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A new gymnospermous stem from the Moscovian (Carboniferous) of North China, and its palaeoecological significance for the Cathaysian Flora at the early evolutionary stage

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abstract

A new permineralized gymnospermous fossil stem, Parnaiboxylon wangi sp. nov., is described from the Moscovian Benxi Formation of Yangquan City, Shanxi Province, North China. It is composed of pith, primary and secondary xylems. The pith is solid, heterogeneous, with numerous secretory canals, ducts, and parenchymatous cells at the periphery. The primary xylem is endarch to mesarch. The secondary xylem is pycnoxylic, characterized by the presence of uni- to quariseriate araucarian radial tracheidal pitting, cupressoid to araucarioid

cross-field pitting, and axial parenchyma. The fossil stem represents the fourth species of gymnosperms with anatomical features preserved from the Pennsylvanian of the Cathaysia. Anatomical characters, including solenoid pith and growth interruptions, and sedimentological evidence suggest a coastal environment with intermittent droughts or occasional incursions of seawater when the tree was alive. The presence of fungal hyphae, coprolites, and decayed tunnels in the secondary xylem of P. wangi sp. nov. indicate well-developed fungi–plant and animal–plant interactions when the Cathaysian flora at its early evolutionary stage.

1. Introduction

There exists a substantial unconformity between the Middle–Upper Ordovician and the upper Carboniferous across nearly the entire North China Craton (e.g., Wang et al., 2010; Cocks and Torsvik, 2013), representing ca. 135 million years of missing time. The Pennsylvanian Benxi Formation just above the unconformity is the oldest Pennsylvanian deposits in North China (Shao et al., 2006, 2008, 2015). Therefore, fossil plants from the Benxi Formation have been regarded as the oldest vascular vegetation colonizing the terrestrial landscape of North China Craton, and as an early evolutionary stage of the Cathaysian flora (Cleal and Wang, 2002; Hilton and Cleal, 2007; Cheng et al., 2019). Sixty species of thirty genera of fossil plants have been identified from the Benxi Formation (Wu, 1995). However, most of them are preserved as fragmentary impressions. Their identification and affinities are commonly

obscure (Hilton and Cleal, 2007). Pennsylvanian fossil plants with preserved anatomical features are extremely rarely documented in North China Craton (Cleal and Wang, 2002; Feng et al., 2008; Wang et al., 2022b). Hence, systematic studies of permineralized plants will significantly expand our knowledge of the taxonomy and composition of past vegetation in Cathaysia (Hilton et al., 2001, 2002; Wang et al., 2003a, 2003b; Zheng et al., 2008; Cheng et al., 2017, 2021; Wan et al., 2017c, 2017d, 2019a, 2019b, 2020a, 2020b, 2021a, 2021c).

Anatomy of permineralized stems from clastic deposits also provides additionally palaeoecological and environmental information on plants (Falcon-Lang, 1999a, 1999b, 2003; Feng et al., 2010a, 2010b, 2013, 2017, 2021, 2022; Falcon-Lang et al., 2014, 2016; Wan et al., 2014, 2016a, 2016b, 2017a, 2017b, 2019c, 2020c, 2021b). Fossil arthropods and their ecology from the upper Paleozoic of North China are poorly known in comparison to those from the Mesozoic and Cenozoic (Huang et al., 2022; Wang et al., 2022a). Plant–arthropod associations observed from fossil stems provide data on the feeding behaviors and strategies of arthropods (e.g., Wan et al., 2014, 2016a). Previous documented wood–arthropod associations in China are based exclusively on materials from the Permian (Feng et al., 2010b, 2012, 2021; D'Rozario et al., 2011; Feng, 2012; Wei et al., 2019). In addition, fungi are important contributors to multiple levels of ecosystem functioning in both modern and ancient ecosystems (e.g., Taylor, 1993; Taylor and Krings, 2005; Oberwinkler, 2012; Taylor et al., 2014). Similar to plant–arthropod associations, the interactions between fungi and Pennsylvanian plants in Cathaysia have never been discovered before.

In this contribution, we describe materials of a fossil stem from the Benxi Formation in Yangquan City, Shanxi Province, North China. The age of the fossiliferous interval is Moscovian according to the biostratigraphy of invertebrates (Wang and Zhang, 1983). The fossil stem is characterized by a solenoid pith, endarch to mesarch primary xylem, and Agathoxylon-type secondary xylem. A new species of Parnaiboxylon Kurzawe et Merlotti is established based on pith and wood anatomy. This is the fourth gymnospermous stem species that has been reported from Pennsylvanian in Cathaysia. Coprolites and fungal hyphae in the wood of the stem are documented for the first time from the Carboniferous of China. Their palaeoecological implications are discussed.

2. Geological setting, material and methods

The research area is in Yinying Town, Yangquan City, Shanxi Province, North China (Fig. 1, A; GPS: 113°34′49.45″ E, 37°58′45.13″ N). It was a part of the North China Block and located in the coastal of the equatorial Palaeo-Tethys Ocean during the Permo-Carboniferous (Fig. 1, B; Lin et al., 1984; Zhang, 1984; Wu et al., 1990; Chang and Gao, 1993; Wang and Pfefferkorn, 2013). In the research area, the Benxi Formation overlies the Middle Ordovician Fengfeng Formation with a major unconformity and underlies conformably the GzhelianAsselian Taiyuan Formation (Figs. 1, C; 2, A). The base of the Benxi Formation is a 1 to 11 m thick bauxite. Three limestone units occur above the bauxite and are collectively named as Pingding Limestone 1 to Pingding Limestone 3 upwardly. They are correlated with the Bangou Limestone in the Eastern Hill section, constrained by a well-defined biostratigraphic framework in the city of Taiyuan (Wang and Zhang, 1983; He et al., 1995). The age of the Benxi Formation in eastern Shanxi Province is Moscovian to Gzhelian as indicated by recent chronostratigraphic and biostratigraphic correlation (Shen et al., 2022).

In this study, the fossil stem was collected from the lowermost limestone unit of the Benxi Formation. The fossiliferous interval is a 20 cm thick mudrock in between two carbonates (Fig. 2, B). Fusulinids, including

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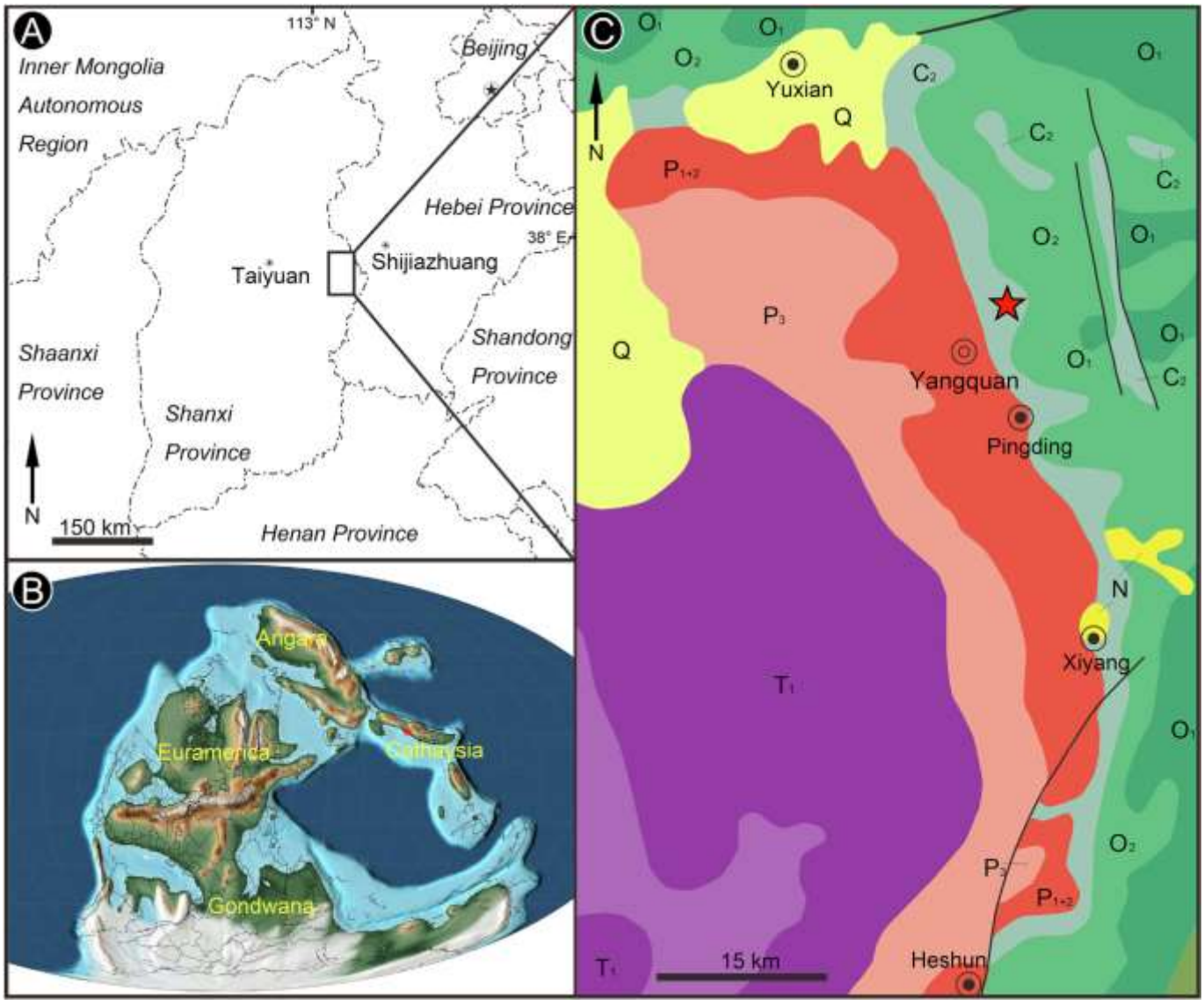


Fig. 1. A. Map showing the research area to the west of Taiyuan City, Shanxi Province, North China. B. Palaeogeographic map showing the research area was situated in palaeoequatorial area of the Cathaysia (red star; after Scotese and Wright, 2018). C. Geological map of research area, showing collection site marked by the red star symbol. O_1: Ordovician Liangjiashan Formation; O_2: Ordovician Fengfeng Formation; C_2: Carboniferous Benxi Formation and lower Taiyuan Formation; P_{1+2}: lower and middle Permian upper Taiyuan, Shanxi, Lower Shihezi and Upper Shihezi formations; P_3: upper Permian Sunjiagou Formation; T_1: Lower Triassic Liujiagou and Heshanggou formations; T_2: Middle Triassic Ermaying and Tongchuan formations; N: Neogene; Q: Quaternary, loess deposit. Modified after Wan et al. (2017b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

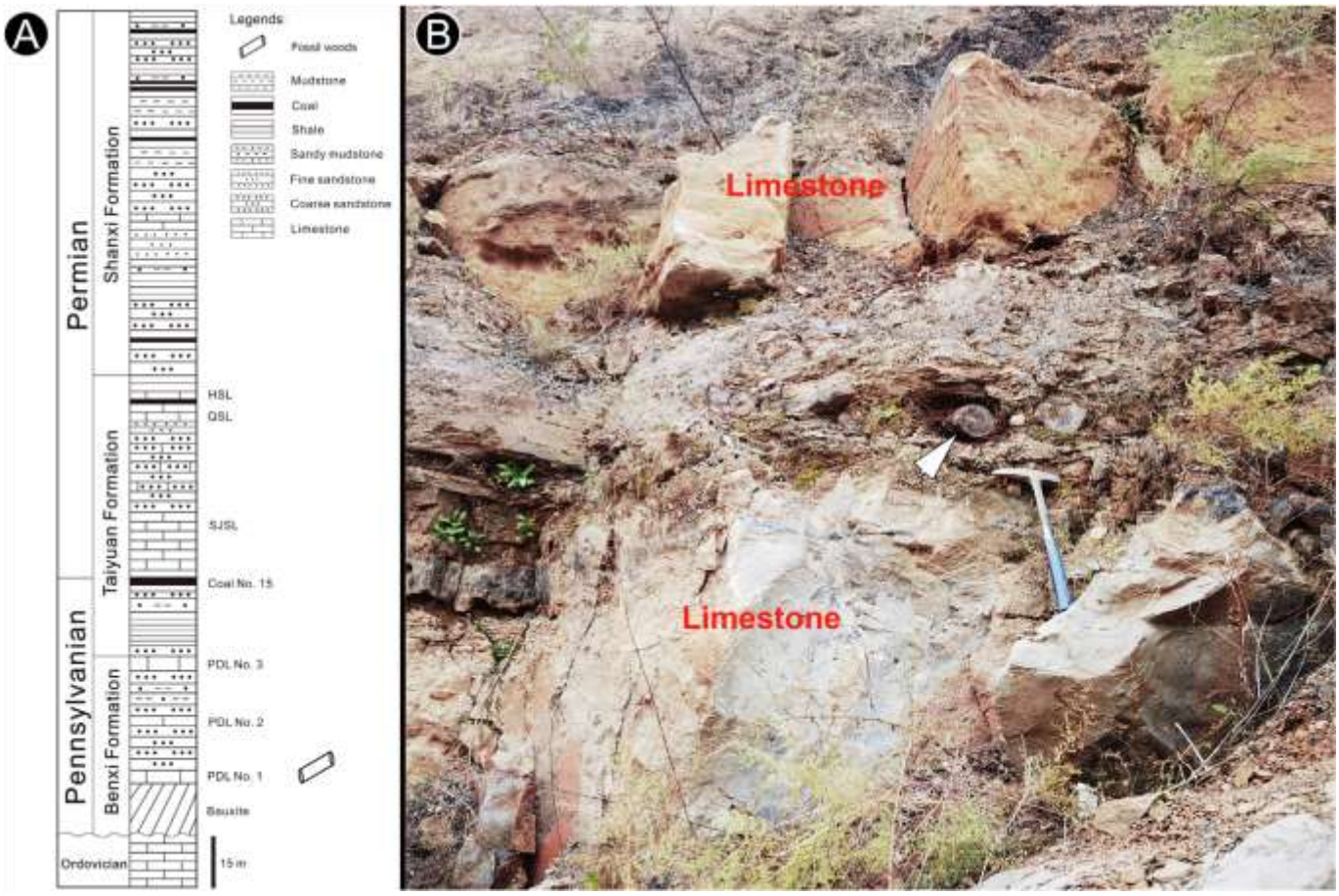


Fig. 2. A. Chrono- and lithostratigraphy of the Benxi, Taiyuan, and Shanxi formations in Yangquan, Shanxi Province, North China (modified after Wang and Zhang, 1983). The wood symbol marks the collection interval from the lowermost limestone unit. In the Benxi Formation, PDL No.1 refers to the lowermost unit of Pingding Limestone; PDL No.2 is the second unit of Pingding Limestone in the middle; and, PDL No.3 points to the uppermost unit of Pingding Limestone. In the Taiyuan Formation, SJSL is the Sijieshi Limestone, QSL means the Qianshi Limestone, and HSL refers to the Houshi Limestone. B. Field photo showing the fossil interval between two carbonate layers. White arrow points to the fossil stem in the mudstone. The hammer is 39 cm long.

Fusulina lanceolata, F. pankouensis, F. pseudokonnoi, F. schellwieni, F. truncatulina, Pseudostaffella sphaeroidea, Ozawainella turgica, and O. vozhgalica from thecarbonates indicate alateMoscovian age. Thepalaeoenvironment of the mudrock interval with the fossil stem is interpreted as a lagoon formed during a sea level fall (Wang and Zhang, 1983).

Thin sections of the fossil stem were studied following the method of Hass and Rowe (1990). The terminology of Richter et al. (2004) and Philippe and Bamford (2008) was used in the description and discussion of wood anatomical features of the fossil stem. The cross section of the stem was photographed with a Nikon D800 digital single-lens reflex camera. Thin section images were taken using a Leica DM5000 compound microscope and Leica DC 500 digital microscope camera system. The specimens and corresponding thin sections are housed in the Palaeobotanical Collection of the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences.

3. Systematics

Division: GYMNOSPERMAE Prantl, 1831

Genus: Parnaiboxylon Kurzawe et Merlotti, 2013

Type species: Parnaiboxylon rohnae Kurzawe, Merlotti et Iannuzzi, 2013

Species: Parnaiboxylon wangi sp. nov.

Holotype: PB201140, and the slides PB201140-1 to PB201140-12; all slides are made of the same specimen.

Repository: Palaeobotanical Collection of Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences.

Type locality: Houwa Village, Yinying Town, Yangquan City, Shanxi Province, China (Fig. 1, GPS: 113°34′49.45″ E, 37°58′45.13″ N).

Stratigraphic horizon: Benxi Formation.

Age: Moscovian, Pennsylvanian.

Etymology: The specific epithet is dedicated to Mr. Jigui Wang, Director of Municipal Congress of the Yangquan City, for his great support to the fieldwork in the research area during the last decade.

Specific diagnosis: Woody tree, stem eustelic. Pith solid, circular, heterocellular, with parenchymatous cells and numerous secretory canals, and ducts at the periphery. Primary xylem strands endarch to mesarch. Tracheids of primary xylem with helical and scalariform thickenings. Secondary xylem pycnoxylic, composed of tracheids, rays, and axial parenchyma. Araucarian radial tracheidal pits uni- to quadriseriate. Bordered pits circular in outline with oblique and slitlike apertures. Rays uniseriate, 1–44 cells high. Ray parenchymatous cells procumbent, rectangular in radial section. Cross-field pitting araucarioid. Each cross-field with 1–7 cupressoid pits. Axial xylem parenchyma irregularly distributed among the secondary xylem tracheids.

4. Description

4.1. General features

The stem is 12 cm in diameter and 36 cm in length in the field, and is weathered into numerous small pieces (Fig. 2, B). They are well preserved with

a cylindrical shape. A relatively complete segment (PB201140) showing all essential features was selected as the holotype.

The center of the specimen displays a prominent broad eustele with a wide solid pith (Fig. 3, A–B). The secondary xylem is pycnoxylic. Cortical and peridermal structures are not preserved. The following description is based on thin section observations of specimen PB201140.

4.2. Pith

The pith is solid, heterogeneous with secretory canals, ducts, cells, and parenchyma (Fig. 4, A–H). It measures 9 × 12 mm in cross section. Secretory canals and ducts occur in the pith periphery among parenchymatous cells (Figs. 4, A; 5, A–D). In cross section, secretory canals are circular to oval in shape, 150–750 μm in diameter, and hollow in the middle (Fig. 5, A–B). Canals are delimitated by a sheath of oblong parenchymatous cells (Fig. 5, A–B). They are up to 9 mm in length in radial section (Fig. 5, C–D). There are 27 separate secretory canals forming a circle at the periphery of the pith (Fig. 4, A). Secretory ducts extend longitudinally up to 400 μm. Secretory cells are circular to sub-circular in transverse view, 40–100 μm in diameter (Fig. 4, B–C, H). They distribute irregularly throughout the pith. They are commonly filled with opaque substance (Fig. 4, B–C, H).

Normal parenchyma has two types of cells: one has thinner cell walls; the other has thicker cell walls. Thinner cell walls are commonly less than 5 μm in thickness (Fig. 4, C, E). Thickness of the thicker cells are up to 40 μm (Fig. 4, D, F). The parenchymatous cells are circular to elliptical and vary from 30 to 100 μm in diameter in cross section (Fig. 4, B). They are largest in diameter at the pith center, decreasing in size toward the periphery (Fig. 4, A). In radial sections, these cells show a subrectangular or rounded shape (Fig. 4, E–F).

4.3. Primary xylem

The primary xylem strands show endarch to mesarch maturation (Fig. 5, E–F). Tracheids are up to 40 μm in diameter. In radial sections, walls of tracheids contain helical and scalariform thickenings (Fig. 5, G). 4.4. Secondary xylem

The secondary xylem consists of tracheids, rays, and axial parenchyma (Fig. 6, A–B). False rings are well developed (Fig. 3, A). Tracheids in false rings vary gradually in diameter from thinner-walled, larger cells to thicker-walled, smaller cells, and change at an opposite direction, forming a symmetrical boundary. In cross section, tracheids are crudely rounded to polygonal in shape, about 25–60 μm in diameter, and arranged in regular radial files (Fig. 6, A–B). Radial tracheidal pits are uni- to quadriseriate, araucarian (sensu Philippe and Bamford, 2008; Fig. 6, C–E). Biseriate pitting is dominant, accounting for about 60% (n = 500). Bordered pits on radial tracheidal walls are rounded to oval, 9–15 μm in diameter, with slit-like apertures. Uniseriate pits arrange continuously on radial tracheidal walls (Fig. 6, C). When multiseriate, radial pits are mostly alternately distributed (Fig. 6, D–E).

Axial parenchyma is isolated and irregularly distributed among the xylem tracheids, with a diameter varying from 25 to 60 μm (Fig. 6, B). In radial section, they appear to have the similar shape and size to adjacent tracheids, but are filled with black opaque substance (Fig. 6, H). Tangential pits are absent.

Rays are homocellular and commonly uniseriate, rarely biseriate (Fig. 6, F–G). In radial section, parenchymatous ray cells are rectangular and range from 50 to 110 μm long and 15 to 30 μm high (Fig. 7, A). Each ray cell spans 1–4, commonly 2–3 tracheids. Cell walls of ray parenchymatous cells are smooth. The vertical walls of ray cells are commonly perpendicular to the horizontal walls. In some cases, the vertical walls are inclined at an angle of 50°–70°. Rays are 1–44 cells high, and 8 cells high on average (n = 200). The cross-field pitting is cupressoid and araucarioid (sensu Richter et al., 2004; Fig. 7, B–D). There are 1–8 pits in each cross-field. Cross-field pits are oval to circular, bordered, with elliptically oval to slit-like apertures (Fig. 7, D).

5. Comparison and discussion

Anatomical features of the pith are diagnostic criteria for the classification and identification of Paleozoic and Mesozoic gymnospermous stems (Lepekhina and Yatsenko-Khmelevsky, 1966; Maheshwari, 1972; Lepekhina, 1969, 1972; Pant and Singh, 1987; Feng, 2012; Wan et al., 2021a, 2021c). Solenoid was defined by Mussa (1986) as fossil stems with a pith having a system of secretory canals and ducts. To our knowledge, at least 20 genera of fossil stems with solenoid pith have been commonly recorded from the Paleozoic in both northern and southern hemispheres (e.g., Kurzawe et al., 2013; Wan et al., 2014, 2017c; Conceição et al., 2022; and references therein). Only two genera, including Europoxylon Vogellehner and Megaporoxylon Kräusel, have been recorded from the Pennsylvanian of Europe and Africa respectively (Kräusel, 1956a, 1956b; Vogellehner, 1965; Bangert and Bamford, 2001). Occurrence of sclereids and absence of secretory canals in the pith of Europoxylon make it distinct from our stem (Vogellehner, 1965). In Megaporoxylon, cross-field pitting is window-like or phyllocladoid, which is distinguishable from the cupressoid and araucarioid pitting in current stem (Kräusel, 1956a; Wan et al., 2021c). Therefore, the stem in current study represents the third Carboniferous fossil taxon with solenoid pith.

The homoxylic wood of current stem is characterized by the araucarian radial tracheidal pits, cupressoid and araucarioid cross-field pitting, and the occurrence of axial parenchyma. These anatomical features make it comparable to Agathoxylon Hartig (Philippe, 1993, 2011; Philippe and Bamford, 2008; Rößler et al., 2014). Fossil stems with solenoid pith containing peripheral secretory canals and ducts, endarch to mesarch primary xylem, and Agathoxylon-type secondary xylem are commonly assigned to Parnaiboxylon Kurzawe et Merlotti (Kurzawe et al., 2013; Conceição et al., 2022). Parnaiboxylon rohnae Kurzawe, Merlotti et Iannuzzi is the only formally named species of the genus. Our specimen is different from the type species in three aspects. First, there are two types of parenchymatous cells with thinner and thicker walls in the pith of current stem. However, parenchymatous cell walls in the pith of P. rohnae is homogeneous. Second, xylem rays in current wood, which are 1–44 (average 8) cells high, are much higher than those (1–9 cells high) in P. rohnae. Last but not least, axial parenchyma is present in our stem but absent in P. rohnae. Kurzawe et al. (2013) described Parnaiboxylon sp. indet. from the Permian Lower Motuca Formation of Brazil. However, the lack of primary xylem of Parnaiboxylon sp. indet. prevent a further comparison with our stem. Therefore, based on the evidence and discussion mentioned above, we establish the new species Parnaiboxylon wangi sp. nov. herein.

The pith of current stem is characterized by the occurrence of secretory canals and ducts distributed at the pith periphery forming a circle. This type of pith is comparable to those in many fossil trees from the Permian of Gondwana (Table 1), including Barakaroxylon jhariense Surange et Maithy, Corticoxylon ampla Merlotti, Ductoabietoxylon solis Kurzawe et al., Ductosolenoxylon guerrae Merlotti, Petalopitys surangei Mussa, Polysolenoxylon whitei Kräusel et Dolianiti, and Solenopitys paulistana Kräusel et Dolianiti (Kräusel and Dolianiti, 1958; Surange and Mathy, 1961; Mussa, 1986; Merlotti, 1989, 2002; Kurzawe et al., 2013). As a diagnostic character of Paleozoic fossil stems, lacunae are present in the pith of C. ampla, Petalopitys surangei, and Polysolenoxylon whitei (Kräusel and Dolianiti, 1958; Mussa, 1986; Merlotti, 1989, 2002). However, this feature is absent from the pith of our stem. It should be noted that the mixed radial tracheidal pitting of B. jhariense, C. ampla, and Ductosolenoxylon guerrae is different from the araucarian pits on radial walls of Parnaiboxylon wangi sp. nov. of current study (Surange and Mathy, 1961; Merlotti, 1989, 2002). Last but not least, the endarch to mesarch primary xylem of Parnaiboxylon wangi sp. nov. is distinguishable from the endarch maturation of primary xylems of those Gondwana tree species mentioned above.

In the Cathaysia, gymnospermous stems are commonly recorded from the Permian (Feng, 2012; Feng et al., 2012; Zheng et al., 2008;

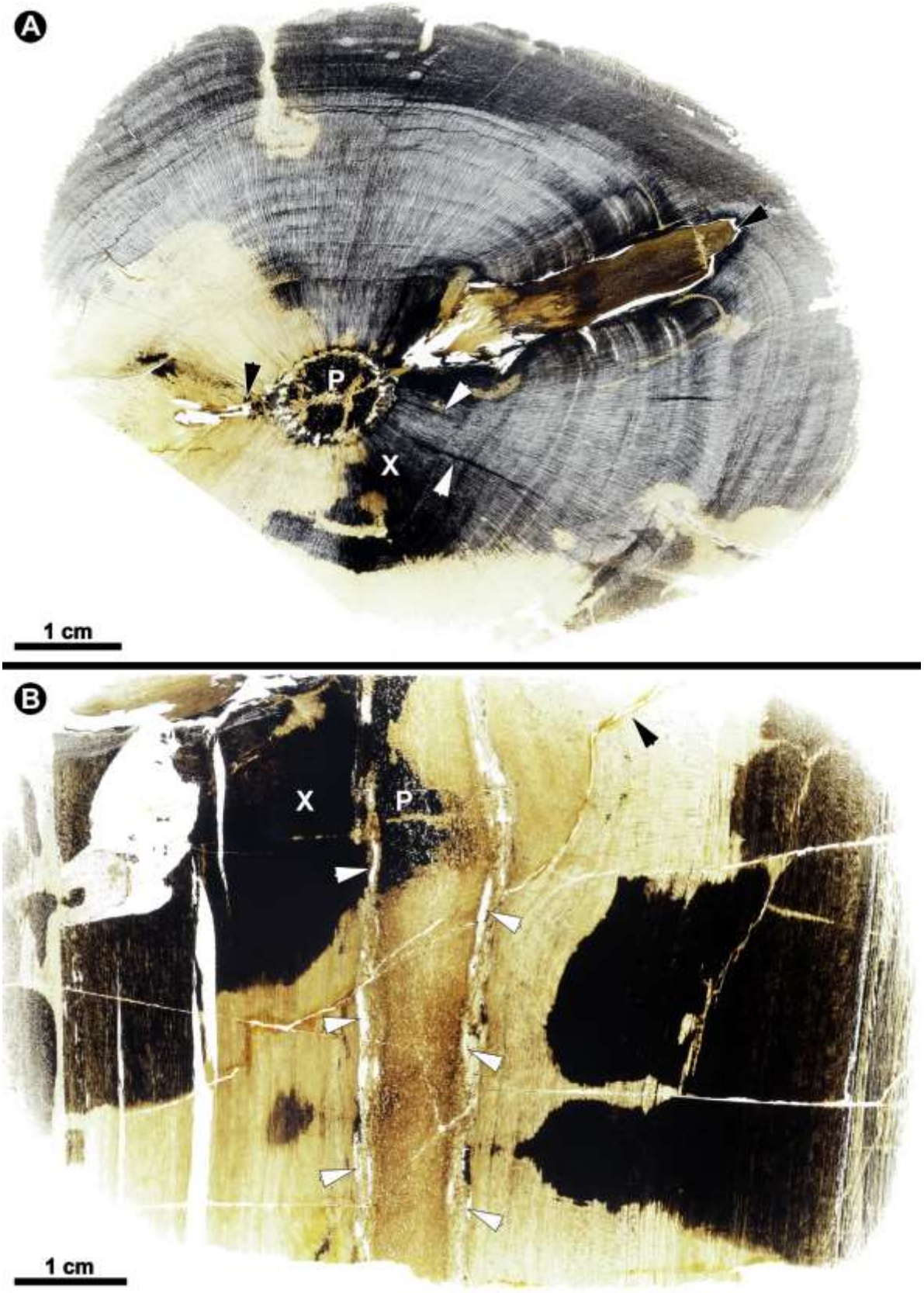


Fig. 3. Photomicrographs showing the gross morphology and pith structure of Parnaiboxylon wangi sp. nov. from the Moscovian of Yangquan City, Shanxi Province, North China. A. Photomicrograph of a cross section of the fossil stem, showing the overview of the plant axis containing pith (P) and secondary xylem (X). Branch traces are shown by black arrows. Leaf traces are indicated by white

arrows. Collection number: PB201140; slide number: PB201140-1; holotype. B. Photomicrograph of a radial section of the fossil stem, the solid heterocellular pith (P) and secondary xylem(X). Collection number: PB201140; slide number: PB201140-2; holotype.

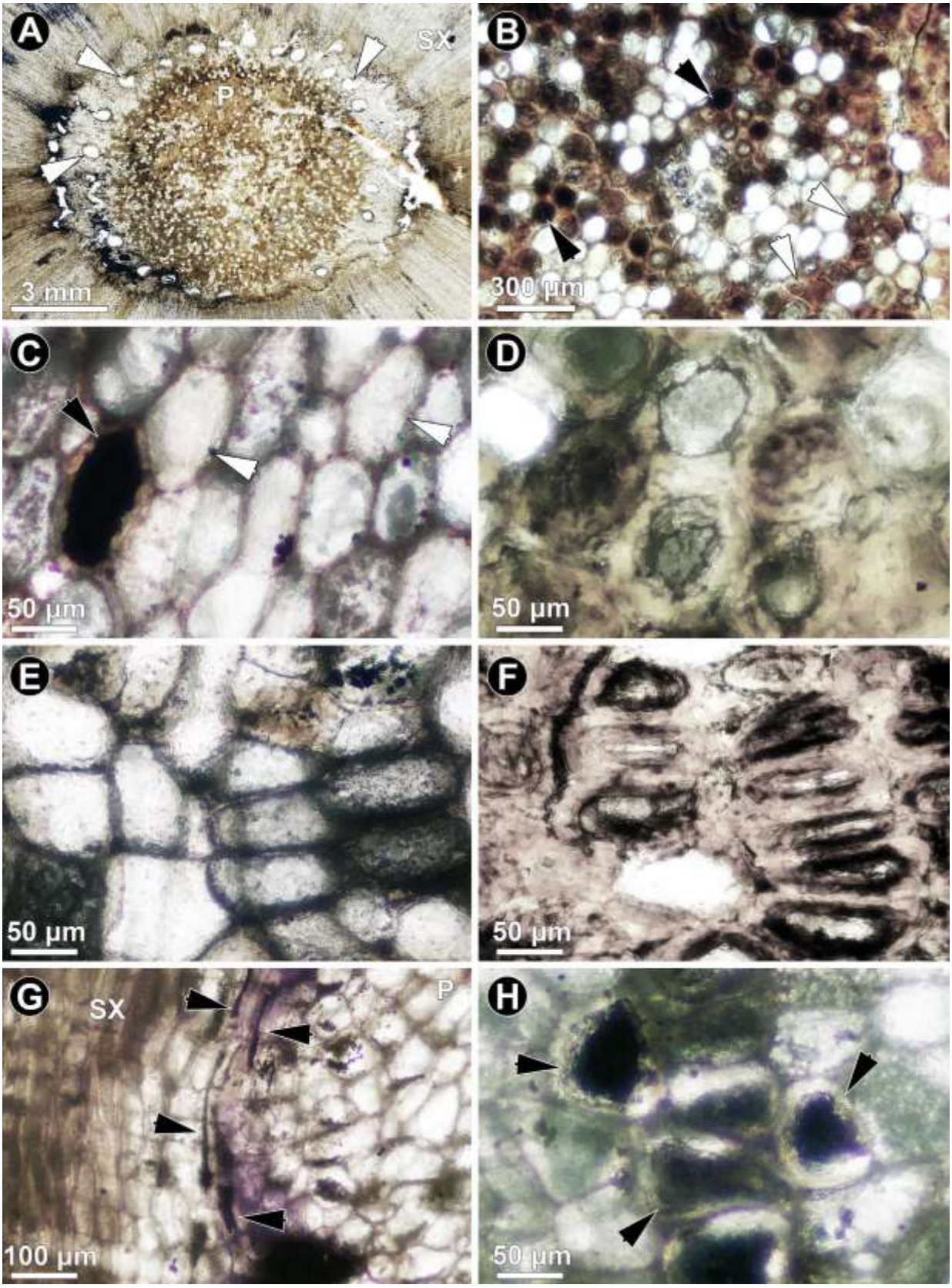


Fig. 4. Photomicrographs showing the characteristics of pith anatomy of Parnaiboxylon wangi sp. nov. from the Moscovian of Yangquan City, Shanxi Province, North China. A. Cross section of the pith (P) and secondary xylem (SX), showing 27 secretory canals (white arrows) at the pith periphery. Collection number: PB201140; slide number: PB201140-3; holotype. B. Cross section of the pith, showing the circular to elliptical parenchymatous cells with secretory cells and ducts with opaque contents (black arrows). White arrows point to the parenchymatous cells with thicker walls. Collection

number: PB201140; slide number: PB201140-3; holotype. C. Cross section of the pith, showing the circular to elliptical parenchymatous cells with thinner (white arrows) and a secretory cell with opaque contents (black arrow). Collection number: PB201140; slide number:PB201140-3; holotype. D. Cross section of the pith, showing the circular to elliptical thicker parenchymatous cells. Collection number: PB201140; slide number: PB201140-3; holotype. E. Radial section of the pith, showing the sub-rectangular or rounded parenchymatous cells with thinner cell walls. Collection number: PB201140; slide number: PB201140-2; holotype. F. Radial section of the pith, showing the sub-rectangular or rounded parenchymatous cells with thicker cell walls. Collection number: PB201140; slide number: PB201140-2; holotype. G. Radial section of the pith (P) and secondary xylem (SX), showing the longitudinal secretory ducts with opaque contents at the pith periphery (black arrows). Collection number:PB201140; slidenumber: PB201140-2–2; holotype. H. Radial section of the pith, showing theub-rectangular or rounded secretory cells with opaque contents.

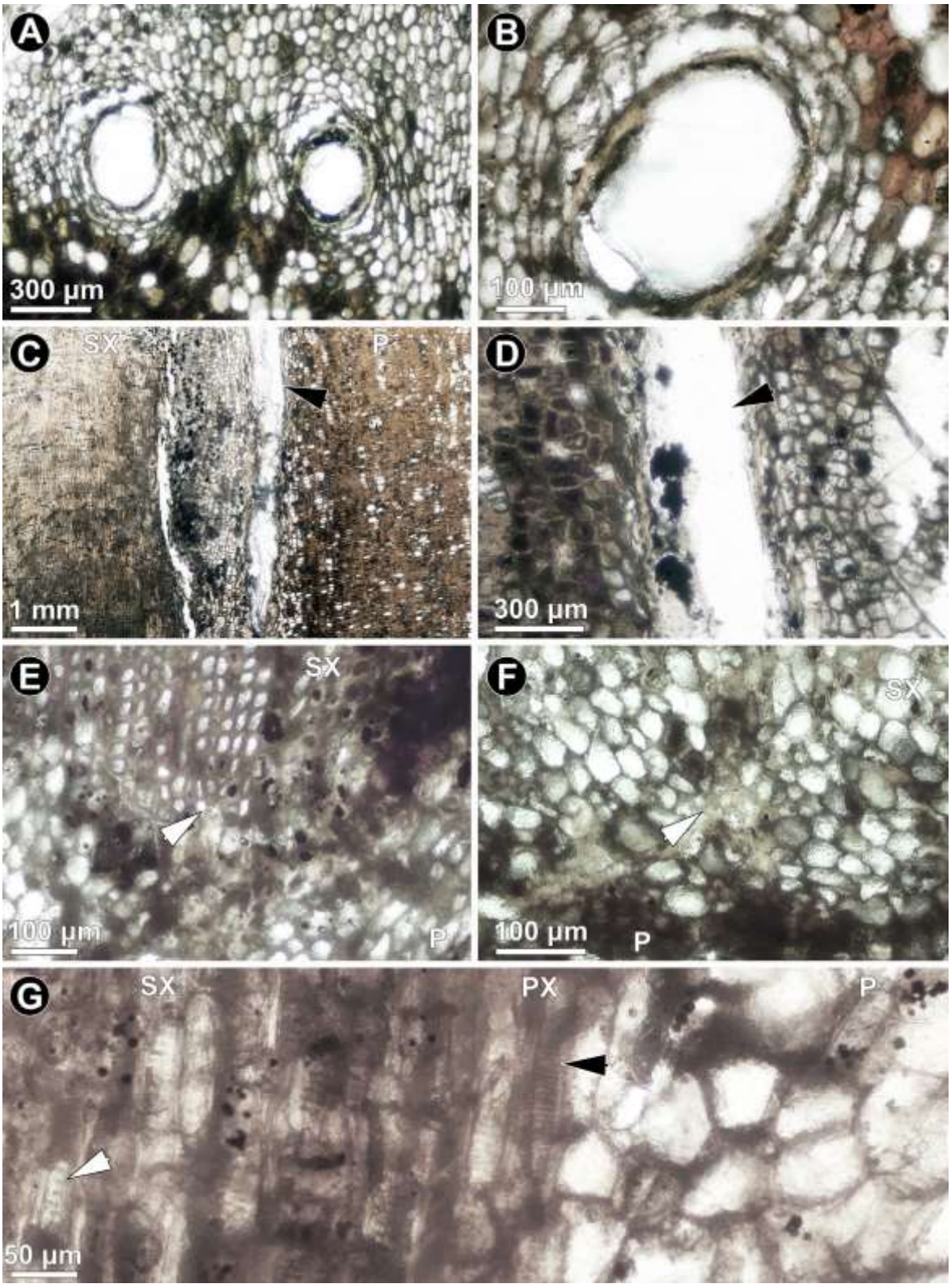


Fig. 5. Photomicrographs showing the anatomy of Parnaiboxylon wangi sp. nov. from the Moscovian of Yangquan City, Shanxi Province, North China. A. Photomicrograph of a cross section of the pith, showing 2 circular secretory canals with a hollow center at the pith periphery. Collection number: PB201140; slide number: PB201140-3; holotype. B. Photomicrograph of a cross section of the pith, showing the secretory canal delimitated by a sheath composed of oblong parenchymatous cells. Collection number: PB201140; slide number: PB201140-3; holotype. C. Photomicrograph of a radial section of the pith (P) and secondary xylem (SX), showing a secretory canal with hollow center (black arrow). Collection number: PB201140; slide number: PB201140-2; holotype. D. Photomicrograph of a radial section of the pith (P) and secondary xylem (SX), showing an enlargement of secretory canal with hollow center (black arrow). Collection number: PB201140; slide number: PB201140-2; holotype. E. Photomicrograph of a cross section of the stem, showing the distribution of the pith (P) and secondary xylem (SX). White arrow points to the endarch primary xylem. Collection number: PB201140; slide number: PB201140-3; holotype. F. Photomicrograph of a cross section of the stem, showing the distribution of the pith (P) and secondary xylem (SX). White arrow points to the mesarch primary xylem. Collection number: PB201140; slide number: PB201140-3; holotype. G. Photomicrograph of a radial section of the stem, showing the distribution of the pith (P) and primary xylem (PX) and secondary xylem (SX). White arrow points to the endarch primary xylem. Black arrow points to the scalariform thickenings on radial tracheidal walls of the primary xylem. White arrow demonstrates bordered pits on radial tracheidal walls of the secondary xylem. Collection number: PB201140; slide number: PB201140-2; holotype.

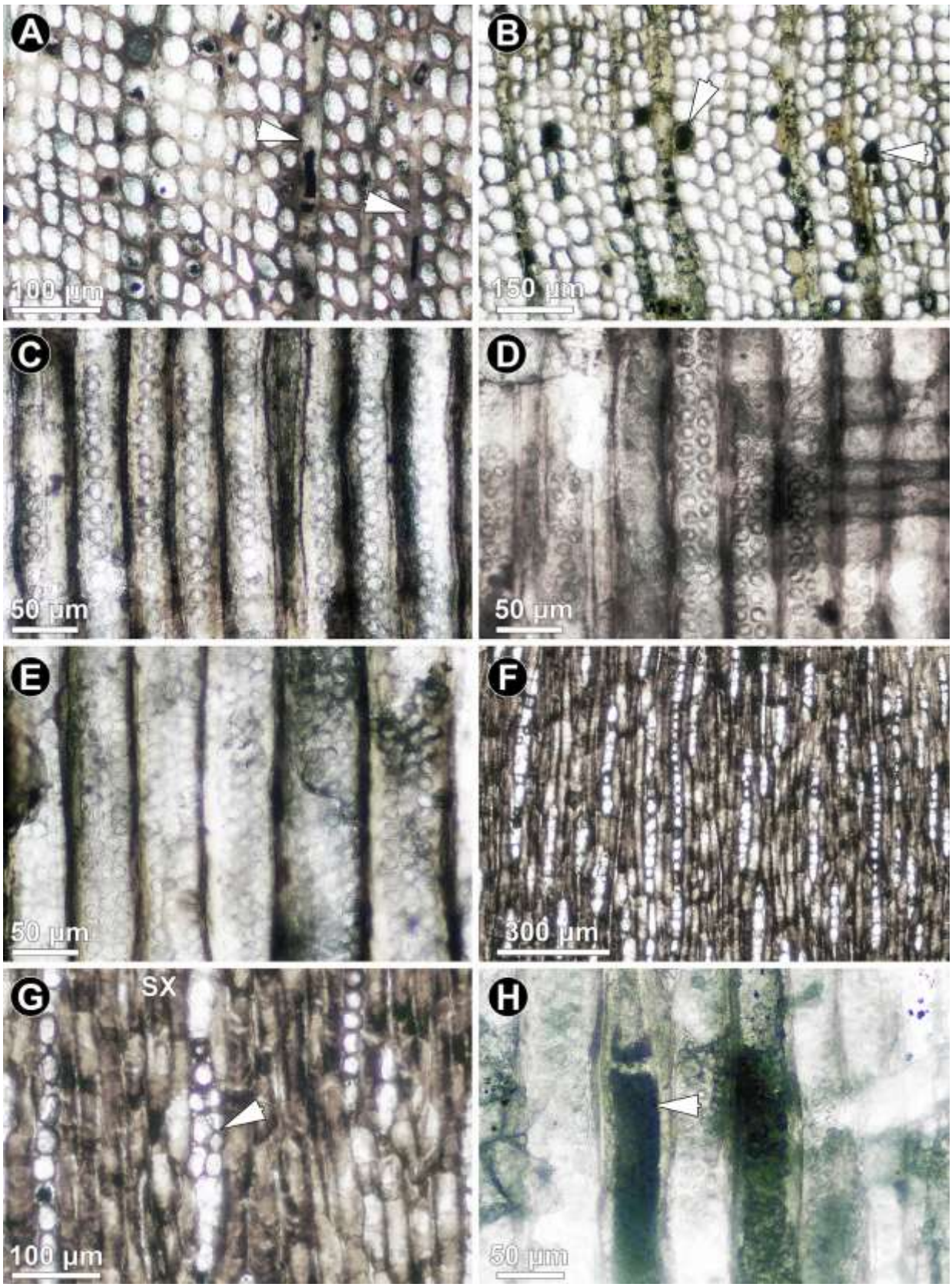
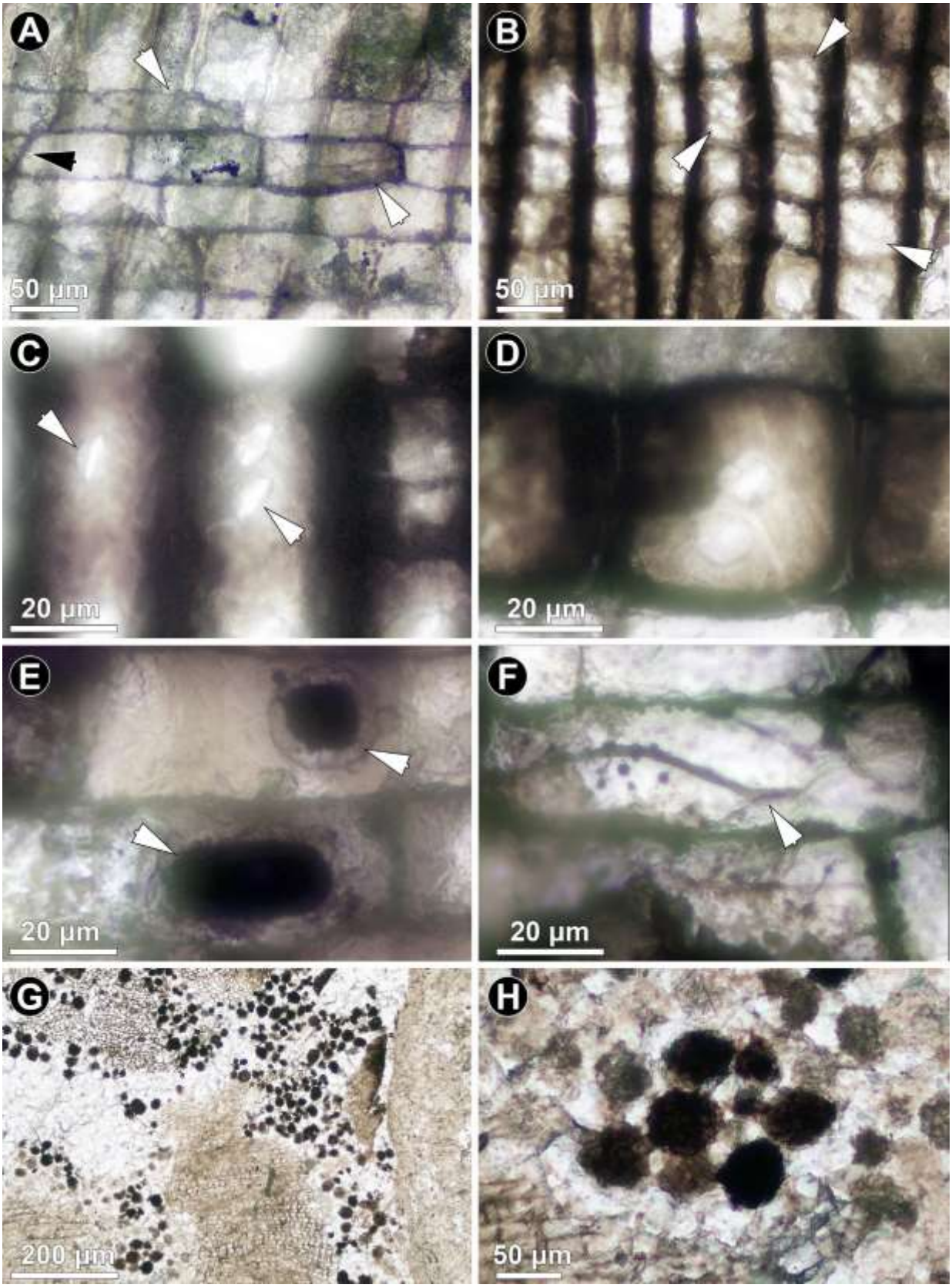


Fig. 6. Photomicrographs showing the anatomy of Parnaiboxylon wangi sp. nov. from the Moscovian of Yangquan City, Shanxi Province, North China. A. Photomicrograph of a cross section of the secondary xylem, showing polygonal to sub-rounded tracheids and uniseriate ray cells (white arrows). Collection number: PB201140; slide number: PB201140-3; holotype. B. Photomicrograph of a cross section of the secondary xylem, showing polygonal to sub-rounded tracheids and axial parenchyma next to uniseriate ray cells with opaque contents (white arrows). Collection number: PB201140;

slide number: PB201140-3; holotype. C. Photomicrograph of a radial section of the secondary xylem, showing the continuously uniseriate pits. Collection number: PB201140; slide number: PB201140-4; holotype. D. Photomicrograph of a radial section of the secondary xylem, showing the biseriate pits with alternate arrangement. Collection number: PB201140; slide number: PB201140-4; holotype. E. Photomicrograph of a radial section of the secondary xylem, showing the tri- to quadriseriate pits with alternate arrangement. Collection number: PB201140; slide number: PB201140-4; holotype. F. Photomicrograph of a tangential section of the secondary xylem, showing the uniseriate rays. Collection number: PB201140; slide number: PB201140-5; holotype. G. Photomicrograph of a tangential section of the secondary xylem, showing the dominant uniseriate rays and rarely partially biseriate rays (white arrow). Collection number: PB201140; slide number: PB201140-5; holotype. H. Photomicrograph of a radial section of the secondary xylem, showing the axial parenchyma with smooth walls and opaque contents (white arrow). Collection number: PB201140; slide number: PB201140-6; holotype.


A
50 μm
B
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C
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D
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E
20 μm
F
20 μm
G
200 μm
H
50 μm

Table 1
Fossil stems with solenoid pith comparable with Parnaiboxylon wangi sp. nov.

Species	Pith	Primary xylem	Secondary xylem			References
			Pits on radial walls	Xylem rays	Cross-field pits	
Parnaiboxylon wangi sp. nov.	Heterocellular, with parenchyma, secretory ducts and cells, periphery canals	Endarch to msearch	Uni to quadriseriate, araucarian	Uniseriate, rarely partly biseriae, 1–44 cells high	Cupressoid and araucarioid, 1–8 pits in each field	The present paper
Barakaroxylon jhariense Surange et Maithy	Heterocellular, with sclereids, secretory cells and canals	Endarch	Uni-to triseriate, mixed	Uni- to bieriate, up to 22 cells high	Araucarioid, up to 7 pits in each field	Surange and Mathy, 1961
Corticoxylon ampla Merlotti	Heterocellular, with secretory cells, canals, and lacunae	Endarch	Uni-to multiseriate, mixed	Uni- to bieriate, 1–20 cells high	Cupressoid	Merlotti, 1989
Ductoabietoxylon solis Kurzawe et al.	Heterocellular, with secretory cells and ducts	Endarch	Uni-to triseriate, araucarian	Uniseriate, 1–12 cells high	Cupressoid, up to 5 pits in each field	Kurzawe et al., 2013
Ductosolenoxylon guerrae Merlotti	Heterocellular, with secretory cells and ducts	Endarch	Uni-to triseriate, mixed	Uniseriate, up to 19 cells high	Araucarioid	Merlotti, 2002
Petalopitys surangei Mussa	Heterocellular, with secretory cells, canals, and lacunae	Endarch	Uniseriate, rarely biseriate, araucarian	Uniseriate, 1–25 cells high	One, large, rarely two, oval, oblique	Mussa, 1986
Polysolenoxylon whitei Kräusel et Dolianiti	Heterocellular, with secretory cells, ducts, canals, and sclerenchyma	Endarch	Uni-to triseriate, araucarian	Uniseriate	Cupressoid, 2–4 pits in each field	Kräusel and Dolianiti, 1958
Solenopitys paulistana Kräusel et Dolianiti	Heterocellular, with secretory cells, and periphery ducts	Endarch	Uni-to triseriate, araucarian	Uniseriate	Cupressoid, 1–5 pits in each field	Kräusel and Dolianiti, 1958

Wei et al., 2019; Wan et al., 2020c). Sixteen species of eleven genera fossil gymnospermous stem with pith, primary and secondary xylems have been formally described (Table 2) from the Permo-Carboniferous. Surprisingly, none of them shows secretary canals in the pith. Three gymnospermous stems, including Agathoxylon leei (Sze) Wang et Wan, Damudoxylon meii Wang et Wan, and Zalesskioxylon xiaheyanense Feng, Wang et Shen, have been reported from the Pennsylvanian of North China (Feng et al., 2008; Wang et al., 2022b). Among them, cellular structures of pith and primary xylem in A. leei from the Benxi Formation of Yangquan, and in Z. xiaheyanense from the lower part of Taiyuan Formation of Ningxia Hui Autonomous Region, are not preserved. The predominantly (94%) uniseriate radial tracheidal pitting in A. leei is different from that of predominantly biseriate pitting on radial tracheidal walls of Parnaiboxylon wangi sp. nov., which has uni- to quadriseriate pits. Damudoxylon meii is established from the Benxi Formation of Yangquan City, which is 6 km away from current research locality. The solid pith of D. meii without any secretory canals in the pith is different from that of P. wangi. Therefore, our finding of Parnaiboxylon wangi sp. nov. from the Benxi Formation represents the fourth wood species from the Pennsylvanian of North China and, expands the knowledge on the diversity of fossil gymnosperms in Yangquan City, Shanxi Province.

Empirical studies suggest that the presence of canals in the pith of fossil tree trunks would be a response of xeromorphism (Mussa, 1986; Guerra-Sommer et al., 2014; Conceição et al., 2022). Parnaiboxylon wangi sp. nov. was collected from lagoonal deposits of the Benxi Formation (Wang and Zhang, 1983) without attached branches or rooting systems. It indicates an allochthonous preservation of the stem. It would have been transported from marine-influenced coastal plain or stream bank into the lagoon. Therefore, the occurrence of solenoid pith in current study is proposed to be related to an environment with episodic salinity and/or water table variations. This explanation is supported by the occurrence of irregularly spaced growth interruptions (sensu FalconLang, 2003) in the stem. Growth interruptions in P. wangi sp. nov. are characterized by a rapid decline in tracheid diameter, followed by an equally rapid return to the normal diameter, resulting in symmetrical growth boundaries. It suggests episodic and irregular growth disturbances when the tree was alive. This type of growth interruptions in fossil trunks commonly indicates an environment with intermittent droughts (Wan et al., 2014; Falcon-Lang et al., 2016) or occasional incursions of seawater (Wang, 1989).

In Parnaiboxylon wangi sp. nov., fungal hyphae are abundant in the ray system of the secondary xylem. They extend through the ray parenchymatous cells, and are non-septate, tubular in shape, relatively uniform in size, ranging from 1 to 3 μm in diameter (Fig. 7, F). Fungi are important mutualistic symbionts, decomposers, or plant pathogens in modern ecosystems (Barbee et al., 2017). In addition, they have had a long and complex geological history and played an important role in ancient ecosystems (Stubblefield and Taylor, 1988; Stubblefield et al., 1984,; Krings et al., 2007, 2011, 2012; Césari et al., 2012; García Massini et al., 2012; Harper et al., 2012, 2016; Taylor et al., 2014; Wan et al., 2014, 2017a; Wei et al., 2019). Saprophytism and parasitism have been documented in fossil woods from the Paleozoic and Mesozoic (e.g., Stubblefield and Taylor, 1988; Wan et al., 2016a). The absence of clear evidence of fungal-induced decay or any tissue damage in the wood of P. wangi sp. nov. indicates that the fungal hyphae in the ray cells may not play the role of a decomposer. Parasitism is difficult to be identified in the fossil wood. In modern plants, it is commonly inferred on the basis of the identity of the fungus, and of the evidence of host response (Stubblefield and Taylor, 1988). Although abundant, the affinity of these fungal hyphae is obscure due to the lack of diagnostic features or reproductive organs. The most distinctive feature of P. wangi sp. nov. in current study is the occurrence of spherical bodies in ray cells (Fig. 7, E). Each spherical body is composed of a dark nuclear surrounded by an outwardly transparent zone. The body ranges from 5 to 30 μm in diameter. Similar contents in ray parenchymatous cells have been recorded from the modern gymnospermous trunk

Fig. 7. Photomicrographs showing the anatomy of Parnaiboxylon wangi sp. nov. from the Moscovian of Yangquan City, Shanxi Province, North China. A. Photomicrograph of a radial section of the secondary xylem, showing rectangular parenchymatous ray cells spanning 1 to 3 tracheids (white arrows). Collection number: PB201140; slide number: PB201140-6; holotype. B. Photomicrograph of a radial section of the secondary xylem, showing araucarioid cross-field pitting, with up to 8 pits in each field (white arrows). Collection number: PB201140; slide number: PB201140-7; holotype. C. Photomicrograph of a radial section of the secondary xylem, showing the cupressoid cross-field pitting (white arrows). Each field contains 1 to 2 bordered pits. Collection number: PB201140; slide number: PB201140-7; holotype. D. Photomicrograph of a radial section of the secondary xylem, showing a cross-field with two cupressoid pits. Collection number: PB201140; slide number: PB201140-7; holotype. E. Photomicrograph of a radial section of the secondary xylem, showing spherical bodies in ray cells with a dark nuclear and an outwardly transparent surrounding zone (white arrows). Collection number: PB201140; slide number: PB201140-6; holotype. F. Photomicrograph of a radial section of the secondary xylem, showing the tube-like fungal hyphae with the ray cells (white arrow). Collection number: PB201140; slide number: PB201140-6; holotype. G. Photomicrograph of a cross section of the secondary xylem, showing the decayed tunnels with abundant coprolites (white arrow). Collection number: PB201140; slide number: PB201140-8; holotype. H. Photomicrograph of a radial section of the secondary xylem, showing the densely distributed spheroidal and ovoidal, dark colored coprolites. Collection number: PB201140; slide number: PB201140-9; holotype.

Table 2

Comparison of gymnospermous stems with pith and primary xylem from the Permo–Carboniferous Cathaysia Flora in China.

Species	Pith	Primary xylem	Secondary xylem			Type locality, horizon and age	Reference
			Pits on radial walls	Xylem rays	Cross–field pits		
Parnaiboxylon wangi sp. nov.	Solid, hetercellular, with parenchyma, secretory ducts and cells, periphery canals	Endarch to msearch	Uni to quadiseriate, araucarian	Uniseriate, rarely partly biseriae, 1–44 cells high	Cupressoid and araucarioid, 1–8 pits in each field	Yangquan, Shanxi; Benxi Formation; Moscovian, Carboniferous	The present paper
Chapmanoxylon taiyuanense Li emend. Wang	Solid and homocellular, parenchyma	Endarch; spiral, reticulate, scalariform and bordered pits thickenings	Uni–biseriate	Uniseriate, rarely partly biseriate, 1–14 cells high, uppermost to 38	1–2 pits	Taiyuan, Shanxi; Taiyuan Fm; Lower Permian	Li, 1986; Wang, 2000
Chapmanoxylon teilhardii Sze comb. Wang	Solid and homogeneous, parenchyma	Endarch	Biseriate, occasionally uniseriate or triseriate	Homogeneous, uniseriate, 1–6 (rarely more than 8) cells high	Simple, 3–6 pits	Datong, Shanxi; Upper Shihhotse Fm; Upper Permian	Sze, 1934; Wang, 2000
Cordaixylon tianii Tian et Wang comb. Wang et Hilton	Septate or hollow, with peripheral parenchyma and a few sclereids	Endarch	Uni–biseriate, uniseriate pits sparsely arranged, biseriate pits alternative	Uniseriate, commonly 2–4 cells high; a few reach heights of 5–6 (more rarely 7–8)	Cupressoid, 1 (or rarely 2) obliquely orientated oval pit	Taiyuan, Shanxi; Taiyuan Fm; Lower Permian	Tian and Wang, 1987; Hilton et al., 2009a
Damudoxylon meii Wang et Wan	Solid, heterogeneous, with parenchymatous cells and secretory cavities	Endarch; scalariform and spiral thickenings	Mostly biseriate; rarely uniseriate	Uniseriate, 2–27 cells high	mall, dispersed bordered pits with circular apertures	Yanquan, Shanxi; Benxi Fm; Upper Carboniferous	Wang et al., 2022a
Damudoxylon zhoui Zhang et Zheng	Heterogeneous, with parenchyma and secretory cells	Endarch	Uni–triseriate	Mostly uniseriate, rarely biseriate	Undescribed	Chaoyang, Liaoning; Taiyuan Fm; Lower Permian	Zheng et al., 2008
Guizhouxylon dahebianense Tian et Li	Solid and heterogeneous, with sclerenchyma, parenchyma, secretory cells	Endarch	Uni–tetraseriate, mostly uniseriate–biseriate	Uniseriate, mostly 1–11 cells high, sometimes up to 15	3–5 oblique elongate trapezoid, or oval pits, rarely 6–8 oval pits	Shuicheng, Guizhou; Longtan Fm； Upper Permian	Tian and Li, 1992
Koleoxylon chinense Zhang et Zheng	Solid and heterocelluar, with parenchyma, sclerenchyma, peripheral conduct sheath	Endarch; scalariform or spiral thickenings	Araucarian, uni–triseriate, mostly uniseriate to biseriate	Uni–biseriate, locally triseriate, mostly 5–20 cells high, uppermost to 35 cells high	1–2 large, obliquely ovate pits	Chaoyang, Liaoning; Taiyuan Fm; Lower Permian	Zheng et al., 2008
Koleoxylon xuetaiziensis Zhang et Zheng	Solid and heterocelluar, with parenchyma, sclerenchyma, peripheral conduct sheath	Endarch; scalariform or spiral thickenings	Araucarian, uni–triseriate, mostly biseriate	Uni–biseriate, locally triseriate, mostly 5–20 cells high, uppermost to 35 cells high	1–2 large and simple, obliquely ovate pits	Chaoyang, Liaoning; Taiyuan Fm; Lower Permian	Zheng et al., 2008
Ningxiaites shitanjingensis Wei et Feng	Solid, with parenchyma	Endarch, annular, helical, scalariformor reticulate thickenings	Uniseriate, sometimes partly biseriate or rarely triseriate	Uniseriate, rarely partly biseriate, 1–14 (average 3.6) cells high	Cupressoid, 1–2 pits	Shitanjing, Ningxia; Sunjiagou Fm; Upper Permian	Wei et al., 2019
Ningxiaites specialis Feng	Solid, with parenchyma	Endarch	Uniseriate, sometimes partially biseriate or triseriate	Homogeneous, uniseriate, partially biseriate, up to 21 (average 7.5) cells high	Cupressoid, 1–2 pits	Shitanjing, Ningxia; Sunjiagou Fm; Upper Permian	Feng, 2012
Palaeoginkgoxylon zhoui Feng, Wang et Rößler	Solid, few pitted cells and parenchyma	Endarch, helical, annular and scalariform or reticulate thickenings	Mixed, uniseriate to biseriate	Uniseriate or biseriate, 1–24 (average 7.9) cells high	Cupressoid, 1–4 pits, rarely up to 6 pits	Hulstai, Inner Mongolia; Lower Shihhotse Fm; Middle Permian	Feng et al., 2010a
Plyophyllioxylon hulstaiense Feng, Wang, Liu et Rößler	Septate, with parenchyma, perimedullary zone present	Endarch, annular, helical, reticulate or scalariform thickenings	Araucarian, uniseriate to biseriate	Uni–biseriate, rarely partially triseriate, 1–22 cells (average 7)	Cupressoid, 1–2 pits, very occasionally up to six pits	Hulstai, Inner Mongolia; Lower Shihhotse Fm; Middle Permian	Feng et al., 2012
Shanxioxylon sinense Tian et Wang emend. Wang, Hilton, Tian et Galtier	Septate and a continuous perimedullary zone	Endarch; annular, spiral, scalariform and scalariform–bordered pits thickenings	Araucarian, uniseriate to pentaseriate	Uniseriate, only very rarely biseriate; 1–9 (mostly 4–5) cells high	Undescribed	Taiyuan, Shanxi; Taiyuan Fm; Lower Permian	Tian and Wang, 1987; Wang et al., 2003a
Shanxioxylon taiyuanense Tian et Wang emend. Wang et Hilton	Septate and heterocelluar, with peripheral parenchyma and secretory ducts	Endarch	Araucarian, mainly biseriate, rarely triseriate	Uniseriate, 1–18 cells high	1–4 oblique and ovate pits	Taiyuan, Shanxi; Taiyuan Fm; Lower Permian	Tian and Wang, 1987; Hilton et al., 2009b
Shenoxylon mirabile Feng, Wang et Rößler	Solid, heterocellular, with sclerenchyma, parenchyma and pitted cells	Endarch; annular, scalariform or reticulate thickenings	Uniseriate, sometimes partially biseriate	Uniseriate or biseriate, up to 14 (average 5.6) cells high	Cupressoid, 1–2 pits	Shitanjing, Ningxia; Sunjiagou Fm; Upper Permian	Feng et al., 2012

(continued on next page)

Table 2 (continued)

Species	Pith	Primary xylem	Secondary xylem		Type locality, horizon and age	Reference
			Pits on radial walls	Xylem rays		
			Cross–field pits			
Walchiopremnon biseriate, 1–17 cupressoid, 2–6 Longtan Fm; Zhao	Heterogeneous, with sclerenchyma and	Endarch; annular and Araucarian, (commonly 7–8) cells	Uniseriate, partly biseriate, pits	Simple or Upper Permian	Nayong, Guizhou; Tian et al., 1996	Tian et al., gaoi Tian, Hu et parenchyma, scalariform thickening secretary cells high

Phellinus pini (Thore) Anes (Blanchette, 1979) and from the Devonian progymnospermous Callixylon newberryi (Dawson) Elkins et Wieland (Arnold, 1931; Stubblefield et al., 1985). They are speculated as a response to fungal infection when the host plant is still alive (Stubblefield et al., 1985; Taylor et al., 2009). Therefore, the interaction between P. wangi sp. nov. and the fungi in the ray cells is interpreted to parasitism.

Complex branching tunnels are present in the secondary xylem of Parnaiboxylon wangi sp. nov., and are filled with spheroidal and ovoidal, dark colored coprolites (Fig. 7, G). Coprolites are commonly densely, rarely loosely distributed, ranging from 30 to 80 μm in diameter (Fig. 7, H). They are all composed of unidentifiable plant fragments. According to their shape, size, surface texture, and contents, the coprolites are interpreted to be produced by oribatid mites, as observed from other Permo-Carboniferous coal balls and petrified woods (Labandeira et al., 1997; Kellogg and Taylor, 2004; Feng et al., 2010b, 2012; Feng, 2012; Wan et al., 2014, 2016a). Carboniferous wood-borings by oribatid mites are mainly documented in Euramerican floras (Baxendale, 1979; Cichan and Taylor, 1982; Labandeira et al., 1997; Feng et al., 2015). In Cathaysia, arthropod–plant associations have patchily and exclusively been reported from the Permian (Hilton et al., 2001, 2002; Glasspool et al., 2003; Wang et al., 2009; Feng et al., 2010b, 2012, 2021; D'Rozario et al., 2011; Feng, 2012). Therefore, based on the occurrence of tunnels and coprolites in the wood of P. wangi sp. nov. from the Benxi Formation in Yangquan, a typical arthropod–plant interaction is proposed to be occurred in Cathaysia as early as the Moscovian.

The distribution of coprolites in Parnaiboxylon wangi sp. nov. is similar to some the previously recorded arthropod–wood interactions from the Permian of Cathaysia. Coprolites are restricted in tunnels of the secondary xylem (Feng et al., 2010b; Feng, 2012). However, in Plyophyllioxylon hulstaiense Feng et al. from the Guadalupian of North China, they are confined to the pith (Feng et al., 2012). In some cases, coprolites are found in both pith and secondary xylem (Wei et al., 2019). The differentiation of coprolite distribution in Permian Cathaysian trunks suggests a selective feeding strategy of ancient oribatid mites (Feng et al., 2012). In P. wangi sp. nov., coprolite producers would have fed preferentially on hard, lignified tissues of the secondary xylem. Thus, we speculate that the Moscovian detritivores in Cathaysia had already evolved distinct feeding behaviors and strategies.

6. Conclusions

A new fossil stem, Parnaiboxylon wangi sp. nov., is described from the Moscovian (Pennsylvanian, upper Carboniferous) Benxi Formation of Yangquan City, North China. The discovery improves the knowledge of the diversity of arborescent gymnosperms of the Cathaysian flora at its early evolutionary stage. The occurrence of solenoid pith and growth interruptions indicates an environment with intermittent droughts or incursions of seawater. The presence of coprolites and fungal hyphae indicates multiple levels of biological association and interaction in the Pennsylvanian terrestrial ecosystems at the coast of Palaeo-Tethys.

Data availability

No data was used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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