

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo



A new Protophyllocladoxylon wood from the Induan (Lower Triassic) Jiucaiyuan Formation in the Turpan–Hami Basin, southern Bogda Mountains, northwestern China

Mingli Wan ^{a,*}, Wan Yang ^b, Jun Wang ^{a,c}

^a State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Palaeoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing

210008, China ^b Geology and Geophysics Program, Missouri University of Science and Technology, Rolla, MO 65409, USA ^c University of Chinese Academy of Sciences, Beijing 100049, China

article

info

abstract

Keywords:

Fossil wood
Anatomy
Gymnosperm
Zhaobishan
Induan
Xinjiang

The presence of distinct and extensive growth rings in all fossil woods from the Induan of the research area were probably caused by the seasonal climate with great precipitation variability during the earliest Triassic in the Turpan–Hami Basin. This is also supported by the occurrence of Calcisols, vertic Calcisols, and calcic Argillisols from coeval deposits nearby. The occurrence of fossil wood with anatomical structures from the Induan confirms that woody gymnosperms, probably conifers, were crucial elements on the Early Triassic landscape in northeastern Pangaea. It appears that some gymnosperms had survived the end-Permian biotic crisis based on the continuous records of Protophyllocladoxylon-type woods from the Wuchiapingian (upper Permian) to Norian (Upper Triassic) in Bogda Mountains.

© 2019 Elsevier B.V. All rights reserved.

Article history:

Received 24 December 2018
Received in revised form 2 April 2019
Accepted 14 May 2019

A silicified gymnospermous wood, *Protophyllocladoxylon zhaobishanensis* sp. nov., is described from the Induan (Lower Triassic) Jiucaiyuan Formation in Zhaobishan section, Shanshan County, southern Bogda Mountains, Xinjiang Uygur Autonomous Region, northwestern China. The pycnoxylic wood contains thick-walled tracheids and parenchymatous ray cells. It is characterized by uni- to triseriate araucarian radial tracheidal pitting, uniseriate rays, one to two large, simple pits in each cross-field, and uni- to biseriate tangential tracheidal pits.

1. Introduction

Wood is an important organ of gymnosperms, providing support and conduction (Beck, 2010). Fossil woods contain valuable information on biotic

diversity in the geological history (Creber and Francis, 1999; Zhang et al., 2007; Zheng et al., 2008; Wan et al., 2017d). In addition, silicified fossil woods with well-preserved internal structures in clastic sediments provide taxonomic, environmental and ecological information on plants (e.g., Wan et al., 2016c, 2017b). A variety of fossil woods have been described from Xinjiang Autonomous Region, northwestern China over the past few years in the Permian, Upper Triassic and Jurassic (Wang et al., 2000; Shi et al., 2014, 2015, 2017; Wan et al., 2014, 2016b,c, 2017a,c, 2019a, b; Wei et al., 2016; Chen et al., 2018). They have provided tremendous information about the floral composition, paleoclimatic conditions and plant paleoecology (Wan et al., 2014, 2016a, 2019a,b). However, fossil woods from the Lower Permian are poorly represented, both in this region and globally (Zheng et al., 2008). In this

* Corresponding author.

E-mail address: mlwan@nigpas.ac.cn (M. Wan).

<https://doi.org/10.1016/j.revpalbo.2019.05.005> 0034-6667/© 2019 Elsevier B.V. All rights reserved.

contribution, we describe a silicified wood, *Protophyllocladoxylon zhaobishanensis* sp. nov., from the Induan (Lower Triassic) Jiucaiyuan Formation in Zhaobishan section, Shanshan County, Xinjiang Uygur Autonomous Region, northwestern China. Our study represents the evidence of woody plant macrofossil from the Lower Triassic in northeastern Pangaea, and provides significant information on the climatic condition during that time.

2. Geological setting, material and methods

The study area is located in the southern foothill of Bogda Mountains, Xinjiang Uygur Autonomous Region, northwestern China (Fig. 1A–B). The Bogda Mountains are a large complex anticline, contain the Devonian to Quaternary rocks, and separate the Turpan–Hami Basin to the south from the Junggar Basin to the north–northwest (Zhang, 1981; Yang et al., 2010). Along the northern and southern foothills of the Bogda Mountains, Permian–Triassic fluvial and lacustrine deposits are exposed, overlying the uppermost Carboniferous volcanic-arc basement (Allen et al., 1995; Carroll et al., 1995; Wartes et al., 2002; Greene et al., 2005; Yang et al., 2007, 2010, 2018; Metcalfe et al., 2009). Paleocurrent and petrographic studies indicate that the

Greene et al., 2005) and, therefore, the Junggar and Turpan–Hami basins were most likely connected during the Permian to Early Triassic (Wartes et al., 2002; Yang et al., 2010). Tens of Permian–Triassic stratigraphic sections have been measured in Zhaobishan and Tarlong–Taodonggou in the Turpan–Hami Basin, and Dalongkou in the Junggar Basin in the last 15 years (Yang et al., 2007, 2010; Thomas et al., 2011; Obrist-Farner and Yang, 2015, 2016, 2017; Fredericks, 2017). Correlations among the sections are largely based on lithostratigraphy, biostratigraphy, and cyclostratigraphy. Here, we use the stratigraphic terminology of Yang et al. (2007, 2010).

In the Zhaobishan section (Figs. 1C and 2), six cyclostratigraphic units, or

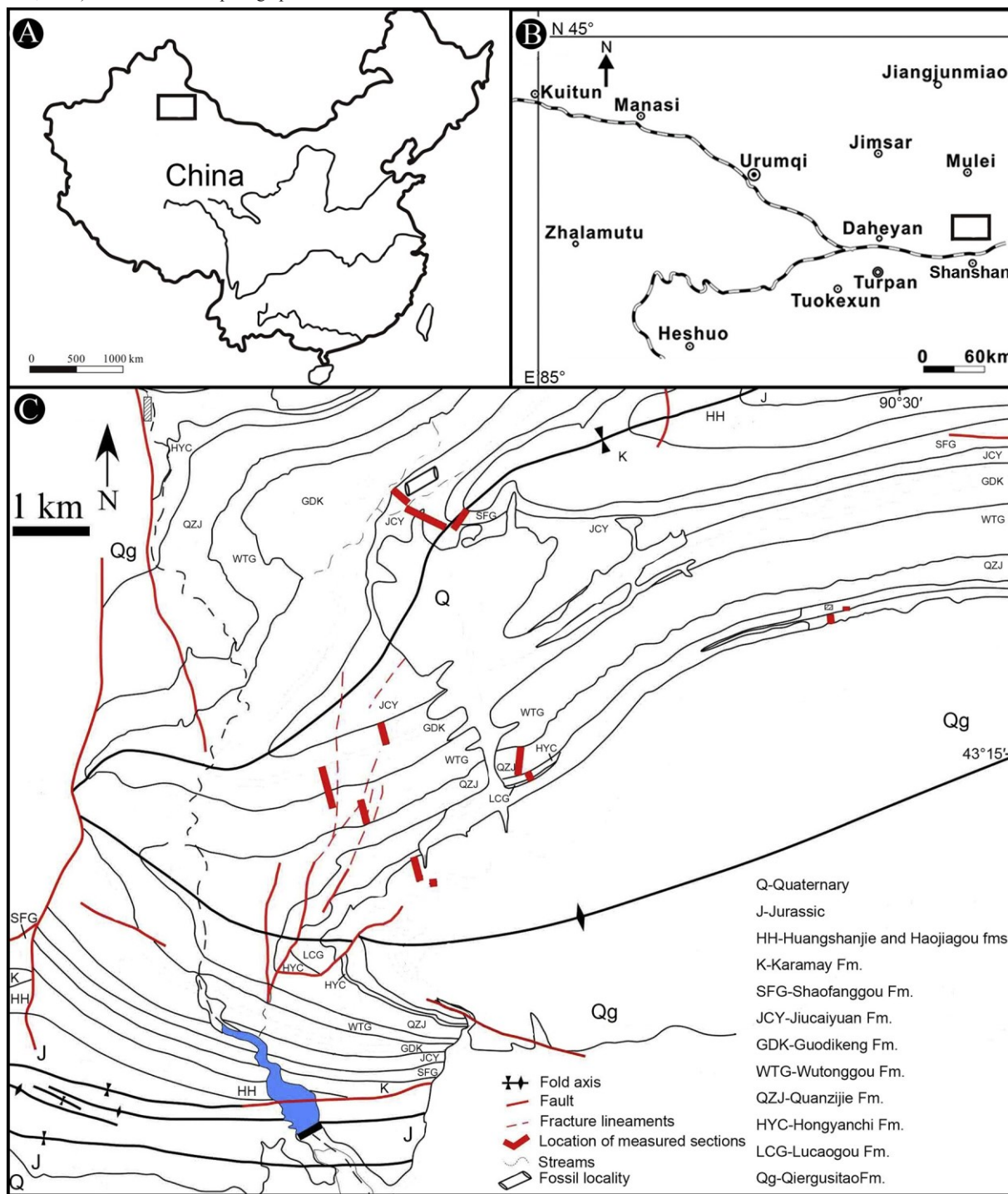


Fig. 1. Maps showing the location of study area in northwestern China (A, rectangle). The collection site indicated by a rectangle (B), and the geological map of the Zhaobishan area in Turpan–Hami Basin, southern Bogda Mountains (C), modified from (Yang, 2016; Fredericks, 2017; Yang et al., 2018).

Bogda Mountains were not uplifted by the Early Triassic (Shao et al., 2001;

low-order cycles (LCs) are identified as: Lucaogou, Hongyanchi, Quanzijie,

Wutonggou, the Jiucaiyuan, the Shaofanggou, and Karamay LCs (Fredericks, 2017; Yang, 2016; Yang et al., 2018). Correlation between lithostratigraphic formations and the cyclostratigraphic units is shown in Fig. 2. The Lucaogou, Hongyanchi, Quanzijie, Jiucaiyuan, Shaofanggou, and Karamay LCs correlate with so-named formations respectively. The Wutonggou LC, on the other hand, includes the Wutonggou and Guodikeng formations (see also, Yang et al., 2010). Silicified wood fragments were collected from the middle part of the Jiucaiyuan LC, about 103 m above the Wutonggou–Jiucaiyuan LCs

Formation, and no single excursion can be uniquely interpreted to represent the late Changhsingian global negative excursion as seen in the marine records.

Commonly, the lowest occurrence of vertebrate *Lystrosaurus* has been considered as the base of the Triassic in terrestrial records (cf. Lucas, 1998). In Junggar and Turpan basins, *Lystrosaurus* fossils have been found in the middle to upper parts of the Guodikeng Formation (Cheng and Lucas, 1993; Cheng et al., 1996, 1997; Liu et al., 2002; Liu and Abdala, 2017). However, recent chronostratigraphic, magnetostratigraphic and biostratigraphic studies in Karoo

System	Epoch	Lithostratigraphy	Cyclostratigraphy Low-Order Cycles (Yang et al., 2010; Obrist-Farner and Yang, 2015)	Revised chronostratigraphy (Yang et al., 2010, Yang, 2016)	
				Dates	Stages
Triassic	Middle	Karamay	Karamay		~242 Ladinian
					247.2 Anisian
	Lower	Shaofanggou	Shaofanggou	250.31	251.2 Olenekian
		Jiucaiyuan	Jiucaiyuan		251.902 Induan
Permian	Lopingian	Guodikeng	Wutonggou	253.11	Changhsingian
				253.63	
		Wutonggou		254.22	254.14 Wuchiapingian
	Guadalupian	Quanzijie	Upper Quanzijie		259.1
					Capitanian
					265.1
	Cisularian		Lower Quanzijie		268.8 Wordian
					272.95 Roadian
		Hongyanchi	Hongyanchi	281.42	283.5 Kungurian
		Lucaogou	Lucaogou		290.1 Artinskian
					293.52 Sakmarian
Carboniferous	Upper	Daheyan	Upper Daheyan		298.9 Asselian
			Middle Daheyan		
			Lower Daheyan		
				301.26 ± 0.05	Gzhelian
		Qiergusitao		301.37 ± 0.07	303.7
				304.1	Kasimovian
				305.50 ± 0.11	
				306.48 ± 0.32	307.0

Fig. 2. Chrono-, litho-, and cyclostratigraphy of Permian–Triassic strata in the Bogda Mountains. Absolute ages at stage boundaries from the International Chronostratigraphic Chart (2018/08); Hachured areas indicate missing strata. Wavy lines are major unconformities. Dashed lines indicate uncertain age correlations.

boundary. In the Zhaobishan section, the Jiucaiyuan LC is 221.9 m thick, and composed mainly of meandering and braided stream deposits (Fredericks, 2017).

Foothills surrounding the Turpan–Hami and Junggar basins contain a continuous sedimentary record across the Permian–Triassic boundary (PTB) with abundant vertebrate, invertebrate and plant fossils (Metcalf et al., 2009; Yang et al., 2010). The PTB is not well constrained in Turpan–Hami and Junggar basins. Palynological (Qu and Wang, 1986; Ouyang and Norris, 1999; Liu, 2000; Hou, 2004; Afonin and Foster, 2005; Foster and Afonin, 2005), invertebrate (Liu, 1994; Pang and Jin, 2004), vertebrate (Cheng and Lucas, 1993; Cheng et al., 1996, 1997; Liu et al., 2002; Liu and Abdala, 2017), and paleomagnetic (Li et al., 2003) data result in various interpretations of the PTB. Nevertheless, most of the data point to the PTB in the middle to upper part of the Guodikeng Formation. Cao et al. (2008) used a negative excursion on the stable organic carbon isotope curve to place a Permian–Triassic event boundary (PTEB) in the upper part of the Guodikeng Formation in the Taoshuyuan section (synonymous with Taodonggou section, ~37 m below the base of the Jiucaiyuan Formation) and Dalongkou section (~53 m below the base of the Jiucaiyuan Formation). However, Metcalf et al. (2009) pointed out that multiple $\delta^{13}\text{C}_{\text{org}}$ negative excursions occur in the Guodikeng

Basin have confirmed that the first occurrence of *Lystrosaurus* is older than previously thought, and should not be used as the PTB in non-marine sections (Lucas, 2009; Gastaldo et al., 2015). Lucas (2009) suggested the last occurrence of *Dicynodon* be much closer to the PTB, although exact correlation is not certain. According to biostratigraphic and magnetostratigraphic data from the Junggar Basin, Metcalf et al. (2009) proposed that the most likely position of the PTB is close to the base of Jiucaiyuan Formation. Considering all previous results as described above, we assign the Jiucaiyuan Formation in Zhaobishan section of the Turpan–Hami Basin, where current fossil wood fragments were collected, as Lower Triassic, probably of an Induan age. Additional geochronological studies are needed in the future to further constrain the Permian–Triassic chronostratigraphy in Turpan–Hami and Junggar basins.

The description and discussion of anatomical features of the fossil wood in this study use the terminology of Richter et al. (2004) and Philippe and Bamford (2008). A thin-section microscopic study of the stems indicates that they are well silicified. Thin section images were taken using a Leica DM5000 compound microscope and Leica DC 500 digital microscope camera system. The fossil woods and thin sections are stored in the Paleobotanical Collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

3. Systematics

Genus: *Prototaphyllocladoxylon* Kräusel, 1939Type species: *Prototaphyllocladoxylon leuschii* Kräusel, 1939

Division: Gymnospermae

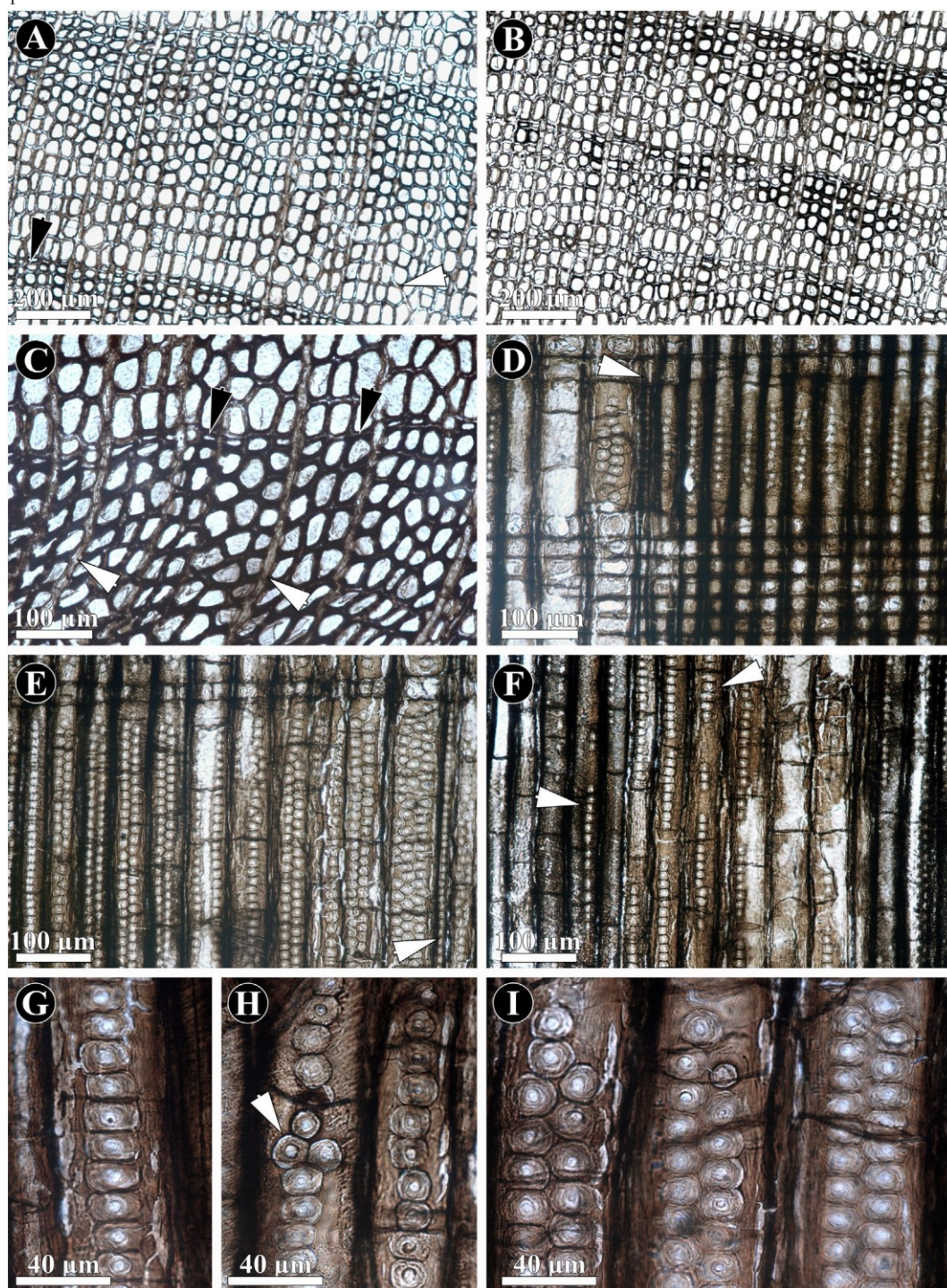


Fig. 3. Photographs showing anatomical structures of *Prototaphyllocladoxylon zhaobishanensis* sp. nov. from the Induan Jiucaiyuan Formation in Zhaobishan area, Shanshan County, Turpan–Hami Basin, southern Bogda Mountains. (A) Transverse section of the fossil wood, showing the arrangement of tracheids, and distinct growth rings. White arrow points to the earlywood. Black arrow points to the latewood with thicker walls and smaller diameters. Collection number: PB22937; slide number: PB22937-1; holotype. (B) Transverse section of the fossil wood, showing three distinct growth rings. Collection number: PB22937; slide number: PB22937-1; holotype. (C) Transverse section of the fossil wood, showing morphology of tracheids in the latewood (black arrows) and earlywood respectively. White arrows point to the uniseriate parenchymatous rays. Collection number: PB22937; slide number: PB22937-1; holotype. (D) Radial section of the fossil wood, showing the sharp transition from the latewood to the earlywood. White arrow points to the last tracheid in the latewood, which is next to the earlywood with smallest diameter. Collection number: PB22937; slide number: PB22937-2; holotype. (E) Radial section of the fossil wood, showing the uni- to triseriate pitting on radial tracheidal walls. White arrow point to the continuous uniseriate pits on radial tracheidal walls of the latewood. Collection number: PB22937; slide number: PB22937; holotype. (F) Radial section of the fossil wood, showing the uniseriate pitting on radial tracheidal walls of the earlywood. White arrows point to the pits which are distributed in groups. Collection number: PB22937; slide number: PB22937-2; holotype. (G) Radial section of the earlywood, showing the uniseriate pitting on tracheidal walls with slightly flattened pits.

Collection number: PB22937; slide number: PB22937-3; holotype. (H). Radial section of the earlywood, showing the uniseriate pitting with partially biseriate pits on tracheidal walls (white arrow). Collection number: PB22937; slide number: PB22937-3; holotype. (I). Radial section of the earlywood, showing the biseriate pitting on tracheidal walls. Pits are rounded, bordered with circular apertures. Collection number: PB22937; slide number: PB22937-3; holotype.

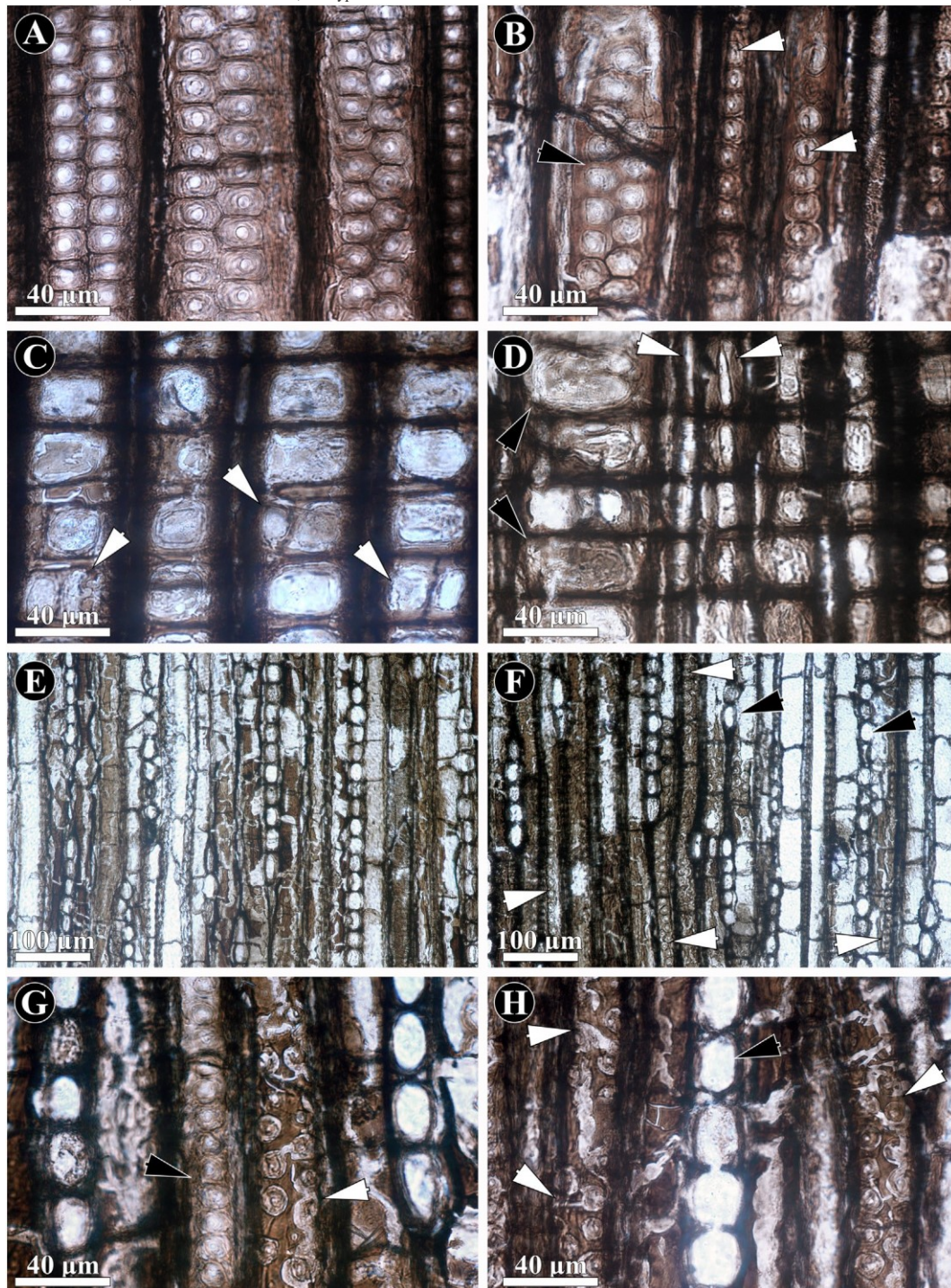


Fig. 4. Photographs showing anatomical structures of *Protophyllocladoxylon zhaobishanensis* sp. nov. from the Induan Jiucayuan Formation in Zhaobishan area, Shanshan County, Turpan–Hami Basin, southern Bogda Mountains. (A). Radial section of the earlywood, showing the biseriate pitting on tracheidal walls. Pits are hexagonal, bordered with circular apertures, continuously and alternatively arranged. Collection number: PB22937; slide number: PB22937-4; holotype. (B). Radial section of the fossil wood, showing the biseriate pitting on tracheidal walls of earlywood (black arrow) and uniseriate pitting on tracheidal walls of latewood (white arrows). Bordered pits of latewood are continuous arranged with slit-like apertures (white arrows). Collection number: PB22937; slide number: PB22937-5; holotype. (C). Radial section of the earlywood, showing the simple pitting in cross-fields, occupying nearly the entire field. There is commonly one large pit in each field. In some cases, there are two pits in each field, which are commonly horizontally arranged (white arrows). Collection number: PB22937; slide number: PB22937-5; holotype. (D). Radial section of the fossil wood, showing the simple pitting in cross-fields of the latewood (white arrows) and earlywood (black arrows). Walls of parenchymatous rays are smooth. Collection number: PB22937; slide number: PB22937-6; holotype. (E). Tangential section of the fossil wood, showing the uniseriate parenchymatous rays. Collection number: PB22937; slide number: PB22937-7; holotype. (F). Tangential section of the fossil wood, showing the uniseriate parenchymatous rays (black arrows) and pits on tangential walls (white arrows). Collection number: PB22937; slide number: PB22937-8; holotype. (G). Tangential section of the fossil wood, showing the uniseriate (black arrow) to biseriate pitting (white arrow) on tangential walls. Uniseriate pits are bordered, arranged continuously (black arrow). Biseriate pits are

alternatively and loosely distributed. Collection number: PB22937; slide number: PB22937-8; holotype. (H). Tangential section of the fossil wood, showing uniseriate rays (black arrow) and the biseriate pitting (white arrows) on tangential walls. Biseriate pits are bordered, with circular apertures, alternatively and loosely distributed. Collection number: PB22937; slide number: PB22937-8; holotype.

Protophyllocladoxylon zhaobishanensis Wan, Yang et Wang sp. nov. (Figs. 3–4)

Holotype: The specimens with catalog PB 22937, and the slides PB 22937-1 to PB 22937-8

Repository: Paleobotanical Collection of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences

Type locality: Zhaobishan, Shanshan County, Turpan, Xinjiang Uygur Autonomous Region, China

Stratigraphic horizon: Jiucayuan Formation

Age: Induan, Early Triassic

Etymology: The specific epithet indicates that the specimens were collected from the Zhaobishan section.

Diagnosis: Secondary xylem pycnoxylic, composed of tracheids and parenchymatous rays. Growth ring distinct. Tracheids rounded or polygonal, sometimes squarish in transverse section. Radial tracheidal pits of early wood commonly uniseriate to biseriate, rarely triseriate. Uniseriate pits commonly continuous, rarely arranged in groups. Multiseriate pits contiguously and alternatively arranged. Bordered pits on radial tracheidal walls commonly rounded to polygonal, rarely flattened in outline, with circular apertures. Radial pits on radial walls of late wood commonly uniseriate, rounded in outline, continuously arranged, with slit-like apertures. Tangential tracheidal pits present on tracheid walls, uniseriate to biseriate, rounded with circular apertures. Bordered pits contiguous or separate. Rays uniseriate, 1–28 cells high. Ray parenchymatous cells procumbent, rectangular. Cross-field pitting window-like. Each cross-field with 1–2, rectangular, circular, oval simple pits. Axial xylem parenchyma and ray tracheids absent.

4. Description

Woody specimens are decorticated, with only secondary xylems. The secondary xylem is composed of tracheids and parenchymatous rays. Axial parenchyma and resin canals are absent. Growth rings are distinct and of varying widths, ranging from 200 μm to 1 mm (Fig. 3A–B). Boundaries of growth rings are well-defined by the presence of early wood with thinner cell walls and late wood with thick walls. The transition from early wood to late wood is gradual.

Tracheids in early wood are crudely rounded to polygonal and, in some cases, squarish in transverse section (Fig. 3A–C). They are distributed in regular radial files. The diameter of tracheids in early wood is ranging from 45 to 85 μm . Diameters of tracheids in late wood vary from 15 to 55 μm . Tracheids are long and fusiform with blunt ends in radial section. Radial pits are uni- to triseriate, commonly uni- to biseriate on tracheidal walls of early wood (Fig. 3D–F). The triseriate pitting is commonly confined to the first one to two tracheids of the early wood (Fig. 3E). In early wood, uniseriate radial pitting is commonly contiguously arranged (Fig. 2E, G–H), with partially biseriate pits (Fig. 3H). Occasionally, they are clustered in groups with 1–17 pits (Fig. 3F). Biseriate radial pitting is contiguously and alternatively arranged (Figs. 3I; 4A–B). Radial pits in early wood are commonly bordered, rounded to hexagonal (Figs. 3I; 4A–B), and rarely flattened (Fig. 3G) in outline, with circular apertures (Figs. 3G; 4A). The diameter of bordered pits on radial walls of early wood is ranging from 15 to 35 μm . Uniseriate pits in late wood are bordered, contiguous, with slit-like to oval apertures (Fig. 4B).

Rays are homogenous and commonly uniseriate (Fig. 4E–F). Cell walls of ray parenchyma are smooth. Rays are 1–28, commonly 4–16 cells high. The cross-field pitting is window-like (sensu Richter et al., 2004), with commonly 1–2 large simple pits in each field (Fig. 4C–D). Pits in each field are rounded, square, elliptical or rectangular, occupying nearly the entire field. In cases of two pits in a cross-field, they are commonly arranged in horizontal (Fig. 4C).

Uniseriate to biseriate pits are present on tangential tracheidal walls (Fig. 4F). They are bordered, rounded, with circular apertures. The diameter of tangential pits varies from 7 to 15 μm . Uniseriate pits are commonly continuous, rarely separated (Fig. 4G). Biseriate pits are commonly alternatively arranged (Fig. 4G). In some instances, tangential pits are separately distributed (Fig. 4G–H). Some of the tracheids contain numerous tylosis-like membranous structures. They are thin and separate tracheids into many lumens (Figs. 3E–F; 4E–F). In some cases, such structures originate from the ray cells (Fig. 4F).

5. Discussion

5.1. Paleoxtolotomy and comparison

Pycnoxylic tracheidoxyls that have dominantly or exclusively araucarian radial pitting and, less than three simple, large pits in each cross field are commonly assigned to Protophyllocladoxylon Kräusel (Kräusel, 1939; Lepekina and Yatsenko-Khmelevsky, 1966; Lepekina, 1972; Pant and Singh, 1987; Zheng et al., 2008). At least 29 species of Protophyllocladoxylon have been recorded from the late Paleozoic to Cenozoic (Zhang et al., 2010; Pujana et al., 2014; Fletcher et al., 2014). Among them, only six species, including *P. derbyi* (Oliveira) Maheshwari, *P. dolianitii* Mussa; *P. henanense* Yao et al., *P. indicum* Pant and Singh, *P. jingyuanense* Zhang et al. and *P. natalense* (Warren) Schultze-Motel, are from the Paleozoic (Mussa, 1958; Schultze-Motel, 1961; Maheshwari, 1972; Pant and Singh, 1987; Yao et al., 1994; Zhang et al., 2010). These species, and our Early Triassic wood specimens, are similar to the type species, *P. leuchsii* Kräusel, with exclusively araucarian radial pitting. The specific radial pitting in our wood differs from that in some of the Mesozoic species, such as *P. chudeaui* Batton, *P. capense* (Walton) Kräusel, *P. korubaense* Serra, *P. maurianum* Gazeau, *P. quedlinburgense* Schultze-Motel, *P. thylloides* Serra, and *P. xenoxylloides* Serra, which have dominantly araucarian and rarely abietinean pits on radial walls (Kräusel, 1939, 1949; Schultze-Motel, 1961; Batton, 1965; Serra, 1966a, 1966b; Gazeau, 1969). Protophyllocladoxylon chaoyangense

Zhang et al., *P. derbyi*, *P. franconicum* Vogellehner, *P. haizhouense* Ding, *P. jingyuanense*, *P. maurianum*, *P. oolithicum* Vogellehner, *P. quedlinburgense*, and *P. szei* Wang are characterized by the dominantly uniseriate radial pitting, which differs from the uni- to triseriate pits in our wood (Schultze-Motel, 1961; Vogellehner, 1966; Gazeau, 1969; Maheshwari, 1972; Wang, 1993b; Ding et al., 2000; Zhang et al., 2000, 2010). Tangential tracheidal pitting is an important characteristic for fossil wood taxonomy (Zheng et al., 2008). Eleven species of Protophyllocladoxylon have uniseriate bordered pits on tangential walls of tracheids (Zhang et al., 2010; Pujana et al., 2014). The occurrence of uni- to biseriate tangential pits in our wood makes it distinct from all of the species of Protophyllocladoxylon. Seven genera of fossil stems with pith and primary xylem, including *Junggaropitys* Shi et al., *Medullopitys* Kräusel, *Megaporoxyton* Kräusel, *Phyllocladopitys* Kräusel, *Septomedullopitys* Lepekina and *Turpanopitys* Shi et al., contain Protophyllocladoxylon-type secondary xylem (Kräusel, 1928, 1956; Lepekina, 1969, 1972; Shi et al., 2014, 2015, 2017; Wan et al., 2014). In addition, a cordaitalean wood, *Cordaixylon andresii* Césari et al., was described with Protophyllocladoxylon-type secondary xylem from the Pennsylvanian of Spain (Césari et al., 2015). However, none of those stems with Protophyllocladoxylon-type wood have biseriate tangential pitting that is comparable to the specimens described here.

Cross-field pitting is one of the critical taxonomic characteristics in extant (Richter et al., 2004) and fossil (Pant and Singh, 1987; Philippe and Bamford, 2008) gymnospermous woods. In general, three types of cross-field pitting are present in the species of Protophyllocladoxylon, including phyllocladoid (sensu Philippe and Bamford, 2008), window-like (sensu Richter et al., 2004), and small to medium oval/rounded pitting. All pits in cross fields of the

Protophyllcladoxylon wood are simple without borders. The type species of Protophyllcladoxylon (*P. leuchsii*) has phyllocladoid cross-field pitting, with 1–2 simple, elliptical pits with pointed to sub-pointed tips in each field (Kräusel, 1939; Philippe and Bamford, 2008). However, the morphology of pits in cross fields of Protophyllcladoxylon is variable. Some species have at least two types of cross-field pitting. In *P. henanense*, cross-field pits are phyllocladoid, circular, and oval (Yao et al., 1994). Protophyllcladoxylon *owensii* has both phyllocladoid and rounded (circopores) pits (Fletcher et al., 2014). When there are more than one pit present in each cross field, they are commonly horizontally distributed (e.g., Pant and Singh, 1987; Fletcher et al., 2014), rarely vertically arranged (Zhang et al., 2010). Similar to the current material, six species of Protophyllcladoxylon have window-like cross-field pitting. Protophyllcladoxylon *dephtericum* Batton et Bureau, *P. franconicum* Vogellehner, *P. lechangense* Wang, and *P. szei* are different from our Early Triassic wood in the relatively lower (less than 15 cells high) rays (Batton and Bureau, 1965; Vogellehner, 1966; Wang, 1991; Wang, 1993a). Protophyllcladoxylon *chudeaui* Batton and *P. dephtericum* are characterized by the occurrence of axial parenchyma, which is absent in our wood (Batton, 1965; Batton and Bureau, 1965).

Tens of fossil woods have been described from the Permian and Triassic of northern Xinjiang during the past few years (e.g., Wan et al., 2016b, 2016c, 2017a, 2017c). Four species are documented with Protophyllcladoxylon-type secondary xylems (Shi et al., 2014, 2015, 2017; Wan et al., 2014). Among them, *Junggaropitys dalongkouense* Shi et al., *Septomedullopitys szei* Wan et al., and *Xinjiangoxylon turpanense* Shi et al. have both phyllocladoid and window-like cross-field pitting (Shi et al., 2014, 2015; Wan et al., 2014). Our wood is comparable with the secondary xylem of *Turpanopitys taoshuyuanense* Shi et al., which has dominantly window-like cross-field pitting (Shi et al., 2017). However, *T. taoshuyuanense* does not have tangential pitting as in our material.

Our wood fragments from the Lower Triassic have unique anatomical characteristics which are consistent with the fossil genus Protophyllcladoxylon, and are different from all of the described species of this genus. Based on the evidence and discussion mentioned above, we establish a new species *P. zhaobishanensis* sp. nov. herein. Protophyllcladoxylon is commonly associated with eusteles composed of piths and primary xylems (Kräusel, 1928, 1956; Lepekhina, 1969, 1972; Shi et al., 2014, 2015, 2017; Césari et al., 2015). Its anatomical features are different from those of seed ferns, cycads and ginkgoes. Protophyllcladoxylon-type woods from the Mesozoic are commonly proposed as conifers (e.g., Fletcher et al., 2014; Pujana et al., 2014). Therefore, *P. zhaobishanensis* is tentatively regarded to be of a coniferous affinity.

5.2. Paleocological implications

The growth pattern of fossil wood may provide key information on regional paleoclimate and plant paleoecology in deep time (Creber and Chaloner, 1984; Falcon-Lang, 2005; Yang et al., 2013). Presence of growth rings in silicified woods indicates seasonal variations in precipitation, temperature and light availability (e.g., Taylor and Ryberg, 2007; Yang et al., 2013). Growth rings are distinct in all silicified wood samples from the Lower Triassic Jiucaiyuan LC in the Zhaobishan section. They occur in the secondary xylem of Protophyllcladoxylon *zhaobishanensis* and indicate a seasonal climate in the area during the Early Triassic. Moreover, they show a gradual transition from earlywood to latewood suggesting gradual changes of environmental and climatic conditions during the growth seasons (Creber and Chaloner, 1984). This type of growth ring is different from those occurred in fossil woods from high latitudes. The latter is characterized by extensive earlywood and very little late wood (Ryberg and Taylor, 2007). During the Permian and Early Triassic, Turpan–Hami Basin was located at about 40 to 50°N paleo-latitude (Yang et al., 2010; Scotese and Wright, 2018). Therefore, annual light/dark cycle is not the reason for growth rings in *P. zhaobishanensis*. In the Early Triassic middle latitude of NE Pangaea, a region with a mean annual temperature were 11–

14 °C, and a mean annual temperature range of only 4.4 °C (Thomas et al., 2011), indicate that unusually low temperatures are not responsible for the growth ring in current study. The absence of traces of arthropods and fungi in *P. zhaobishanensis* suggests arthropod attack and fungal infection are not the cause of growth rings.

The thick braided stream deposits in the lower and middle parts of Jiucaiyuan LC in Zhaobishan section contain little sedimentary evidence on paleoclimatic conditions; but the stacked Calcisols developed in lake plain mudrocks in the uppermost part suggest semi-arid to subhumid, highly seasonal conditions (Fredericks, 2017; Yang et al., 2018). In addition, abundant interpretation of the climatic conditions conforms to those based on sedimentary, paleosol, and geochemical evidence from the Tarlong–Taodonggou area, ~90 km east to the Zhaobishan section in the Turpan–Hami Basin (Yang et al., 2010; Thomas et al., 2011; Liu et al., 2019) substantiate our climatic interpretation. Calcisols, vertic Calcisols, and calcic Argillisols are common in floodplain and lakeplain deposits of the Jiucaiyuan LC in Tarlong–Taodong area. Their occurrence indicates a period of landscape stability and a semi-arid to sub-humid climate, at least during the time of pedogenesis (Retallack, 1990; Mack and James, 1994). The calcareous paleosols suggest periods of low ground water table and soil moisture deficiency (Yang et al., 2010). Thomas et al. (2011) estimated 290–1014 mm/yr MAP (mean annual precipitation) value using the CIA-K (chemical index of alteration minus Potassium) proxy data of the paleosols and suggested a great precipitation variability in a highly seasonal semi-arid to sub-humid climate during the Early Triassic in the Turpan–Hami Basin. Although the Zhaobishan section and Tarlong–Taodonggou area may have been located in two different half-grabens in the Early Triassic, the two areas would likely have had similar climatic conditions as indicated by regional trend of lake contraction and expansion (Fredericks, 2017; Yang et al., 2018). Consequently, we speculate that the growth rings in *P. zhaobishanensis* may have been mainly triggered by droughts during the growing season, causing the physiological water stress of the trees due to great precipitation variability.

5.3. Implications for the end-Permian mass extinction

Our findings add to the complex field of plant evolution across the Permian–Triassic boundary (PTB). The end-Permian mass extinction event is considered to be the most severe biotic catastrophe in the Phanerozoic (e.g., Sepkoski, 1984; Erwin, 1994; Shen et al., 2011; Shen and Zhang, 2017). It is generally accepted that this crisis had a substantial influence on marine invertebrates (e.g., Jin et al., 2000; Payne and Clapham, 2012; Stanley, 2016) over a geologically short time (Bowring et al., 1998; Shen et al., 2011, 2018). However, the impact of the event on land plants has long been controversial. Evidence for floral changes has commonly been documented using palynological data of the Permian–Triassic interval (Ouyang and Utting, 1990; Looy et al., 1999, 2001; Ouyang and Norris, 1999; Lindström and McLoughlin, 2007; Hochuli et al., 2010a,b, 2016; Schneebeil-Hermann et al., 2015, 2017; Fielding et al., 2019), but yielded conflicting results (Schneebeil-Hermann et al., 2017; Nowak et al., 2019). Palynological data from Jameson Land, East Greenland, demonstrate that the terrestrial ecosystem had collapsed in a multi-phase process; and the subsequent extinction of typical late Permian subangaran gymnospermous forests preceded the Permian–Triassic boundary and was followed by a dominant vegetation of herbaceous lycopsids throughout the Early Triassic (Looy et al., 2001; Twitchett et al., 2001). However, palynological records from the southern Barents Sea of offshore Norway and the Kap Stosch, East Greenland indicate a gymnosperm extinction at the Induan–Olenekian boundary in the Early Triassic (Hochuli et al., 2010a, 2016; Schneebeil-Hermann et al., 2017), and no significant floral diversity decrease at the Permian–Triassic boundary (Schneebeil-Hermann et al., 2017). In northern Xinjiang, palynomorphs are diverse and well-preserved, and show similar species composition and percentage from the Guodikeng and Jiucaiyuan formations (Qu and Wang, 1986; Yu et al., 1986; Ouyang and Norris, 1999; Liu, 2000). The Early Triassic

(Induan) palynological assemblage from the Jiucayuan Formation is characterized by dominant and diverse pteridophytic spores and subordinate but almost equally diverse gymnospermous pollen. Ouyang and Norris (1999) suggested that the presence of transitional palynofloras in the lowermost Triassic of northern Xinjiang, and there is no catastrophic mass extinction of terrestrial floras at the global scale at the end of the Permian.

Plant macrofossil data are also used to interpret that the vegetation suffered enormous losses during the end-Permian mass extinction event (Wang, 1989; Wang, 1993a, 1996; Retallack, 1995a,b; Wang and Chen, 2001; Grauvogel-Stamm and Ash, 2005; Yu et al., 2007, 2015; Shen et al., 2011; Zhang et al., 2016). In Australia, macrofloral records show that the peat-forming *Glossopteris* flora was replaced by the Triassic vegetation dominated by herbaceous lycopside and voltzialean conifers at the PTB (Retallack, 1995b). However, it should be noted that glossopterids have been reported from the Triassic of Gondwana (Srivastava, 1969; Anderson and Anderson, 1985; Holmes, 1992). Recently, Gastaldo et al. (2015) reported a *Glossopteris*-dominated megafloral assemblage and a Permian palynoflora above the highest occurrence (HO) of *Dicynodon* in the Karoo Basin. If the HO of *Dicynodon* marks the PTB, there are significant range extensions of typical Permian plants into Triassic strata. Research on the evolution and extinction of plants across the PTB from west Guizhou and eastern Yunnan (WGEY) of South China have been deeply conducted (e.g., Yao et al., 1980; Yu et al., 2007; Feng et al., 2018). Vegetation in this area is marked by a severe decline in biodiversity around the PTB and, a dramatic turnover from the typical *Gigantopteris* flora to the *Annalepis*-dominated flora (Yu et al., 2015). However, the bone of contention is whether the plant extinction WGEY was synchronous with the marine animals, or not, and if it was a rapid collapse of the tropical rainforest or a long-term changeover process and extinction pattern (Yu et al., 2007, 2010, Yu et al., 2015; Shen et al., 2011; Zhang et al., 2016). Early Triassic floral data in the mid- to high-latitude Angara are scarce (Dobruskina, 1994, 1995; Grauvogel-Stamm and Ash, 2005; Karasev, 2015). In eastern Siberia (eastern Taimyr, Lena–Anabar Trough, Verkhoyansk region), the Permian cordaitalean coal-forming flora was replaced by the lycopside-dominant (*Tomostrobus* Neuburg) flora (Mogucheva, 1980, 1989; Dobruskina, 1994). In the Tunguska and Kuznetsk basins and partially in the Verkhoyansk region, fossil records show a dramatic transformation from the late Permian *Tatarina* flora to a diverse equisetale- and fern-dominated flora in the Induan (Mogucheva and Naugolnykh, 2010; Mogucheva, 2016). However, there is a sedimentary hiatus at the boundary between the Permian and Triassic in the Angaraland (Mogucheva and Krugovikh, 2009; Mogucheva, 2016; and references therein). In North China, the Changhsingian flora was replaced by the *Pleuromeia*-dominant flora around the PTB (Wang, 1989, 1996, 2000; Tian et al., 2000; Wang and Chen, 2001). However, the diversity of the late Permian flora in North China decreased since the Wuchiapingian (Wang and Wang, 1986; Wang, 1989). Typical *Cathaysia* floral elements have a dramatic decline at the beginning of deposition of the Capitanian–Wuchiapingian Upper Shihhotse Formation (Shen, 1995; Wang, 2010). In addition, it is important to note that there is a 300-m thick sandstone interval between the last Permian flora assemblage and the earliest Triassic *Pleuromeia*-dominated flora in North China (Wang, 1996). No fossil has been found from this interval. Therefore, Wang (Wang, 1993b, p. 474) suggested that plant extinction at the PTB in North China was a long-term and complex evolutionary event, rather than a single catastrophic event.

Studies by Cascales-Miñana and Cleal (2012, 2014) demonstrated a long-term decline of 55% of plant families across the Permian–Triassic interval. Global compilations of land plant diversity show no substantial land plant mass extinction at the end of the Permian (Knoll, 1986; Traverse, 1988; Rees, 2002; McElwain and Punyasena, 2007; Xiong and Wang, 2011). The Permian–Triassic interval records a long period of vegetational turnover in a time frame of millions of years, during which there was extensive replacement of higher-level taxa (Knoll, 1986; Wing and Sues, 1992). There is hardly any evidence for the extinction of major groups of plants at the PTB (Kerp, 2000). Most of

the major plant groups that characterize Mesozoic floras had already evolved during the latest Carboniferous or Permian (Meyen, 1979; Kerp, 2000; DiMichele et al., 2001; Kerp et al., 2006; Abu Hamad et al., 2008). Recently, Lopingian plant fossils from Jordan studied by Blumenkemper et al. (2018) confirmed that three seed-plant lineages (*Corynospermales*, *Bennettiales* and *Podocarpaceae*) that were dominant during the Mesozoic had evolved during the Permian. In northern Xinjiang, the composition of flora in the uppermost Permian and Lower Triassic is poorly documented in well-exposed Permian–Triassic continental deposits. Five species, including *Viatcheslavia* cf. *vorcutensis* (Zalessky) Neuberg, *Lepidostrobusphyllum* sp., *Paracalamites* sp., *Zamiopteris* cf. *glossopteroides* Schmalhausen, *Walchia* sp. and *Samaropsis* sp., were described from the Changhsingian Guodikeng Formation (Zhou and Zhou, 1986). Only one fossil plant fragment, *Pecopteris* sp., was found from the Lower Triassic (Induan) Jiucayuan Formation (Zhou and Zhou, 1986). Records of Early Triassic flora are scarce globally (Zhou and Li, 1979; Bose et al., 1990; Wang and Wang, 1990; Fuchs et al., 1991; Retallack, 1995a; Yu et al., 2010; Naugolnykh, 2012; Feng et al., 2018). Therefore, current state of knowledge on the latest Permian and Early Triassic plants, and the resolution of correlation between marine and non-marine deposits is too limited to conclude patterns in extinction, recovery, and radiation across the Permian–Triassic boundary.

Fossil gymnospermous wood is rarely used to identify the patterns of extinction and survival in the geological history. In most cases, woody fragments cannot be related to the macrofossil of their parent plants (Boulter et al., 1988). In addition, the spatio-temporal distribution of gymnospermous woods is commonly not well constrained (e.g., Wan et al., 2016b). Occurrence of *Protophyllocladoxylon*-type wood ranges from the Mississippian to Eocene (Zhang et al., 2010; Pujana et al., 2014; Fletcher et al., 2014). In northern Xinjiang, this type of wood has been reported from the Wuchiapingian Wutonggou Formation (Wan et al., 2014), Changhsingian–Induan (?) Guodikeng Formation (Shi et al., 2014, 2017), and Anisian–Carnian Karamay Formation (Shi et al., 2015). In addition to current discovery in the Induan Jiucayuan Formation, it seems that this type of wood is continuously distributed from the base of upper Permian to Middle–Upper Triassic. The similarities in anatomical structures except the presence of tangential pitting on tracheidal walls in *P. zhaobishanensis*, and their occurrence in the same region, suggest the *Protophyllocladoxylon*-type woods from the upper Permian to Triassic in northern Xinjiang represent a single coniferous group. Triassic elements of this group represented by the wood-species are most likely developed and evolved from the Permian in this geographic region. This suggests the group was not drastically affected by the end-Permian mass extinction. The prevailing model for the end-Permian terrestrial catastrophe is the extinction of woody trees in response to extreme environmental stress (Looy et al., 1999; Shen et al., 2011; Zhang et al., 2016), and increased sediment loads as a function of profound soil erosion due to deforestation (Benton and Newell, 2014; Sephton et al., 2005). However, occurrence of *P. zhaobishanensis* from the Induan of northern Xinjiang shows that there existed survivors of woody plants after greatest biotic crisis in Earth history.

6. Conclusions

A new type of coniferous wood, *Protophyllocladoxylon zhaobishanensis*, is proposed from the Induan (Lower Triassic) Jiucayuan Formation in the southern Bogda Mountains, northwestern China. Description of this species adds to the knowledge on the diversity of the Early Triassic flora in the northeastern Pangaea in the earliest Triassic. The presence of distinct and extensive growth rings in all fossil woods from the Induan of the research area and the occurrence of *Calcisols*, *vertic Calcisols*, and *calcic Argillisols* from coeval deposits nearby suggests a seasonal climate with great precipitation variability during the earliest Triassic in the Turpan–Hami Basin. Continuous records of *Protophyllocladoxylon*-type wood from the upper Permian to Middle–Upper Triassic in northern Xinjiang suggest that conifers may have

suffered a strong decline at the end of Permian, but some survived the end-Permian biotic crisis.

Acknowledgements

We thank Mr. Shengwu Mei of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Jaimeson Fredericks and Yiran Lv of Missouri University of Science and Technology for field assistance. We acknowledge Mr. Xiting Cheng of NIGPAS for helping make the thin sections. We are grateful to Ms. Jing Feng of NIGPAS for helping prepare the images and plates. We are grateful to Dr. Tamara Fletcher, an anonymous reviewer and Prof. Maria Gandolfo for their valuable comments, which have helped to significantly improve the paper. This research was supported by the National Natural Science Foundation of China (41872013 and 41530101), the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB26000000, XDB18000000), the National Science Foundation (NSF EAR 1714749), and State Key Laboratory of Palaeobiology and Stratigraphy (20181102).

References

- Abu Hamad, A., Kerp, H., Vöding, B., Bandel, K., 2008. A Late Permian flora with *Dicroidium* from the Dead Sea region, Jordan. *Rev. Palaeobot. Palynol.* 149, 85–130.
- Afonin, S.A., Foster, C.B., 2005. Palynological assemblages and Permian–Triassic boundary in continental deposits of Dalongkou section (Xinjiang, N.-W., China). In: Afonin, S.A., Tokarev, P.N. (Eds.), XI All-Russian Palynological Conference Palynology: Theory and Applications, Proceedings of the Conference 27th September–1st October, Moscow. Russian Academy of Science, Palaeontological Institute, pp. 14–18 in Russian.
- Allen, M.B., Şengör, A.M.C., Natal'in, B.A., 1995. Junggar, Turfan and Alakol basins as Late Permian to ?Early Triassic extensional structures in a sinistral shear zone in the Altai orogenic collage, Central Asia. *J. Geol. Soc.* 152, 327–338.
- Anderson, J.M., Anderson, H.M., 1985. Palaeoflora of Southern Africa. *Prodromus of South African Megafloras Devonian to Lower Cretaceous*. Balkema, Rotterdam, Netherlands, p. 416.
- Batton, C., 1965. Contribution à l'étude anatomique et biostratigraphique de la flore du continental intercalaire saharien. Centre National Recherche Scientifique, Série Géologique 6. Publication Centre Recherche sur les Zones Arides, Paris, pp. 11–88.
- Batton, C., Boureau, E., 1965. Étude des flore fossiles du Nord du Cameroun: *Protophylladoxylon diphtericum* n. sp., bois fossile du Crétacé moyen du Lagon. Centre National Recherche Scientifique, Série Géologique 6. Publication Centre Recherche sur les Zones Arides, Paris, pp. 97–114.
- Beck, C.B., 2010. An Introduction to Plant Structure and Development: Plant Anatomy for the Twenty-First Century. Second edition. Cambridge University Press, Cambridge, pp. 1–441.
- Benton, M.J., Newell, A.J., 2014. Impacts of global warming on Permo-Triassic terrestrial ecosystems. *Gondwana Res.* 25, 1308–1337.
- Blumenkemper, P., Kerp, H., Abu Hamad, A., DiMichele, W.A., Bomfleur, B., 2018. A hidden cradle of plant evolution in Permian tropical lowlands. *Science* 362, 1141–1146.
- Bose, M.M., Taylor, E.L., Taylor, T.N., 1990. Gondwana floras of India in Antarctica—a survey and appraisal. In: Taylor, T.N., Taylor, E.L. (Eds.), *Antarctic Paleobiology: Its Role in the Reconstruction of Gondwana*. Springer, New York, pp. 102–117.
- Boulter, M.C., Spicer, R.A., Thomas, B.A., 1988. Patterns of plant extinction from some palaeobotanical evidence. In: Larwood, G.P. (Ed.), *Extinctions and Survivals in the Fossil Record*. Systematic Association Special Volume 34. Charles Press, Oxford, pp. 1–36.
- Bowring, S.A., Erwin, D.H., Jin, Y.G., Martin, M.W., Davidek, K., Wang, W., 1998. U/Pb Zircon Geochronology and Tempo of the End-Permian Mass Extinction. *Science* 280, 1039–1045.
- Cao, C.Q., Wang, W., Liu, L.J., Shen, S.Z., Summons, R.E., 2008. Two episodes of ¹³C depletion in organic carbon in the latest Permian: evidence from the terrestrial sequences in northern Xinjiang, China. *Earth Planet. Sci. Lett.* 270, 251–257.
- Carroll, A.R., Graham, S.A., Hendrix, M.S., Ying, D., Zhou, D., 1995. Late Paleozoic tectonic amalgamation of northwestern China: sedimentary record of the northern Tarim, northwestern Turpan, and southern Junggar Basins. *Geol. Soc. Am. Bull.* 107, 571–594.
- Cascales-Miñana, B., Cleal, C.J., 2012. Plant fossil record and survival analyses. *Lethaia* 45, 71–82.
- Cascales-Miñana, B., Cleal, C.J., 2014. The plant fossil record reflects just two great extinction events. *Terra Nova* 26, 195–200.
- Césari, S.N., Álvarez-Vázquez, C., Méndez-Bedia, I., Álvarez-Laó, D., Turrero, P., Arbizu, M., 2015. First report of permineralised plants in the Stephanian of Arnao (Asturias, northwestern Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 440, 475–486.
- Chen, F.Y., Shi, X., Yu, J.X., Chi, H.F., Zhu, J., Li, H., Huang, C., 2018. Permineralized calamitean axes from the Upper Permian of Xinjiang, Northwest China and its paleoecological implication. *J. Earth Sci.* 29, 237–244.
- Cheng, Z.W., Lucas, S.G., 1993. A possible nonmarine GSSP for the Permian–Triassic boundary. *Albertina* 12, 39–44.
- Cheng, Z.W., Wu, S.Z., Fang, X., 1996. The Permian–Triassic sequences in the southern margin of the Junggar basin and the Turpan basin, Xinjiang, China. 30th International Geological Congress Field Trip Guide T394 (25 pp).
- Cheng, Z.W., Wu, S.Z., Fang, X.S., 1997. The Permian–Triassic sequences in the southern margin of the Junggar Basin and the Turpan Basin, Xinjiang. *Xinjiang Geol.* 15, 155–173.
- Creber, G.T., Chaloner, W.G., 1984. Influence of environmental factors on the wood structure of living and fossil trees. *Bot. Rev.* 50, 357–448.
- Creber, G.T., Francis, J.E., 1999. Fossil tree-analysis: palaeodendrology. In: Jones, T.P., Rowe, N.P. (Eds.), *Fossil plants and spores: modern techniques*. Geological Society, London, pp. 245–250.
- DiMichele, W.A., Mamay, S.H., Chaney, D.S., Hook, R.W., Nelson, W.J., 2001. An Early Permian flora with Late Permian and Mesozoic affinities from North-Central Texas. *J. Paleontol.* 75, 449–460.
- Ding, Q.H., Zhang, W., Zheng, S.L., 2000. Research on fossil wood from the Fuxin Formation in western Liaoning Province, China. *Liaoning Geol.* 17, 284–286 in Chinese with English abstract.
- Dobruskina, I.A., 1994. Triassic floras of Eurasia. *Österreichische Akademie der Wissenschaften Schriftenreihe der Erdwissenschaftlichen Kommissionen Band 10*, 1–422.
- Dobruskina, I.A., 1995. Keuper (Triassic) flora from Middle Asia (Madygen, Southern Fergana). *New Mexico Mus. Nat. Hist. Sci. Bull.* 5, 1–49.
- Erwin, D.H., 1994. The Permo-Triassic extinction. *Nature* 367, 231–236.
- Falcon-Lang, H.J., 2005. Intra-tree variability in wood anatomy and its implications for fossil wood systematic and palaeoclimatic implications. *Palaeontology* 48, 171–183.
- Feng, Z., Wei, H.B., Guo, Y., Bomfleur, B., 2018. A conifer-dominated Early Triassic flora from Southwest China. *Sci. Bull.* <https://doi.org/10.1016/j.scib.2018.09.011>.
- Fielding, C.R., Frank, T.D., McLoughlin, S., Vajda, V., Mays, C., Tevyaw, A.P., Winguth, A., Winguth, C., Nicoll, R.S., Bocking, M., Crowley, J.L., 2019. Age and pattern of the southern high-latitude continental end-Permian extinction constrained by multiproxy analysis. *Nat. Commun.* 10, 385. <https://doi.org/10.1038/s41467-018-07934-z>.
- Fletcher, T.L., Cantrill, D.J., Moss, P.T., Salisbury, S.W., 2014. A new species of *Protophylladoxylon* from the Upper Cretaceous (Cenomanian–Turonian) portion of the Winton Formation, central-western Queensland, Australia. *Rev. Palaeobot. Palynol.* 208, 43–49.
- Foster, C.B., Afonin, S.A., 2005. Abnormal pollen grains: an outcome of deteriorating atmospheric conditions around the Permian–Triassic boundary. *J. Geol. Soc.* 162, 653–659.
- Fredericks, J.G., 2017. Provenance and Depositional Environments of Fluvial-Lacustrine Deposits in a Non-marine Rift Basin, Lower-Triassic Jiucayuan and Shaofangou Loworder Cycles Bogda Shan, NW China. Master Thesis. Missouri University of Science and Technology, p. 276.
- Fuchs, G., Grauvogel-Stamm, L., Mader, D., 1991. Une remarquable flore à *Pleuromeia* et *Anomopteris mougeotii* in situ du Buntsandstein moyen (Trias inférieur) de l'Eifel (R.F. Allemagne). *Morphologie, paléocologie et paléogéographie. Palaeontogr. Abteilung B, Band 222*, 89–120.
- Gastaldo, R.A., Kamo, S.L., Neveling, J., Geissman, J.N., Bamford, M., Looy, C.V., 2015. Is the vertebrate defined Permian–Triassic boundary in the Karoo basin, South Africa, the terrestrial expression of the end-Permian marine event? *Geology* 43, 939–942.
- Gazeau, F., 1969. Étude de quelques bois fossils du Mésozoïque du Maroc–Sur quelques structures des bois mésozoïques du Maroc–Étude de *Protophylladoxylon maurianum* Gazeau 1967, du Jurassique du Haut Atlas. Notes et mémoires du Service Géologique du Maroc 210, 108–116.
- Grauvogel-Stamm, L., Ash, S., 2005. Recovery of the Triassic land flora from the end-Permian life crisis. *Comptes Rend. Palevol.* 4, 593–608.
- Greene, T.J., Carroll, A.R., Warts, M., Graham, S.A., Wooden, J.L., 2005. Integrated provenance analysis of a complex orogenic terrane: Mesozoic uplift of the Bogda Shan and inception of the Turpan-Hami Basin, NW China. *J. Sediment. Res.* 75, 251–267.
- Hochuli, P.A., Hermann, E., Vigran, J.O., Bucher, H., Weissert, H., 2010a. Rapid demise and recovery of plant ecosystems across the end-Permian extinction event. *Glob. Planet. Chang.* 74, 144–155.
- Hochuli, P.A., Vigran, J.O., Hermann, E., Bucher, H., 2010b. Multiple climatic changes around the Permian–Triassic boundary event revealed by an expanded palynological record from mid-Norway. *Geol. Soc. Am. Bull.* 122, 884–896.
- Hochuli, P.A., Sanson-Barrera, A., Schneebeli-Hermann, E., Bucher, H., 2016. Severest crisis overlooked—worst disruption of terrestrial environments postdates the Permian–Triassic mass extinction. *Sci. Rep.* 6, 28372.
- Holmes, W.B.K., 1992. *Glossopteris*-like leaves from the Triassic of eastern Australia. In: Venkatchala, B.S., Jain, K.P., Awasthi, N. (Eds.), *Proceedings of Birbal Sahni Birth Centenary Palaeobotanical Conference*. Geophytology 22, pp. 119–125.
- Hou, J.P., 2004. Two sporo-pollen assemblages of Guodikeng formation and discussion on the Permo-Triassic boundary in Junggar Basin, Xinjiang. *Prof. Pap. Stratigr. Palaeontol.* 28, 177–204 in Chinese.

- Jin, Y.G., Wang, Y., Wang, W., Shang, Q.H., Cao, C.Q., Erwin, D.H., 2000. Pattern of marine mass extinction near the Permian-Triassic boundary in South China. *Science* 289, 432–436.
- Karasev, E., 2015. On small pinnate leaves of peltasperm pteridosperms from the Early Triassic of the Kuznetsk Basin (Mal'tsevo Formation, Babii Kamen Locality). *Bot. Pacif.* 4, 131–136.
- Kerp, H., 2000. The modernization of landscapes during the Late Palaeozoic–Early Mesozoic. *Paleontol. Soc. Pap.* 6, 79–114.
- Kerp, H., Abu Hamad, A., Vöröding, B., Bandel, K., 2006. Typical Triassic Gondwanan floral elements in the Upper Permian of the paleotropics. *Geology* 34, 265–268.
- Knoll, A.H., 1986. Patterns of change in plant communities through geological time. In: Diamond, J., Case, T. (Eds.), *Community Ecology*. Harper and Row, New York, pp. 126–141.
- Kräusel, R., 1928. Palaeobotanical notes 10, a Keuper wood with cordaitoid marrow. *Senckenb. Lethaea* 10, 443–451 (In German).
- Kräusel, R., 1939. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. IV–Die fossilen Floren Ägyptens. 3–die fossilen Pflanzen Ägyptens. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung* 47, 1–140 (in German).
- Kräusel, 1949. Die fossilen Koniferen-Hölzer (Unter Ausschluss von Araucarioxylon Kraus) II. Teil. Kritische Untersuchungen zur Diagnostik lebender und fossiler Koniferen-Hölzer. *Palaeontogr. Abteilung B, Band* 89, 83–203 (in German).
- Kräusel, R., 1956. Timber from the southern area of Karro layers South West Africa. *Senckenb. Lethaea* 37, 447–453 In German.
- Lepekina, V.G., 1969. Paleoecological characterization of the Upper Palaeozoic coal-bearing deposits of the Kuznetsk Basin. *Trans. Acad. Sci. USSR, Geol. Inst.* 130, 126–140 (in Russian).
- Lepekina, V.G., 1972. Woods of Palaeozoic pycnoxylic gymnosperms with special reference to North Eurasia representatives. *Palaeontogr. Abt. B* 138, 44–106.
- Lepekina, V.G., Yatsenko-Khmelevsky, A.A., 1966. Classification and nomenclature of woods of Palaeozoic pycnoxylic plants. *Taxon* 15, 66–70.
- Li, Y.A., Jin, X.C., Sun, D.J., Cheng, Z.W., Pang, Q.Q., Li, P.X., 2003. Paleomagnetic properties of non-marine Permo-Triassic transitional succession of the Dalongkou Section, Jimsar, Xinjiang. *Geol. Rev.* 49, 525–536 in Chinese with English abstract.
- Lindström, S., McLoughlin, S., 2007. Synchronous palynofloristic extinction and recovery after the end-Permian event in the Prince Charles Mountains, Antarctica: implications for palynofloristic turnover across Gondwana. *Rev. Palaeobot. Palynol.* 145, 89–122.
- Liu, S., 1994. The non-marine Permian-Triassic boundary and Triassic conchostracan fossils in China. *Albertina* 13, 12–24.
- Liu, Z.S., 2000. The Permian-Triassic boundary on the northern margin of the Turpan-Hami Basin of Xinjiang NW China. *J. Stratigr.* 24, 310–314 in Chinese with English abstract.
- Liu, J., Abdala, F., 2017. The rocephalian (Therapsida) and chroniosuchian (Reptiliomorpha) from the Permo-Triassic transitional Guodikeng Formation of the Dalongkou Section, Jimsar, Xinjiang, China. *Vertebr. Palasiatica* 55, 24–40 (in Chinese with English summary).
- Liu, J., Li, J.L., Cheng, Z.W., 2002. The *Lystrosaurus* fossils from Xinjiang and their bearing on the terrestrial Permian-Triassic boundary. *Vertebr. Palasiatica* 40, 267–275 in Chinese with English summary.
- Liu, D.D., Zhang, C., Yang, D.X., Pan, Z.K., Kong, X.Y., Huang, Z.X., Wang, J.B., Song, Y., 2019. Petrography and geochemistry of the Lopingian (upper Permian)-lower Triassic strata in the southern Junggar and Turpan basins, NW China: implications for weathering, provenance, and palaeogeography. *Int. Geol. Rev.* 61, 1016–1036.
- Looy, C.V., Brugman, W.A., Dilcher, D.L., Visscher, H., 1999. The delayed resurgence of equatorial forests after the Permian-Triassic ecologic crisis. *Proc. Natl. Acad. Sci. U. S. A.* 96, 13857–13862.
- Looy, C.V., Twitchett, R.J., Dilcher, D.L., Konijnenburg-van Cittert, J.H.A., Visscher, H., 2001. Life in the end-Permian dead zone. *Proc. Natl. Acad. Sci. U. S. A.* 98, 7879–7883.
- Lucas, S.G., 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 143, 347–384.
- Lucas, S.G., 2009. Timing and magnitude of tetrapod extinctions across the Permo-Triassic boundary. *J. Asian Earth Sci.* 36, 491–502.
- Mack, G.H., James, W.C., 1994. Paleoclimate and the global distribution of paleosols. *J. Geol.* 102, 360–366.
- Maheshwari, H.K., 1972. Permian wood from Antarctica and revision of some Lower Gondwana wood taxa. *Palaeontogr. Abt. B* 138, 1–43.
- McElwain, J.C., Punyasena, S.W., 2007. Mass extinction events and the plant fossil record. *Trends Ecol. Evol.* 22, 548–557.
- Metcalfe, I., Foster, C.B., Afonin, S.A., Nicoll, R.S., Mundil, R., Wang, X.F., Lucas, S.G., 2009. Stratigraphy, biostratigraphy and C-isotopes of the Permian-Triassic non-marine sequence at Dalongkou and Lucaogou, Xinjiang Province, China. *J. Asian Earth Sci.* 36, 503–520.
- Meyen, S.V., 1979. Permian predecessors of the Mesozoic pteridosperms in western Angaraland, U.S.S.R. *Rev. Palaeobot. Palynol.* 28, 191–201.
- Mogucheva, N.K., 1980. Distribution of peltasperm pteridosperms in the Triassic flora of Eastern Taimyr. *Paleontology and Stratigraphy of the Triassic of Central Siberia*. Nauka, Moscow, pp. 93–96.
- Mogucheva, N.K., 1989. Flora transformation at the Permian-Triassic boundary in Angarida. Upper Paleozoic and Triassic of Siberia. *Nauka, Novosibirsk*, pp. 4–12.
- Mogucheva, N.K., 2016. Flora from the Induan Stage (Lower Triassic) of Middle Siberia. *Stratigr. Geol. Correl.* 24, 252–266.
- Mogucheva, N.K., Naugolnykh, S.V., 2010. *Gagariostrobus cylindricus* (Prynada) Mogutcheva and the Permian-Triassic ecosystem flora reorganization in the Tunguska Basin. *Stratigr. Geol. Correl.* 18, 31–41.
- Mogutcheva, N.K., Krugoviykh, 2009. New data on the stratigraphic chart for Triassic deposits in the Tunguska Syncline and Kuznetsk Basin. *Stratigr. Geol. Correl.* 17, 510–518.
- Mussa, D., 1958. Conifera fóssil do Carbonífero Superior de Sanata Catarina. *Servicio Grafico do Instituto Brasileiro de Geografia e Estatística, Boletim* 182, 1–22.
- Naugolnykh, S.V., 2012. Sporophyll morphology and reconstruction of the heterosporous lycopod *Tomostrobus radiatus* Neuburg emend. from the Lower Triassic of Siberia (Russia). *The Palaeobotanist* 61, 387–405.
- Nowak, H., Schneebeli-Hermann, E., Kustatscher, E., 2019. No mass extinction for land plants at the Permian-Triassic transition. *Nat. Commun.* 10, 384. <https://doi.org/10.1038/s41467-018-07945-w>.
- Obrist-Farner, J., Yang, W., 2015. Nonmarine time-stratigraphy in a rift setting: an example from the Mid-Permian lower Quanzijie low-order cycle, Bogda Mountains, NW China. *J. Palaeogeogr.* 4, 27–51.
- Obrist-Farner, J., Yang, W., 2016. Implications of loess and fluvial deposits on paleoclimatic conditions during an icehouse-hothouse transition, Capitanian upper Quanzijie low-order cycle, Bogda Mountains, NW China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 441, 959–981.
- Obrist-Farner, J., Yang, W., 2017. Provenance and depositional conditions of fluvial conglomerates and sandstones and their controlling processes in a rift setting, midPermian lower and upper Quanzijie low order cycles, Bogda Mountains, NW China. *J. Asian Earth Sci.* 138, 317–340.
- Ouyang, S., Norris, G., 1999. Earliest Triassic (Induan) spores and pollen from the Junggar Basin, Xinjiang, northwestern China. *Rev. Palaeobot. Palynol.* 106, 1–56.
- Ouyang, S., Utting, J., 1990. Palynology of Upper Permian and lower Triassic rocks, Meishan, Changxing County, Zhejiang Province, China. *Rev. Palaeobot. Palynol.* 66, 65–103.
- Pang, Q.Q., Jin, X.C., 2004. *Ostrocod* in the Guodikeng formation and continental Permo-Triassic boundary of Dalongkou section, Jimsar, Xinjiang. In: Editorial Committee of Professional Papers of Stratigraphy and Palaeontology of Chinese Academy of Geological Sciences (Ed.), *Professional Papers of Stratigraphy and Palaeontology*. vol. 28. Geological Publishing House, Beijing, pp. 205–246.
- Pant, D.D., Singh, V.K., 1987. Xylotomy of some woods from Raniganj Formation (Permian) Raniganj Coalfield. *Palaeontogr. Abt. B* 203, 1–82.
- Payne, J.L., Clapham, M.E., 2012. End-Permian mass extinction in the oceans: an ancient analog for the twenty-first century? *Annu. Rev. Earth Planet. Sci.* 40, 89–111.
- Philippe, M., Bamford, M.K., 2008. A key to morphogenera used for Mesozoic conifer-like woods. *Rev. Palaeobot. Palynol.* 148, 184–207.
- Pujana, R.R., Santillana, S.N., Marenssi, S.A., 2014. Conifer fossil woods from the La Meseta Formation (Eocene of Western Antarctica): evidence of Podocarpaceae-dominated forests. *Rev. Palaeobot. Palynol.* 200, 122–137.
- Qu, L.F., Wang, Z., 1986. Triassic spore and pollen. In: Institute of Geology, Chinese Academy of Geological Sciences, Institute of Geology, Xinjiang Bureau of Geology and Mineral Resources (Ed.), *People's Republic of China Ministry of Geology and Mineral Resources, Geological Memoirs Series 2; Number 3, Permian and Triassic Strata and Fossil assemblages in the Dalongkou Area of Jimsar, Xinjiang*. Geological Publishing House, Beijing, pp. 113–173 (in Chinese with English abstract).
- Rees, P.C., 2002. Land-plant diversity and the end-Permian mass extinction. *Geology* 30, 827–830.
- Retallack, G.J., 1990. *Soil of the Past—An Introduction to Paleopedology*. Springer, Netherlands, Dordrecht, p. 520.
- Retallack, G.J., 1995a. An Early Triassic fossil flora from Culvida Soak, Canning Basin, western Australia. *J. R. Soc. West. Aust.* 78, 57–66.
- Retallack, G.J., 1995b. Permian-Triassic life crisis on land. *Science* 267, 77–80.
- Richter, H.G., Grosser, D., Heinz, I., Gasson, P.E., 2004. IAWA list of microscopic features for softwood identification. *IAWA J.* 25, 1–70.
- Schneebeli-Hermann, E., Kürschner, W.M., Kerp, H., Bomfleur, B., Hochuli, P.A., Bucher, H., Ware, D., Roohi, G., 2015. Vegetation history across the Permian-Triassic boundary in Pakistan (Amb section, Salt Range). *Gondwana Res.* 27, 911–924.
- Schneebeli-Hermann, E., Hochuli, P.A., Bucher, H., 2017. Palynofloral associations before and after the Permian-Triassic mass extinction, Kap Stosch, East Greenland. *Glob. Planet. Chang.* 155, 178–195.
- Schultze-Motel, J., 1961. Gymnospermenhölzer aus dem Jura des nördlichen Harzvorlandes: *Protophyllocladoxylon quedinburgense* n. sp. *Monatsberichte der Deutschen Akademie der Wissenschaften zu Berlin* 3, 418–426.
- Scotese, C.R., Wright, N., 2018. PALEOMAP Paleodigital Elevation Models (PaleoDEMS) for the Phanerozoic. <https://www.earthbyte.org/paleodem-resource-scotese-andwright-2018/>.
- Sephton, M.A., Looy, C.V., Brinkhuis, H., Wignall, P.B., de Leeuw, J.W., Visscher, H., 2005. Catastrophic soil erosion during the end-Permian biotic crisis. *Geology* 33, 941–944.
- Sepkoski, J.J., 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10, 246–267.
- Serra, C., 1966a. Étude anatomique et paléogéographique de quelques espèces homoxylées du Sud Viêt-Nam et du Cambodge. *Arch. Géol. Viet-Nam* 8, 94–116.

- Serra, C., 1966b. *Protophyllocladoxylon korubaense* nov. sp., bois fossile du Cambodge. Comptes-rendus du Congrès des Sociétés Savantes de Paris et des Départements. Section du Scientifique 91, 199–215.
- Shao, L., Stattegger, K., Garbe-Schoenberg, C., 2001. Sandstone petrology and geochemistry of the Turpan Basin (NW China): implications for the tectonic evolution of a continental basin. *J. Sediment. Res.* 71, 37–49.
- Shen, G.L., 1995. Permian floras. In: Li, X.X. (Ed.), *Fossil Floras of China Through the Geological Ages*, English edition Guangdong Science and Technology Press, Guanzhou, pp. 127–223.
- Shen, S.Z., Zhang, H., 2017. What caused mass extinction? *Chin. Sci. Bull.* 62, 1119–1135 in Chinese.
- Shen, S.Z., Crowley, J.L., Wang, Y., Bowring, S.A., Erwin, D.H., Sadler, P.M., Cao, C.Q., Rothman, D.H., Henderson, C.M., Ramezani, J., Zhang, H., Shen, Y.N., Wang, X.D., Wang, W., Mu, L., Li, W.Z., Tang, Y.G., Liu, X.L., Liu, L.J., Zeng, Y., Jiang, Y.F., Jin, Y.G., 2011. Calibrating the End-Permian mass extinction. *Science* 334, 1367–1372.
- Shen, S.Z., Ramezani, J., Chen, J., Cao, C.Q., Erwin, D.H., Zhang, H., Xiang, L., Schoepfer, S.D., Henderson, C.M., Zheng, Q.F., Bowring, S.A., Wang, Y., Li, X.H., Wang, X.D., Yuan, D.X., Zhang, Y.C., Mu, L., Wang, J., Wu, Y.S., 2018. A sudden end-Permian mass extinction in South China. *GSA Bull.* <https://doi.org/10.1130/B31909.1>.
- Shi, X., Yu, J.X., Li, H., Chi, H.F., Zhang, W., 2014. *Xinjiangoxylon* gen. nov., a new gymnosperm from the latest Permian of China. *Acta Geol. Sin. (English Edition)* 88, 1356–1363.
- Shi, X., Yu, J.X., Broutin, J., Pons, D., 2015. *Junggaropitys*, a new gymnosperm stem from the Middle–Late Triassic of Junggar Basin, Northwest China, and its palaeoecological and palaeoclimatic implications. *Rev. Palaeobot. Palynol.* 223, 10–20.
- Shi, X., Yu, J.X., Broutin, J., Pons, D., Rossignol, C., Bourquin, S., Crasquin, S., Li, Q., Shu, W.C., 2017. *Turpanopitys taoshuyuanense* gen. et sp. nov., a novel woody branch discovered in Early Triassic deposits of the Turpan Basin, Northwest China, and its palaeoecological and palaeoclimatic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 468, 314–326.
- Srivastava, S.C., 1969. Two new species of *Glossopteris* from the Triassic of Nidpur, Madhya Pradesh, India. In: Santapau, H., Sen, J. (Eds.), *J. Sen Memorial Volume*. Botanical Society of Bengal, J. Sen Memorial Committee and Botanical Society of Bengal, Calcutta, pp. 229–303.
- Stanley, S.M., 2016. Estimates of the magnitudes of major marine mass extinctions in earth history. *Proc. Natl. Acad. Sci. U. S. A.* 113, E6325–E6334.
- Taylor, E.L., Ryberg, P.E., 2007. Tree growth at polar latitudes based on fossil tree ring analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 255, 246–264.
- Thomas, S.G., Tabor, N.J., Yang, W., Myers, T.S., Yang, Y., Wang, D., 2011. Palaeosol stratigraphy across the Permian–Triassic boundary, Bogda Mountains, NW China: implications for palaeoenvironmental transition through earth's largest mass extinction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 308, 41–64.
- Tian, B.L., Wang, S.J., Li, C.S., Chen, G.R., 2000. An approach on the origin center, evolution center and the mechanics of evolution and extinction of the late Palaeozoic Cathaysian Flora. *Chin. Bull. Bot.* 17, 21–33.
- Traverse, A., 1988. Plant evolution dances to a different beat: plant and animal evolutionary mechanisms compared. *Hist. Biol.* 1, 277–301.
- Twitchett, R.J., Looy, C.V., Morante, R., Visscher, H., Wignall, P.B., 2001. Rapid and synchronous collapse of marine and terrestrial ecosystems during the end-Permian biotic crisis. *Geology* 29, 351–354.
- Vogelheiner, D., 1966. Zwei neue Vertreter der fossilen Sekundärholzgattung *Protophyllocladoxylon* Kräusel aus dem deutschen Mesozoikum. *Geologisches Jahrbuch*, Band 84, 307–326 (in German).
- Wan, M.L., Yang, W., Wang, J., 2014. *Septomedullopitys zsei* sp. nov., a new gymnospermous wood from Lower Wuchiapingian (Upper Permian) continental deposits of NW China, and its implication for a weakly seasonal humid climate in mid-latitude NE Pangaea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 407, 1–13.
- Wan, M.L., Yang, W., Liu, L.J., Wang, J., 2016a. Plant–arthropod and plant–fungus interactions in late Permian gymnospermous woods from the Bogda Mountains, Xinjiang, northwestern China. *Rev. Palaeobot. Palynol.* 235, 120–128.
- Wan, M.L., Zhou, W.M., Yang, W., Wang, J., 2016b. Charred wood of *Prototoxylon* from the Wuchiapingian Wutonggou Formation (Permian) of Dalongkou, northern Bogda Mountains, northwestern China. *Palaeoworld* 25, 21–31.
- Wan, M.L., Zhou, W.M., Tang, P., Liu, L.J., Wang, J., 2016c. *Xenoxylon junggarensis* sp. nov., a new gymnospermous fossil wood from the Norian (Triassic) Huangshanjie Formation in northwestern China, and its palaeoclimatic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 441, 679–687.
- Wan, M.L., Yang, W., Liu, L.J., Wang, J., 2017a. *Ductoagathoxylon jimsarensis* gen. nov. et sp. nov., a gymnospermous stem from the Wuchiapingian (upper Permian) Wutonggou Formation in the Junggar Basin, northern Bogda Mountains, northwestern China. *Rev. Palaeobot. Palynol.* 241, 13–25.
- Wan, M.L., Yang, W., He, X.Z., Liu, L.J., Wang, J., 2017b. First record of fossil basidiomycete clamp connections in cordate (Cordaitales) stems from the Asselian–Sakmarian (lower Permian) of Shanxi Province, North China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 466, 353–360.
- Wan, M.L., Yang, W., Tang, P., Liu, L.J., Wang, J., 2017c. *Medulloprotaxodioxylon triassicum* gen. et sp. nov., a taxodiaceous conifer wood from the Norian (Triassic) of northern Bogda Mountains, northwestern China. *Rev. Palaeobot. Palynol.* 241, 70–84.
- Wan, M.L., Yang, W., He, X.Z., Zhou, W.M., Liu, L.J., Wang, J., 2017d. *Yangquanoxylon miscellum* gen. nov. et sp. nov., a gymnospermous wood from the Upper Pennsylvanian–lower Permian Taiyuan Formation of Yangquan City, Shanxi Province, with reference to the palaeoclimate in North China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 479, 115–125.
- Wan, M.L., Yang, W., Wang, J., 2019a. *Amyelon bogdense* sp. nov., a silicified gymnospermous root from the Changhsingian–Induan (?) in southern Bogda Mountains, northwestern China. *Rev. Palaeobot. Palynol.* 263, 12–27.
- Wan, M.L., Yang, W., Wang, J., 2019b. *Sclerospiroxylon xinjiangensis* sp. nov., a gymnospermous wood from the Kungurian (lower Permian) southern Bogda Mountains, northwestern China: systematics and palaeoecology. *Geobios* 52, 85–97.
- Wang, Z.Q., 1989. Permian gigantic palaeobotanical events in North China. *Acta Paleontol. Sin.* 28, 314–343.
- Wang, S.J., 1991. A new permineralized wood of later Triassic from northern Guangdong Province. *Acta Scient. Nat. Univers. Sunyatseni* 30, 66–69 in Chinese with English abstract.
- Wang, S.J., 1993a. Late Triassic plants from northern Guangdong Province. *Universitatis Sunyatseni Press*, Guangzhou, pp. 1–100 in Chinese with English summary.
- Wang, Z.Q., 1993b. Evolutionary ecosystem of Permian–Triassic redbeds in North China: a historical record of global desertification. In: Lucas, S.G., Morales, M. (Eds.), *The Nonmarine Triassic*. New Mexico Museum of Natural History and Science Bulletin 3, pp. 471–476.
- Wang, Z.Q., 1996. Recovery of vegetation from the terminal Permian mass extinction in North China. *Rev. Palaeobot. Palynol.* 91, 121–142.
- Wang, Z.Q., 2000. Vegetation declination on the eve of the P–T event in North China and plant survival strategies: an example of upper Permian refugium in northwestern Shanxi, China. *Acta Palaeontol. Sin.* 39 (Supplementary Issue), 127–153.
- Wang, J., 2010. Late Paleozoic macrofloral assemblages from Weibei Coalfield, with reference to vegetational change through the Late Paleozoic Ice-age in the North China Block. *Int. J. Coal Geol.* 83, 292–317.
- Wang, Z.Q., Chen, A.S., 2001. Traces of arborecent lycopsids and dieback of the forest vegetation in relation to the terminal Permian mass extinction in North China. *Rev. Palaeobot. Palynol.* 117, 217–243.
- Wang, Z.Q., Wang, L.X., 1986. Late Permian fossil plants from the lower part of the Shiqianfeng (Shichienfeng) Group in North China. *Bull. Tianjin Inst. Geol. Miner. Resour. Chin. Acad. Geol. Sci.* 15, 1–120 (in Chinese with English summary).
- Wang, Z.Q., Wang, L.X., 1990. Late early Triassic fossil plants from the upper part of the Shiqianfeng Group in North China. *Shanxi Geol.* 5, 97–154 in Chinese with English summary.
- Wang, Y.D., Zhang, W., Saiki, K., 2000. Fossil woods from the Upper Jurassic of Qitai, Junggar Basin, Xinjiang, China. *Acta Palaeontol. Sin.* 39 (Suppl.), 176–185.
- Wartes, M.A., Carroll, A.R., Greene, T.J., 2002. Permian sedimentary record of the Turpan–Hami Basin and adjacent regions, Northwest China: constraints on postamalgamation tectonic evolution. *Geol. Soc. Am. Bull.* 114, 131–152.
- Wei, X.X., Zhang, X.H., Shi, G.R., Zhao, X.M., Huang, X., Luan, T.F., 2016. First report of a phytogeographically mixed (transitional) Middle–Late Permian fossil wood assemblage from the Hami area, northwest China, and implications for Permian phytogeographical, paleogeographical and paleoclimatic evolution in central Asia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 448, 125–140.
- Wing, S.L., Sues, H., 1992. Mesozoic and Early Cenozoic terrestrial ecosystems. In: Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H., Wing, S.L. (Eds.), *Terrestrial Ecosystems Through Time: Evolutionary Paleocology of Terrestrial Plants and Animals*. University of Chicago Press, Chicago, pp. 327–416.
- Xiong, C.H., Wang, Q., 2011. Permian–Triassic land-plant diversity in South China: was there a mass extinction at the Permian/Triassic boundary? *Paleobiology* 37, 157–167.
- Yang, W., 2016. Multi-order tectonic and climatic signals in Permian–Lower Triassic terrestrial sedimentary successions in Bogda Mountains, NW China. Abstract of the 35th International Geological Congress (Cape Town, South Africa), no. 2957.
- Yang, W., Liu, Y.Q., Feng, Q., Lin, J.Y., Zhou, D.W., Wang, D., 2007. Sedimentary evidence of Early–Late Permian mid-latitude continental climate variability, southern Bogda Mountains, NW China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 252, 239–258.
- Yang, W., Feng, Q., Liu, Y.Q., Tabor, N., Miggins, D., Crowley, J.L., Lin, J.Y., Thomas, S., 2010. Depositional environments and cyclo- and chronostratigraphy of uppermost Carboniferous–lower Triassic fluvial-lacustrine deposits, southern Bogda Mountains, NW China—a terrestrial palaeoclimatic record of mid-latitude NE Pangea. *Glob. Planet. Chang.* 73, 15–113.
- Yang, X.J., Wang, Y.D., Zhang, W., 2013. Occurrences of early cretaceous fossil woods in China: implications for paleoclimates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 385, 213–220.
- Yang, W., Wan, M.L., Zhan, X., 2018. Cyclostratigraphy of uppermost Permian–Lower Triassic terrestrial deposits in Bogda Mountains, Greater Turpan–Junggar Basin, NW China – updates from sedimentary, geochemical, and paleobotanical data. *Geol. Soc. Am. Abstr. Programs* 50, 194. <https://doi.org/10.1130/abs/2018AM-321878>
- Yao, Z.Q., Xu, J.T., Zheng, Z.G., Zhao, X.H., Mo, Z.G., 1980. Late Permian biostratigraphy in western Guizhou and eastern Yunnan and the Permian–Triassic boundary. In: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Ed.), *Late Permian*

- Coal-Bearing Strata and Palaeontological Fauna in Western Guizhou and Eastern Yunnan. Science Press, Beijing, pp. 1–69 in Chinese.
- Yao, Z.Q., Liu, L.J., Zhang, S., 1994. Permian wood from western Henan, China: implications for palaeoclimatological interpretations. *Rev. Palaeobot. Palynol.* 80, 277–290.
- Yu, J.X., Broutin, J., Huang, Q.S., Grauvogel-Stamm, L., 2010. *Annalepis*, a pioneering lycopsid genus in the recovery of the Triassic land flora in South China. *Comptes. Rendus. Palevol.* 9, 479–486.
- Yu, J.X., Sun, M.R., Zhang, W.P., Qu, L.F., Hou, J.P., Yang, J.D., Sun, S.Y., 1986. Palynological assemblage sequence from Late Permian to Tertiary in northern Xinjiang. *Bull. Inst. Geol. Chin. Acad. Geol. Sci.* 15, 140–151 (in Chinese with English abstract).
- Yu, J.X., Peng, Y.Q., Zhang, S.X., Yang, F.Q., Zhao, Q.M., Huang, Q.S., 2007. Terrestrial events across the Permian–Triassic boundary along the Yunnan–Guizhou border, SW China. *Glob. Planet. Chang.* 55, 193–208.
- Yu, J.X., Broutin, J., Chen, Z.Q., Shi, X., Li, H., Chu, D.L., Huang, Q.S., 2015. Vegetation changeover across the Permian–Triassic Boundary in Southwest China. *Extinction, survival, recovery and palaeoclimate: a critical review. Earth Sci. Rev.* 149, 203–224.
- Zhang, X., 1981. Regional Stratigraphic Chart of Northwestern China, Branch of Xinjiang UygurAutonomous Region. Geological PublishingHouse, Beijing, p. 496 in Chinese.
- Zhang, H., Cao, C.Q., Liu, X.L., Mu, L., Zheng, Q.F., Liu, F., Xiang, L., Liu, L.J., Shen, S.Z., 2016. The terrestrial end-Permian mass extinction in South China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 448, 108–124.
- Zhang, W., Zheng, S.L., Ding, Q.H., 2000. Early Jurassic coniferous woods from Liaoning, China. *Liaoning Geol.* 17, 89–97 in Chinese with English summary.
- Zhang, W., Wang, Y.D., Zheng, S.L., Yang, X.J., Li, Y., Fu, X.P., Li, N., 2007. Taxonomic investigations on permineralized conifer woods from the Late Palaeozoic Angaran deposits of northeastern Inner Mongolia, China and their palaeoclimatic significance. *Rev. Palaeobot. Palynol.* 144, 261–285.
- Zhang, Y., Wang, J., Liu, L., Li, N., 2010. *Protophyllocladoxylon jingyuanense* sp. nov., a gymnospermous wood of the Serpukhovian (Late Mississippian) from Gansu, Northwest China. *Acta Geol. Sin. (English Edition)* 84, 257–268.
- Zheng, S.L., Li, Y., Zhang, W., Li, N., Wang, Y.D., Yang, X.J., Yi, T.M., Yang, J.J., Fu, X.P., 2008. Fossil Woods of China. English edition. China Forestry Press, Beijing, p. 356.
- Zhou, Z.Y., Li, B.X., 1979. A preliminary study of the early Triassic plants from the Qionghai District, Hainan Island. *Acta Palaeontol. Sin.* 5, 444–462 in Chinese with English abstract.
- Zhou, T.S., Zhou, H.Q., 1986. Palaeobotany. In: Institute of Geology, Chinese Academy of Geological Sciences, Institute of Geology, Xinjiang Bureau of Geology and Mineral Resources (Ed.), People's Republic of China Ministry of Geology and Mineral Resources, Geological Memoirs Series 2; Number 3, Permian and Triassic Strata and Fossil assemblages in the Dalongkou Area of Jimsar, Xinjiang. Geological Publishing House, Beijing, pp. 39–69 in Chinese with English summary.