Xuanweioxylon damogouense sp. nov., a gymnosperm stem from the Lopingian (late Permian) of southwestern China and its systematic and paleoecological implications

Yang, Yang; Xiao-Yuan, He; Hilton, Jason; Zhou, Fu-Guang; Chen, Xin-Shi; Wang, Shi-Jun

DOI:
10.1016/j.revpalbo.2019.06.012

Xuanweioxylon damogouense sp. nov., a gymnosperm stem from the Lopingian (late Permian) of southwestern China and its systematic and palaeoecological implications

Yang Yang[a], Xiao–Yuan He[a,]*, Jason Hilton[b], Fu–Guang Zhao[a], Xin–Shi Chen[a], Shi–Jun Wang[c]

[a] *Institute of Deep Time Terrestrial Ecology, Yunnan University, Kunming 650091, China*

[b] *School of Geography, Earth and Environmental Sciences and Birmingham Institute of Forest Research, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK*

[c] *State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China.*

* Corresponding author. E-mail address hexiaoy68@163.com (X.Y. He)

Keywords: Conifer, wood anatomy, palaeoclimate, false rings, Xuanwei Formation, volcaniclastic tuff

ABSTRACT

A new species of permineralized gymnosperm stem is described from volcaniclastic tuffs in Lopingian (late Permian) Xuanwei Formation from eastern Yunnan province, China. The stem comprises well-preserved tissues of the pith, primary and secondary xylem. Pith is divided into a thick-walled parenchymatous peripheral zone and an inner parenchymatous part. Primary xylem strands are numerous and indistinct with mesarch maturation. Secondary xylem is pycnoxylic with scalariform bordered pits on radial tracheid walls, with rays normally uniseriate or partly biseriate. Cross-field pits are mixed and including circular, elliptical and scalriform pitting. Comparisons indicate a close affinity with the contemporaneous plant *Xuanweioxylon scalariforme*, but differences with it lead to the erection of the new *Xuanweioxylon damogouense* sp. nov. We evaluate the systematic affinity of both species of *Xuanweioxylon* and conclude they represent conifers based on features of their wood anatomy. We consider the Xuanwei Formation includes at least four species of conifer, and show that *X. damogouense* possessed weak growth rings and false rings that suggest it grew in a climate with low seasonality and occasional periods of drought.

1. Introduction

Fossil woods are important in the geological record in providing valuable information to help determine the organization, structure and habit of woody plants in the past and also providing a key line of evidence for palaeoclimate analysis. In addition, fossil woods can also help determine the composition of vegetation in geological history (Zhang et al., 2006; Wang et al., 2011; Wei et al., 2016). In China, approximately 60 species belonging to 35 genera of gymnospermous wood have been recorded from the Permian (Li and Taylor, 1998, 1999; Wang et al., 2003, 2009, 2011; Zhang et al., 2006, 2007; Hilton et al., 2009a,b; Seyfullah et al., 2009; Feng et al., 2010, 2011, 2012; Feng, 2012; He et al., 2013; Shi et al., 2014; Wei et al., 2016; Wan et al., 2014, 2016, 2017a,b,c). Most of these accounts come from the northern China palaeo-landmass, and with no more than 10 species to date identified from the southern China palaeo-landmass.

Here we described a new species of gymnospermous wood that was collected from the upper Permian of Yunnan Province, southwestern China. Through detailed comparisons, we assigned it into *Xuanweioxylon* (He et al., 2013) and establish the new species *X. damogouense*. The discovery of this new species not only complements the anatomical characteristics of *Xuanweioxylon*, but also provides information on the palaeoecology and diversity of conifers from the Xuanwei Formation in the run up to Permian/Triassic mass extinction (Neregato et al., 2016).

2. Material and methods

Two permineralized specimens (numbered YNUPB11002 and YNUPB11003) were collected from the Xuanwei Formation (Lopingian; late Permian) of the Damogou coalfield and Qinyun coalfield, Fuyuan County, Yunnan Province (fig. 1). The Xuanwei Formation was deposited during the late Wuchipingian to

Changhsingian stages of the Permian period, approximately 260–251 Ma (Wang et al., 2011).

Both specimens were cut to reveal cross, longitudinal and tangential sections using a rock saw with a diamond blade. Cut surfaces were then then prepared by the acetate peel method (Galtier and Phillips, 1999). Grinding was undertaken with #400 and #600 grade carborundum. Ground surfaces were etched in 5% HCL to leave the organic contents exposed on the etched surface. Peels were mounted on glass slides with coverslips using Canada Balsam. Photography was undertaken on an Axio Imager A2, and Nikon D3X digital camera with AF–S Micro 105mm 1:2.8 GED lens. Scanning Electron Microscopy (SEM) was undertaken at Yunnan University. Figures were constructed in CorelDraw. The specimens, peels and slides are deposited in the Institute of Deep Time Terrestrial Ecology of Yunnan University, China.

3. Systematic palaeobotany

Phylum Coniferophyta (Serbet et al., 2010)

Genus *Xuanweioxylon* He, Wang, Hilton et Shao, 2013

Type species: *Xuanweioxylon scalariform* He, Wang, Hilton et Shao, 2013

Species *Xuanweioxylon damogouense* sp. nov. (Plates I–V)

Holotype: YNUPB11002

Paratype: YNUPB11003

Depository: Institute of Deep Time Terrestrial Ecology, Yunnan University, Kunming, China.

Collecting locality: Damogou coalfield and Qinyun coalfield in Fuyuan County of Eastern Yunnan Province, China.

Stratigraphic horizon and age: Xuanwei Formation, Late Wuchiapingian to Changhsingian stages, Lopingian series, Permian period (Wang et al., 2011).

Etymology: The specific epiphet *damogouense* is derived from the fossil location of Damogou coalfield, Yunnan Province.

Diagnosis: Gymnosperm wood with pith divided into two parts: thick-walled parenchymatous peripheral zone and parenchymatous central part. Sclerenchymatous cells absent. Primary xylem elements numerous and indistinct, maturation mesarch. Secondary xylem pycnoxylic, mainly with uniseriate scalariform bordered pits on radial tracheid walls. “Leaf gaps” absent. Ray cells homogeneous, uniseriate and partially biseriate, 1–13 cells high. Cross-fields with 3–19 circular, oval, polygonal and scalariform bordered pits with the pores nearly horizontal.

4. Description

4.1. General features

The species is represented by two decorticated stems in which the pith, primary xylem and secondary xylem are preserved. The two specimens vary in size from which the larger specimen (YNUPB11002; Plates I–IV) has a preserved length of c.

65 mm and an incomplete diameter in cross section of c. 68×126 mm (Plate I, 1). The smaller specimen (YNUPB11003; Plates V–VI) is 40 mm long and c. 12×14 mm in diameter in cross section (Plate V, 1). According to the preserved extent of the large stem, it is estimated that its entire diameter may be more than 20 cm. In the following account, we describe the specimens separately in order to characterise each first before considering their variation.

4.2. Specimen YNUPB11002

This is the larger of the two specimens described.

4.2.1. Pith

The pith is oval in the cross section, c. 12×18 mm in diameter (Plate I, 1–2) and is divided into a peripheral zone and central parenchyma region (Plate I, 3). The width of the peripheral zone varies slightly at different levels and is absent in some areas due to poor preservation. Cells of the peripheral zone are normally thick-walled parenchymatous and circular, oval and polygonal in cross section (Plate I, 3–4). The diameter of the thick-walled parenchyma cells decreases gradually in cross section from the inner part where they are 115×142–127×137 μm to 41×46–45×53 μm in the outer part (Plate I, 3–4). Secretory cells are scattered across the peripheral zone (Plate I, 4) and are circular, oval and polygonal. The secretory cells usually contain dark-coloured contents and form a discontinuous band located close to the internal parenchyma region of the pith. In longitudinal section, the thick-walled parenchyma cells are usually longitudinally elongated (Plate I, 5), and many of them have circular pits on the walls (Plate I, 8).

The central parenchymatous region of the pith is composed of parenchyma cells that are isodiametric, polygonal and oval in cross section (Plate I, 6). Parenchyma cells are from 43×44–44×50 μm to 152×183–177×185 μm in diameter in cross section. In the longitudinal section, parenchyma cells usually are polygonal and rectangular and somewhat longitudinally elongated, but some of them are square, circular or even horizontally elongated (Plate I, 7).

4.2.2. Primary xylem

In cross section, primary xylem strands are indistinct as they are small, low and are almost at the same level with the innermost secondary xylem (Plate II, 1–3). Primary xylem strands are numerous but the exact number is unknown due to incomplete preservation of the stem. The primary xylem is mesarch (Plate II, 3) and in some places double primary xylem strands can be seen (Plate ?, ?). In longitudinal section, there are helical and scalariform thickenings on the primary xylem tracheid walls (Plate II, 4).

4.2.3. Secondary xylem

The secondary xylem is pycnoxylic, consisting of rays and tracheids. Growth rings are very weakly developed (Plate III, 1); a few false rings occur where they are formed by bands of broken tracheid walls (Plate II, 5–6).

In cross section, tracheids are sub–circular, square, rectangular with tangential dimensions larger than radial dimensions, or flat with tangential width smaller than radial width (Plate III, 2). Tracheid diameters varies from 29×25 to 79×62 μm. Rays are normally uniseriate, occasionally partly biseriate. Ray cells are rectangular, 17–82 μm in radial direction and 10–34 μm in tangential direction. There are no pits in the horizontal wall of ray cells. Rays density is 3–10 rays per mm^2.

In radial section, tracheid end walls are blunt and occasionally straight. Pitting on the radial tracheid walls is normally uniseriate scalariform (Plate III, 3–6). The width of the bordered pits is c. 9–37 μm and their height is c. 4–8 μm. Pits are usually located in the middle part of the tracheid, covering about 1/3 to 5/6 of the tracheid width. Occasionally, there are uniseriate oval or circular (Plate III, 7), or bi– to multiseriate opposite (Plate III, 8–10) bordered pits on the radial tracheid walls. Pits are usually contiguous. Ray cells are rectangular with thin walls. The horizontal walls of ray cells are often slightly wavy, and tangential walls are vertical or oblique (Plate III, 11). The cross-field show circular, oval, polygonal and scalariform bordered pits (Plate IV, 1–6); oval bordered pits are dominant, followed by scalariform bordered pits, while circular and polygonal bordered pits are rare. When the cross-field is occupied only by oval bordered pits, they are small and crowded, numbering about 5–19 with nearly horizontal apertures, and 3×4 to 12×15 μm in diameter. When the cross-field pits are occupied only by scalariform bordered pits, they number about 3–6, each with diameters varying from 3×13 to 8×33 μm. Circular and polygonal bordered pits are rare and they are randomly distributed in the cross-field.

In tangential section, tracheid end walls are apiculate or partly straight. Individual tracheids are bent to varying degrees, and ornamentation on the tangential tracheid walls is absent. Rays are normally uniseriate and some are partially biseriate (Plate III, 12, 13) and 1–13 (typically 1–7) cells high. The width or tangential diameter of ray cells is 23–56 μm (mean = 36 μm, n = 50), while their height ranges from 18–61 μm (mean = 42 μm). Pits are absent on the walls of ray cells.

4.3. The smaller stem (YNUPB11003)

Features of this specimen largely agree with those of the larger stem. This stem is c. 40 mm long and c. 12×14 mm in diameter in cross section (Plate V, 1). In cross section, the pith consists of oval or isodiametric parenchyma cells with some secretory cells. In the middle of the pith, there is a band composed of broken cell walls (Plate V, 2). In longitudinal section, parenchyma cells are usually longitudinally elongated (Plate V, 3, 4). The primary xylem is indistinct and mesarch (Plate V, 5, 6), and secondary xylem is pycnoxylic (Plate V, 7) with uniseriate or occasionally bi– to multiseriate scalariform bordered pits on the radial tracheid walls (Plate V, 8, 9). Rays are normally uniseriate and partly biseriate. The cross–field pits are well-preserved, with oval, circular and scalariform bordered pits (Plate V, 10–12).

5. Discussion

The two stems investigated have common features allowing them to be considered as a single species including indistinct primary xylem strands, absence of a “leaf gap” in the secondary xylem, scalariform bordered pits on secondary tracheid walls, and well developed pits in cross-field. The larger specimen has an estimated diameter of >20 cm if it was completely preserved, suggesting it was a trunk or a large lateral branch of a larger tree. However, the small specimen has a stem diameter only 12×14 mm and while the external tissues are absent, was either a small trunk or a lateral branch of a larger tree.

5.1. Comparisons

The genus *Xuanweioxylon* was established by He et al. (2013) based on permineralized gymnosperm stems collected from the Lopingian of Panxian district, Guizhou Province, China, a short distance from the present locality (Fig. 1). The main features of *Xuanweioxylon* are that it possesses a heterocellular pith, which consists of parenchyma cells, transfusion tissue and sclerotic cells, and is divided into central part of thin-walled parenchymatous cells and peripheral part of thick-walled parenchyma cells. In *X. salariforme* primary xylem strands are numerous, secondary xylem is pycnoxylic and possesses scalariform bordered pits on radial tracheid walls throughout the secondary xylem. The features of the specimens described here conform to these characters and allow their assignment to *Xuanweioxylon*.

Xuanweioxylon is monotypic and includes the sole species *X. scalariforme*. Although our specimens are quite similar to *X. scalariforme,* there are obvious differences between them. Firstly, in the pith of our specimens lacks sclerenchymatous cells but they are present in *X. scalariforme*. Secondly, the primary xylem strand in our specimens is indistinct and the margin between pith periphery and xylm is smooth without any projections of the primary xylem strands (Plate II, 1–3; Plate V, 5, 6), while the primary xylem strand of *X. scalariforme* is distinct and forms a triangle that extends into the pith (Plate VI, 1–3). Thirdly, cells of the peripheral zone of the pith are isodiametric in our specimens while they are mostly radially elongated in *X. scalariforme*, especially in places where the primary xylem strand is present. Fourthly, our specimens lack a "leaf gap" in the secondary xylem (Plate VI, 4–6), but in *X. scalariforme* "leaf gaps" are well-developed and obvious. These differences indicate that the present specimens differ from *X. scalariforme*, leading to the establishment of *Xuanweioxylon damogouense* sp. nov.

As outlined above, *Xuanweioxylon damogouense* had a diameter of > 20 cm if it was completely preserved, suggesting it was a trunk or a large lateral branch of a larger tree. However, *Xuanweioxylon scalariforme* has a stem with the diameter of only 2.8 x 3.2 cm, being much smaller than *X. damogouense* sp. nov. and was probably a small tree or a lateral branch of a larger tree.

He et al. (2013) made a detailed comparison between *Xuanweioxylon* and other gymnosperm stems with scalariform pits on secondary xylem tracheid walls; this information will not be repeated here as with the addition of a second species the same features still distinguish *Xuanweioxylon* from these taxa. Recently Wan et al. (2017c) described a gymnosperm wood, *Yangquanoxylon miscellum*, from the Upper Pennsylvanian–lower Permian Taiyuan Formation of Yangquan City, Shanxi Province, North China. *Y. miscellum* shows scalariform pits on secondary xylem tracheid walls and mixed pits in the cross-fields, however differing from *Xuanweioxylon*. While scalariform pits in *Y. miscellum* are only occasionally present, in X. damogouense the scalariform pits are present on nearly all secondary xylem tracheid walls, and the mixed pits in cross-fields are mainly bordered. The mixed pits in cross-field in *Y. miscellum* are mainly simple. Thus *Y. miscellum* is obviously different from *Xuanweioxylon*.

5.2. Affinity of *Xuanweioxylon damogouense*

He et al. (2013) discussed the systematic position of *X. scalariforme* and considered it to be a coniferophyte of uncertain systematic affinity. In the secondary xylem of our specimens, there are some bi- to multiseriate opposite, circular to elliptical pits on radial tracheid walls, and the pits in cross field possess nearly horizontal pores. This suggests that *Xuanweioxylon* is a conifer, rather than a cordaitalean plant in which pits on radial tracheid walls of secondary xylem are typically alternatively arranged and the pits in cross-field possess oblique pores

(Wang et al., 2003; Hilton et al., 2009a, b).

Previous palaeobotanical studies from the Xuanwei Formation have documented four species of conifer from compression/impression fossils. These comprise leaves of *Podozamites lanceolatus* (L. et H.) Braun and *P. permica* Zhao, *Ullmannia bronnii* Goeppert and *Ull*. cf. *bronnii* Goeppert (Zhao et al., 1980; Zhao, 1990; Tian et al., 1993). In addition, interpreting *Xuanweioxylon scalariforme* as a conifer (see above), four species of conifer wood have also been reported from the Xuanwei Formation. These comprise *Walchiopremnon gaoi* Tian et al. (1993), *Xuanweioxylon scalariforme* He et al. (2013), *X. damogouense* sp. nov. and *Parapodocarpoxylon huopuense* He (2013). At present, there is no anatomical or co-occurrence data to help associate any of these conifer species with other conifer species from the Xuanwei Formation to develop whole-plant relationships (Bateman and Hilton, 2010). Furthermore, taphonomic studies of the fossil plant-bearing tuffaceuous sediments from the Xuanwei Formation remain in their infancy (e.g. Neregato *et al*., 2016), also not offering additional evidence of whole-plant reconstructions (Bateman and Hilton, 2010). The available evidence from adpression/impression foliage species and permineralized wood species demonstrate that at least four species of conifer were present in the Xuanwei Formation.

5.3. Environmental implications

Growth rings refer to a growth layer of wood and bark in cross section of a trunk that represents a layer of wood and bark produced during a growing period. Growth rings are an important tool to help evaluate palaeoclimate and tree habit (e.g., Creber and Chaloner, 1984; Ash and Creber, 1992; Schweingruber, 1992; Zhou and Jiang, 1994; Falcon-Lang et al., 2000a,b; Brea et al., 2008, 2011; Wan et al., 2017c). Through the study of the growth rings, growth conditions from the region in which the tree grew can be deduced including also information on season (Creber, 1977; Wan et al., 2017c). Growth rings are often formed on trees when the seasons vary significantly. During the early stages of the growth season, as the light intensifies and temperature generally raises, cambial activities increases forming early or spring wood that has larger diameter of tracheid with thinner walls (Creber and Chaloner, 1984; Zhou and Jiang, 1994). Early or spring wood has a lighter colour. By contrast, in the late stages of a growth season as the light weakness and temperature generally decreases, cambial activity slows and forms late or summer wood that has smaller diameter of tracheids. These thicker cell walls produce a dark colour (Creber and Chaloner, 1984; Zhou and Jiang, 1994). Such features can be readily identified in permineralized fossil woods. Change in growth ring colour, cell thickness and cell wall thickness can reflect fluctuations in dryness, temperature and other environmental factors during the period of plant growth (Zhou and Jiang, 1994; Shi et al., 2015, 2017). By contrast, absence or weak growth rings could indicate that the environmental factors affecting the growth of plants in the growth period is small, having less noticeable seasonality. In our specimens, the growth rings are very weakly developed (Plate III, 1), which indicates that variation in environmental factors that affected plant growth when it was alive was small, thus, suggests low seasonality.

Both specimens of *Xuanweioxylon damogouense* have faint false rings which are normally 1–5 cells wide and discontinuous. False rings are formed by the short–term environmental disturbance during the growing period of a tree. Disturbance to growth can be caused by phenomena such as flood, pathogen or insect attack, drought, light availability, wind or fire damage and temperature fluctuations (Creber and Chaloner, 1984; Weaver et al., 1997; Falcon-Lang, 2003; Wan et al., 2017c). During the Permian period, the Southern China tectonic plate was located in the region between the tropics and subtropics, with a seasonal rainforest developing under a temperate and humid climate (Tian and Zhang, 1980; Shen, 1995; Tian and Wang, 1995; He et al., 2013). The structure of the false rings in *X. damogouense* were most likely caused by temporary drought during the growing period (Wan et al., 2017c). However, considering the abundance of volcanic ash horizons in the lower member of the Xuanwei Formation (Wang et al., 2011; Neregato et al. 2016), this could also represent episodes of volcanic activity influencing environmental conditions that in turn disrupted plant growth, for instance by producing gaseous emissions or ash fall events. Detailed palaeoenvironmental analysis of the tuffaceous units in the Xuanwei Formation are now required to further assess the causal mechanisms of climate change during the deposition of the Xuanwei Formation.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (Awards No. 41162001, 41472021, 41530101, U1702242) and the Strategic Priority Research Program of Chinese Academy of Sciences (XDB26000000). We thank R. Rößler and an anonymous reviewer for constructive reviews of the manuscript.

References

Ash, S.R., Creber, G.T., 1992. Palaeoclimatic interpretation of the wood structures of the trees in the Chinle Formation (Upper Triassic), petrified Forest National Park, Arizona, USA. Palaeogeog., Palaeoclimatol., Palaeoecol. 96, 299–317.

Bateman, R. M. and Hilton, J., 2009. Palaeobotanical systematics for the phylogenetic age: applying organ–species, form–species and phylogenetic species concepts in a framework of reconstructed fossil and extant whole–plants. Taxon 58, 1254–1280.

Brea, M., Artabe, A., Luis., Spalletti, A., 2008. Ecological reconstruction of a mixed Middle Triassic forest from Argentina. Alcheringa 32, 365–393.

Brea, M., Matheos, S.D., Raigemborn, M.S., Iglesias, A., Zucol, A.F., Prámparo, M., 2011. Paleoecology and paleoenvironments of Podocarp trees in the Ameghino petrified forest (Golfo San Jore Basin, Patagonia, Argentina): constraints for early Paleogene paleoclimate. Geologica Acta 9, 13–28.

Creber, G.T., 1977. Tree ring: a natural data–storage system. Biol. Rev. 52, 349–381.

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

Falcon-Lang, H.J., 2000a.The relationship between leaf longevity and growth ring markedness in modern conifer woods and its implications for palaeoclimatic studies. Palaeogeogr., Palaeoclimatol., Palaeoecol. 160, 317–328.

Falcon-Lang, H.J., 2000b. A method to distinguish between woods produced by evergreen and deciduous coniferopsids on the basis of growth ring anatomy: a new palaeoecological tool. Palaeontology 43, 785–793.

Falcon-Lang, H.J., 2003. Growth interruptions in silicified conifer woods from the Upper Cretaceous Two Medicine Formation, Montana, USA: Implications for palaeoclimate and dinosaur palaeoecology. Palaeogeogr., Palaeoclimatol., Palaeoecol. 199, 299–314.

Feng, Z., Wang, J., Röβler, R., 2010. *Palaeoginkgoxylon zhoui*, a new ginkgophyte wood from the Guadalupian (Permian) of China and its evolutionary implications. Rev. Palaeobot. Palynol. 162, 146–158.

Feng, Z., Wang, J., Rößler, R., 2011. A unique gymnosperm from the latest Permian of China, and its ecophysiological implications. Rev. Palaeobot. Palynol. 165, 27–40.

Feng, Z., Wang, J., Liu, L.J., Rößler, R., 2012. A novel coniferous tree trunk with septate pith from the Guadalupian (Permian) of China: ecological and evolutionary significance. Int. J. Plant Sci. 173, 835–848.

Feng, Z., 2012. *Ningxiaites specialis*, a new woody gymnosperm from the uppermost Permian of China. Rev. Palaeobot. Palynol. 181, 34–46.

Galtier J., Phillips T. L., 1999. The acetate peel technique. In: Jones, T. P., Rowe, N. P.

(Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society of London, London, pp. 67–71.

He, J., 2013. Fossil conifers of Late Permian age in Panxian, southwestern China. Master Degree Thesis of Institute of Botany, the Chinese Academy of Sciences.

He, J., Wang, S.J., Hilton, J., Shao, L.Y., 2013. *Xuanweioxylon scalariforme* gen. et sp. nov.: novel Permian coniferophyte stems with scalariform bordered pitting on secondary xylem tracheids. Rev. Palaeobot. Palynol. 197, 152–165.

Hilton, J., Wang, S.J., Galtier, J., Bateman, R.M. 2009a. Cordaitalean seed plants from the early Permian of north China. II. Reconstruction of *Cordaixylon tianii*. Int. J. Plant Sci. 170, 400–418.

Hilton, J., Wang, S.J., Galtier, J., Bateman, R.M. 2009b. Cordaitalean seed plants from the early Permian of north China. □. Reconstruction of the *Shanxioxylon taiyuanense* plant. Int. J. Plant Sci. 170, 951–967.

Li, H.Q., Taylor, D.W., 1998. *Aculeovinea yunguiensis* gen. et sp. nov. (Gigantopteridales), a new taxon of Gigantopterid stem from the Upper Permian of Guizhou Province, China. Int. J. Plant Sci. 159, 1023–1033.

Li, H.Q., Taylor, D.W., 1999. Vessel–bearing stems of *Vasovinea tianii* gen. et sp. nov. (Gigantopteridales) from the Upper Permian of Guizhou Province, China. Amer. J. Bot. 86, 1563–1575.

Neregato, R., D’Apolito, C., Glasspool, I. J., Wang, S. J., Feng, L., Windslow, P., Lu, J., Shao, L., and Hilton, J. 2016. Palynological constraints on the provenance and stratigraphic range of a Lopingian (late Permian) inter-extinction floral lagerstätte from the Xuanwei Formation, Guizhou Province, China. Int. J. Coal Geol. 62, 139–150.

Schweingruber, F.H., 1992. Annual growth rings and growth zones in woody plants in southern Australia. Iawa Journal 13, 359–379.

Seyfullah, L.J., Hilton, J., Wang, S.J., Galtier, J. 2009. Anatomically preserved pteridosperm stems and rachises from Permian Floras of China. Int. J. Plant Sci. 170, 814–828.

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, Guangzhou, China, pp. 127–223.

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 palaeoclimate implications. Palaeogeogr., Palaeoclimatol., Palaeoecol. 468, 314–326.

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 Geologica Sin. (English Edition) 88, 1356–1363.

Tian, B.L., Zhang, L.W., 1980. Fossil atlas of Wangjiazhai Mine Region in Shuicheng, Guizhou Province. China Coal Industry Publishing House, Beijing (in Chinese).

Tian, B.L., Wang, S.J., 1995. Palaeozoic coal ball floras in China, In: Li, X.X. (Ed.), Fossil Floras of China through the geological ages, English edition. Guangdong Science and Technology, Guangzhou, pp. 202–211.

Tian, B.L., Hu, T., Zhao, H., 1996. The first discovery of *Walchiopremnon gaoi* sp. nov. in China. In: Geological Section of Beijing Graduate School, China University of Mining and Technology (Eds.), Selected papers on coal geology. China Coal Industry Publishing House, Beijing, pp. 118–125 (in Chinese with English abstract).

Wan, M.L., Yang, W., Wang, J., 2014. *Septomedullopitys szei* 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., Zhou, W.M., Yang, W., Wang, J., 2016. Charred wood of *Prototaxoxylon* from the Wuchiapingian Wutonggou Formation (Permian) of Dalongkou, northern Bogda Mountains, northwestern China. Palaeoworld 25, 21–31.

Wan, M.L., Yang, W., He, X.Z., Liu, L.J., Wang, J., 2017a. First record of fossil basidiomycete clamp connections in cordaitalean stems from the Asselian–Sakmarian (Lower Permian) of Shanxi Province, north China. Palaeogeog., Palaeoclimatol., Palaeoecol. 466, 353–360.

Wan, M.L., Yang, W., Liu, L.J., Wang, J., 2017b. *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., Zhou, W.M., Liu, L.J., Wang, J., 2017c. *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.

Wang, H., Shao, L.Y., Hao, L.M., Zhang, P.F., Glasspool, I.J., Wheeley, J.R., Wignall, P.B., Yi, T.S., Zhang, M.W., Hilton, J., 2011. Sedimentology and sequence stratigraphy of the Lopingian (Late Permian) coal measures in southwestern China. Int. J. Coal Geol. 85, 168–183.

Wang, S.J., Hilton, J., Tian, B.L., Galtier, J., 2003. Cordaitalean seed plants from the Early Permian of North China. I. Delimitation and reconstruction of the *Shanxioxylon sinense* plant. Int. J. Plant Sci. 164, 89–112.

Wang, S.J., Sun, K.Q., Cui, J.Z., Ma, S.M., 2009. Fossil plants from coal balls in China. In: Cui, J.Z. (Ed.), Fossil Flora of China. Higher Education Press, Beijing, China.

Wang, S.J., He, X.Y., Shao, L.Y., 2011. Cycad wood from the Lopingian (late Permian) of southern China: *Shuichengoxylon tianii* gen. et sp. nov. Int. J. Plant Sci. 172, 725–734.

Weaver, L., McLoughlin, S., Drinnan, A.N., 1997. Fossil woods from the Upper Permian Bainmedart Coal Measures, northern Prince Charles Mountains, east Antarctica. J. Australian Geol. Geophys. 16, 655–676.

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.

Yao, Z.Q., Liu, L.J., Rothwell, G.W., Mapes, G., 2000. *Szecladia* new genus, a Late Permian conifer with multiveined leaves from South China. J. Paleontol. 74, 524–531.

Zhang, W., Li, Y., Zhen, S.L., Li, N., Wang, Y.D., Yang, X.J., Yang, J.J., Yi, T.M., Fu, X.P., 2006. Chinese Fossil Wood. Chinese Forestry Press, Beijing China.

Zhang, W., Wang, Y.D., Zheng, S.L., Yang, X.J., Li, Y., Fu, X.P., Nan Li., 2007. Taxonomic investigations on permineralized conifer woods from the Late Paleozoic Angaran deposits of northeastern Inner Mongolia, China and their palaeoclimatic significance. Rev. Palaeobot. Palynol. 144, 261–285.

Zhao, H., 1990. The Permian flora of eastern Yunnan and the division and correlation of Xuanwei Formation. Master Degree Thesis of China University of Mining and Technology (Beijing)

Zhao, X. H., Mo, Z. G., Zhang, S. Z., Yao, Z. Q., 1980. Late Permian flora from western Guizhou and eastern Yunnan. In: Nanjing Institute of Geology and

Palaeontology, Academia Sinica (Ed.), Late Permian Coal Bearing Strata and Biota from Western Guizhou and Eastern Yunnan. Science Press, Beijing, pp. 70–122 (In Chinese).

Zhou, Y., Jiang, X.M., 1994. Wood anatomy and ultrastructure of gymnospermous woods in China. China Forestry Publishing House.

Figure and plate captions

Fig. 1. Left—Outline map of China showing province positions and with box showing border area of NE Yunnan Province and SW Guizhou Province. Right—enlargement of box area to show collection locality in black square (Figure modified from He et al., 2013).

Plate I. *Xuanweioxylon damogouense* sp. nov. from the Lopingian of southwestern China. Holotype, YNUPB11002. 1–4, 6 in cross section, 5, 7, 8 in radial section. 1. Tissue of the pith (P) and secondary xylem (SX). Area in the box is enlarged in Plate II, 5. Bar = 1 cm. Slide YH–0100. 2. Pith with central part (CP) and peripheral zone (PZ). Bar = 2 mm. Slide YH–0100. 3. Pith central part (CP) and peripheral zone (PZ). Bar = 200 µm. Slide YH–0101. 4. Secretory cells in the peripheral zone of pith. Bar = 200 µm. Slide YH–0101. 5. Longitudinally elongated thick–walled parenchyma cells of the peripheral zone of pith. Bar = 100 µm. Slide YH–0104. 6. Parenchyma cells in the central part of pith and the residual cell walls (arrows). Bar = 500 µm. Slide YH–0101. 7. Parenchyma cells of the central part of pith and the residual cells wall (arrows). Bar = 500 µm. Slide YH–0105. 8. Thick–walled parenchyma cells of the peripheral zone of pith with circular pits (arrow) on the walls. Bar = 20 µm. Slide YH–0104

Plate II. *Xuanweioxylon damogouense* sp. nov. from the Lopingian of southwestern

China. Holotype in cross section except 4 that is in radial section. 1. Three indistinct primary xylem strands (arrows). Bar = 100μm. Slide YH–0100. 2. Indistinct mesarch primary xylem strand (arrow). Bar = 50 μm. Slide YH–0100. 3. Mesarch primary xylem strand (arrow). Bar = 50 μm. Slide YH–0102. 4. Helical and scalariform thickenings on tracheid walls of the primary xylem. Bar = 20 μm. Slide YH–0104. 5. Discontinuous false rings in the box indicated at Plate I, 1. Bar = 2 mm. Slide YH–0100. 6. A false ring. Bar = 100 μm. Slide YH–0100.

Plate III. *Xuanweioxylon damogouense* sp. nov. from the Lopingian of southwestern China. Holotype, 1, 2, 12 and 13 in cross section, 3-11 in radial section. 1. Discontinuous and inconspicuous growth ring (arrow). Bar = 2 mm. Slide YH–0101. 2. Tracheids and uniseriate rays of secondary xylem. Bar = 100 μm. Slide YH–0103. 3. Uniseriate scalariform bordered pits on the radial tracheid walls of secondary xylem. Bar = 20 μm. Slide YH–0104. 4. SEM image of the secondary xylem showing uniseriate scalariform bordered pits. Bar = 100 μm. 5–6. SEM photos of the secondary xylem, showing uniseriate scalariform bordered pits. Bars = 50 μm. 7. Uniseriate oval bordered pits on radial tracheid walls. Bar = 20 μm. Slide YH–0104. 8. Uniseriate to multiseriate scalariform bordered pits and oval bordered pits on tracheid walls. Bar =10 μm. Slide YH–0111. 9. Uniseriate to triseriate scalariform bordered pits on tracheid walls. Bar = 10 μm. Slide YH–0106. 10. Uniseriate to triseriate scalariform bordered pits on tracheid walls. Bar = 10 μm. Slide YH–0132. 11. Parenchyma cells of the ray. Bar = 50 μm. Slide YH–0106. 12. Uniseriate rays. Bar = 200 μm. Slide

YH–0107. 13. Uniseriate and partly biseriate rays. Bar = 200 µm. Slide YH–0107.

Plate IV. *Xuanweioxylon damogouense* sp. nov. from the Lopingian of southwestern China. Holotype in radial section. 1–6. Variation in cross-field pits. Bar = 20 µm. Slide YH–0104.

Plate V. *Xuanweioxylon damogouense* sp. nov. from the Lopingian of southwestern China. Paratype with 1, 2, 5–7 in cross section 3, 4, and 8 in radial section. 1. Tissue overview including pith (P) and secondary xylem (SX). Bar = 1 mm. Slide YH–0240. 2. Pith cells. Bar = 1 mm. Slide YH–0240. 3. Longitudinally elongated thick–walled parenchyma cells of pith's peripheral zone. Bar = 40µm. Slide YH–0241. 4. Parenchyma cells of the pith. Bar = 40 µm. Slide YH–0241. 5. Indistinct primary xylem strand (arrows). Bar = 200 µm. Slide YH–0240. 6. Mesarch primary xylem strand (arrow). Bar = 50 µm. Slide YH–0240. 7. Tracheids of the secondary xylem. Bar = 40 µm. Slide YH–0240. 8. Uniseriate scalariform bordered pits on radial tracheid walls of secondary xylem. Bar = 20 µm. Slide YH–0241. 9. Uni– to triseriate scalariform bordered pits. Bar = 20µm. Slide YH–0241. 10–12. Cross–field bordered pits. Bars = 20 µm. Slide YH–0241.

Plate VI. *Xuanweioxylon scalariforme* He et al. from the Lopingian of southwestern China. All Bars = 200 µm unless otherwise stated. 1. Primary xylem strand (arrows). Slide WP2L–0077. 2. Primary xylem strand (arrows). Slide WP2L–0076. 3. Primary xylem strands (arrows). Slide WP2–0085. 4. “Leaf gap” in the secondary xylem. Bar = 100 µm. Slide WP2–0085. 5. “Leaf gap” in the secondary xylem. Slide WP2L–0076. 6. “Leaf gap” in the secondary xylem. Slide WP2–0085.