Journal of Earth Science, *Online 2017* *ISSN 1674-487X*
Printed in China
DOI: 10.1007/s12583-017-0941-3

Permineralized Calamitean Axes from the Upper Permian of Xinjiang, Northwest China and Its Palaeoecological Implication

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ABSTRACT: Two anatomically preserved calamitean axes are reported for the first time from the Late Permian Wutonggou Formation in the southern Bogda Mountains, Xinjiang Uygur Autonomous Region, Northwest China. Based on the anatomical features, these axes are assigned to *Arthropitys*. A new species *Arthropitys taoshuyuanensis* sp. nov. is established. *A. taoshuyuanensis* sp. nov. possesses a large pith comprises large pith cavity and a narrow perimedullary zone at the nodes and diaphragms at the internodes. Carinal canals are circular and surrounded by a single layer of metaxylem tracheids. Secondary xylem is divided into interfascicular rays and fascicular wedges. Interfascicular rays are initially four to five cells wide and taper abruptly centrifugally. Fascicular wedge consists of thick-walled tracheids and thin-walled fascicular ray cells. Radial tracheid walls have uniseriate or biseriate circular pits, or scalariform pits. The absence of growth rings in the *Arthropitys* specimens indicates that they probably lived in the wetland area under stable annual temperature and water sufficient conditions.
KEY WORDS: *Arthropitys*, calamitean, horsetail, late Permian, Xinjiang.

0 INTRODUCTION

Horsetails, extending back to the Late Devonian (Taylor et al., 2009), were an important component of the Carboniferous and Early Permian coal-forming swamp forest where they obtained the greatest diversity and became the dominant group of Arthrophyta (DiMichele and Hook, 1992; Li et al., 1995; Tian et al., 1996; Feng et al., 2012a; Rößler et al., 2012). The decline of the once-booming taxon began in the late Permian. Its herbal types became the majority of the group in Mesozoic (Yang, 1994; Li et al., 2004). The genus *Equisetum*, which consists of about 29 species, is the only extant relict (Hauke, 1963, 1978; Wu and Ching, 1991).

The Palaeozoic arborescent horsetails, represented by *calamites*, are among the most common and frequently elements in Carboniferous and Permian continental strata (DiMichele and Phillips, 1994; Hilton et al., 2001; Taylor et al., 2009). However, compared to the large amount of impressions/compressions, the axes with anatomical details preserved remain rather rare (Rößler and Noll, 2010). The term "calamitean" is usually used to refer to axis remains of plants ascribable to the Calamitaceae (Andrews, 1952).

Anatomically preserved calamitean axes are usually distinguished into three genera: i.e., *Arthroxylon* Reed, 1952, *Calamitea* (Cotta, 1982) emend. Rößler and Noll, 2007 and *Arthropitys* Goeppert, 1864. As the most common genus, *Arthropitys* contains up to 27 species (the varieties are not counted) have previously been recognized (Renault, 1896; Andrews, 1952; Anderson, 1954; Eggert, 1962; Cichan and Taylor, 1983; Wang et al., 2003, 2006; Rößler and Noll, 2010; Feng et al., 2012a; Rößler et al., 2012; Neregato et al., 2015). While there are only two species of *Arthropitys*, *A. junlianensis* Wang, Hilton, Li and Galtier, 2003 and *A. yunnanensis* (Tian and Gu) ex Wang, Hilton, Galtier and Tian, 2006, have been reported from the Permian of China and they are both from the upper Permian of South China.

The Bogda Mountain area of Xinjiang Uygur Autonomous Region belongs to the Subangaran phytoprovince during the late Permian (Meyen, 1981, 1982). The former researches about the permineralized axes from the upper Permian of China have been abundant (e.g. Wang, 1985; Tian and Li, 1992; Tian BL et al., 1996; Wang, 2000; Wang et al., 2003, 2006; Feng, 2012; Feng et al., 2008, 2010, 2011, 2012b, 2013; Wei et al., 2015). Yet, there are a few studies involved the subangaran province (Sze, 1934; Wan et al., 2014; Shi et al., 2014; Wei et al., 2016), and permineralized calamitean axes have never been reported in that region. Recently, we found two anatomically preserved calamitean axes from the Upper Permian of the Taoshuyuan area in the Southern Bogda Mountains for the first time. These specimens provide important materials for the anatomy of calamiteans and the palaeoecology reconstruction of the Late Permian Bogda Mountains.

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Manuscript received November 10, 2015.
Manuscript accepted July 18, 2016.

Chen, F. Y., Shi, X., Yu, J. X., et al., 2017. Permineralized Calamitean Axes from the Upper Permian of Xinjiang, Northwest China and Its Palaeoecological Implication. *Journal of Earth Science*. doi: 10.1007/s12583-017-0941-3 . http://en.earth-science.net

1 MATERIAL AND METHODS

The terrestrial facies Taoshuyuan section lays in the southern foothills of Bogda Mountains, contains whole exposed continuous Permian-Triassic strata that distribute as a syncline in space (Fig. 1). These strata were deposited in the Tarlong-Taodonggou half graben, which was located near the northwestern coast of the Paleo-Tethys at the easternmost Kazakhstan Plate (Sengor and Nat'lin, 1996; Ziegler et al., 1997; Scotese, 2001; Yang et al., 2010). The specimens were collected in the bottom of the Wutonggou Formation at the Taoshuyuan section (XTT-A-06: 43° 13' 54.70" N, 88° 58' 24.27" E; XTT-BW-03: 43° 13' 54.90" N, 88° 59' 38.26" E). The Wutonggou Formation is about 56 m thick, mainly composed of uneven interbed of yellowish green mudstone and medium to fine sandstone and intercalated with dark gray mudstone, coal seams and three thin-bedded limestone layers, contains plant fossils: *Callipteris changi*, *C. zeilleri*, *Comia* sp. etc (WGRSTXUAR, 1981). Yang et al. (2007, 2010) defined the Wutonggou low-order cycle, which includes the Wutonggou, Guodikeng, and the lower part of Jiucaiyuan formations and spans the Wuchiapingian, Changhsingian and early Induan stages, on the basis of interpreted depositional environments and palaeoclimatic conditions. The age of the fossil-bearing interval is Wuchiapingian, as indicated by cyclostratigraphic correlation of the Taoshuyuan Section with the northeastern Tarlong Section where three U-Pb zircon radiometric ages of Wutonggou low-order cycle are available (Yang et al., 2010).

To examine the anatomy of the fossils, we made thin slides of three plans (transversal, longitudinal and tangential) in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan) and Shenyang Institute of Geology and Mineral Resources. The slides are examined and photographed under light microscope Leica DM4000 B and SPOT Flex Color with SPOT Advanced microscope software. All the specimens and the slides are housed in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan).

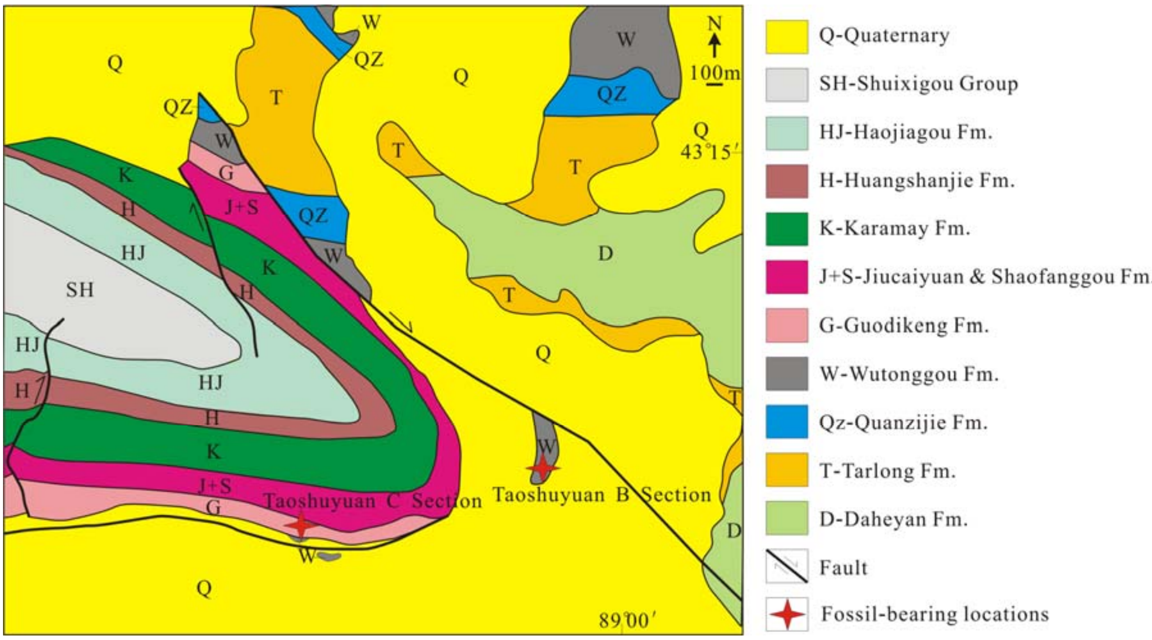

Figure 1. Geological map of the study area. Specimen XTT-A-06 was collected from the Taoshuyuan B Section, and specimen XTT-BW-03 was from the Taoshuyuan C Section.

2 RESULTS

Class: Sphenopsida

Order: Equisetales

Family: Calamitaceae

Genus: *Arthropitys* Goeppert, 1864-65

Type species: *Arthropitys bistriata* (Cotta) Goeppert emend. Rößler, Feng and Noll, 2012

***Arthropitys taoshuyuanensis* sp. nov.**

Holotype: Specimen XTT-A-06.

Type locality: Taoshuyuan C Section, Turpan, Xinjiang Uygur Autonomous Region, China

Geological horizon: Wutonggou Formation

Stratigraphic position: Early Late Permian (Wuchiapingian)

Etymology: The species name refers to the fossil locality.

Diagnosis: Plant axis possesses pith, primary and secondary vascular tissues. Pith consists of a large central cavity and a narrow perimedullary zone in internodal region and diaphragm in nodal region. Carinal canals are circular and surrounded by a single layer of metaxylem tracheids. Secondary xylem consists of interfascicular rays and fascicular wedges. Fascicular wedges comprise thick-walled tracheids and thin-walled fascicular ray cells. Interfascicular rays are initially four to five cells wide, gradually diminished distally. Radial tracheid walls have uniseriate or biseriate circular pits, or scalariform pits. Fascicular rays parenchymatous, vary from five to more than 45 cells high and one to up to seven cells wide in the middle of the secondary xylem. Fascicular ray cells rectangular in cross section, polygonal in tangential section.

Description

General features The specimen XTT-A-06 is 250 mm in length and 58 mm in diameter. It is composed of pith, primary xylem and secondary xylem.

Detailed description Pith of the specimen XTT-A-06 has an elliptical outline, which is likely to the consequence of partial compression (Fig. 2a). The diameter is about 17×11 mm. The pith is filled with calcite contents. The pith diaphragms are poorly preserved, but the protuberances at the nodes are visible (Fig. 2b). At the internodes, the pith constitutes a large cavity and a narrow perimedullary (Figs. 2c and 2d, black arrows). Between the perimedullary zone and xylem, some dark cell contents are preserved.

A discrete ring of primary xylem strands surrounding the pith (Fig. 2d and 3). There are approximately 55 primary xylem strands. The carinal canals are surrounded by a single layer of metaxylem tracheids (Fig. 2c, 2d and 3). These tracheids are 16-34 μm in diameter.

The secondary xylem of XTT-A-06 is between 13 and 25 mm wide. It consists of interfascicular parenchymatous rays and fascicular wedges. Interfascicular rays start at the outer periphery of the pith at a width of four to five cells (ca. 0.3 mm) (Fig. 2d and 3). After a short distance, they gradually diminished. The fascicular wedges start from the external side of the primary xylem at a width of four to six rows of tracheids and rays. The widths of the fascicular wedges rapidly increase as new files of tracheids and rays are added. In the inner part of the secondary xylem the tracheids and the ray cells are both rectangular in the cross section and the former are smaller in dimension. In the outer part of the secondary xylem, the fascicular ray cells are always rectangular, 29×47-49×97 μm. Tracheids are nearly square and smaller, 31×38-48×57 μm. In radial section the ray cells are rectangular, 76-117 μm high (Fig. 2f). The radial walls of tracheids possess uniseriate or biseriate circular pits, or scalariform pits (Figs. 2e and 2g). In tangential section through the inner part of the secondary xylem, the interfascicular ray cells are rectangular or polygonal, 57-106 μm high (Fig. 2h). The fascicular rays are one or two cells wide and the ray cells are rectangular. In tangential section through the middle region of the secondary xylem, the fascicular ray cells are polygonal, and the walls are smooth (Fig. 2i). The rays vary from five to more than 45 cells (400-3125 μm) high and up to seven cells (~500 μm) wide.

Comparisons

The nature of the secondary xylem, particularly the interfascicular rays, plays as the basis to distinguish the three fossil genera among anatomically preserved calamitean axes (e.g. Andrews, 1952; Eggert, 1962; Cichan and Taylor, 1983; Rößler and Noll, 2007). *Arthropitys* and *Arthroxylon* both show a high portion of parenchyma and uniform type of tracheids (Andrews, 1952; Reed, 1952; Hass, 1975; Rößler and Noll, 2010; Rößler et al., 2012). In *Arthropitys* the interfascicular rays consist of parenchymatous cells with rectangular to isodiametric shape and horizontal cell end walls (Andrews, 1952; Wang et al., 2003; Rößler and Noll, 2010; Rößler et al., 2012). In *Arthroxylon* the interfascicular rays are mainly composed of vertically elongated prosenchymatous cells with tapering end walls (Reed, 1952). In contrast, the wood of *Calamitea* contains a relatively small proportion of parenchyma and possesses two types of tracheids in different diameter (Rößler and Noll, 2007).

The studied specimens show a high portion of parenchyma. Interfascicular rays consist of only parenchymatous cells with rectangular or polygonal shape and horizontal cell end walls. Tracheids are of uniform diameter. These characteristics all conform to those of *Arthropitys*.

For the delimitation of different species of *Arthropitys*, the constant characteristics such as interfascicular rays, nature of tracheid pitting, size of carinal canals and development patterns in the primary and secondary body could be taken into account (Andrews, 1952; Wang et al., 2003; Rößler and Noll, 2007). And secondary xylem contains most of the features that considered to be important in classification of anatomically preserved calamitean axes (Wang et al., 2003).

About 27 species of *Arthropitys* have previously been reported as far as we know. Of these species, *A. jongmansi* Hirmer, 1927 (in Knoell, 1935), *A. herbacea* Hirmer and Knoell (in Knoell, 1935), *A. bistriatoides* Hirmer and Knoell (in Knoell, 1935) and *A. renaultii* Boureau, 1964 either have very thin secondary xylem or not. That makes it difficult to compare with other species. *Arthropitys hirmeri* Knoell, 1935 is an unique species in *Arthropitys* that lacks interfascicular rays (Anderson, 1954).

Nine species possess well-developed interfascicular rays: *Arthropitys kansana* Andrews, 1952, *A. versifoveata* Anderson, 1954, *A. felixi* Hirmer and Knoell (in Knoell, 1935), *A. bistriata* (Cotta) Goeppert emend. Rößler and Noll, 2012, *A. gallica* Renault, 1896, *A. deltoides* Cichan and Taylor, 1983, *A. yunnanensis* (Tian and Gu) ex Wang, Hilton, Galtier and Tian, 2006, *A. isoramis* Neregato, Rößler, et Noll, 2015 and *A. iannuzzii* Neregato, Rößler, et Noll, 2015. Their interfascicular rays extend throughout the secondary xylem. While the interfascicular rays of *Arthropitys taoshuyuanensis* sp. nov. are only four to five cells wide and abruptly taper centrifugally. *Arthropitys major* (Weiss) Renault, 1896 and *A. approximata* (Schlotheim) Renault, 1896 have very broad interfascicular rays that are different from those of the new species.

The radial tracheid walls of *Arthropitys taoshuyuanensis* sp. nov. possess uniseriate or biseriate circular pits or scalariform pits. But *A. lineata* Renault, 1896 and *A. rochei* Renault, 1896 are characterised by elongate bordered pits on their tracheid walls; *Arthropitys gigas* (Brongniart) Renault, 1896 and *A. cacundensis* Mussa, 1984 (in Coimbra and Mussa, 1984) have round pits; *Arthropitys illinoensis* Anderson, 1954 possesses multiseriate oval to elongate pits; *Arthropitys sterzelii* Rößler and Noll, 2010 shows equally spaced reticulate wall thickenings. The tracheid radial walls of *A. porosa* Renault, 1896 are composed of circular reticulate, elongate reticulate and scalariform thickenings. These pitting patterns are all different from those of the new species.

The carinal canal of *Arthropitys taoshuyuanensis* sp. nov. is lined by a single row of elements. In *A. communis* (Binney)

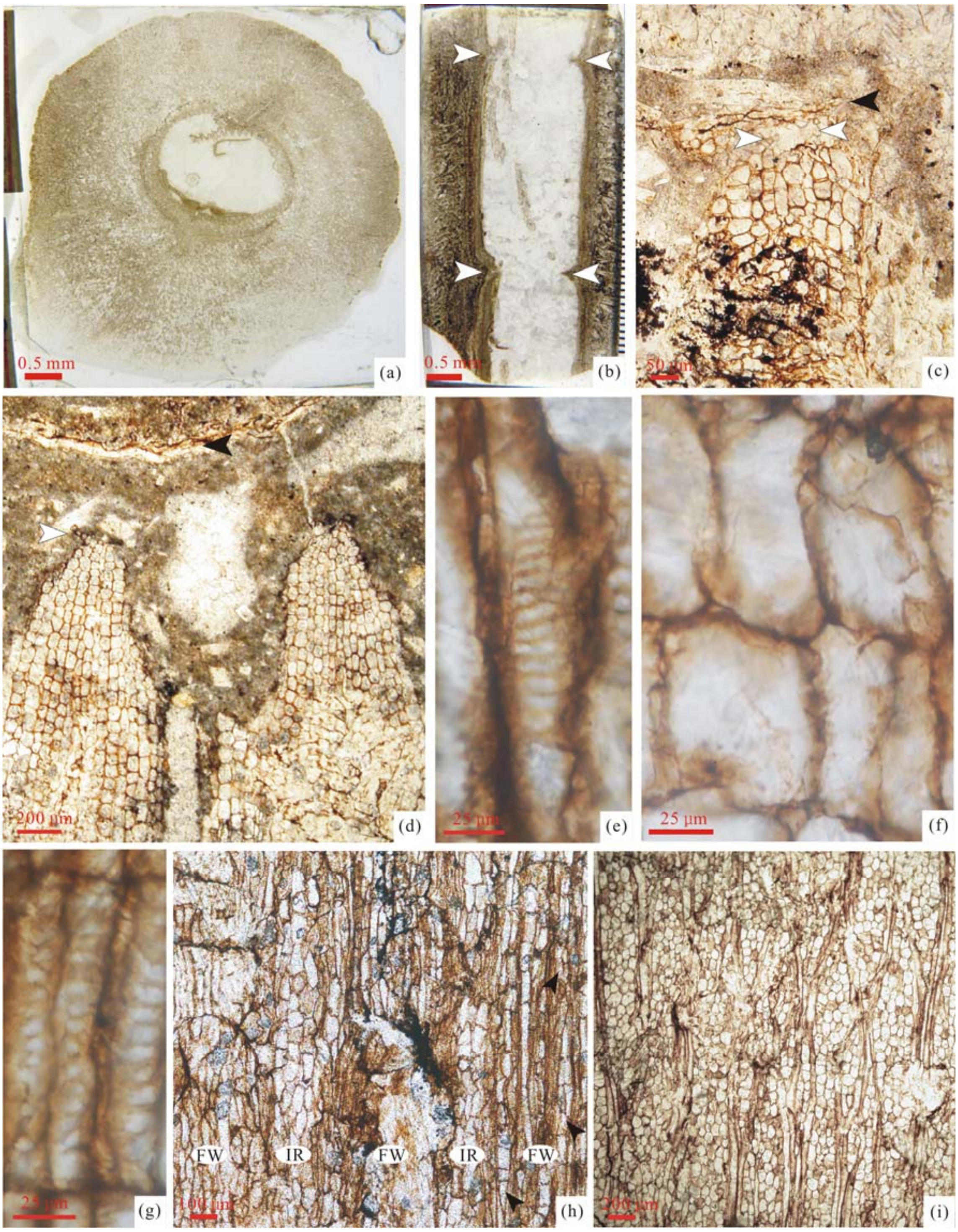

Figure 2. Photomicrographs showing anatomical features of *Arthropitys taoshuyuanensis* sp. nov. (a) Transverse section (TS) showing the overview of the pith, primary xylem and secondary xylem, scale bar = 0.5 mm. Slide no. XTT-A-06a1; (b) Radial section (RL) showing the overview of the pith, primary xylem and secondary xylem, white arrows indicate the protuberances, likely to relate to diaphragms, at the nodes, scale bar = 0.5 mm. Slide no. XTT-A-06b1; (c) TS showing the layer of perimedullary cells (black arrow), the carinal canal with metaxylem tracheids (white arrows), scale bar = 50 μm. Slide no. XTT-A-06a1; (d) TS showing the layer of perimedullary cells (black arrow), the single layer of metaxylem tracheids (white arrow), the secondary xylem strands and interfascicular ray cells, scale bar = 200 μm. Slide no. XTT-A-06a1; (e) RL showing the scalariform pits of the tracheids, scale bar = 25 μm. Slide no. XTT-A-06b2; (f) RL showing the ray cells, scale bar = 25 μm. Slide no. XTT-A-06b2; (g) RL showing the circular pits and scalariform pits of the tracheids, scale bar = 25 μm. Slide no. XTT-A-06b2; (h) Tangential section (TGS) through the inner part of the secondary xylem showing the interfascicular rays (IR) and fascicular wedges (FW) that comprise fascicular rays (black arrows) and tracheids, scale bar = 100 μm. Slide no. XTT-A-06d1; (i) TGS through the middle part of the secondary xylem showing the fascicular rays, scale bar = 200 μm. Slide no. XTT-A-06c2.

Hirmer and Knoell (in Knoell, 1935) and *A. junlianensis* Wang, Hilton, Li and Galtier, 2003 the carinal canal and protoxylary traicheids are surrounded by an arch of multiple layers of iso-diametric cells.

The new species possesses multiseriate fascicular rays, similar with *A. medullata* Renault, 1896. While the pith of *A. medullata* is weakly developed, in comparison, *A. taoshuyuanensis* sp. nov. has a large pith. The secondary rays of *A. ezonata* Goeppert, 1864–65 are only two cells wide.

Therefore, the specimen should be designated to a new species that is here described as *Arthropitys taoshuyuanensis* sp. nov.

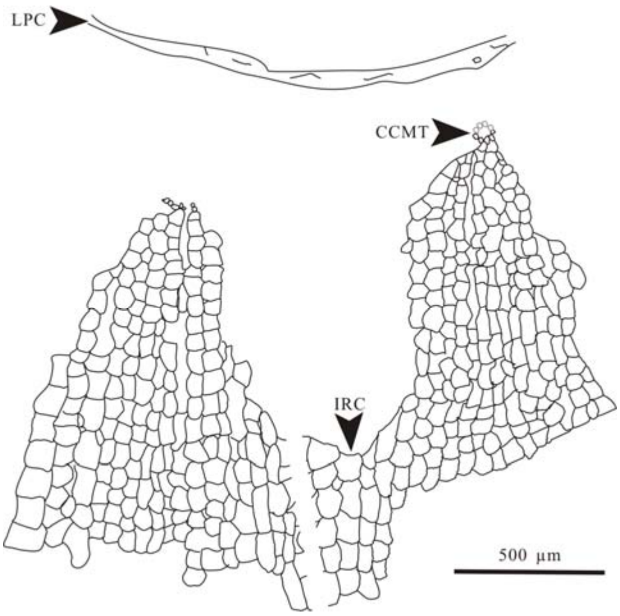

Figure 3. Diagrammatic sketch of Figure 2d showing the layer of perimedullary cells (LPC), the carinal canal and metaxylem tracheids (CCMT) and interfascicular ray cells (IRC).

***Arthropitys* sp.**

Specimen: XTT-BW-03.

Locality: Taoshuyuan B Section,Turpan, Xinjiang Uygur Autonomous Region, China

Geological horizon: Wutonggou Formation

Stratigraphic position: Early Late Permian (Wuchiapingian)

Description

General features XTT-B-03 is 100 mm long, and only secondary xylem was preserved. In cross section, the outline is sub-rectangular, 53 × 26 mm.

Detailed description In cross section, the fascicular ray cells are rectangular, 53×102-85×169 μm (Fig. 4a). The tracheids are smaller, rectangular or square, 22×49-70×101 μm (Fig. 4a). In radial section, the fascicular ray cells are rectangular, 60-142 μm high (Fig. 4b). The radial walls of tracheids possess reticulate pits (Fig. 4c), or scalariform thickenings (Fig. 4d). There are many simple pits in the cross-field units (Fig. 4e). In tangential section, the fascicular ray cells are polygonal with smooth walls (Figs. 4f and 4g). The rays vary from three to more than 39 cells (350-3225 μm) high and up to seven cells (~425 μm) wide.

Comparisons

The absence of pith and primary xylem makes it impossible to determine which species the specimen belongs to. Although the width and height of fascicular rays are similar to that of *Arthropitys taoshuyuanensis* sp. nov., the tracheid pitting pattern of this specimen is different. Besides, the cross-fields show many simple pits in the present specimen. That is also different from those of *Arthropitys taoshuyuanensis* sp. nov.

3 DISCUSSIONS

Palaeozoic horsetail trees preferred wetland environments as the extant *Equisetum*. They formed hygrophilous stands surrounding lakes or grew in swamps and along river banks (Scott, 1979; Pfefferkorn et al., 2001). There are many geological facts confirm the ecological preference of the horsetail trees. In Euramerica, it is well-documented that the Late Carboniferous coal swamp ecosystems collapsed near the Permo-Carboniferous boundary (DiMichele and Hook, 1992; DiMichele et al., 2001). The geographical extinction of certain plant taxa in this event is primarily related to the more seasonal and dry climate, and the lycopsids and sphenopsids (including the calamitean plants) who cannot adapt to the changed environments in Euramerica (DiMichele and Hook, 1992; Gastaldo et al., 1996; DiMichele et al., 2001). In Cathaysian flora, these taxa lived in the waterlogged swamp environments during the early Permian of North China (Hilton et al., 2001, 2002) and the late Permian of South China (Li et al., 1995; Wang et al., 2003, 2006). Accordingly, the calamitean axes found in the upper Permian of the southern Bogda Mountains indicate the presence of waterlogged environments in that region during the late Permian in which calamitean plants lived.

Growth rings are absent in *Arthropitys taoshuyuanensis* sp. nov. and *A.* sp. and the tracheids in the secondary xylem are of uniform size. In *Septomedullopitys szei* Wan, Yang et Wang, a coniferopsid wood also found in the lower part of the Wutonggou Formation, annual growth rings are absent as well but irregular growth interruptions are developed (Wan et al., 2014). The climate of the study area during the late Permian was humid to subhumid with a wet-dry seasonality as indicated by abundant Histosols, Gleysols, and Argillisols capping thick meandering stream and freshwater deltaic deposits in the Wutonggou low-order cycle (Yang et al., 2010). Wan et al. (2014) proposed that the absence of true growth rings in *S. szei* indicates a subhumid to perhumid climate and the irregular growth interruptions reflect drought-induced fluctuations in groundwater table caused by short-lived, irregular droughts. The development of growth rings in a tree is affected by both intrinsic and extrinsic factors. In general, the extrinsic factors exert a greater influence than the intrinsic ones (Creber and Chaloner, 1984). Moreover, as hygrophilous taxa, calamitean plants are supposed to be more sensitive to the changes in water availability than coniferopsids. Additionally, growth rings related to droughts or changes in water availability have been previously reported in *A. yunnanensis* from South China and *A.*

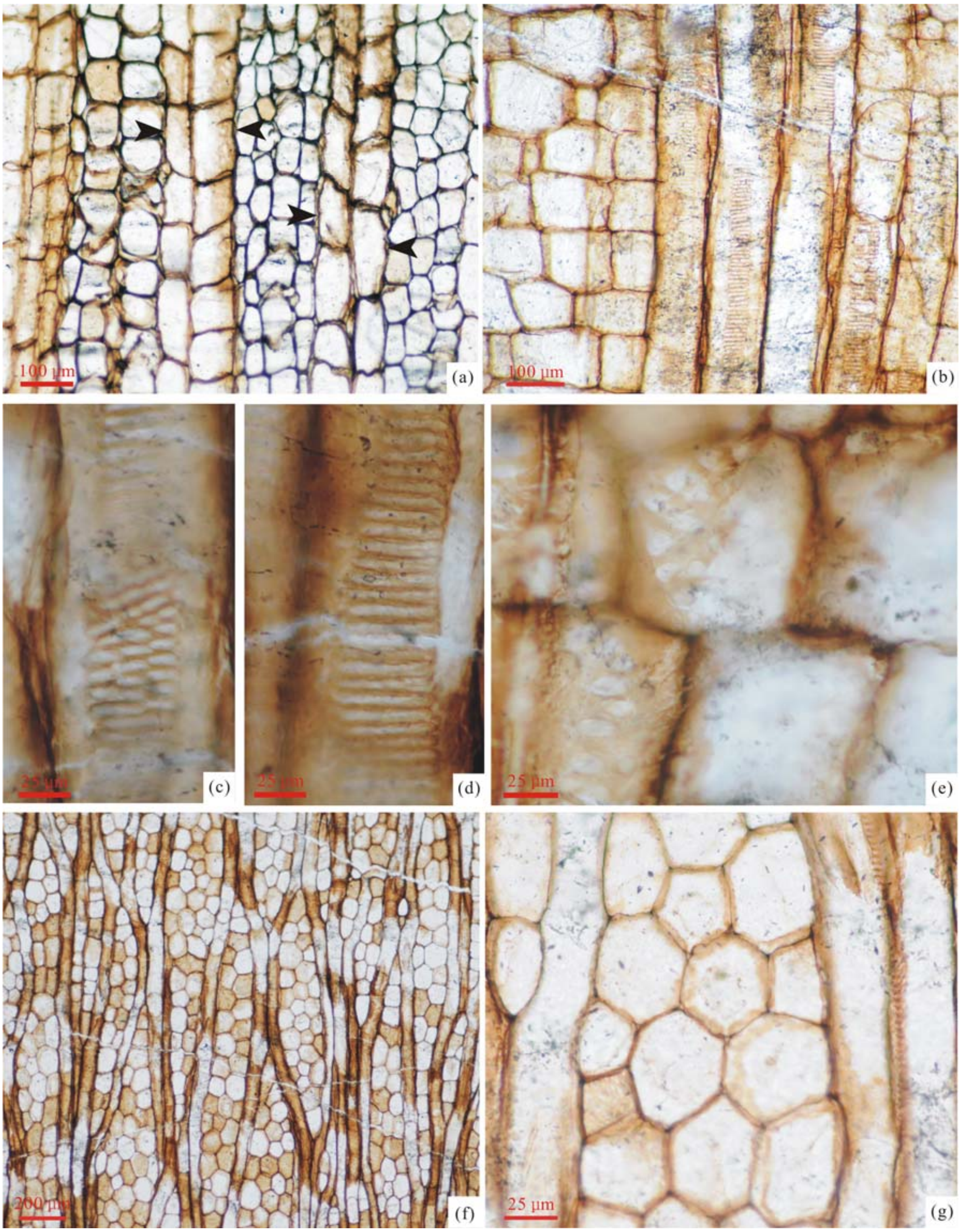

Figure 4. Photomicrographs showing anatomical features of *Arthropitys* sp. (a) Transverse section (TS) showing the tracheids and fascicular ray cells (black arrows), scale bar = 100 µm. Slide no. XTT-BW-03a1; (b) Radial section (RL) showing the tracheids and fascicular ray cells, scale bar = 100 µm. Slide no. XTT-BW-03b1; (c) RL showing the reticulate pits of the tracheids, scale bar = 25 µm. Slide no. XTT-BW-03b1; (d) RL showing the scalariform pits of the tracheids, scale bar = 25 µm. Slide no. XTT-BW-03b1; (e) RL showing the simple pits in the cross-field units, scale bar = 25 µm. Slide no. XTT-BW-03b1; (f) Tangential section (TGS) showing the fascicular ray cells and tracheids, scale bar = 200 µm. Slide no. XTT-BW-03c1; (g) TGS showing the close-up of the fascicular ray cells, scale bar = 25 µm. Slide no. XTT-BW-03c1.

isoramis and *A. iannuzzi* from the Parnaíba Basin (Wang et al., 2006; Neregato et al., 2015). Given the above, the absence of growth rings and growth interruptions in *Arthropitys taoshuyuanensis* sp. nov. and *A.* sp. indicates that their habitats are different from where *S. szei* and the other trees with growth interruptions lived. Considering the ecological preference of the calamitean plants, they probably grew in the lowland area where kept humid all the year round like lakeside and riverside, the enough supply of moisture contributed to the absence of growth rings and growth interruptions. In comparison, *S. szei* and the other trees grew on the higher grounds or the place away from rivers and lakes, and the short-lived droughts controlled the development of the growth interruptions. Temperature plays as another important factor that influences the development of growth rings (Creber and Chaloner, 1984). To some extent, the absence of annual growth rings in both *A. taoshuyuanensis* and *S. szei* indicates a limited range of annual temperature in the late Permian southern Bogda Mountains. More detail work on growth rings is needed to document the annual temperature range.

4 CONCLUSIONS

1. Two calamitean axes include a new species *Arthropitys taoshuyuanensis* sp. nov. are firstly found in the late Permian Subangaran flora of China. The new discovery increased diversity of the Subangaran flora and the genus *Arthropitys* that were only two species previously found in China.

2. The absence of growth rings and growth interruptions in the calamitean axes indicates the limited range of annual temperature and sufficient water supply of their habitats.

3. In the late Permian southern Bogda Mountains, the calamitean plants probably lived in the lowland humid areas, and *Septomedullopitys szei* and some other trees with growth interruptions grew on the higher grounds where there were short-lived droughts.

ACKNOWLEDGMENTS

We gratefully acknowledge the anonymous reviewers for their critical comments and constructive suggestions, which have improved the quality of the paper greatly. We also thank Prof. Shucheng Xie of China University of geosciences and Ms. Qingting Wu of Ohio State University for collecting the samples. This research was supported by the National Natural Science Foundation of China (Nos: 40972002, 41272024 and 41572005).

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