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Giant cordaitalean trees in early Permian riparian canopies in North China: Evidence from anatomically preserved trunks in Yangquan, Shanxi Province

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Abstract

Cordaitaleans, as close relatives of modern conifers, had a long geological history in the Cathaysia from the Visean (Mississippian, lower Carboniferous) to the end of Permian. They became prominent since the late Pennsylvanian, and best developed during the Cisuralian (early Permian) in North China, serving as the volumetrically dominant to subdominant elements of wetland floras. Architecture and ecology of the Cathaysian cordaitaleans from non-peat-forming environments are poorly known. Here, we report giant cordaitalean trunks and describe their morphology and brief anatomical features from the Cisuralian Taiyuan Formation in Yangquan, Shanxi Province, North China. These trunks are characterized by the Artisia-like pith and pycnoxylic xylem. Absence of growth rings in the logs suggests they grew under non-seasonal humid tropical conditions. They are preserved in sandstone bodies interpreted as deposits of distributary river channels on the delta plain. Several trunks with attached rooting systems indicate that these trees may have been growing on channel levees or delta plains, and brought into the channels by lateral bank erosion. Allometric estimates of tree height suggests that the largest trees were up to approximately 43.5 m tall. Mature cordaitaleans with straight trunks were probably the tallest trees and formed the canopy of the riparian forest in North China during the Cisuralian.

Keywords: Fossil wood; Cisuralian; Wetland flora; Plant palaeoecology; Palaeoclimate; Cathaysia

1. Introduction

Cordaitaleans are an extinct group of gymnosperms with large strap-shaped coriaceous leaves, woody stems, axillary branching, and platyspermic seeds (Falcon-Lang and Bashforth, 2005; Hilton and Bateman, 2006; Raymond et al., 2010). They were taxonomically and ecologically diverse, ranged in size from small scrambling forms to large forest trees (Falcon-Lang and Scott, 2000; Falcon-Lang and Bashforth, 2004, 2005). They first appeared in the palaeoequatorial regions during the Mississippian (Sze, 1951). In the Pennsylvanian, they became more widespread, occurring in both humid peat-forming habitats and well-drained hinterlands (e.g., Phillips and Peppers, 1984; Falcon-Lang and Bashforth, 2004). This group of plant gradually diminished in Euramerica during the late Pennsylvanian and became rare since the earliest Permian (Raymond et al., 2010; DiMichele, 2014). However, cordaitalean plants extended into high latitudes, were of a global distribution during the Permian, and went extinct at the end of Permian.

In Cathaysia, cordaitaleans persisted for a longer time than those in Euramerica. They were the volumetrically dominant to subdominant elements of the early Permian Cathaysian wetland floras (Shen, 1995; Wang, S.J. et al., 1995; Wang, S.J., 1997, 1998; Wang, J., 2010; Wang, J. et al., 2012). Many records of

the coal and coal floors (Sun, 1991; Zhou et al., 2015), indica that they were significant components of the clastic substrate

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cordaitalean plants from siliciclastic deposits, such as roof-shales of wetland floras. However, from this type of habitat they are exclusively represented by leaves. Diversity of this group is underestimated due to the fragmentary preservation and limited number of characters that can be used to differentiate taxa (DiMichele, 2014). Their growth habitat preference can hardly be interpreted from only allochthonously preserved fossil leaves. Finally, the architecture of Cathaysian cordaitaleans from clastic substrate wetlands is unknown so far.

In this contribution, we report giant cordaitalean trunks from sandstones of the Asselian upper Taiyuan Formation (Cisuralian, lower Permian) in Yangquan City, Shanxi Province, North China (Fig. 1A). They are characterized by the septate pith and pycnoxylic xylems. Estimation of their heights based on the trunk diameter shows they were one of the tallest groups of plants in the research area. Their growth habitat is briefly discussed. The results improve our knowledge of the palaeoecology of cordaitaleans and wetland ecosystems in the Cathaysia.

2. Geological setting, materials, and methods

The research area, Yangquan, situates at the northeastern corner of the Qinshui Basin (Shao et al., 2015). During the Carboniferous and Permian periods, the basin was part of the North China Craton at palaeoequatorial areas of the Palaeo-Tethys Ocean (Fig. 1B). In the research area, the Taiyuan Formation conformably overlies the MoscovianKasimovian Benxi Formation, and conformably underlies the ArtinskianKungurian Shanxi Formation (Fig. 1C; Ge et al., 1985; Sun et al., 1986; Wang, 1989). Taiyuan Formation is a diachronous lithostratigraphic unit in North China, ranging from the late Pennsylvanian to early Permian (Fig. 2A; Ge et al., 1985; Wang and Pfefferkorn, 2013). It is composed of cyclic deposits of coal, mudstone, limestone, and sandstone that were deposited in fluvial, deltaic and shallow marine environments. Taiyuan Formation has been divided into three parts (Jia and Wang, 1989). The lower part consists

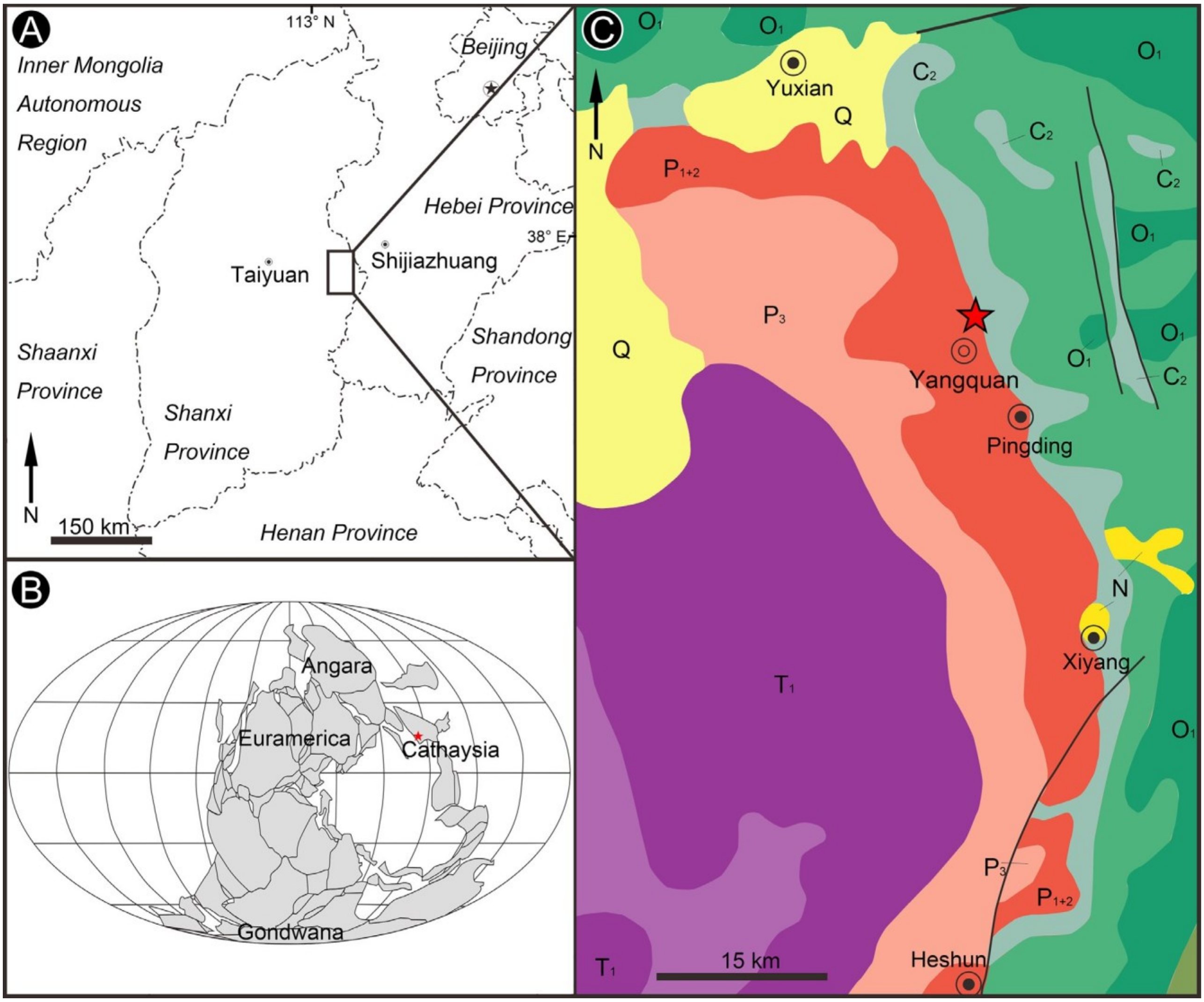

Fig. 1. (A) Map of the research area, it is located to the west of Taiyuan City. (B) Palaeogeographic map showing the research area was situated in palaeoequatorial area of the Cathaysia (red star; midified after Shen et al., 2013). (C) Geological map of research area, showing collection site marked by the red star symbol; O_1: Ordovician Liangjiashan Formation; O_2: Ordovician Fengfeng Formation; C_2: Carboniferous lower Taiyuan Formation; P_{1+2}: lower and middle Permian upper Taiyuan, Shanxi, Lower Shihezi and Upper Shihezi formations; P_3: upper Permian Sunjiagou Formation; T_1: Lower Triassic Liujiagou and Heshanggou formations; T_2: Middle Triassic Ermaying and Tongchuan formations; N: Neogene; Q: Quaternary, loess deposit (modified after Wan et al., 2017b).

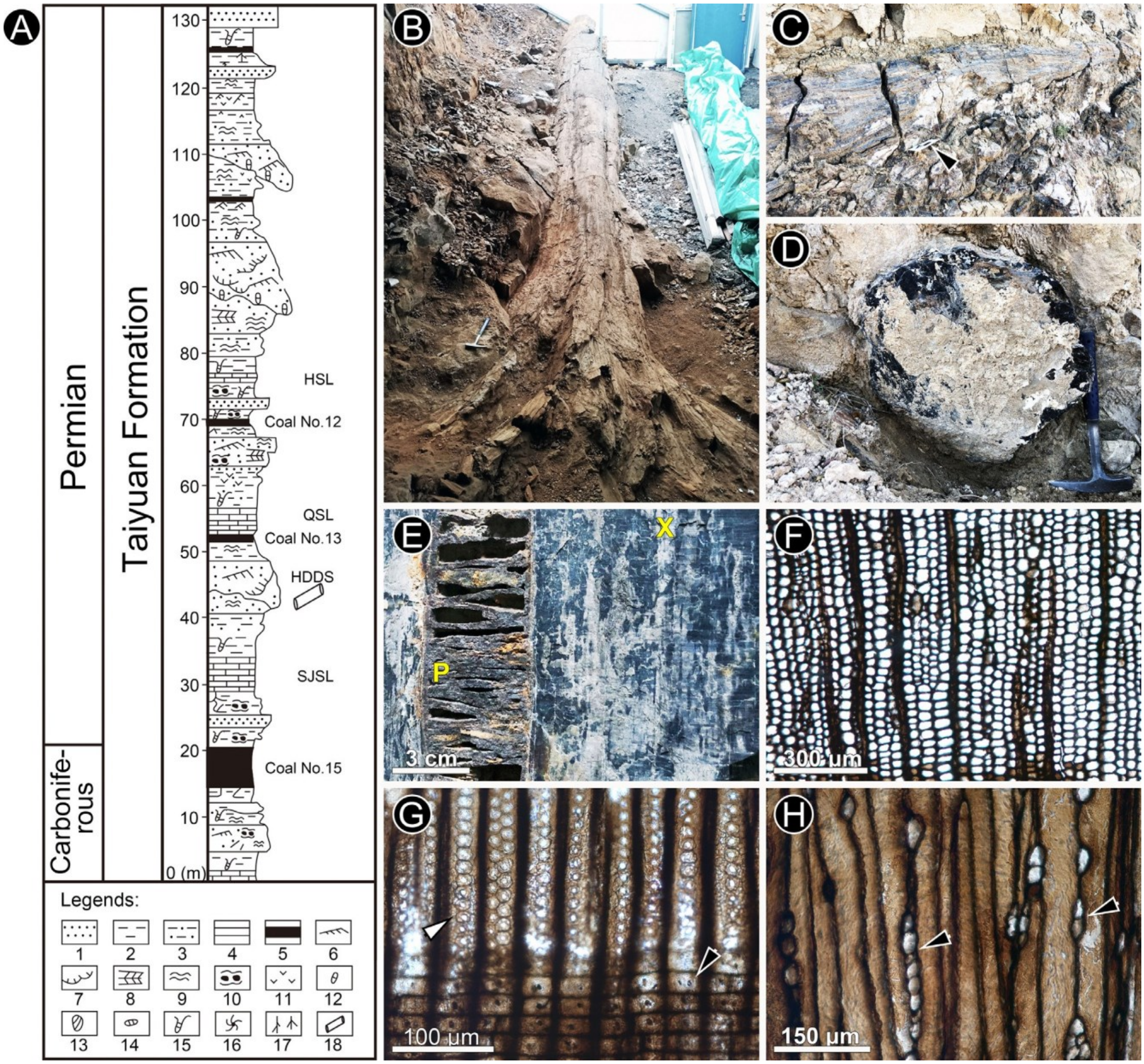

Fig. 2. (A) Chrono- and lithostratigraphy of the Taiyuan Formation in Yangquan, Qinshui Basin, Shanxi Province, North China (modified after Jia and Wang, 1989 and Fan et al. 1999); the wood symbol mark the collection strata distributary channel sandstone interval in the middle part of the Taiyuan Formation. Legends: 1, sandstone; 2, mudstone; 3, siltstone; 4, limestone; 5, coal bed; 6, tabular cross-bedding; 7, trough cross-bedding; 8, herringbone cross-bedding; 9, wavy bedding; 10, lenticular bedding; 11, flaser bedding; 12, boulder clay; 13, invertebrate fossil; 14, lingual and bivalve; 15, burrow; 16, zoophycos; 17, roots; 18, fossil wood; SJSL: Sijieshi Limestone; HDDS: Huangdadu Sandstone; QSL: Qianshi Limestone; HSL: Houshi Limestone. (B) Field photo showing a giant trunk with basal flare and attached roots; this is the largest trunk that have been found with a diameter of 136 cm at the base of the stem; hammer is 28 cm in length as a scale. (C) Field photo showing a large trunk being preserved in the sandstone interval parallel to the bedding; black arrow point to the scale which is 10 cm long. (D) Field photo showing a trunk with a diameter greater than 30 cm submerged in the sandstones; hammer is 28 cm in length as a scale. (E) Photo of the largest trunk in current research, showing the septate pith (P) and pycnoxylic xylem (X). (F) Photomicrograph of a transverse section showing secondary xylem without growth rings. (G) Photomicrograph of a radial section of the xylem, showing uniseriate and biseriate radial tracheidal pitting and, cross-field pits; uniseriate pits are bordered, continuous and slightly flattened (white arrow); biseriate pits are circular to polygonal, alternately and contiguously arranged; black arrow points the cross-fields, showing commonly 12 bordered pits in each cross-field. (H) Photomicrograph of a tangential section of the xylem, showing the uniseriate rays (black arrows).

of tidal and lagoon deposits, and is assigned as MoscovianGzhelian. The middle and upper parts are dominated by deltaic and shoreface deposits, and are assigned as AsselianSakmarian (Fan et al., 1999).

Cordaitalean trunks occur in a 611 m thick sandstone interval, named “Huangdadu Sandstone” locally in the middle part of the Taiyuan Formation in the suburb of the Yangquan City (37˚55⁰13⁰⁰N, 113˚34⁰27⁰⁰E). It is an upward-fining succession with local lenses of conglomerates and gravelly sandstone, and has been interpreted as distributary channel deposits on the delta plain (Sun et al., 1986; Wang, 1989). Most of the trunks are distributed at the base, and approximately parallel to the bedding. Fossil plants in the sandstones are rare and poorly preserved, including Cathaysiodendron Li, Lepidodendron Sternberg, Calamites Suckow, Artisia Sternberg, and Cordaites Unger. Overlying the sandstone interval is a light grey to bluish grey, massive, and rooted mudstone unit. Root fossils Stigmaria Broningart are desultorily distributed, indicating the presence of arborescent lycopsids. A thin coal bed, which is named as Coal No. 13, is present on the top of the mudstone unit, and develops continuously in the whole Yangquan area.

The anatomy of fossil woods is studied by thin sections using the method summarized by Hass and Rowe (1990). The description and discussion of anatomical features of the fossil stem use the terminology of Philippe and Bamford (2008). The stems are strongly silicified. Thin section images are taken using a Leica DM5000 compound microscope and Leica DC 500 digital microscope camera system. The maximum buckling height of the host tree is inferred using Niklas' (1994) empirically derived, biomechanical relationship between basal trunk diameter (D) and tree height (H) for woody plants:

$$\log_{10}H = 1.59 + 0.39(\log_{10}D) - 0.18(\log_{10}D)^2.$$

Due to their large size, limited samples have been collected. Specimen and thin sections used in this study are housed in the Palaeobotanical Collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. Access number of the specimen is PB 23200. Thin section number ranges from PB 23200-1 to PB 23200-10.

3. Results and discussion

Two hundred and eleven petrified fossil trunks composed of septate pith and pycnoxylic wood, are exposed in three outcrops. Most of them have a diameter greater than 30 cm (Fig. 2BD; Table S1). They are straight, decorticated, and up to 10 m long with parallel sides (Fig. 2B, C). Attached lateral branches and branch scars are absent, suggesting that they are the lower or middle parts of the trees. The largest trunk is approximate 8 m in length with an attached rooting system (Fig. 2B). It is 136 cm in diameter at the base of the stem immediately above the locus of root departure. To the position where the two sides of the trunk became parallel, the diameter is 82 cm, and keeps stable to the top. Rooting system of the trunk is morphologically complex (Fig. 2B), and characterized by an increasing diameter comparing with the stem. At the point of maximum flare, the radius of the root system is to 2.4 m. Large numbers of roots extend from the stump up to 1.5 m downwards with variable departure angles ranging from 25° to 60°. Bifurcation of the roots is not preserved.

The biggest trunk has a broad Artisia pith, which has densely spaced septa and is 4 cm in diameter at the top of the specimen (Fig. 2E). Primary xylem is poorly preserved. Secondary xylem is pycnoxylic composed of tracheids and parenchymatous rays (Fig. 2F). Growth rings are absent. Tracheids are crudely rounded to polygonal and, in some cases, squarish in transverse section (Fig. 2F). They are distributed in regular radial files. The diameter of tracheids ranges from 30 to 65 mm. Tracheids are long and fusiform with blunt ends in radial section. Radial pits are dominantly uniseriate, rarely biseriate, on tracheidal walls (Fig. 2G, white arrow). Uniseriate radial pitting is commonly contiguously arranged. Biseriate radial pitting is contiguously and alternately arranged. Radial pits are commonly bordered, rounded to hexagonal in outline, with circular apertures. The diameter of bordered pits on radial walls ranges from 13 mm to 32 mm. Rays are homogenous and commonly uniseriate, partially biseriate, with smooth cell walls (Fig. 2G, black arrow). They are 112 cells high (Fig. 2H, black arrow). Tangential pits are absent. The crossfield pitting is cupressoid, with commonly 12 bordered pits in each field (Fig. 2G, black arrow). Other identifiable trunks have similar wood anatomy. Comparing with the ubiquitous occurrence of Cordaites leaves from the Cisuralian (lower Permian) clastic deposits in lowland of North China (Sun, 1991; Shen, 1995; Wang, 2010), petrified stems, branches and roots with certain cordaitalean affinity are rare (Wang, 1997, 1998; Wan et al., 2017a). Up to now, 15 species in 11 genera of gymnospermous fossil wood have been described from the upper Pennsylvanianlower Permian of North China (Wan et al., 2017b). Current trunks are anatomically similar to the Cordaioxylon sahnii (Hs€u et Bose) Wang from the Taiyuan Formation in Yangqu (YangCh€u) of Shanxi Province, ca. 100 km to the east of the research area (Hs€u and Bose, 1952). Both of them have septate pith, uni- to biseriate araucarian radial tracheidal pitting, commonly one cupressoid pit in each cross-field, and low rays. However, it should be noted that C. sahnii is a small stem with a radius less than 6 cm. The diameter of its pith is less than 1 cm, four time smaller than that of this study. Therefore, we assign current trunks to Cordaioxylon sp. tentatively.

Cordaitaleans were one of the major groups of seed plants in Pennsylvanian wetlands (DiMichele, 2014). Drastic floristic turn-over related to high frequency climatic oscillations occurred around the CarboniferousPermian transition in western and central Pangaea (Gastaldo et al., 1996; Kerp, 1996; DiMichele et al., 2008). Euramerican cordaitaleans started to decline in the late Pennsylvannian in both wetlands (Phillips and Peppers, 1984; Raymond et al., 2010) and seasonally dry areas (DiMichele, 2014). Cordaitalean-dominated floras gradually changed to coniferalean-dominated dry biome (Gastaldo et al., 1996; DiMichele, 2014) due to the gradual drying trend in palaeotropics (Roscher and Schneider, 2006; Tabor and Poulsen, 2008). However, North China, a part of a chain of microcontinents between Palaeotethys and Panthalassa and surrounded by tropical oceans, was still under a humid climate during the CarboniferousPermian transition (Rees et al., 2002; Wang and Pfefferkorn, 2013). Diverse wetland vegetation persisted and flourished in the North China Block (Hilton and Cleal, 2007). The palaeogeographic configuration and humid palaeoclimatic conditions had facilitated continued large-scale peat accumulation and persistent growth of wetland floral elements (Wang et al., 2012; Wan et al., 2017b), including the cordaitaleans, which had been extirpated in the Euramerican floral realm in the early Permian.

Cordaitaleans are commonly assumed as one of the tallest trees in Cathaysian wetland floral communities of North China (Sun, 1991; Wang et al., 2012; Zhou et al., 2015). However, the exact height of the Cathaysian cordaitaleans in clastic substrate habitats is unknown. This group is anatomically and ecologically better understood from the peat-forming environments (e.g., Wang et al., 1995; Wang, 1998). Coal ball floras from the lower Permian of Shanxi and Shandong provinces, North China, indicate that the cordaitaleans were a dominant group of the peat-forming swamp, volumetrically important in the plant assemblage, and were of low-stature forms with a diameter less than 20 cm (Wang, 1998). Pennsylvanianoxylon cf. nauertianum Costanza is so far the largest cordaitalean plant documented from the coal balls. It is proposed to be as high as 10 m. The early Permian Wuda Tuff Flora, which represents a peat-forming forest, is locally dominated by cordaitaleans (Wang et al., 2012). Their stems from the latest excavation are commonly less than 30 cm in diameter (Zhou, 2017). From this point of view, they were trees of a medium height, similar to Cordaites borassifolius (Sternberg) Unger from the middle Pennsylvanian peat-forming flora preserved also in tuff in the Czech Republic (Simu nek et al., 2009). Using Niklas' (1994) formula, the largest cordaitalean tree in Yangquan is calculated as 43.54 m tall, much taller than those previously reported from elsewhere in North China. The majority of the trees reported here are calculated to be more than 21.72 m tall for those have a diameter greater than 30 cm. Therefore, cordaitaleans growing on a clastic substrate were morphologically and ecologically different from those living in peat-forming swamps in other places of North China during the Cisuralian, playing roles as canopies.

Allochthonous accumulation of large cordaitalean trunks as logjams has been reported extensively from the Pennsylvanian in the Euramerica (Falcon-Lang and Scott, 2000; Gibling et al., 2010). They were found in proximity to upland areas, from which the logs are speculated to have been derived (Falcon-Lang and Bashforth, 2004, 2005; Gibling et al., 2010). Autochthonous and parautochtonous cordaitalean stumps are rarely documented. They are interpreted to grow in seasonallydry palaeosols in the fluvial overbanks on the basis of the associated Vertisols (Bashforth et al., 2014) and in alluvial fans (Falcon-Lang, 2007). It is speculated that Pennsylvanian giant cordaitaleans inhabited well-drained substrates in seasonallydry precipitation regimes (Falcon-Lang and Bashforth, 2004, 2005; Bashforth et al., 2011, 2014; Falcon-Lang et al., 2011; DiMichele, 2014). In contrast, low- and medium-stature forms occupied peat-forming swamps and clastic wetlands (Simu nek et al., 2009; Raymond et al., 2010; Bashforth et al., 2014). However, our evidence shows that giant cordaitalean trees were not restricted to uplands or seasonally-dry settings, at least in North China during the early Permian.

The research area is located around the center of the North China Craton (Wan et al., 2017b). Palaeogeographical reconstruction based on various evidence shows that this area was about 1000 km from any contemporaneous upland areas (Wang, 1985; Shao et al., 2015). The trunks are preserved in distributary channel deposits on the delta plain between and underlying marine limestone and an overlying coal bed, representing a falling stage of sea level (Sun et al., 1986; Wang, 1989). No indicator of moisture deficits, such as Calcisols and Vertisols, has been found from the entire Taiyuan Formation in the research area (Wang, 1989; Shao et al., 2015). Siderite nodules and bauxite are present, indicating a high ground water table (Sun et al., 1986; Wang, 1989; Shao et al., 2015). The absence of growth rings in woods of the cordaitalean trunks (Fig. 2F) indicates that these trees grew in a non-seasonal climate without periodic large fluctuations in temperature and ground water table. Lycopsids stems and roots present in the sandstones where our trunks are preserved and the overlying palaeosol respectively suggest that the regional climate was not dry. Coal beds (locally named Coal No. 13) were generated from peats accumulated in areas with high-productivity floras and preserved in a reducing delta plain swamps (Ge et al., 1985; Jia and Wang, 1989; Cheng et al., 1990; Shao et al., 2015), and indicate a humid climate.

The cordaitalean trunks documented here are not autochthonous. Research on the transport potential of tree trunks demonstrates that the majority of logs in modern deltaic deposits can be sourced from various environments of the tributaries (Eggertsson, 1994). Therefore, it is impossible to determine the exact growth habitat of our cordaitalean trees from taphonomy. The 16 trunks in the fossil interval, including the largest one we have, all occur together with the attached rooting system (Fig. 2B). This phenomenon indicates that at least these logs were parautochthonous, and have been transported over a limited distance before burying (Falcon-Lang and Bashforth, 2004; Falcon-Lang et al., 2009; Tr€umper et al., 2020). Therefore, we suggest that some of the cordaitalean trees lived closely on river banks of the delta plain. They probably grew on the levee and floodplain, and fell into the channel when the bank collapse due to the phases of lateral channel migration with bank erosion or catastrophically environmental disturbance to the vegetation. Other trunks may be from the trees growing in streamside niches of the deltaic and coastal plains, or upstream areas in the upper drainage basin up to hundreds of kilometers away. This interpretation is supported by the common occurrence of cordaitalean leaves from the channel deposits of the research area and other places in North China (e.g., Zhou et al., 2015). The leaves were probably from the adjacent floodplain, as documented by an actualistic study in the modern Orinoco Delta (Scheihing and Pfefferkorn, 1984).

4. Conclusions

Large petrified cordaitalean trunks are reported from fluvial channel-fill sandstones of the Asselian (lower Permian) Taiyuan Formation in Yangquan, Shanxi Province, North China. They are characterized by septate (Artisia) pith and pycnoxylic secondary xylems. They are estimated to be up to 43.54 m tall, and may have formed the canopy of a wetland forest growing on a clastic substrate in the Cathaysia. The attached rooting system indicate that the giant cordaitalean trees, if not all, grew in the riparian environment on a delta plain under a humid climate. The trees are different from those restricted to Pennsylvanian uplands or a seasonally-dry habitat in Euramerica.

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Supplementary materials

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References

Bashforth, A.R., Drabkova, J., Oplustil, S., Gibling, M.R., Falcon-Lang, H.J., 2011. Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nyrany Member, Central and Western Bohemian Basin, Czech Republic). Review of Palaeobotany and Palynology 163, 153–189.

Bashforth, A.R., Cleal, C.J., Gibling, M.R., Falcon-Lang, H.J., Miller, R.F., 2014. Paleoecology of Early Pennsylvanian vegetation on a seasonally dry tropical landscape (Tynemouth Creek Formation, New Brunswick, Canada). Review of Palaeobotany and Palynology 200, 229–263.

Cheng, B.Z., Wang, H.S., Zhang, Y.N., 1990. Sedimentary environments and coal accumulation regularity of Late Palaeozoic coal-bearing strata in Shanxi Province. Shanxi Geology 5, 319–332 (in Chinese, with English abstract).

DiMichele, W.A., 2014. Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics. International Journal of Plant Sciences 175, 123–164.

DiMichele, W.A., Kerp, H., Tabor, N.J., Looy, C.V., 2008. The so-called “PaleophyticMesophytic” transition in equatorial Pangea-Multiple bimes and vegetational tracking of climate change through geological time. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 152–163.

Eggertsson, O., 1994. MacKenzie River driftwood — a dendrochronological study. Arctic 47, 128–136.

Falcon-Lang, H.J., 2007. A Cordaixylon axis from well-drained alluvial plain facies in the Lower Pennsylvanian Joggins Formation of Nova Scotia. Atlantic Geology 43, 87–90.

Falcon-Lang, H.J., Bashforth, A.R., 2004. Pennsylvanian uplands were forested by giant cordaitalean trees. Geology 32, 417–420.

Falcon-Lang, H.J., Bashforth, A.R., 2005. Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland. Review of Palaeobotany and Palynology 135, 223–243.

Falcon-Lang, H.J., Scott, A.C., 2000. Upland ecology of some Late Carboniferous cordaitalean trees from Nova Scotia and England. Palaeogeography, Palaeoclimatology, Palaeoecology 156, 225–242.

Falcon-Lang, H.J., Nelson, W.J., Elrick, S., Looy, C.V., Ames, P.R., DiMichele, W.A., 2009. Incised channel fills containing conifers indicate that seasonally dry vegetation dominated Pennsylvanian tropical lowlands. Geology 37, 923–926.

Falcon-Lang, H.J., Pendleton, J.L., Wellman, C.H., 2011. Dryland plant communities in the Pennsylvanian (mid- to late Bolsovian) Winterbourne Formation of Bristol, southern Britain: Further evidence for taphonomic megabias. Review of Palaeobotany and Palynology 166, 268–285.

Fan, B.H., Zhu, W.B., He, X.L., 1999. Early early Permian brachiopod fauna from Yangquan, Shanxi Province. Acta Palaeontologica Sinica 38, 352–364 (in Chinese, with English summary).

Gastaldo, R.A., DiMichele, W.A., Pfefferkorn, H.W., 1996. Out of the icehouse into the greenhouse: a late Paleozoic analogue for modern global vegetational change. GSA Today 6, 1–7.

Ge, B.X., Yin, G.X., Li, C.S., 1985. A preliminary study on sedimentary environments and law of coal-bearing formation in Yangquan, Shanxi. Acta Sedimentologica Sinica 3, 33–44 (in Chinese, with English abstract).

Gibling, M.R., Bashforth, A.R., Falcon-Lang, H.J., Allen, J.P., Fielding, C.R., 2010. Log jams and flood sediment buildup caused channel abandonment and avulsion in the Pennsylvanian of Atlantic Canada. Journal of Sedimentary Research 80, 268–287.

Hass, H., Rowe, N.P., 1990. Thin sections and wafering. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. The Geological Society of London, London, pp. 76–81.

Hilton, J., Bateman, R.M., 2006. Pteridosperms are the backbone of seed-plant phylogeny. The Journal of the Torrey Botanical Society 133, 119–168.

Hilton, J., Cleal, C.J., 2007. The relationship between Euramerican and Cathaysian tropical floras in the Late Paleozoic: Palaeobiogeographical and palaeogeographical implications. Earth-Science Reviews 85, 85–116.

Hs€u, J., Bose, M.N., 1952. On a new cordaitean stem, Cordaites sahnii, from central Shansi, China. Palaeobotanist 1, 241–244.

Jia, B.W., Wang, P.Z., 1989. The preliminary study on the sedimentary environment of Taiyuan Formation of upper Carboniferous in Pingxi Mining District of Qinshui Coal Field in Shanxi Province. Acta Sedimentologica Sinica 7, 71–77 (in Chinese, with English abstract).

Kerp, H., 1996. Post-Variscan late Palaeozoic Northern Hemisphere gymnosperms: the onset to the Mesozoic. Review of Palaeobotany and Palynology 90, 263–285.

Niklas, K.J., 1994. Predicting the height of fossil plant remains: An allometric approach to an old problem. American Journal of Botany 81, 1235–1243.

Philippe, M., Bamford, M.K., 2008. A key to morphogenera used for Mesozoic conifer-like woods. Review of Palaeobotany and Palynology 148, 184–207.

Phillips, T.L., Peppers, R.A., 1984. Changing patterns of Pennsylvanian coalswamp vegetation and implications of climatic control on coal occurrence. International Journal of Coal Geology 3, 205–255.

Raymond, A., Lambert, L., Costanza, S., Slone, E.J., Cutlip, P.C., 2010. Cordaiteans in paleotropical wetlands: An ecological re-evaluation. International Journal of Coal Geology 83, 248–265.

Rees, P.M., Ziegler, A.M., Gibbs, M.T., Kutzbach, J.E., Behling, P.J., Rowley, D.B., 2002. Permian phytogeographic patterns and climate data/ model comparisons. The Journal of Geology 110, 1–31.

Roscher, M., Schneider, J.W., 2006. Permo-Carboniferous climate: Early Pennsylvanian to late Permian climate development of central Europe in a regional and global context. Geological Society, London, Special Publications 265, 95–136.

Scheihing, M.H., Pfefferkorn, H.W., 1984. The taphonomy of land plants in the Orinoco Delta: a model for the incorporation of plant parts in clastic sediments of Late Carboniferous age of Euramerica. Review of Palaeobotany and Palynology 41, 205–240.

Shao, L.Y., Yang, Z.Y., Shang, X.X., Xiao, Z.H., Wang, S., Zhang, W.L., Zheng, M.Q., Lu, J., 2015. Lithofacies palaeogeography of the Carboniferous and Permian in the Qinshui Basin, Shanxi Province, China. Journal of Palaeogeography 4, 384–412.

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, Guangzhou, pp. 127–223.

Shen, S.Z., Zhang, H., Shi, G.R., Li, W.Z., Xie, J.F., Mu, L., Fan, J.X., 2013. Early Permian (Cisuralian) global brachiopod palaeobiogeography. Gondwana Research 24, 104–124.

Simu nek, S., Oplustil, S., Drabkova, J., 2009. Cordaites borassifolius (Sternberg) Unger (Cordaitales) from the Radnice Basin (Bolsovian, Czech Republic). Bulletin of Geoscience 84, 301–336.

Sun, G., 1991. Cuticle of Cordaites baodeensis sp. nov. from lower Permian of Baode, NW Shanxi, China with discussion of taxonomy of Cordaites. Acta Palaeontologica Sinica 30, 167–185 (in Chinese, with English abstract).

Sun, Y.C., Li, H.S., Deng, X.H., Cai, S., 1986. CarboniferousPermian sedimentary environments and their sedimentary characteristics in ShouyangYangquan area, Shanxi Province. Earth Science Journal of Wuhan College of Geology 11, 273–280 (in Chinese, with English abstract).

Sze, H.C., 1951. Eine kulmflora aus der Tseshui kohlen-serie in Hunan. Science Record 4, 299–309.

Tabor, N.J., Poulsen, C.J., 2008. Palaeoclimate across the Late PennsylvanianEarly Permian tropical palaeolatitudes: a review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 293–310.

Tr€umper, S., Gaitzsch, B., Schneider, J.W., Ehling, B.-C., Kleeberg, R., R€obler, R., 2020. Late Palaeozoic red beds elucidate fluvial architectures preserving large woody debris in the seasonal tropics of central Pangaea. Sedimentology 67, 1973–2012.

Wan, M.L., Yang, W., He, X.Z., Liu, L.J., Wang, J., 2017a. First record of fossil basidiomycete clamp connections in cordaite (Cordaitales) stems from the AsselianSakmarian (lower Permian) of Shanxi Province, North China. Palaeogeography, Palaeoclimatology, Palaeoecology 466, 353–360.

Wan, M.L., Yang, W., He, X.Z., Zhou, W.M., Liu, L.J., Wang, J., 2017b. Yangquanoxylon miscellum gen. nov. et sp. nov., a gymnospermous wood from the Upper Pennsylvanianlower Permian Taiyuan Formation of Yangquan City, Shanxi Province, with reference to the palaeoclimate in North China. Palaeogeography, Palaeoclimatology, Palaeoecology 479, 115–125.

Wang, H.Z., 1985. Atlas of the Palaeogeography of China. Cartographic Publishing House, Beijing, 143 pp. (in Chinese, with English abstract).

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. International Journal of Coal Geology 83, 292–317.

Wang, J., Pfefferkorn, H.W., 2013. The CarboniferousPermian transition on the North China microcontinent — Oceanic climate in the tropics. International Journal of Coal Geology 119, 106–113.

Wang, J., Pfefferkorn, H.W., Zhang, Y., Feng, Z., 2012. Permian vegetational Pompii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. Proceedings of the National Academy of Sciences of the United States of America 109, 4927–4932.

Wang, S.J., 1997. A study on origin and evolution of Cordaitaceae in late Paleozoic. Acta Phytotaxonomica Sinica 35, 303–310 (in Chinese, with English abstract).

Wang, S.J., 1998. The cordaitean fossil plants from Cathaysian area in China. Acta Botanica Sinica 40, 573–579 (in Chinese, with English abstract).

Wang, S.J., Tian, B., Guo, Y.T., 1995. Palaeocommunity and its succession of peat swamp no. 7 seam in Xishan coal-field. Journal of China Coal Society 20, 88–92 (in Chinese, with English abstract).

Wang, W.H., 1989. The research on the sedimentary environments of PermoCarboniferous coalfield of Yangquan-Jingxing, North China. Scientia Geologica Sinica 4, 338–347 (in Chinese, with English abstract).

Zhou, W.M., 2017. Community ecology of the early Permian “Vegetational Pompeii” from the Wuda Coalfield, Inner Mongolia. PhD thesis, Nanjing University, Nanjing, 162 pp. (in Chinese, with English abstract).

Zhou, W.M., Wan, M.L., Yan, M.X., Cheng, C., Wang, J., 2015. The succession sequence of early Permian wetland vegetational communities in the Shanxi Formation of the Wuda Coalfield, Inner Mongolia. Acta Palaeontologica Sinica 54, 66–83 (in Chinese, with English abstract).