unpaired and borne alternately or suboppositely [18]. Either the main axes or primary branches in both plants contain a clepsydroid stele. By contrast, in *R. zygopteroides*, the primary branches are helical on the main axis (probably) containing an actinostele [15]. Alternate branching and clepsydroid stele are also seen in *Eoeladoxylon* [19] and now, in *Xinghangia*. As to the triseriate primary or secondary branches of *Xinghangia*, the unpaired branches and the common base of the paired branches are alternately attached. Therefore, in these four plants, the common bases of the paired branches and/or unpaired branches occur in a single plane, correlating to the clepsydroid stele with the primary xylem bearing two peripheral protoxylem strands. This suggests that the clepsydroid stele may not be highly stressed in discussing relationships among plants such as rhacophytaleans.

The co-evolution of the vegetative and fertile organs has been suggested for the fern-like plants [4]. The derivation of the laminate leaves from planate ultimate appendages is accompanied by the increase in complexity of the fertile organs (number of internal divisions and terminal sporangia). Of *Xinghangia* as a plesiomorphic taxon, the vegetative ultimate appendages, with the distal recurving and rare divisions, are simple and far from planation. Accordingly, the fertile organs divide usually only 1–2 times to produce few
terminal sporangia. The secondary xylem provides mechanical support and, fundamentally, water conductance for fern-like plants with plateate ultimate appendages or laminate leaves, e.g., *Rhacophyton* and *Shougangia* [3,5]. As to *Xinhangia* lacking leaf-like organs or leaves, the secondary xylem appears necessary to perform a supporting function. Of course, the explanation of such a function in *Xinhangia* may also depend on the growth habit and understanding of its habitat (under study).

7. Conclusions

*Xinhangia spina* gen. et sp. nov. is known from both its morphology and anatomy. It is characterized by primary and secondary branches borne in an alternate and sometimes a triseriate pattern, vegetative and fertile ultimate appendages with rare divisions and a clepsydroid-shaped primary xylem surrounded by secondary xylem. By comparison with other fern-like plants, *Xinhangia* represents a new and primitive taxon with uncertain affinity. Based on stelar architecture in relation to branching pattern, the anatomical features of some fern-like plants are reconsidered.

**Author Contributions:** Conceptualization, J.-N.Y. and D.-M.W.; field work, collecting material, J.-N.Y. and D.-M.W.; material handling and experiment, J.-N.Y. All authors have read and agreed to the published version of the manuscript.

**Funding:** This work was supported by the National Natural Science Foundation of China (Grant No.: 42072016).

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** The specimens are deposited in the Department of Geology, Peking University, Beijing, China.

**Acknowledgments:** We thank Le Liu, Min Qin, Yi Zhou and Xue Gao for their help in the field work.

**Conflicts of Interest:** The authors declare no conflict of interest.

**References**

1. Soria, A.; Meyer-Berthaud, B. Reconstructing the Late Devonian cladoxylopsid *Pietzschia schulleri* from new specimens from southeastern Morocco. *Int. J. Plant Sci.* 2005, 166, 857–874. [CrossRef]
2. Taylor, T.N.; Taylor, E.L.; Krings, M. Paleobotany: The Biology and Evolution of Fossil Plants, 2nd ed.; Academic Press: Burlington, VT, USA, 2009; pp. 383–417.
3. Galtier, J. The origins and early evolution of the megaphyllous leaf. *Int. J. Plant Sci.* 2010, 171, 641–661. [CrossRef]
4. Wang, D.M.; Xu, H.H.; Xue, J.Z.; Wang, Q.; Liu, L. Leaf evolution in early-diverging ferns: Insights from a new fern-like plant from the Late Devonian of China. *Ann. Bot.* 2015, 115, 1133–1148. [CrossRef]
5. Wang, D.M.; Zhang, Y.Y.; Liu, L.; Xu, H.H.; Qin, M.; Liu, L. Reinvestigation of the Late Devonian *Shougangia bella* and new insights into the evolution of fernlike plants. *J. Syst. Palaeontol.* 2018, 16, 309–324. [CrossRef]
6. Xue, J.Z.; Basinger, J. *Melvillipteris quadriseriata* gen. et sp. nov., a new plant assigned to Rhacophytales from the Upper Devonian (Famennian) of Arctic Canada. *Geol. Mag.* 2016, 153, 601–617. [CrossRef]
7. Wang, D.M.; Qin, M.; Liu, L.; Liu, L.; Zhou, Y.; Zhang, Y.Y.; Huang, P.; Xue, J.Z.; Zhang, S.H.; Meng, M.C. The most extensive Devonian fossil forest with small lycopsid trees bearing the earliest stigmarian roots. *Curr. Biol.* 2019, 29, 2604–2615. [PubMed]
8. Gao, X.; Liu, L.; Qin, M.; Zhou, Y.; Mao, L.; Wang, D.M. Re-study of *Guangdedendron micrum* from the Late Devonian Xinhang forest. *BMC Ecol. Ecol.* 2022, 22, 69. [CrossRef]
9. Berry, C.M.; Stein, W.E. A new iridopteridalean from the Devonian of Venezuela. *Int. J. Plant Sci.* 2000, 161, 807–827. [CrossRef]
10. Meyer–Berthaud, B.; Soria, A.; Young, G.C. Reconsidering differences between Cladoxylopsida and Iridopteridales: Evidence from *Polyxylon australe* (Upper Devonian, New South Wales, Australia). *Int. J. Plant Sci.* 2007, 168, 1085–1087. [CrossRef]
11. Leclercq, S.; Banks, H.P. *Pseudosporochnus nodosus* sp. nov., a Middle Devonian plant with Cladoxyloideae affinities. *Palaeontogr. Abt. B* 1962, 110, 1–34.
12. Wang, Z.; Geng, B.Y. A new Middle Devonian plant: *Metacladophyton tetraxylum* gen. et sp. nov. *Palaeontogr. Abt. B Palaeophytol.* 1997, 243, 85–102.
13. Xue, J.Z.; Hao, S.G. *Denglongia hubeiensis* gen. et sp. nov., a new plant attributed to Cladoxyloides from the Upper Devonian (Frasnian) of South China. *Int. J. Plant Sci.* 2008, 169, 1314–1331. [CrossRef]
14. Xue, J.Z.; Hao, S.G.; Basinger, J.F. Anatomy of the Late Devonian Denglingia hubeiensis, with a discussion of the phylogeny of the Cladoxylopsida. *Int. J. Plant Sci.* 2010, 171, 107–120. [CrossRef]

15. Leclercq, S. Étude morphologique et anatomique d’une fougère du Dévonien Supérieur, le *Rhacophyton zygopteroides* nov. sp. *Ann. De l’Académie Géologique De Belg.* 1951, 9, 1–62.

16. Andrews, H.N.; Phillips, T.L. Rhacophyton from the Upper Devonian of West Virginia. *Bot. J. Linn. Soc.* 1968, 61, 37–64. [CrossRef]

17. Cornet, B.; Phillips, T.L.; Andrews, H.N. The morphology and variation in *Rhacophyton ceratangium* from the Upper Devonian and its bearing on front evolution. *Palaeontogr. Abt. B* 1976, 158, 105–129.

18. Hill, S.A.; Scheckler, S.E.; Basinger, J.F. *Rhacophyton* from the earliest Carboniferous of Jiangsu, China. *Alcheringa* 2022, 18, 107–117. [CrossRef]

19. Berry, C.M.; Wang, Y. *Iridopteris protrusion* (Protopteridium) minutum (Halle) Koidzumi from the Middle Devonian of Yunnan, China: An early Rhacophyton–like plant? *Int. J. Plant Sci.* 2006, 167, 551–566. [CrossRef]

20. Li, C.S.; Hsü, J. Studies on a new Devonian plant *Protopteridophyton devonicum* assigned to primitive fern from South China. *Palaeontogr. Abt. B* 1987, 207, 111–131.

21. Wang, Y. A new plant from the earliest Carboniferous of Jiangsu, China. *Alcheringa* 2003, 27, 51–61.

22. Meyer-Berthaud, B.; Decombeix, A.-L.; Dunstone, R.; Gerrienne, P.; Momont, N.; Young, G. *Tetraxylopteris* Beck emend. Hammond and Berry (2005), the first aneurophtyalean genus recorded in Australia. *Rev. Palaeobot. Palynol.* 2016, 224, 54–65. [CrossRef]

23. Durieux, T.; Lopez, M.A.; Bronson, A.W.; Tomescu, A.M.F. A new phylogeny of the cladoxylopsid plexus: Contribution of an early cladoxylopid from the Lower Devonian (Emsian) of Quebec. *Botanical Soc. Am.* 2021, 108, 2066–2095. [CrossRef] [PubMed]

24. Berry, C.M.; Edwards, D. *Anapaulia moodyi* gen. et sp. nov.: A probable iridopteridalean compression fossil from the Devonian of western Venezuela. *Rev. Palaeobot. Palynol.* 1996, 93, 127–145. [CrossRef]

25. Stein, W.E. The morphology and variation in *Protopteridium* from the Upper Devonian (Famennian) of South China. *Can. J. Bot.* 1983, 61, 1283–1299. [CrossRef]

26. Scheckler, S.E.; Skog, J.E.; Banks, H.P. *Langoxylon asterochlaenoideum* Stockmans: Anatomy and relationships of a fern-like plant from the Middle Devonian of Belgium. *Rev. Palaeobot. Palynol.* 2006, 142, 193–217. [CrossRef]

27. Fu, Q.; Wang, Y.; Berry, C.M.; Xu, H.H. Complex branching patterns in a newly recognized species of *Compsocradus* Berry et Stein (iridopteridales) from the middle Devonian of north Xinjiang, China. *Int. J. Plant Sci.* 2011, 172, 707–724. [CrossRef]

28. Skog, J.E.; Banks, H.P. *Ibyka amphikoma* gen. et sp. nov., a new protoarticulate precursor from the late Middle Devonian of New York State. *Am. J. Bot.* 1973, 60, 366–380. [CrossRef]

29. Stein, W.E. *Iridopteris criensis* from the Middle Devonian of North America, with systematics of apparently related taxa. *Bot. Gaz.* 1982, 143, 401–416. [CrossRef]

30. Champreux, A.; Meyer-Berthaud, B.; Decombeix, A.L. *Keraphyton* gen. nov., a new Late Devonian fern-like plant from Australia. *PeerJ* 2020, 8, e9321. [CrossRef]

31. Wang, D.M.; Lin, Y.J. A new species of *Metacladophyton* from the Late Devonian of China. *Int. J. Plant Sci.* 2007, 168, 1067–1084. [CrossRef]

32. Leclercq, S.; Andrews, H.N. *Calamaphyton bicephalum*, a new species from the Middle Devonian of Belgium. *Ann. Mo. Bot. Gard.* 1960, 47, 1–23. [CrossRef]

33. Fairon-Demaret, M.; Li, C.S. *Lorophyton goense* gen. et sp. nov. from the Lower Givetian of Belgium and a discussion of the Middle Devonian Cladoxylopsida. *Rev. Palaeobot. Palynol.* 1993, 77, 1–22. [CrossRef]

34. Berry, C.M. A reconsideration of *Wattieza* Stockmans (here attributed to Cladoxylopsida) based on a new species from the Devonian of Venezuela. *Rev. Palaeobot. Palynol.* 2000, 112, 125–146. [CrossRef]

35. Bertrand, P. Contribution a l’étude des Cladoxyles de Saalfeld. *Palaeontogr. Abt. B* 1935, 18, 101–170.

36. Wang, Y.; Berry, C.M. Morphology of a non-pseudosporochnalean cladoxylopid from the Middle Devonian of Yunnan, south China. *Palaeoworld* 2006, 15, 54–67. [CrossRef]

37. Xue, J.Z.; Huang, P.; Wang, D.M.; Wang, Q.; Hao, S.G. Anatomy of the Middle Devonian cladoxylopid *Panzsia gabata* Y. Wang et Berry from Yunnan Province, southwestern China. *Rev. Palaeobot. Palynol.* 2016, 224, 66–82.

38. Soria, A.; Meyer-Berthaud, B.; Scheckler, S.E. Reconstructing the architecture and growth habit of *Pietzschia levis* sp. nov. from the Late Devonian of southeastern Morocco. *Int. J. Plant Sci.* 2001, 162, 911–926. [CrossRef]

39. Dittrich, H.S.; Matten, L.C.; Phillips, T.L. Anatomy of *Rhacophyton ceratangium* from the Upper Devonian (Famennian) of West Virginia. *Rev. Palaeobot. Palynol.* 1983, 40, 127–147. [CrossRef]