ARTICLE IN PRESS

Available online at www.sciencedirect.com ScienceDirect

Palaeoworld xxx (2023) xxx–xxx

www.elsevier.com/locate/palwor

Palaeoworld

First record of plant-plant facilitative interaction from the Moscovian (Pennsylvanian, upper Carboniferous) of North China

Ke-Yu Wang [a,b], Xing Huang [a,b], Wan Yang [c], Jun Wang [a,b], Ming-Li Wan [a,b,⇑]

[a]State Key Laboratory of Palaeobiology and Stratigraphy, Department of Palaeobotany and Palynology, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China [b]University of Chinese Academy of Sciences, Beijing 100049, China

[c]Geology and Geophysics Program, Missouri University of Science and Technology, Rolla, MO 65409, USA

Received 26 March 2023; received in revised form 7 August 2023; accepted 22 August 2023

Abstract

Fallen logs acting as a seedbed for trees to aid the regeneration of vegetation is a common ecological strategy in modern forests. However, the origin, occurrence, and evolution of this nurse log strategy in the geological time is unclear. Here we report a ca. 310-millionyear-old permineralized cordaitalean tree trunk from the Moscovian (Pennsylvanian, upper Carboniferous) Benxi Formation in Yangquan City, Shanxi Province, North China, with evidence of probable cordaitalean rootlets growing inside the trunk. The specimen is interpreted as a nurse log for regeneration of cordaitaleans in coastal lowlands. It provides the first glimpse of plant-plant facilitative interaction between Pennsylvanian cordaitaleans in Cathaysia. We interpret that the Moscovian cordaitalean seedlings preferentially established on the fallen log owing to the ability of the rotting wood to store fresh water. The nurse log provided a stable substrate in an environment with episodic salinity and/or water table variations. In combination with previous records, it is suggested that a sophisticated terrestrial ecosystem with multiple interactions between plants and other organisms have developed on the central North China Craton no later than the Middle Pennsylvanian.

Keywords: Anatomy; Root; Benxi Formation; Palaeoecology; Cathaysia

1. Introduction

Interactions between plants, including facilitation, competition, and parasitism, have been recognized as key drivers of plant community composition, diversity, structure, and dynamics of modern terrestrial ecosystems (Pannell, 2012; Kunstler et al., 2016; Losapio et al., 2021). Facilitative interactions are commonly observed in response to high environmental stress and disturbance conditions, they generally contribute to improving resistance of neighboring plants, and thus are designated as positive interactions (Callaway et al., 2002; Callaway, 2007). Nurse logs are fallen trunks, stumps, large branches and roots, which serve as microhabitats for seedlings of young plants and facilitate the regeneration of the vegetation (Ce´sari et al., 2010). Therefore, nurse logs are considered as an important strategy for facilitation (Feng et al., 2022). It is a common and significant ecological strategy in modern forest ecosystems of humid to arid landscapes (Sanchez et al., 2009; Fukasawa, 2012). Comparatively, nurse logs have rarely been documented in the fossil record (Daugherty, 1963; Fairon-Demaret et al., 2003; Decombeix et al., 2009, 2021; Ce´sari et al., 2010, 2012; Vera and Loinaze, 2022). Their origin and evolution are not fully understood (Feng et al., 2022).

Please cite this article as: K. Y. Wang, X. Huang, W. Yang et al., First record of plant-plant facilitative interaction from the Moscovian (Pennsylvanian, upper Carboniferous) of North China, Palaeoworld, https://doi.org/10.1016/j.palwor.2023.08.002

⇑ Corresponding author.
E-mail address: mlwan@nigpas.ac.cn (M.L. Wan).

https://doi.org/10.1016/j.palwor.2023.08.002

Here we report a Cathaysian nurse log from the Moscovian (Pennsylvanian, upper Carboniferous) of Yangquan City, Shanxi Province, North China. Young and delicate Amyelon-type rootlets growing through the wood of an older putative cordaitalean trunk. This finding suggests the existence of facilitative interaction between cordaitalean trees growing at the same locality. Possible advantages of nurse logs in tropical forests of Cathaysia during the Pennsylvanian are assessed as well.

2. Geological setting, material, and methods

The specimen described in this study was collected from the Pennsylvanian Benxi Formation at Houwa Village, Yinying Town, Yangquan City, Shanxi Province, central North China (Fig. 1A; GPS: 11334⁰49.45⁰⁰E, 3758⁰45.13⁰⁰N). During the Pennsylvanian, this area was situated in a coastal area fringing the equatorial Palaeo-Tethys Ocean (Fig. 1B; Wangetal.,2022,2023,andreferencestherein).TheBenxiFormation unconformably overlies the Middle Ordovician Fengfeng Formation with a ca. 5-m-thick bauxite at its base, and is overlain by the Gzhelian to Asselian Taiyuan Formation. The nurse log specimen was collected from a 20-cm-thick mudstone interval between two layers of carbonates. The mudstone is gray to dark gray, pure to silty, carbonaceous, noncalcareous, and thin-medium laminated. It contains abundant plant fragments and sparse horizontal rootlets. It is interpreted as a coastal pond and lowland deposits. The fossiliferous interval is 10 m above the bauxite. Recently, Wang et al. (2023) reported a gymnospermous stem, Parnaiboxylon wangi Wang et al., from the same fossil interval.

The Benxi Formation is diachronous in the North China Craton, with an age ranging from the Bashkirian to Gzhelian according to recent chronostratigraphic and biostratigraphic correlation (Yang et al., 2020; Shen et al., 2022). In the Yangquan area, fusulinids (Fig. 1D), including Fusulina lanceolata, F. pankouensis, F. pseudokonnoi, F. pseudokonnoi longa, Fusulina sp. cf. F. schellwieni, Fusulina sp. cf. F. pseudonytvica, Pseudostaffella sphaeroidea cuboides, Pseudostaffella sp. P. larionovae polasnensis, Ozawainella turgica, O. magna and O. praestellae have been identified from the carbonate above the nurse log interval. Most of these species were described from the Mayi Limestone and Hsiaoyu¨ Limestone of Taitzeho valley, Liaoning, Northeast China (Sheng, 1958), and commonly occur in the Fusulina lanceolata-Fusulinella vozhgalensis fusulinid zone in South China (Zhang et al., 2010). They are similar to the Kashirian to Podolskian (Moscovian Stage) assemblages from the Eastern European Basin (RauserChernousova et al., 1951). Therefore, the interval with nurse log in current study is considered Moscovian in age.

Thin sections of the fossil log were studied following the method of Hass and Rowe (1990). The terminology of Richter et al. (2004) and Philippe and Bamford (2008) was used in the description and discussion of wood anatomy. Thin section images were taken using a Leica DM5000 compound microscope and Leica DC 500 digital microscope camera system. The specimen and corresponding thin sections are housed in the Palaeobotanical Collection of the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences.

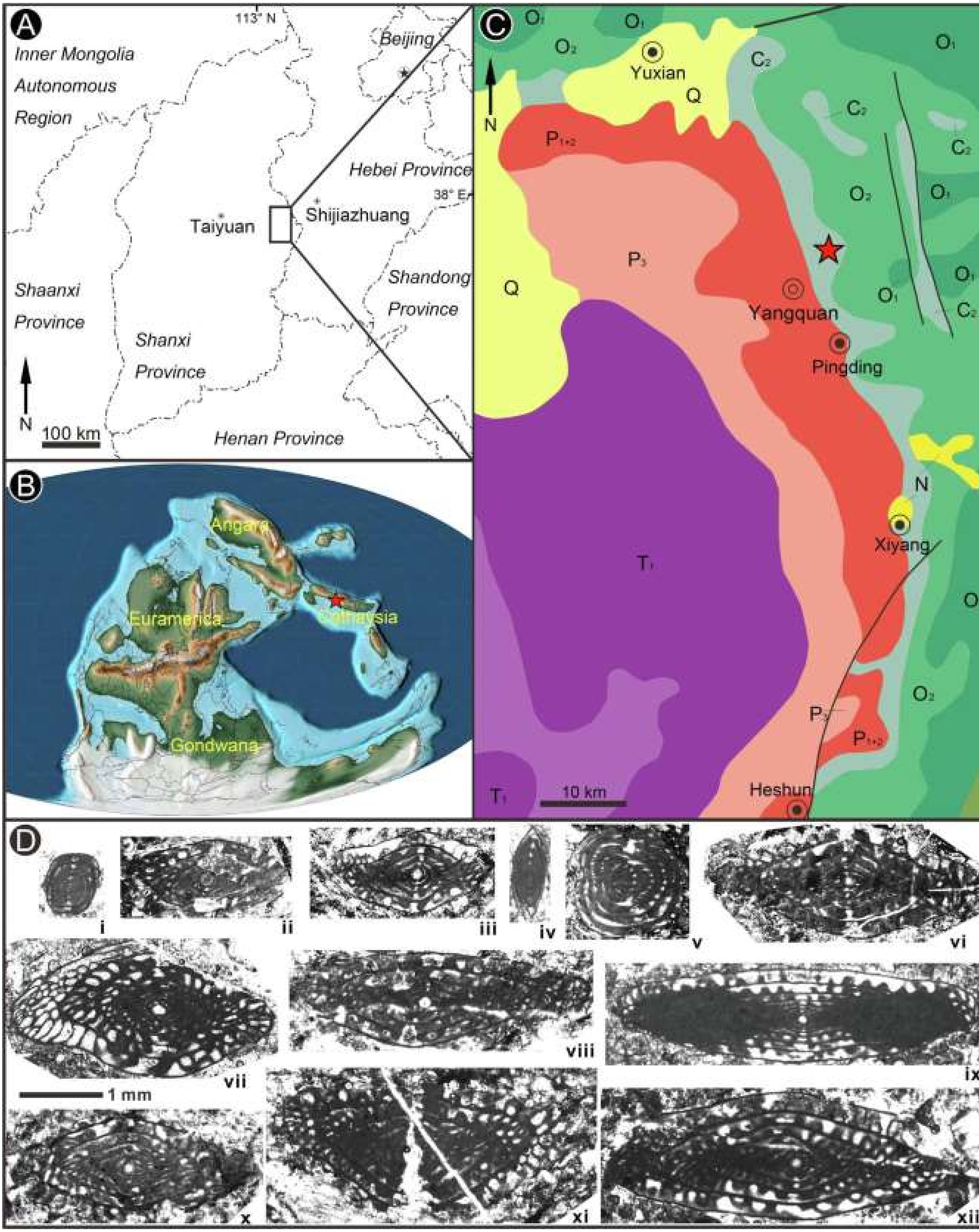
3. Results

3.1. Host trunk

The preserved portion of the trunk is 12 cm 8 cm in size (Fig. 2A). The central part of the trunk, including the pith and primary xylem, is not preserved. It is replaced by a gallery filling with indeterminate plant fragments. The wood consists of tracheids and rays. Growth interruptions (sensu Falcon-Lang, 2003) are well developed. Tracheids in growth interruptions vary gradually in diameter from thinner-walled, larger cells to thicker-walled, smaller cells, then gradually reverse this pattern, forming a symmetrical boundary. In cross-section, tracheids are crudely circular to polygonal, about 25–50 lm in diameter, and arranged in regular radial files. Radial tracheidal walls are dominated by uni- (60%, n = 500) to biseriate (40%, n = 500), araucarian (sensu Philippe and Bamford, 2008; Fig. 2B) pits. Triseriate pits are rare. Tangential pits are absent. Bordered pits on radial tracheidal walls are circular to oval, 8– 12 lm in diameter, with elliptical apertures. Uniseriate pits are arranged contiguously on radial tracheidal walls (Fig. 2B, white arrows). Where biseriate, radial pits are mostly alternately distributed (Fig. 2B, black arrow). Axial parenchymatous cells are absent. Rays are homogeneous. Sixty-seven percent of rays are uniseriate (n = 200). The rest (33%) are biseriate (Fig. 2C, white arrows). Walls of ray parenchymatous cells are smooth. Rays are 1–30 cells high (average = 9; n = 200). The cross-field pitting is cupressoid and araucarioid (sensu Richter et al., 2004;

"

Fig. 1. (A) Map showing the research area to the west of Taiyuan City, Shanxi Province, North China. (B) Palaeogeographic map showing the research area was situated in the palaeoequatorial belt of Cathaysia (red star; after Scotese and Wright, 2018). (C) Geological map of the research area, showing the collection site marked by the red star symbol (modified after Wan et al., 2017). O_1: Ordovician Liangjiashan Formation; O_2: Ordovician Fengfeng Formation; C_2: Carboniferous Benxi Formation and lower Taiyuan Formation; P_{1+2}: lower and middle Permian upper Taiyuan, Shanxi, Lower Shihezi and Upper Shihezi formations; P_3: upper Permian Sunjiagou Formation; T1: Lower Triassic Liujiagou and Heshanggou formations; T_2: Middle Triassic Ermaying and Tongchuan formations; N: Neogene; Q: Quaternary, loess deposit. (D) Age diagnostic fusulinids from the carbonate bed above the interval with the nurse log: i) Pseudostaffella sp. cf. P. larionovae polasnensis Rauser-Chernousova and Safonova; ii), iii), vi), and x) Fusulina lanceolata Lee and Chen; iv) Ozawainella magna Sheng; v) Pseudostaffella sphaeroidea cuboides Rauser; vii) Fusulina sp. cf. F. schellwieni Staff; viii) Fusulina pseudokonnoi longa Sheng; ix) Fusulina pankouensis Lee; xi) Fusulina sp. cf. F. pseudonytvica Sheng; xii) Fusulina pseudokonnoi Sheng.



Please cite this article as: K. Y. Wang, X. Huang, W. Yang et al., First record of plant-plant facilitative interaction from the Moscovian (Pennsylvanian, upper Carboniferous) of North China, Palaeoworld, https://doi.org/10.1016/j.palwor.2023.08.002

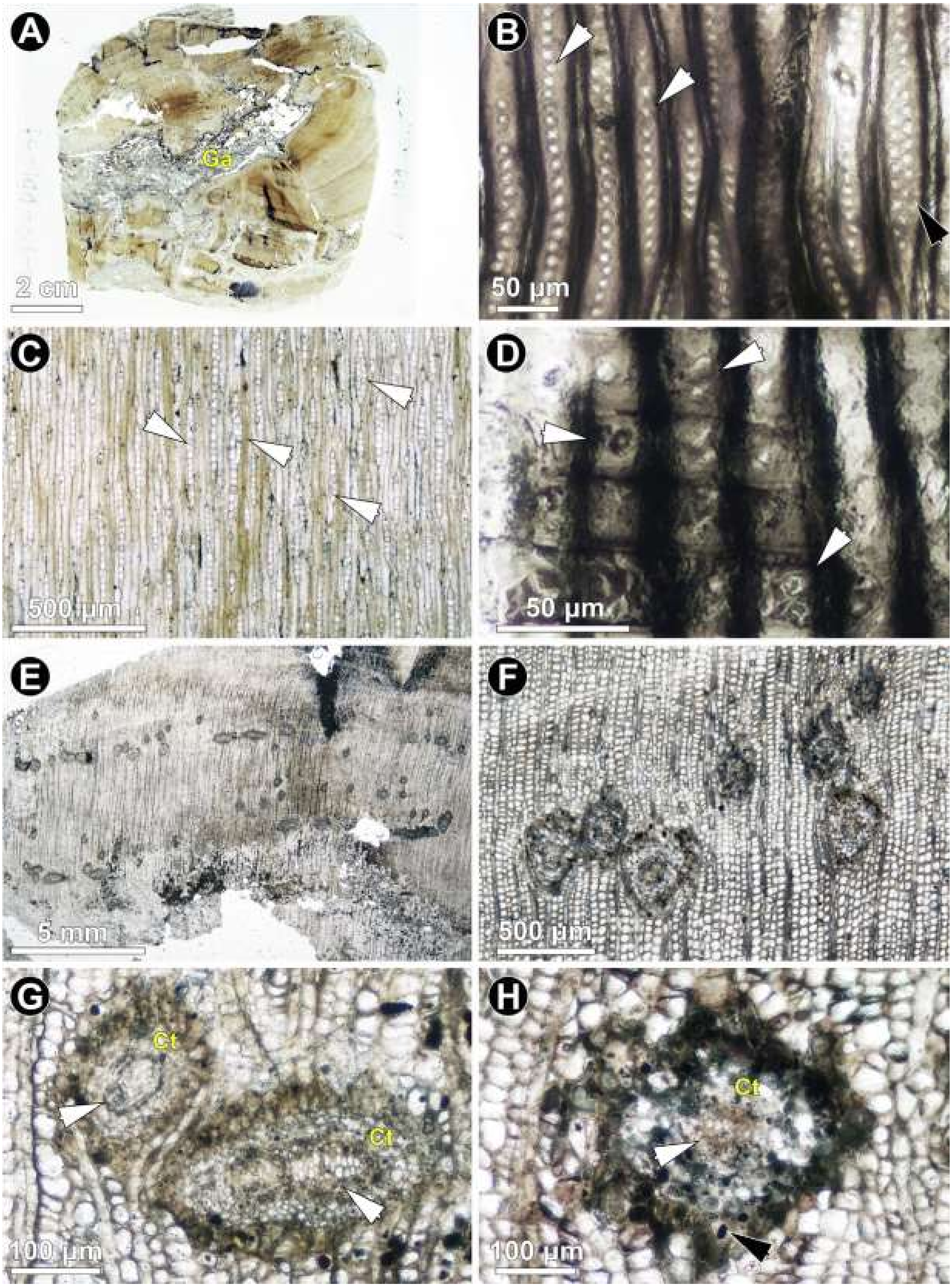


Fig. 2D). There are 1–8 pits in the cross-field. In most cases, each field contains 2–3 pits. Cross-field pits are oval to circular, bordered, with elliptically oval to slit-like apertures (Fig. 2D).

Remarks: The host trunk is characterized by wood with dominantly uni- to biseriate araucarian radial tracheidal pits, cupressioid and araucarioid pitting in each crossfield, and 33%

partially biseriate rays. This type of wood is similar to Araucarioxylon wudense Wang from the Lopingian (upper Permian) Upper Shihhotse Formation of Wuda, Inner Mongolia, North China (Wang, 2000). It should be pointed out that the genus Arauacarioxylon Kraus is illegitimate (Philippe, 1993, 2011; Ro¨ßler et al., 2014). Fossil pycnoxylic wood with araucarian radial tracheidal pitting, cupressoid and araucarioid cross-field pits should be assigned to the genus Agathoxylon Hartig (Bamford and Philippe, 2001; Philippe and Bamford, 2008). Therefore, Araucarioxylon wudense is re-combined as Agathoxylon wudense (Wang) Wang and Wan comb. nov. herein. The affinity of A. wudense is obscure because of the lack of attached leaves or reproductive organs (Wang, 2000). However, during the Moscovian, the dominant gymnospermous plants in the North China Block were medullosaleans and cordaitaleans (Wu, 1995). Conifers have not been recorded in Cathaysia until the Cisuralian, early Permian (Shen, 1995). Wood of medullosaleans is commonly manoxylic (Galtier and Meyer-Berthaud, 2006), which is different from the pycnoxylic wood of the studied trunk. Permo-Carboniferous Cathaysian cordaitalean stems and branches commonly possess a septate pith and Agathoxylon-type wood (Tian and Wang, 1987; Wang, S.J. et al., 2003; Hilton et al., 2009a, 2009b; Wan et al., 2017, 2020). Recently, cordaitalean trunks with a septate pith and Agathoxylon-type wood and have been documented from the Pennsylvanian Benxi Formation in Yangquan City (Wang et al., 2022). Therefore, the host trunk in the current study is inferred to be a member of
Cordaitales.

3.2. Rootlets

Small rootlets are distributed in the outer part of the preserved trunk (Fig. 2E–H), and are interpreted as roots of seedlings. These rootlets commonly invade into the wood vertically (Fig. 3A–C). Most of them are unbranched (Fig. 3A, B). Rare rootlets show lateral branches (Fig. 3C). Their diameters range from 100 lm to 1 mm. More than 90% of the rootlets are less than 500 lm in diameter (Fig. 2F–G). Rootlets are protostelic, composed of a vascular cylinder encircled by cortex (Fig. 2G, H). In most cases, the vascular cylinders are circular with 3–6 strands of primary xylem, and less than 50 lm long. The protoxylem is indistinguishable from the metaxylem. In some larger rootlets, secondary growth is developed (Figs. 2G, 3D). Tracheids of the secondary xylem are commonly less than 50 lm in length in radial section (Fig. 3D). Their primary xylem is diarch in cross-section. Thin scalariform thickenings are present on tracheidal walls of the primary xylem (Fig. 3E).

Remarks: As indicated by Decombeix et al. (2021), root anatomy is very conservative, therefore, the affinities of these rootlets are difficult to determine. An important feature of the studied larger rootlets is the presence of wedgeshaped secondary xylem, encircled by 3–4 layers of parenchymatous cortex cells. This feature makes it comparable to some species of Amyelon Williamson emend. Wang and Tian (Wang et al., 2009; Wan et al., 2019). In Cathaysia, during the Pennsylvanian and Cisuralian, species of Amyelon are commonly designated as roots of cordaitaleans (Hilton et al., 2009a, 2009b; Wang et al., 2009). Hence, it is highly likely that the rootlets in the current study belong to cordaitaleans.

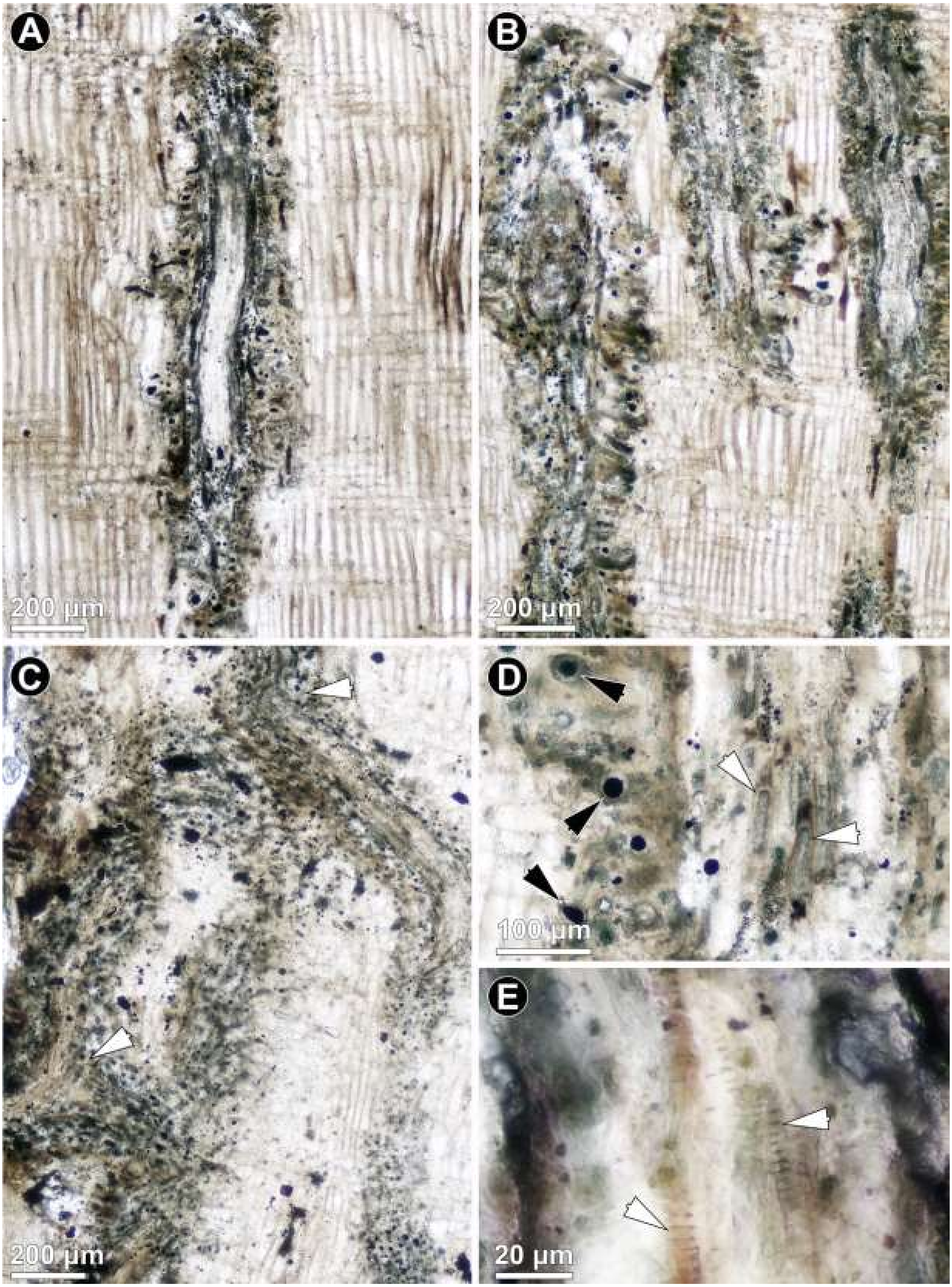
4. Discussion

Cordaitaleans in the Permo-Carboniferous palaeotropical areas had a range of growth habits, including small scrambling forms, mangrove-like architectures, and giant trees (e.g., Cridland, 1964; Rothwell, 1988; Falcon-Lang and Scott, 2000; Falcon-Lang and Bashforth, 2004, 2005; Raymond et al., 2010; Wan et al., 2020). The presence of fossil trunks with a septate pith and Agathoxylon-type wood up to 55 cm in diameter from the Benxi Formation of Yangquan City indicates that cordaitaleans were giant trees with reconstructed heights up to 30 m in the research area (Wang et al., 2022). They formed the canopy of the riparian forest in North China during the Pennsylvanian under a humid climate. Therefore, it is interpreted that

3

Fig. 2. Photomicrographs showing the characteristics of the nurse log from the Moscovian of Yangquan City, Shanxi Province, North China. (A) Crosssection of Agathoxylon wudense comb. nov., showing a broken log with a gallery (Ga) filled with indeterminate plant tissues in the center; collection number: PB201855; slide number: PB201855-1. (B) Radial section of Agathoxylon wudense, showing the uniseriate (white arrows) and biseriate (black arrow) pitting on tracheidal walls; collection number: PB201855; slide number: PB201855-2. (C) Radial section of Agathoxylon wudense, showing the uniseriate and biseriate (white arrows) rays; collection number: PB201855; slide number: PB201855-3. (D) Radial section of Agathoxylon wudense, showing the cupressoid and araucarioid cross-field pitting (white arrows); collection number: PB201855; slide number: PB201855-4. (E) Cross-section of Agathoxylon wudense, showing numerous rootlets inside the wood; collection number: PB201855; slide number: PB201855-1. (F) Cross-section of Agathoxylon wudense, showing seven rootlets closely arranged inside the wood; collection number: PB201855; slide number: PB201855-1. (G) Cross section of Agathoxylon wudense, showing a rootlet inside the wood; the rootlet is composed of a vascular cylinder (white arrow) in the middle and a ring of cortex (Ct) at the periphery; collection number: PB201855; slide number: PB201855-1. (H) Cross section of Agathoxylon wudense, showing a rootlet inside the wood; the rootlet is composed of a vascular cylinder (white arrow) in the middle and a ring of cortex (Ct) at the periphery; collection number: PB201855; slide number: PB201855-1.

Please cite this article as: K. Y. Wang, X. Huang, W. Yang et al., First record of plant-plant facilitative interaction from the Moscovian (Pennsylvanian, upper Carboniferous) of North China, Palaeoworld, https://doi.org/10.1016/j.palwor.2023.08.002


A
200 μm
B
200 μm
C
200 μm
D
100 μm
E
20 μm

the newly documented occurrence of Amyelon-like rootlets growing in an Agathoxylon wudense trunk provides evidence that the cordaitalean trunk acted as a nurse log for young cordaitaleans in a forest during the Moscovian.

Nurse logs as a facilitative interaction between plants are common in modern boreal, temperate, and tropical forests. However, they are rarely documented in fossil records. To date, the only probable Carboniferous nurse log is recorded from the Upper Pennsylvanian–lower Permian San Ignacio Formation of Argentina (Ce´sari et al., 2010, 2012). In a ca. 300-Ma in situ monospecific forest growing on periodically waterlogged soils under an overall humid and warm climate, Amyelon-like rootlets have been found invading the pith and secondary xylem of Cuyoxylon sp. in various directions. The host trunk with Agathoxylontype wood shares great similarities with the cordaitalean stem Mesoxylon Scott et Maslen. However, as pointed out by Ce´sari et al. (2012), Argentina was located at the westernmost margin of Gondwana. Although abundant impression fossil leaves and seeds with similarities to the Cordaites from the Northern Hemisphere have been documented extensively from the upper Palaeozoic of Gondwana, no fertile shoots have been found to confirm the world-wide distribution of members of classical Cordaitales. Fusulinids found from the underlying and overlying carbonates of current fossil interval demonstrate that the nurse log in the current study is of a late Moscovian age, ca. 310 Ma. It demonstrates that this type of regenerative ecological strategy originated during or before the Middle Pennsylvanian.

In some extant forests, dead logs play a role as a significant substrate for germination of some specific plants. Decaying woods provide many nutrients (Ce´sari et al., 2010) and fresh water (Harmon et al., 1986) for other plants. They form a unique microhabitat that could protect the roots of seedlings from pathogenic fungi in the soil and animal browsing (Harmon and Franklin, 1989). Growing on fallen logs would also reduce the competition with other understory plants, including mosses and herbaceous plants on the forest floor (Harmon and Franklin, 1989). However, it is difficult to test the different advantages that might have influenced the development of the fossil nurse log. In the geological record, the nurse tree syndrome has commonly been documented in fossil forests growing in at least partially waterlogged habitats (Daugherty, 1963; FaironDemaret et al., 2003; Ce´sari et al., 2010, 2012; Decombeix et al., 2021), and in some cases subject to volcanic disturbances (Ce´sari et al., 2010, 2012; Vera and Loinaze, 2022). However, fossil nurse logs have also been found from forests that were stressed by arid climates and a shortage of water (Feng et al., 2022). Based on the absence of true growth rings in fossil trunks from the Benxi Formation in Yangquan, and the co-occurrence of arborescent lycopsids, thin coal seams and bauxite, Wang et al. (2022) concluded that the palaeoclimate of the research area during the Moscovian was humid. The presence of growth interruptions in the fossil wood of current study and in the stem of Parnaiboxylon wangi Wang et al. from the same stratigraphic interval (Wang et al., 2023) indicates episodic and irregular growth disturbances when the tree was alive. Considering the fossil trunk was preserved and collected from a coastal pond or lowland deposit, it would be growing in the forest on the marine-influenced coastal plain or stream bank. In such environments with intermittent droughts (Wan et al., 2014; Falcon-Lang et al., 2016) or occasional incursions of seawater (Wang, 1989), a shortage of fresh water is commonly thought as the cause of growth interruptions (Wang et al., 2023). Therefore, it is interpreted that the Moscovian cordaitalean seedlings established on the fallen log which has the ability to store fresh water (Harmon et al., 1986). The nurse log provided a better substrate in an environment with episodic salinity and/or water table variations.

The host trunk, Agathoxylon wudense comb. nov., from the Benxi Formation in Yangquan was in an early stage of decay when it was colonized by the rootlets because of the well-preserved wood with anatomical structures. The gallery in the middle part of the host trunk is speculated to be caused by decaying processes. Contents filling in the gallery of the trunk are unrecognizable plant tissues without a regular shape. Therefore, the gallery-maker of current study cannot be fully determined at present. Similar to modern terrestrial ecosystems, microbes, including fungi and bacteria, were major decomposers in the geological time (e.g., Stubblefield et al., 1985; Stubblefield and Taylor, 1988; Labandeira et al., 1997; Dighton et al., 2005;

3

Fig. 3. Photomicrographs showing the characteristics of the nurse log from the Moscovian of Yangquan City, Shanxi Province, North China. (A) Radial section of Agathoxylon wudense comb. nov., showing a rootlet growing vertically inside the wood; collection number: PB201855; slide number: PB2018555. (B) Radial section of Agathoxylon wudense, showing three rootlets growing vertically inside the wood; collection number: PB201855; slide number: PB201855-6. (C) Radial section of Agathoxylon wudense, showing a complex rootlet system with branching (white arrows) growing vertically inside the wood; collection number: PB201855; slide number: PB201855-7. (D) Radial section of the nurse log, showing the tracheidal walls of a rootlet (white arrows) and abundant spherical bodies composed of a dark nucleus surrounded by an outwardly transparent zone present in tracheids of the host trunk around a rootlet (black arrows); collection number: PB201855; slide number: PB201855-8. (E) Radial section of a rootlet, showing the thin scalariform thickenings (white arrows) are present on tracheidal walls of the primary xylem; collection number: PB201855; slide number: PB201855-9.

Please cite this article as: K. Y. Wang, X. Huang, W. Yang et al., First record of plant-plant facilitative interaction from the Moscovian (Pennsylvanian, upper Carboniferous) of North China, Palaeoworld, https://doi.org/10.1016/j.palwor.2023.08.002

Labandeira, 2006a, 2006b; McLoughlin and Strullu-Derrien, 2016; Wan et al., 2016). Fungal hyphae and bacterial remains are absent in the host trunk of current study. However, probable plant-microbe association

occurs in the nurse log. Abundant spherical bodies which are composed of a dark nuclear surrounded by an outwardly transparent zone present in cortical tissues of the rootlets (Fig. 3D, black arrows). Similar phenomenon has been found in extant gymnospermous trunks which are caused by fungal infection (Blanchette, 1979). However, these structures could also be a link to general bacterial degradation in decayed woods (McLoughlin and StrulluDerrien, 2016; Philippe et al., 2022). Therefore, these spherical bodies in current rootlets are proposed as a response of a living vegetation to parasitic fungal infection (Stubblefield et al., 1985; Taylor et al., 2009; Wang et al., 2023), or bacterial penetration.

The Pennsylvanian Benxi Formation constitutes the oldest deposits of the upper Palaeozoic in the central North China Craton (NCC) (Zhao et al., 2001; Wang, Y.X. et al., 2003). Following uplift and erosion from the late Ordovician to Mississippian, crustal subsidence and sea-level rise in the Pennsylvanian enabled sediments accumulation on the NCC, the region became habitable for coastal plants. Therefore, fossil plants from the Benxi Formation represent the oldest vascular vegetation that we have known on the central NCC (Cleal and Wang, 2002). The Benxi Flora (sensu Hilton and Cleal, 2007) is thus proposed to represent an early evolutionary stage of the Cathaysian Flora (Wu, 1995; Cleal and Wang, 2002; Hilton and Cleal, 2007; Cheng et al., 2019). The majority of the Permian plants on the NCC, including lycopsids, sphenophytes, tingialeans, pteridosperms, and cordaitaleans, have their origin in the Benxi Flora (Wu, 1995). Similarly, our finding, together with the previous records (Wang et al., 2022, 2023), demonstrates that the plant-plant, plant-microbe, and plantarthropod associations that had recently been recorded from the Permian (Wan et al., 2017; Wei et al., 2019; Feng et al., 2022), have evolved no later than the Moscovian in Cathaysia. A sophisticated terrestrial ecosystem with multiple interactions between plants and other organisms had developed on the central NCC during the middle Pennsylvanian.

5. Conclusions

A Moscovian (Middle Pennsylvanian, Late Carboniferous) nurse log is identified from the Benxi Formation in Yangquan City, Shanxi Province, North China. It represents a fallen trunk or stump of a cordaitalean tree acting as a substrate for the regeneration of cordaitalean seedlings in a palaeoequatorial forest, providing a suitable microenvironment with fresh water. This ecological strategy is interpreted to be response to episodic salinity and/or water table variations in the study area. It is the most ancient unequivocal plant-plant facilitative interaction in Cathaysia. Multiple interactions between plants and other organisms indicate a long-ranging facilitative and saprotrophic interactions in the late Palaeozoic terrestrial ecosystems of the North China Craton.

Acknowledgements

We thank Mr. Zhi-Jun Bai from the Bureau of Planning and Natural Resources of Yangquan City, and Mr. Jun Li of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS) for field assistance. We acknowledge You-Dong Chen, Yang Gao, and ZhiKang Kou of NIGPAS for thin sectioning. We are grateful to Jing-Jing Tang of NIGPAS for help in preparing the images and plates. We thank the reviewers and editors for their constructive comments. This study was supported by the National Key R&D Program of China (2022YFF0800200), National Natural Science Foundation of China (42272016, 42230210), Youth Innovation Promotion Association, Chinese Academy of Sciences (2020312), State Key Laboratory of Palaeobiology and Stratigraphy (20212103), and the National Science Foundation (NSF EAR 1714749).

References

Bamford, M.K., Philippe, M., 2001. Jurassic–Early Cretaceous Gondwanan homoxylous woods: a nomenclatural revision of the genera with taxonomic notes. Review of Palaeobotany and Palynology 113, 287–297.

Blanchette, R.A., 1979. Wood decomposition by Phellinus (Fomes) pini: a scanning electron microscopy study. Canadian Journal of Botany 58, 1496–1503.

Callaway, R.M., 2007. Positive Interactions and Interdependence in Plant Communities. Springer, Berlin, 404 pp.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Cook, B.J., Aschehoug, E.T., Armas, C., Newingham, B., 2002. Interdependence among alpine plants increases with stress: A global experiment. Nature 417, 844–848.

Ce´sari, S.N., Busquets, P., Colombo Pin˜ol, F., Me´ndez Bedia, I., Limarino, C.O., 2010. Nurse logs: an ecological strategy in a late Paleozoic forest from the southern Andean region. Geology 38, 295–298.

Ce´sari, S.N., Busquets, P., Me´ndez-Bedia, I., Colombo Pin˜ol, F., Limarino, C.O., Cardo´, R., Gallastegui, G., 2012. A late Paleozoic fossil forest from the southern Andes, Argentina. Palaeogeography, Palaeoclimatology, Palaeoecology 333–334, 131–147.

Cheng, C., Wang, J., Li, D.D., Wu, X.Y., 2019. The late Carboniferous flora (Bashkirian) in the east sector of northern Qilian Mountain: a note on the origin center of the Cathaysia Flora. Geological Review 65, 491–502 (in Chinese, with English abstract).

Cleal, C.J., Wang, Z.Q., 2002. A new and diverse plant fossil assemblage from the upper Westphalian Benxi Formation, Shanxi, China, and its palaeofloristic significance. Geological Magazine 139, 107–130.

Cridland, A.A., 1964. Amyelon in American coal balls. Palaeontology 7, 186–209.

Daugherty, L.H., 1963. Triassic roots from the Petrified Forest National Park. American Journal of Botany 50, 802–805.

Decombeix, A., Taylor, E., Taylor, T., 2009. Secondary growth in Vertebraria roots from the Late Permian of Antarctica: a change in developmental timing. International Journal of Plant Sciences 170, 644–656.

Decombeix, A., Durieux, T., Harper, C.J., Serbet, R., Taylor, E.L., 2021. A Permian nurse log and evidence for facilitation in high-latitude Glossopteris forests. Lethaia 54, 96–105.

Dighton, J., White, J.F., Peter, O., 2005. The Fungal Community: Its Organization and Role in the Ecosystem (3rd Edition). CRC Press, Boca Raton, 960 pp.

Fairon-Demaret, M., Steurbaut, E., Damblon, F., Dupuis, C., Smith, T., Gerrienne, P., 2003. The in situ Glyptostroboxylon forest of Hoegaarden (Belgium) at the Initial Eocene Thermal Maximum (55 Ma). Review of Palaeobotany and Palynology 126, 103–129.

Falcon-Lang, H.J., 2003. Anatomically-preserved cordaitalean trees from Lower Pennsylvanian (Langsettian) dryland alluvial-plain deposits at Joggins, Nova Scotia. Atlantic Geology 39, 255–261.

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., Kurzawe, F., Lucas, S.G., 2016. A Late Pennsylvanian coniferopsid forest in growth position, near Socorro, New Mexico, U.S.A.: tree systematics and palaeoclimatic significance. Review of Palaeobotany and Palynology 225, 67–83.

Feng, Z., Gou, X., McLoughlin, S., Wei, H., Guo, Y., 2022. Nurse logs: A common seedling strategy in the Permian Cathaysian flora. iScience 25, 105433.

Fukasawa, Y., 2012. Effects of wood decomposer fungi on tree seedling establishment on coarse woody debris. Forest Ecology and Management 266, 232–238.

Galtier, J., Meyer-Berthaud, B., 2006. The diversification of early arborescent seed ferns. The Journal of the Torrey Botanical Society 133, 7–19.

Harmon, M.E., Franklin, J.F., 1989. Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. Ecology 70, 48–59.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. In: MacFadyen, A., Ford, E.D. (Eds.), Advances in Ecological Research. Academic Press, Orlando, pp. 133–302.

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

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. International Journal of Plant Sciences 170, 400– 418.

Hilton, J., Wang, S.J., Galtier, J., Bateman, R.M., 2009b. Cordaitalean seed plants from the early Permian of North China. III. Reconstruction of the Shanxioxylon taiyuanense Plant. International Journal of Plant Sciences 170, 951–967.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., GourletFleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Pen˜uelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.F., Sta˚hl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529, 204–207.

Labandeira, C.C., 2006a. The four phases of plant-arthropod associations in deep time. Geologica Acta 4, 409–438.

Labandeira, C.C., 2006b. Silurian to Triassic plant and insect clades and their associations: new data, a review, and interpretations. Arthropod Systematics and Phylogeny 64, 53–94.

Labandeira, C.C., Phillips, T.L., Norton, R.A., 1997. Oribatid mites and the decomposition of plant tissues in Paleozoic coal-swamp forests. Palaios 12, 319–353.

Losapio, G., Scho¨b, C., Staniczenko, P.P.A., Bascompte, J., 2021. Network motifs involving both competition and facilitation predict biodiversity in alpine plant communities. Proceedings of the National Academy of Sciences of the United States of America 118, e2005759118.

McLoughlin, S., Strullu-Derrien, C., 2016. Biota and palaeoenvironment of a high middle-latitude Late Triassic peat-forming ecosystem from Hopen, Svalbard Archipelago. In: Kear, B.P., Lindgren, J., Hurum, J. H., Mila`n, J., Vajda, V. (Eds.), Mesozoic Biotas of Scandinavia and its Arctic Territories. Geological Society of London Special Publications 434, 87–112.

Pannell, J.R., 2012. The ecology of plant populations: their dynamics, interactions and evolution. Annals of Botany 110, 1351–1355.

Philippe, M., 1993. Nomenclature ge´ne´rique des trache´idoxyles me´sozo¨ıques a` champs araucario¨ıdes. Taxon 42, 74–80. Philippe, M., 2011. How many species of Araucarioxylon? Comptes Rendus Palevol 10, 201–208.

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

Philippe, M., McLoughlin, S., Strullu-Derrien, C., Bamford, M., Kiel, S., Nel, A., The´venard, F., 2022. Life in the woods: taphonomic evolution of a diverse saproxylic community within fossil woods from Upper Cretaceous submarine mass flow deposits (Mzamba Formation, southeast Africa). Gondwana Research 109, 113–133.

Rauser-Chernousova, D.M., Gryzlova, N.D., Kireeva, G.D., Leontovich, G.E., Safonova, T.P., Chernova, E.I., 1951. Middle Carboniferous fusulinids of the Russian Platform and Neighboring Regions. Academy of Sciences USSR, Moscow, 380 pp. (in Russian).

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.

Richter, H.G., Grosser, D., Heinz, I., Gasson, P.E., 2004. IAWA list of microscopic features for softwood identification. IAWA Journal 25, 1–70.

Ro¨ßler, R., Philippe, M., van Konijnenburg-van Cittert, J.H.A., McLoughlin, S., Sakala, J., Zijlstra, G., Bamford, M., Booi, M., Brea, M., Crisfulli, A., Decombeix, A., Dolezych, M., Dutra, T., Esteban, L.G., Falaschi, P., Feng, Z., Gnaedinger, S., GuerraSommer, M., Harland, M., Herbst, R., Iamandei, E., Iamandei, S., Jiang, H.E., Kunzmann, L., Kurzawe, F., Merlotti, S., Naugolnykh, S., Nishida, H., Noll, R., Oh, C., Orlova, O., de Palacios, P.P., Poole, I., Pujana, R.R., Rajanikanth, A., Ryberg, P., Terada, K., The´venard, F., Torres, T., Vera, E., Zhang, W., Zheng, S.L., 2014. Which name(s) should be used for Araucaria-like fossil wood? — results of a poll. Taxon 63, 177–184.

Rothwell, G.W., 1988. Cordaitales. In: Beck, C.B. (Ed.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 273–297.

Sanchez, E., Gallery, R., Dalling, J.W., 2009. Importance of nurse logs as a substrate for the regeneration of pioneer tree species on Barro Colorado Island, Panama. Journal of Tropical Ecology 25, 429–437. Scotese, C.R., Wright, N., 2018. PALEOMAP Paleodigital Elevation Models (PaleoDEMS) for the Phanerozoic. Available at: https://www. earthbyte.org/paleodem-resource-scotese-andwright-2018/.

Shen, B.H., Shen, S.Z., Wu, Q., Zhang, S.C., Zhang, B., Wang, X.D., Hou, Z.S., Yuan, D.X., Zhang, Y.C., Liu, F., Liu, J., Zhang, H., Shi, Y.K., Wang, J., Feng, Z., 2022. Carboniferous and Permian integrative stratigraphy and timescale of North China Block. Science China Earth Sciences 65, 983–1011.

Shen, G.L., 1995. Permian floras. In: Li, X.X., Zhou, Z.Y., Cai, C.Y., Sun, G., Ouyang, S., Deng, L.H. (Eds.), Fossil Floras of China through the Geological Ages. Guangdong Science and Technology Press, Guangzhou, pp. 94–173.

Sheng, J.Z., 1958. Fusulinids from the Penchi Series of the Taitzeho valley, Liaoning. Palaeontologia Sinica, Whole Number 143, New Series B, Number 7, 1–119 (in Chinese, with English abstract).

Stubblefield, S.P., Taylor, T.N., 1988. Tansley review no. 12: recent advances in palaeomycology. New Phytologist 108, 3–25.

Stubblefield, S.P., Taylor, T.N., Beck, C.B., 1985. Studies of Paleozoic fungi. IV. Wood-decaying fungi in Callixylon newberryi from the Upper Devonian. American Journal of Botany 72, 1765–1774.

Taylor, T.N., Taylor, E.L., Krings, M., 2009. Paleobotany: The Biology and Evolution of Fossil Plants (Second Edition). Elsevier/Academic Press, London, San Diego CA, Waltham MA, Oxford, 1230 pp.

Tian, B.L., Wang, S.J., 1987. On cordaitean stems in coal balls from Taiyuan Formation in Xishan, Taiyuan, Shanxi. Acta Palaeontologica Sinica 26, 196–204 (in Chinese, with English abstract).

Vera, E.I., Loinaze, V.S.P., 2022. Ecological interactions in conifers (Agathoxylon and Protocupressinoxylon) from the Punta del Barco Formation (Baquero´ Group, upper Aptian), Patagonia, Argentina. Cretaceous Research 129, 105035.

Wan, M., 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. Palaeogeography, Palaeoclimatology, Palaeoecology 407, 1–13.

Wan, M., Yang, W., Liu, L., Wang, J., 2016. Plant-arthropod and plantfungus interactions in late Permian gymnospermous woods from Bogda Mountains, Xinjiang, northwestern China. Review of Palaeobotany and Palynology 235, 120–128.

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

Wan, M., Yang, W., Wang, J., 2019. Amyelon bogdense sp. nov., a silicified gymnospermous root from the Changhsingian–Induan (?) in southern Bogda Mountains, northwestern China. Review of Palaeobotany and Palynology 263, 12–27.

Wan, M., Yang, W., Wan, S., Li, D., Zhou, W., He, X., Wang, J., 2020. Giant cordaitalean trees in early Permian riparian canopies in North China: Evidence from anatomically preserved trunks in Yangquan, Shanxi Province. Palaeoworld 29, 469–475.

Wang, J., 2000. Permian wood from Inner Mongolia, North China: with special reference to Palaeozoic climate change of North China Block. The Palaeobotanist 49, 353–370.

Wang, K.Y., Yang, W., Li, D.D., Wang, J., Wan, M.L., 2022. Anatomically preserved cordaitalean trees from the Pennsylvanian of Yangquan City, Shanxi Province, and their implication for a perhumid climate in North China Block. Palaeoworld 31, 294–310.

Wang, K., Huang, X., Yang, W., Wang, J., Wan, M., 2023. A new gymnospermous stem from the Moscovian (Carboniferous) of North China, and its palaeoecological significance for the Cathaysian Flora at the early evolutionary stage. Review of Palaeobotany and Palynology 311, 104858.

Wang, S.J., 1989. Cordaites in coal balls of Taiyuan Formation of Shanxi and Shandong provinces and their living environment. Journal of China University of Mining and Technology 18, 71–80 (in Chinese, with English abstract).

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. International Journal of Plant Sciences 164, 89–112.

Wang, S.J., Sun, K.Q., Cui, J.Z., Ma, S.M., 2009. Fossil Flora of China. Volume 1: Fossil Plants from Coal Balls in China. Higher Education Press, Beijing, 141 pp.

Wang, Y.X., Li, H.M., Gu, L.X., Wu, C.Z., Chai, D.H., Chen, P., Wang, S.S., Zhang, J.J., 2003. Rb-Sr isotope dating of bauxite deposits in Shanxi Province. Acta Geologica Sinica 24, 589–592 (in Chinese, with English abstract).

Wei, H.B., Gou, X.D., Yang, J.Y., Feng, Z., 2019. Fungi–plant– arthropods interactions in a new conifer wood from the uppermost Permian of China reveal complex ecological relationships and trophic networks. Review of Palaeobotany and Palynology 271, 104100.

Wu, X.Y., 1995. Carboniferous floras. In: Li, X.X., Zhou, Z.Y., Cai, C.Y., Sun, G., Ouyang, S., Deng, L.H. (Eds.), Fossil Floras of China through the Geological Ages. Guangdong Science and Technology Press, Guangzhou, pp. 58–93.

Yang, J., Cawood, P.A., Montan˜ez, I.P., Condon, D.J., Du, Y., Yan, J., Yan, S., Yuan, D., 2020. Enhanced continental weathering and large igneous province induced climate warming at the Permo-Carboniferous transition. Earth and Planetary Science Letters 534, 116074.

Zhang, L.X., Zhou, J.P., Sheng, J.Z., 2010. Upper Carboniferous and Lower Permian fusulinids from western Guizhou. Palaeontologia Sinica, Whole Number 195, New Series B, Number 34, 1–296 (in Chinese, with English abstract).

Zhao, S.S., Chai, D.H., Bo, G.L., 2001. Isotopic age of bed G bauxite of Shanxi massif and its geological significance. Light Metal 8, 5–9 (in Chinese, with English abstract).

Please cite this article as: K. Y. Wang, X. Huang, W. Yang et al., First record of plant-plant facilitative interaction from the Moscovian (Pennsylvanian, upper Carboniferous) of North China, Palaeoworld, https://doi.org/10.1016/j.palwor.2023.08.002