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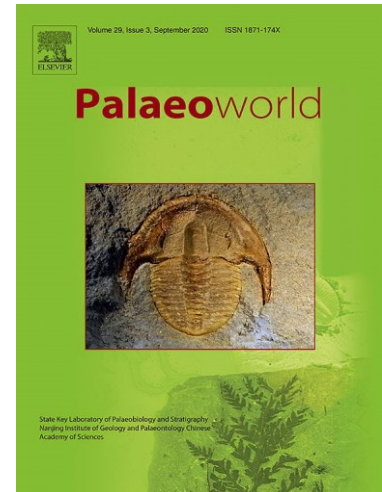
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# Anatomically preserved cordaitalean trees from the Pennsylvanian of Yangquan City, Shanxi Province, and their implication for a perhumid climate in North China Block

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## Abstract

Fifty-six cordaitalean trunks with anatomical features are discovered and described from the Moscovian (Pennsylvanian) Benxi Formation in Yangquan City, Shanxi Province, North China. They are allochthonously preserved in fluvial channel deposits and classified into two types based on the anatomy. The first type is characterized by a solid and heterocellular pith, endarch primary xylem and pycnoxylic secondary xylem with araucarian radial tracheidal pits and araucarioid cross-field pitting. The second type contains a septate pith and a pycnoxylic secondary xylem which is comparable to that of the first type. Primary xylem is absent in the second type. The diameter of these trunks ranges from 0.11 m to 0.55 m. The largest tree is estimated to be 29.96 m high using an allometric approach. The trunks represent the oldest and largest trees from the North China Block during the Pennsylvanian due to the absence of Silurian, Devonian, and Mississippian there. The

fossil evidence shows that cordaitaleans were large arborescent trees growing on clastic substrates in the Cathaysia during the Pennsylvanian. Their occurrence from the upper Pennsylvanian in North China Block suggests that the previously reported diversity of cordaitaleans, which were estimated based on impressions, is a gross underestimate. The absence of growth rings in the trunks and co-occurrence of arborescent lycopsids in the same interval, together with coal seams and barroisite around the fossil-bearing horizons, indicate that the trees grew under perhumid tropical conditions.

**Keywords:** Fossil wood; Anatomy; Carboniferous; Cathaysia; Palaeoecology

## 1. Introduction

Fossil plants from the Benxi Formation are the oldest documented tracheophytes in central North China Block. They represent the early evolutionary stage of the Cathaysia Flora (Wu et al., 1987; Cheng et al., 2019), and are considered to be a link between the Cathaysian and Euramerican floras (Cleal and Wang, 2002). However, as pointed out by Hilton and Cleal (2007), shortage of anatomically preserved plant fossils prevents a detailed comparison and discussion of the relationship between these two floras developed in the palaeotropical regions during the Pennsylvanian. Systematic studies of fossil stems are effective to improve the knowledge of the composition of past vegetation (Zheng et al., 2008; Yang et al., 2013). Anatomy of permineralized stems from clastic deposits provides additionally taxonomic, palaeoecological, and environmental information on plants (Wan et al., 2017a, 2017b). Woody detritus is an important component of modern forest ecosystems and plays a significant role in energy flow, hydrologic and geomorphologic processes as well as in carbon and nutrient cycling (Harmon, 2021). Allochthonous accumulation of large cordaitalean trunks as logjams have been reported from the Pennsylvanian in

the Euramerica (Falcon-Lang and Scott, 2000; Gibling et al., 2010) and recently documented from the Cisuralian (lower Permian) in the Cathaysia (Wan et al., 2020b). However, similar records have never previously been found from the Pennsylvanian in North China.

Cordaitaleans are an extinct group of gymnosperms closely related to conifers (Rothwell, 1988; Hilton and Bateman, 2006), characterized by large, strap-shaped and coriaceous leaves, woody stems, axillary branching, and platyspermic seeds (e.g., Gu and Zhi, 1974; Falcon-Lang and Bashforth, 2005; Taylor et al., 2009). The earliest *Cordaite*s leaves were recorded from the Visean (Mississippian, lower Pennsylvanian) of both South and North China (Sze, 1951; Cheng, 1982; Jin, 1995; Mi et al., 2001). Cordaitalean gymnosperms were common elements on the Pennsylvanian landscapes of palaeotropical areas (Costanza, 1985; Raymond, 1988; Wang, 1989, 1997, 1998; DiMichele and Hook, 1992; DiMichele and Phillips, 1994; Li et al., 1995; Wu, 1995; Falcon-Lang and Scott, 2000; Falcon-Lang, 2003, 2007; Falcon-Lang and Bashforth, 2004, 2005; Falcon-Lang et al., 2006, 2009, 2011; DiMichele et al., 2010; Raymond et al., 2010; Wang, 2010; DiMichele, 2014). They became prominent since the Cisuralian (early Permian) in the Cathaysia, serving as significant components of the peat-forming and clastic wetlands (Tian and Wang, 1987, 1988; Wang, 1989, 1997, 1998; Sun, 1991; Chen, 1994; Wang et al., 1995; Tian et al., 1996; Liu et al., 1998; Hilton et al., 2001, 2009a, 2009b; Yang et al., 2006; Pfefferkorn and Wang, 2007; Wang, 2010; Yang, 2010; Wang et al., 2012; Zhou et al., 2015, 2017; Wan et al., 2017a; Backer et al., 2019; Liang et al., 2019). However, the Pennsylvanian cordaitaleans are extremely poorly preserved in the Cathaysia comparing with those from the Permian. Their inner structures of cellular anatomy are not yet found and described. They were recorded sporadically as fragmentary leaves (Stockmans and

Mathieu, 1939; Zhang et al., 1987; He et al., 1990, 1995; Li et al., 1993; Lavine et al., 2003; Cheng et al., 2019). Hence, their growth habits and habitat preference are still unclear.

In this contribution, we report large tree trunks from the Moscovian Benxi Formation (Pennsylvanian) in Yangquan City, Shanxi Province, North China. The wood anatomy suggests that they are cordaitaleans. Conceivable tree heights are calculated based on trunk diameters. Their growth habitat is briefly discussed. The Moscovian palaeoclimate in the research area is interpreted as humid with little seasonality as indicated by the absence of growth rings in the trunks, and the lithological and other palaeobotanical evidence from the Benxi Formation.

## 2. Geological setting, materials and methods

Fifty-six fossil trunks were found and collected from the Benxi Formation in Yaxinyuan section, Yangquan City, Shanxi Province, North China (Fig. 1A; 37°55'45''N, 113°33'40''E). During the Pennsylvanian, this area was part of the North China Block in palaeoequatorial Palaeo-Tethys Ocean (Fig. 1B). The Benxi Formation overlies the Middle Ordovician Fengfeng Formation with a major unconformity and underlies conformably the Gzhelian–Sakmarian Taiyuan Formation (Fig. 1C; Wang and Zhang, 1983; Shao et al., 2006, 2008). It is composed of carbonaceous mudstones, limestones, conglomerates, and bauxitic mudstones (Shao et al., 2015). A 1–10 m thick bauxite occurs at the base of the formation and overlies the unconformity. Three limestone units occur in the Benxi Formation, and are collectively named as Pingdingshi Limestone locally. The limestones in Yangquan are correlated with the Bangou Limestone in the Eastern Hill section, constrained by a well-defined biostratigraphic framework in the city of Taiyuan (Wang and Zhang, 1983; He et al., 1995). The age of Benxi Formation in eastern Shanxi Province is Moscovian as indicated by fusulinids, brachiopods, conodonts and fossil plants (Zhang et al., 1987; He et al., 1995; Cleal and Wang, 2002).

[Approximate position for Fig. 1]

The fossil-bearing interval is between the middle and upper units of Pingdingshi Limestone (Fig. 2). It is about 28 m thick, composed of four upward-thinning successions of conglomerates, gravelly sandstones, ferruginous siltstone, and mudstone (Fig. 3A). The sandstones are greenish gray and contain coarse to very coarse, moderately to well sorted and rounded to well-rounded quartz and feldspar framework grains. Large to medium tabular and trough cross beddings are common. The sandstones are interpreted as fluvial channel-fill deposits, and mudstones as overbank deposits. Fossil trunks are commonly preserved parallel to the bedding in basal channel-fill sandstones and conglomerates, suggesting an allochthonous origin (Fig. 3B–D). In some cases, cordaitalean leaves with parallel venation are present in the sandstone bodies (Fig. 3E).

[Approximate position for Fig. 2]

Thin sections of fossil trunks are studied following the method introduced by Hass and Rowe (1990). The terminology of Richter et al. (2004) and Philippe and Bamford (2008) are used in the description and discussion of wood anatomical features of the fossil stems. The polished cross section of large specimens were photographed with a Nikon D800 digital single-lens reflex camera (Figs, 4A, 6A). Thin section images were taken using a Leica DM5000 compound microscope and Leica DC 500 digital microscope camera system. The maximum height of the host tree is estimated using Niklas' (1994) empirically derived, biomechanical relationship between basal trunk diameter (D) and tree height (H) for woody plants:

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

The specimens and corresponding thin sections are housed in the Palaeobotanical Collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

[Approximate position for Fig. 3]

### 3. Results

The trunks are straight, decorticated, and have a diameter ranging from 0.11 m to 0.55 m. Margins of each trunk are parallel. Attached lateral branches and branch scars are absent, suggesting that they are the lower or middle parts of the trees. The allometric estimates of tree height are 11.24–29.96 m (Table S1). Two types of trunks are identified on the basis of pith morphology and wood anatomy. **3.1. Type I: fossil trunks with solid pith and pycnolytic wood**

#### 3.1.1. Systematic palaeontology

Genus *Damudoxylon* Maheshwari, 1967

**Type species:** *Damudoxylon waltonii* Maheshwari, 1967.

*Damudoxylon mei* Wang and Wan, n. sp.

(Figs. 4, 5)

**Etymology:** The specific epithet is dedicated to Mr. Sheng-Wu Mei (Senior Experimentalist of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) for his finding the current material and his continuous exploration of petrified woods in the research area during the last decade.

**Holotype:** The specimen with Catalog No. PB23311, and the slides PB23311-1 to PB23311-9.

**Repository:** Nanjing Institute of Geology and Palaeontology, Chinese Academic of

Sciences.

**Diagnosis:** Woody tree, stem eustelic. Pith solid, circular, heterocellular, with spherical secretory cavities at the periphery. Primary xylem endarch, with helical and scalariform thickenings on radial tracheidal walls. Secondary xylem pycnoxylic, composed of tracheids and ray parenchyma. Radial tracheidal pits arranged alternately, commonly biseriate, rarely uniseriate. Rays uniseriate, 2 to 27 cells high. Cross-field pitting araucarioid. Axial parenchyma and tangential tracheidal pits absent.

**Type locality:** Yaxinyuan section, Sanquan Village, Yangquan City, Shanxi Province, China.

**Stratigraphic horizon:** Benxi Formation.

**Age:** Moscovian, Pennsylvanian, Carboniferous

### 3.1.2. Description

Nine specimens belong to this type. Their diameters range from 0.13 m to 0.33 m. They are cylindrical in a preserved shape in the field. The following description is based on slides from the specimen which has been catalogued as PB23311.

The trunk is composed of pith, primary and secondary xylems. Phloem, cortex and periderm are not preserved (Fig. 4A, B). The pith is circular in cross section, solid and heterogeneous, and consists of parenchymatous cells and secretory cavities (Fig. 4C, D). In cross section, the diameter of pith varies from 0.02 m to 0.03 m (Fig. 4A, B). Parenchymatous cells are commonly rounded, oval, and polygonal (Fig. 5A). Their diameters range from 40  $\mu\text{m}$  to 144  $\mu\text{m}$ . The smaller cells are distributed at the marginal portion of the pith. Some opaque contents are present in the parenchyma (Fig. 5A, red arrows). In the radial section of the pith, cells are commonly quadrangular, rarely rounded (Fig. 5C). They are of a larger size at the central pith, and the width is greater than height. At the periphery, their sizes decrease, and horizontal walls are shorter than the vertical walls. Secretory cavities distribute at the periphery of the pith (Fig. 4C, white arrow). Diameters of the cavities vary from 100



$\mu\text{m}$  to  $260 \mu\text{m}$ . Each cavity is surrounded by 2–3 rings of small, elongate, and oval parenchymatous cells (Fig. 4D, E, white arrows). The primary xylem is endarch (Fig. 5A, B, white arrows). In radial section, scalariform and spiral thickenings are present on the radial tracheidal walls (Fig. 5C, white arrows).

The wood is pycnoxylic, containing tracheids and rays. Growth rings are absent. Tracheids are rounded and polygonal in the cross section (Fig. 5A, B). Diameters of the tracheids are  $40\text{--}72 \mu\text{m}$ . In radial section, rounded and hexagonal bordered pits are present on the tracheidal walls. They are mostly biseriate (92%,  $n = 300$ ), rarely uniseriate (Fig. 5D, E). Uniseriate pits are continuously arranged (Fig. 4E, red arrows). When biseriate, pits are alternatively distributed (Fig. 5D, E, white arrows). Tangential pitting and axial parenchyma are absent. Rays are parenchymatous, with smooth cell walls. They are uniseriate, 2 to 27 cells high (Fig. 5F, white arrows). In radial section, ray cells are rectangular, spanning 2 to 5 tracheids. Pits in cross-fields are obscure. In some cases, some dispersed bordered pits with circular apertures are present (Fig. 5G, white arrows). They are small in size, with a diameter less than  $7 \mu\text{m}$ .

[Approximate position for Figs. 4, 5]

### 3.1.3. Remarks

The solid pith, with secretory cavities, endarch primary xylem, and pycnoxylic secondary xylem of the trunks are consistent with the anatomical diagnosis of

*Damudoxylon* Maheshwari (Maheshwari, 1967, 1972; Pant and Singh, 1987).

Originally, the pith structure of *Damudoxylon* is of two types, one is homogeneous, the other is heterogeneous with secretory cells (Maheshwari, 1967, 1972). Eight species with similar characteristics were put under this genus. However, Pant and Singh (1987) proposed that these two types of pith would represent host plants with totally different affinities. They established *Chapmanoxylon* Pant and Singh for those with homogeneous pith, endarch primary xylem, and pycnoxylic woods. Five species, including *Damudoxylon daintreei* (Chapman) Maheshwari, *D. jamuriense*

Maheshwari, *D. parenchymosum* (Surange and Maithy) Maheshwari, *D. porosum* (Kräusel) Maheshwari, and *D. rangei* (Kräusel) Maheshwari, have been transferred to *Chapmanoxylon daintreeii* (Chapman) Pant and Singh, *C. jamuriense* (Maheshwari) Pant and Singh, *C. parenchymosum* (Surange and Maithy) Pant and Singh, *C. porosum* (Kräusel) Pant and Singh, and *C. rangei* (Kräusel) Pant and Singh, respectively (Pant and Singh, 1987). In addition, *Dadoxylon adhariense* Prasad, *Dadoxylon chandrapuraensis* Prasad, and *Dadoxylon maharashtraensis* Prasad, were reclassified as *Damudoxylon adhariense* (Prasad) Pant and Singh, *Damudoxylon chandrapuraensis* (Prasad) Pant and Singh, and *Damudoxylon maharashtraensis* (Prasad) Pant and Singh respectively. Further, *Damudoxylon zhoui* Zhang and Zheng was erected based on the early Permian material from the Taiyuan Formation in North China (Zheng et al., 2008). Kurzawe et al. (2013) established *D. buritiranaense* Kurzawe, Merlotti, Rohn and Iannuzzi, *D. humile* Kurzawe, Merlotti and Iannuzzi, and *D. roessleri* Kurzawe, Merlotti and Iannuzzi according to the fossil trunks from the Permian of the Parnaíba Basin, northeastern Brazil. In summary, ten species of *Damudoxylon* are formally established and accepted (Table 1).

The mostly biseriata radial tracheidal pitting in the wood of current trunks is distinguishable from the uni- to triseriate pits in *Damudoxylon arberi* (Walton) Pant and Singh, *D. maharashtraensis*, *D. roessleri*, *D. waltonii* Maheshwari and *D. zhoui* (Maheshwari, 1967, 1972; Zheng et al., 2008; Kurzawe et al., 2013). The transitional sheath in the pith and paired leaf trace in *D. indicum* are not present in current material (Maheshwari, 1967, 1972). Uni- to biseriata rays in *D. adhariense* and *D. chandrapuraensis* are different from the entirely uniseriate rays in our trunks (Prasad, 1982). Pits on ray parenchymatous cells and axial parenchyma in the wood of *D. zhoui* is absent in our material (Zheng et al., 2008). *Damudoxylon buritiranaense* and

*D. humile* is featured by mostly uniseriate radial tracheidal pitting (Kurzawe et al., 2013), which is different from that of our trunk. The occurrence of tangential

tracheidal pitting in *D. humile* makes it distinct from the trunks in this study.

However, it should be noted that the assignment of *D. buritiranaense* and *D. roessleri* with homocellular pith is suspicious. According to Pant and Singh (1987), the pith of *Damudoxylon* is heterogenous with parenchyma and secretory cells. Secretory cavities present at the pith periphery, which are diagnostic features of current trunks, have never been recorded from any species of *Damudoxylon*. Due to its unique anatomical features and dissimilarities to the established species, we propose a new species, *Damudoxylon meii* Wang and Wan herein.

[Approximate position for Table 1]

It should be noted that *Damudoxylon* was erected based on fossil stems from the Permian of Gondwana (Maheshwari, 1972). Species of this genus have extensively been reported from the Southern Hemisphere, including the Antarctic (Maheshwari, 1967, 1972), Brazil (Kurzawe et al., 2013), India (Pant and Singh, 1987), and South Africa (Pant and Singh, 1987). However, the occurrence of *D. zhoui* from the lower Permian of Chaoyang City, Liaoning Province, northeastern China (Zheng et al., 2008), demonstrate that this genus was not constrained within the Gondwana. Our trunk from the Moscovian of Yangquan City, Shanxi Province, North China, represent the second species of *Damudoxylon* in the Cathaysia. Its presence indicates that *Damudoxylon* may not have any palaeogeographic implications.

Secretory structures are common in the pith of fossil stems from the upper Palaeozoic all over the world (e.g., Pant and Singh, 1987; Feng et al., 2010; FalconLang et al., 2016; Wan et al., 2017c). Among them, secretory cells and ducts are characterized by slightly thickened walls and opaque contents. They are circular in cross section, with a larger size than normal parenchymatous cells (Kulkarni et al., 1971), and distributing separately (Pant and Singh, 1987; Kurzawe et al., 2013) or in cluster (Wan et al., 2017c). Secretory ducts are canular in cross section. In some

cases, they are joined by narrow transverse connections (Maheshwari, 1972).

However, in the pith of *Damudoxylon meii* n. sp., secretory cavities are spherical and distribute at the periphery. Their middle parts are hollow. Each secretory cavity is surrounded by two to three rings of small, elongate, and oval parenchymatous cells, which is distinguishable from secretory cells/ducts without any adjacent ornament. Similar secretory cavities have only been recorded from the pith of *Shanxioloxylon taiyuanense* Hilton et al., a cordaitalean plant from the lower Permian of North China (Hilton et al., 2009b).

The eustelic trunk with thick development of wood of *Damudoxylon meii* n. sp. suggests that it is a member of gymnosperms. The absence of irregular arrangement of tracheid elements, bent endings of tracheids, abnormal ray cells and, axial parenchymatous tissue makes *D. meii* n. sp. different from trunks of ginkgophyte (Feng et al., 2010). Flora from the Moscovian Fenxi Formation in North China, where current materials were collected, is dominated by neuropterid forliage (*Paripteris* Gothan) and *Linopteris* Presl (Wu, 1995). Although their affinities are still on debate, they are commonly found associated with medullosan seeds and pollen organs (Cleal and Shute, 1995). Wood of medullosan seed ferns is commonly manoxylic (Galtier and Meyer-Berthaud, 2006), which is distinguishable from the pycnoxylic wood of *D. meii*. Trunks of cordaitaleans have a similar wood anatomy with that of conifers (e.g., Falcon-Lang et al., 2016). However, unequivocal remains of conifer have never been found from the Carboniferous in the Cathaysia. The oldest coniferous leaves are recorded from the lower Permian in North China (Shen, 1995). In contrast, cordaitalean leaves are common in the Cathaysia since the beginning of Pennsylvanian (Wu, 1995). Commonly, the trunks and branches of cordaitaleans are characterized by a septate pith (e.g., Stewart and Rothwell, 1993; Taylor et al., 2009). However, as noted by Falcon-Lang (2007), in the basal part of cordaitalean trunks and their young shoots, pith is commonly solid with an incompletely developed

diaphragm. Cordaitalean stems and shoots with solid pith have been well documented from the Pennsylvanian in palaeotropical areas (Falcon-Lang, 2007; Césari et al., 2015). Therefore, a cordaitalean affinity of *D. meii* n. sp. is preferred in current study.

### 3.2. Type II: fossil trunks with septate pith and pycnoxylic wood

#### 3.2.1. Description

Forty-seven trunks, including the biggest one with a diameter of 0.25 m, are of comparable anatomical features, and thus attributed to this type. The description is based on slides from the specimen which has been catalogued as PB23312.

The trunk is composed of pith and secondary xylem (Fig. 6A). Structures of the primary xylem are indiscernible due to the poor preservation. The pith is circular and 0.025 m in diameter (Fig. 6A). It shows closely spaced septa in radial section (Fig. 6B, C, white arrows). Each septum is 1–2 mm thick. Cellular features of the pith are not preserved. The secondary xylem is pycnoxylic, consisting of tracheids and rays (Fig. 6C). Growth rings are absent (Fig. 6A). In radial section, predominantly uniseriate pitting (94%,  $n = 700$ ) occurs on tracheidal walls (Fig. 6D, white arrows). Pits are bordered and continuously distributed. In some cases, partially biseriate pits with alternate arrangement are present (Fig. 6D, red arrows). Rays are parenchymatous and 1 to 12 cells high in tangential section (Fig. 6E, white arrows). Cross-field pits are not well-preserved. Only some dispersed small, bordered pits are present in each cross-field (Fig. 6F). Tangential pitting and axial parenchyma are absent.

[Approximate position for Fig. 6]

#### 3.2.2. Remarks

The second type of trunk is featured by the septate pith with horizontal diaphragms, which is distinct from *Damudoxylon meii* n. sp. with solid pith described above. In addition, its mostly uniseriate radial tracheidal pitting and relatively lower

rays in tangential section are different from those of *D. meii* n. sp. The absence of cellular features of the pith and primary xylems prevents further comparisons between these two types of trunks from the same fossil interval. Traditionally, fossil woods with septate pith from the Cathaysia were attributed to *Cordaioxylon* Grand'Eury (Hsü and Bose, 1952; Wang, 2000; Zheng et al., 2008). It should be pointed out that the primary xylem of *Cordaioxylon* shows an endarch maturation (Rothwell and Warner, 1984; Césari et al., 2015; Conceição et al., 2020). Therefore, it is inappropriate to assign current trunks to *Cordaioxylon* due to the lack of primary xylem. The wood described here is characterized by predominantly uniseriate araucarian radial pitting and scattered bordered cross-field pits, which is comparable to the fossil species *Araucarioxylon leei* (Sze) Wang from the Permian of North China (Sze, 1952). However, the genus *Araucarioxylon* Karst is illegitimate (Philippe, 1993, 2011). The species that formerly assigned to this genus should be re-assigned to *Agathoxylon* Hartig (Bamford and Philippe, 2001; Philippe and Bamford, 2008). From this point of view, *Araucarioxylon leei* (Sze) Wang is re-combined as *Agathoxylon leei* (Sze) Wang and Wan, n. comb. herein. *Agathoxylon leei* n. comb. in current study is proposed to be of Cordaitalean affinity due to the occurrence of septate pith, and the characteristic of the Cordaitales with mostly uniseriate radial tracheidal pitting and short rays in the wood (Doubinger and Marguerier, 1975; Noll et al., 2005).

## 4. Discussion

Permineralized plants with anatomical characteristics are extremely rare from the Pennsylvanian of Cathaysia. The oldest Cordaitalean axis from the Cathaysia is recorded from the Bashkirian Hongtuwa Formation in Jingyuan, Gansu Province, China, and was named as *Dadoxylon* (?*Mesoxylon*) sp. by Tian et al. (1996). However, the description of inner structures of this species has never been provided or formally published (Feng et al., 2008). Feng et al. (2008) described a fossil wood

named as *Zalesskioxylon xiaheyense* Feng, Wang and Shen from the lower part of Taiyuan Formation in Ningxia, China. The age of their fossil interval is proposed to be Stephanian (Kasimovian–Gzhelian), which is younger than that of the Benxi Formation in North China. Pith and primary xylem of *Z. xiaheyense* are absent. Therefore, the affinity of this fossil wood is unknown. *Zalesskioxylon xiaheyense* is characterized by numerous simple pits in each cross-field, which is distinct from the bordered pits in our trunks. Anatomically preserved fossil plants from the Moscovian in North China are only documented from the Benxi Formation in Western Hill, Taiyuan City, Shanxi Province (Cleal and Wang, 2002). Charcoalified fragments of lycopsids, sphenophytes, and tingaleans were described in detail. However, anatomical structures of plants with gymnospermous affinities were not found. Therefore, the two types of trunks described in this study represent the first gymnosperms with definite anatomy from the Moscovian in Cathaysia.

The diversity of Pennsylvanian cordaitaleans in palaeotropical regions is not well understood. Common characteristics that have been used to differentiate species of cordaitalean leaves, including size, shape, and venation schemes, are thought to be artificial and not diagnostic (Šimůnek, 2007). The limited number of characteristics and fragmentary preservation of the fossils themselves further compound the problem (DiMichele, 2014). Cuticular analyses based on cordaitalean leaves demonstrate that the diversity of this group was grossly underestimated (Zodrow et al., 2000; Šimůnek, 2007; Šimůnek and Florjan, 2013). Cordaitaleans are commonly represented by the occurrence of leaf adpressions and permineralized materials from the Permian of Cathaysia (Wang, 1998). However, they are of a low diversity and a sporadic distribution in North China during the Pennsylvanian (Wu, 1995). Only one species, *Cordaite principalis* (Germar) Geinitz, has previously been recorded from the Moscovian Benxi Formation in four localities of the Cathaysia, including Eastern and Western Hills in Taiyuan, Shanxi Province, Zhungeerqi and Hulusitai in Inner Mongolia, and Kaiping in Hebei Province (Stockmans and Mathieu, 1939; Gu and



Zhi, 1974; Zhang et al., 1987; He et al., 1990; Laveine et al., 2003). In Yangquan area, six species of plants including *Lepidodendron* sp., *Annularia* sp., *Sphenophyllum oblongifolium* (Germar) Unger *Cyathocarpus hemitelioides* (Brongniart) Mosbrugger and *Paripteris gigantea* (Sternberg) Gothan, have previously been reported from the Benxi Formation (Lee, 1957; Wang and Zhang, 1983). Cordaitaleans have never been found and recorded in this region. The presence of *Damudoxylon meii* n. sp. and *Agathoxylon leei* n. comb. with septate pits from Yangquan provides the first evidence of Moscovian cordaitaleans in this area. The two species of fossil trunks in current research area indicate that previously inferred low diversity of cordaitaleans from the Moscovian of Cathaysia was biased. This observation is further supported by the cuticular research on *C. principalis* from the Canadian Carboniferous Maritimes Basin, which reveals five distinct epidermal morphotypes within one taxon (Zodrow et al., 2000).

There is a substantial unconformity between the Middle–Upper Ordovician and the upper Carboniferous across nearly the entire North China Block (e.g., Wang et al., 2010; Cocks and Torsvik, 2013), representing ca. 135 million years of missing time. This gap makes the investigation of the origination and evolution of vascular plants during the Silurian, Devonian, and early Carboniferous impossible. Geochemical evidence shows that North China Block was uplifted as a continental upland during this time (Wang et al., 2010). The Benxi flora represents the oldest vascular plants colonizing the terrestrial landscape in North China Block (Cleal and Wang, 2002). According to the statistical work by Wu (1995), sixty species of thirty genus have been recorded from the Benxi Formation of this region. However, due to the fragmentary preservation of the fossils, the occurrence of tall trees and the completeness of Moscovian floral communities in North China are obscure. It has been proposed that lycophytes were the only candidate of arborescent trees based on empirical analysis (Cleal and Wang, 2002). Arborescent trees are crucial for liana-like plants, providing physical and physiological supports (Cai and Guo, 2000). The rarity



of arborescent groups has been used to explain the absence of scrambling and climbing plants in Benxi flora (Hilton and Cleal, 2007). Cordaitaleans had a range of growth habits, including small scrambling forms, mangrove-like and giant trees (Cridland, 1964; Rothwell, 1988; Falcon-Lang and Scott, 2000; Falcon-Lang and Bashforth, 2004, 2005; Raymond et al., 2010; Wan et al., 2020b). The trunks with a diameter up to 0.55 m in current study suggest that the cordaitalean trees could grow to a height of 29.96 m and is, at present, the tallest plants in Cathaysia during the Moscovian. In addition, *Damudoxylon meii* n. sp. and *Agathoxylon leei* n. comb. with septate pith from Yangquan represent the oldest trees, if not all, in North China Block. And arborescent cordaitaleans were one of the first groups migrating to North China during the Moscovian. Recent finding of a small latero-phyllous vine climbing on *Cordaites* trees from the lower Permian of Inner Mongolia indicates that cordaitaleans were suitable for hosting vines during the Palaeozoic (Pšenička et al., 2020). Considering the fact that less than 15 localities with Moscovian fossiliferous intervals have been excavated in North China (Wu, 1995, and references therein), the lack of scrambling and climbing plants is probably caused by the insufficient fossil collection.

The cordaitalean trunks documented here are allochthonous indicated by their occurrence as fluvial channel lag deposits and the absence of attached leaves, rooting systems, or branches. Pennsylvanian cordaitaleans were ecological diverse, with growth habits varying from marine-influenced coastal margins (Falcon-Lang, 2005), peat-forming and clastic-substrate swamps (DiMichele, 2014), dry lands (Bashforth et al., 2014), to uplands (Falcon-Lang and Bashforth, 2004, 2005). The dispersed logs are a time-averaging assemblage, and their provenance is highly variant (Trümper et al., 2020). Hence, it is difficult to determine the exact growth habitat of current cordaitalean trees from taphonomy. One possibility is that host trees of these trunks were from streamside niches in the upper drainage basin up to hundreds of kilometers away. Fossil trunks from the intermontane alluvial conglomerates suggest that

Pennsylvanian uplands in Euramerica were forested by arborescent cordaitaleans (Falcon-Lang and Bashforth, 2004). However, for the trunks in current study, an origin from stream riparian zones of the river in lowland is preferred. This interpretation is supported by the presence of abundant cordaitalean leaves from the same interval, which are parautochthonous, presenting an “ecological snapshot” of the local vegetation (Wing and DiMichele, 1995; DiMichele and Gastaldo, 2008). Cordaitalean trees probably grew in the overbank area and fell into the streams when the bank collapsed due to erosion caused by lateral channel migration (Wan et al., 2020b).

Fossil woods provide important clues in palaeoclimatic and palaeoenvironmental reconstruction (Wan et al., 2017b, 2020a). Presence of growth rings in fossil woods is indicative of palaeoclimatic seasonality (Chaloner and Creber, 1973, 1990; Creber and Chaloner, 1985; Wan et al., 2020a). On the other hand, absence of growth rings may indicate a non- to weakly seasonal climate with a short or no dry season (Falcon-Lang, 2003; Wan et al., 2014, 2017b). Therefore, the absence of growth rings in all the trunks from Yangquan suggests that these trees grew in an environment without large seasonal fluctuations in temperature, precipitation, and ground water table. Indicators of moisture deficiency, such as Calcisols and Vertisols, are not present from the entire Benxi Formation in the research area (Wang and Zhang, 1983; Shao et al., 2015). The occurrence of arborescent lycopsids (Lee, 1957; Wang and Zhang, 1983), which are commonly interpreted as hydrophytes (e.g., DiMichele, 2014), from the same fossil interval, also suggests that the regional climate was not dry. Siderite nodules and bauxite, which are indicative of tropical–subtropical humid climate (Boucot et al., 2013), are present around the fossil interval (Wang and Zhang, 1983). In summary, the climate in Yangquan area of Shanxi Province was likely perhumid (*sensu* Cecil and Dulong, 2003) during the Moscovian when these tall cordaitalean trees thrived.

## 5. Conclusions

Fifty-six trunks, with diameters ranging from 0.11 m to 0.55 m, are recorded from the Moscovian Benxi Formation in Yangquan City, Shanxi Province, North China. They belong to two types. The first type is identified as *Damudoxylon meii* n. sp., characterized by a solid pith with secretory cavities, endarch primary xylem, and pycnoxylic secondary xylem. The second type with septate pith is assigned to *Agathoxylon leei* n. comb., featured by predominantly uniseriate radial tracheidal pitting and scattered bordered cross-field pits. Both types are designated to be members of cordaitaleans mainly based on their anatomical features. Presence of *D. meii* n. sp. and *A. leei* n. comb. with septate pith suggests that previous speculations on the diversity of cordaitaleans and diversity of the entire Moscovian flora in North China based only on impressions are inaccurate. The trees are estimated to be up to about 30 m tall and probably the tallest trees in Cathaysia during the Moscovian. They also represent the oldest arborescent trees in North China because the Late Ordovician to early Carboniferous sedimentary records are missing. The absence of growth rings in the trunks, together with the occurrence of bauxite, siderite nodules, and lycopsid stems, suggests that these cordaitalean trees would have grown in a stream riparian environment under a perhumid climate.

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### Figure captions

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 situated in palaeoequatorial area of the Cathaysia (red star, after Scotese and Wright, 2018). (C) Geological map of research area (modified after Wan et al., 2017b), showing collection site marked by the red star. O<sub>1</sub>: Ordovician Liangjiashan Formation; O<sub>2</sub>: Ordovician Fengfeng Formation; C<sub>2</sub>: Carboniferous Benxi Formation and lower part of the Taiyuan Formation; P<sub>1a</sub>: lower to middle Permian including the upper part of the Taiyuan Formation, Shanxi Formation, Lower Shihezi Formation and Upper Shihezi Formation; P<sub>3</sub>: upper Permian Sunjiagou Formation; T<sub>1</sub>: Lower Triassic Liujiagou Formation and Heshanggou Formation; T<sub>2</sub>: Middle Triassic Ermaying Formation and Tongchuan Formation; N: Neogene; Q: Quaternary, loess deposit.

Fig. 2. Chrono- and lithostratigraphy of the Benxi, Taiyuan, and Shanxi formations in Yangquan, Shanxi Province, North China (modified after Wang and Zhang, 1983).

The wood symbol marks the collection interval between the upper two limestones units. In the Benxi Formation, PDL No. 1 refers to the lowermost unit of Pingdingshi Limestone; PDL No. 2 is the second unit of Pingdingshi Limestone in the middle; and, PDL No. 3 points to the uppermost unit of Pingdingshi Limestone. In the

Taiyuan Formation, SJSL is the Sijieshi Limestone; QSL means the Qianshi Limestone; and, HSL refers to the Houshi Limestone.

Fig. 3. (A) Field photo showing an upward thinning succession of sandstones with a basal channel lag composed of conglomerates (red arrow) overlying an erosional channel base; white arrow points to the large cross beddings. (B) Field photo showing three fossil trunks and axes in the channel lag deposits (red arrows). (C) Field photo showing a large trunk with an inflated base preserved parallel to bedding (red arrow); hammer is 0.28 m long. (D) Field photo showing a fossil stem with a central pith in the middle preserved in gravelly sandstone. (E) Field photo showing cordaitalean leaves present in the same fossil interval with distinct parallel venation.

Fig. 4. Photographs showing the gross morphology and anatomical features of *Damudoxylon meii* n. sp. from the Moscovian Benxi Formation in Yangquan, Shanxi Province, North China. (A) Photograph of a cross section of the fossil wood, showing the overview of the plant stem containing a solid pith (P) and secondary xylems (SX); Catalog No.: PB23311, holotype. (B) Photograph of a cross section of the fossil wood, showing the circular pith (P) surrounded by secondary xylems (SX); Catalog No.: PB23311, holotype. (C) Photograph of a cross section of the fossil wood, showing a secretory cavity (white arrow) situating at the periphery of the pith (P); SX refers to the secondary xylem; Catalog No.: PB23311, holotype. (D) Photograph of a cross section of the fossil wood, showing a secretory cavity surrounded by 2–3 rings of parenchymatous cells (white arrows); Catalog No.: PB23311, holotype. (E) Photomicrograph of a cross section of the fossil wood, showing the hollow secretory cavity enveloped by parenchymatous cells (white arrows); red arrow points to the normal circular parenchymatous cell in the pith; Catalog No.: PB23311, slide number: PB23311-1, holotype.

Fig. 5. Photomicrographs showing the anatomical features of *Damudoxylon meii* n. sp. from the Moscovian Benxi Formation in Yangquan, Shanxi Province, North China. (A) Cross section of the fossil stem, showing the endarch primary xylem (white arrow); red arrows point to the parenchymatous cells in the pith (P) with opaque contents; the size of parenchymatous cells decreases from the center to the marginal part of the pith; SX refers to the secondary xylem; Catalog No.: PB23311, slide number: PB23311-1, holotype. (B) Cross section of the fossil stem, showing the distribution of the pith (P), primary xylem (white arrow) and secondary xylem (SX); Catalog No.: PB23311, holotype. (C) Radial section of the fossil wood, showing the large cells with greater width in the central pith (CP) and the smaller cells at the periphery pith (PP); white arrows point to the scalariform thickenings of the primary xylem (PX); Catalog No.: PB23311, slide number: PB23311-2, holotype. (D) Radial section of the fossil wood, showing the dominantly biseriate bordered pits on tracheidal walls (white arrows); Catalog No.: PB23311, slide number: PB23311-2, holotype. (E) Radial section of the wood, showing the predominant biseriate (white arrows) and partially uniseriate (red arrows) pitting on tracheidal walls; Catalog No.: PB23311, slide number: PB23311-3, holotype. (F) Tangential section of the wood, showing the uniseriate rays (white arrows); Catalog No.: PB23311, slide number: PB23311-4, holotype. (G) Radial section of the wood, showing the dispersed bordered pits (white arrows) in the cross-field; Catalog No.: PB23311, slide number: PB23311-3, holotype.

Fig. 6. Photographs showing the gross morphology and anatomical features of *Agathoxylon leei* n. comb. from the Moscovian Benxi Formation in Yangquan, Shanxi Province, North China. (A) Photograph of a cross section of the fossil wood, showing the overview of the plant stem containing a pith (P) and secondary xylems (SX); Catalog No.: PB23312. (B) Photograph of a radial section of the fossil wood, showing the septate pith with horizontal diaphragms (white arrows); Catalog No.: PB23312.

(C) Photograph of a radial section of the fossil wood, showing the distribution of septate pith (P) and secondary xylem (SX); Catalog No.: PB23313. (D) Radial section of the fossil wood, showing the dominantly uniseriate (red arrows), partially biseriate (white arrow) bordered pits on tracheidal walls; Catalog No.: PB23312, slide number: PB23312-1. (E) Tangential section of the wood, showing the uniseriate rays (white arrows); Catalog No.: PB23312, slide number: PB23312-2. (F) Radial section of the wood, showing the dispersed bordered pits (white arrows) in the cross-field. Catalog No.: PB23312, slide number: PB23312-1.

**Anatomically preserved cordaitalean trees from the Pennsylvanian of Yangquan**

**City, Shanxi Province, and their implication for a perhumid climate in North**

**China**

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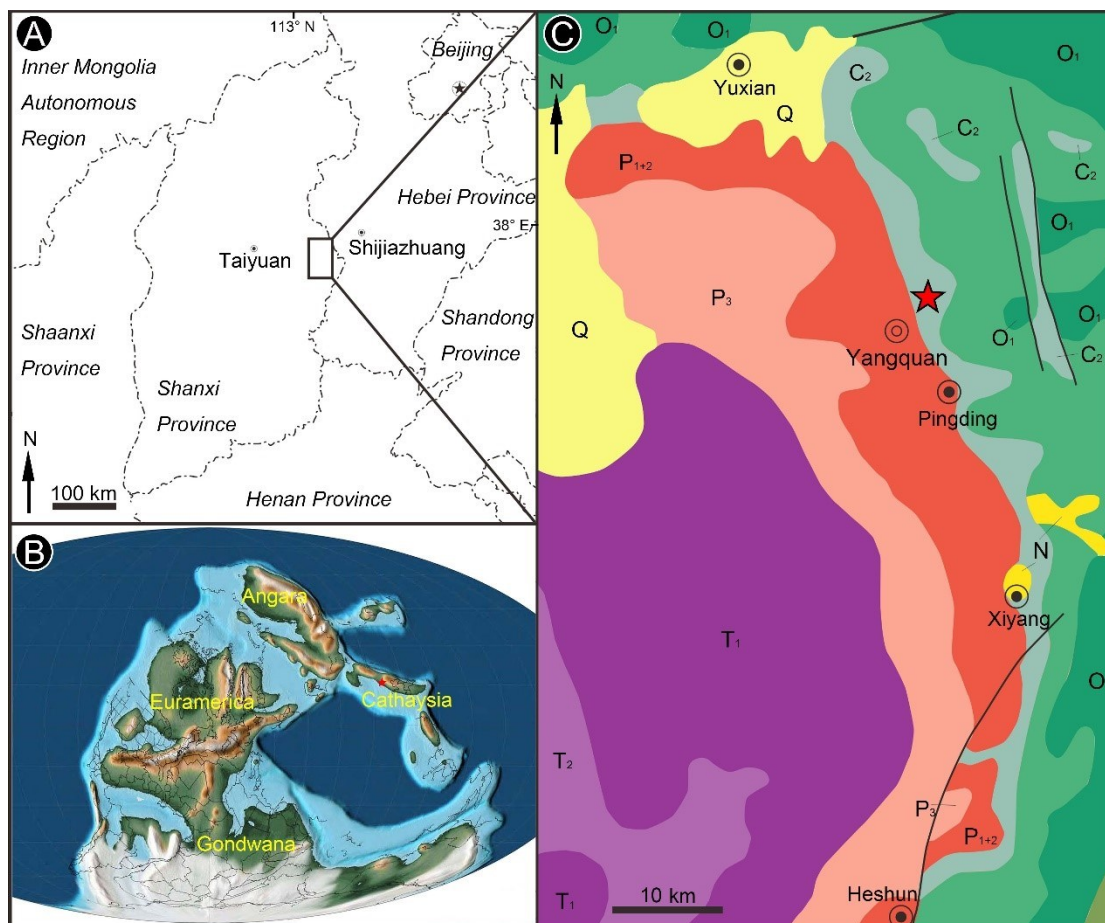
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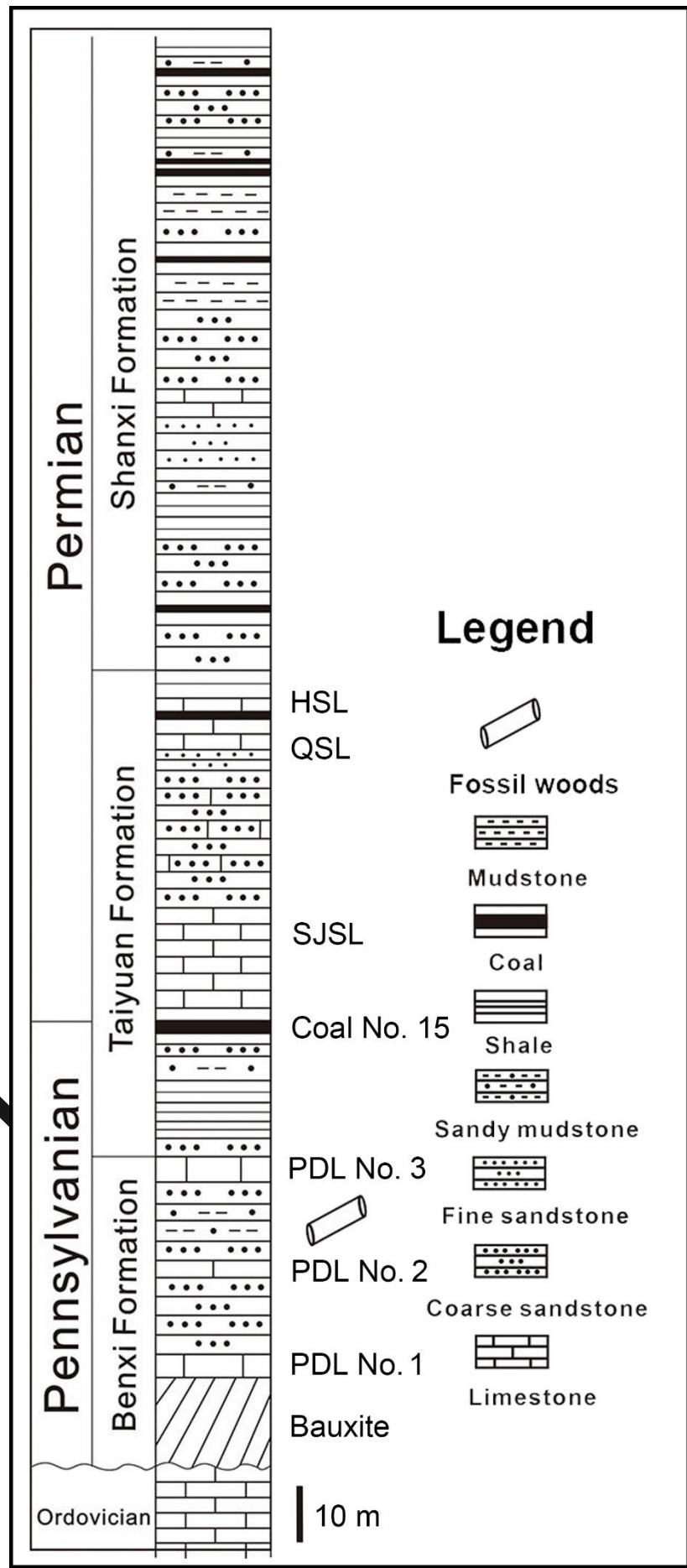
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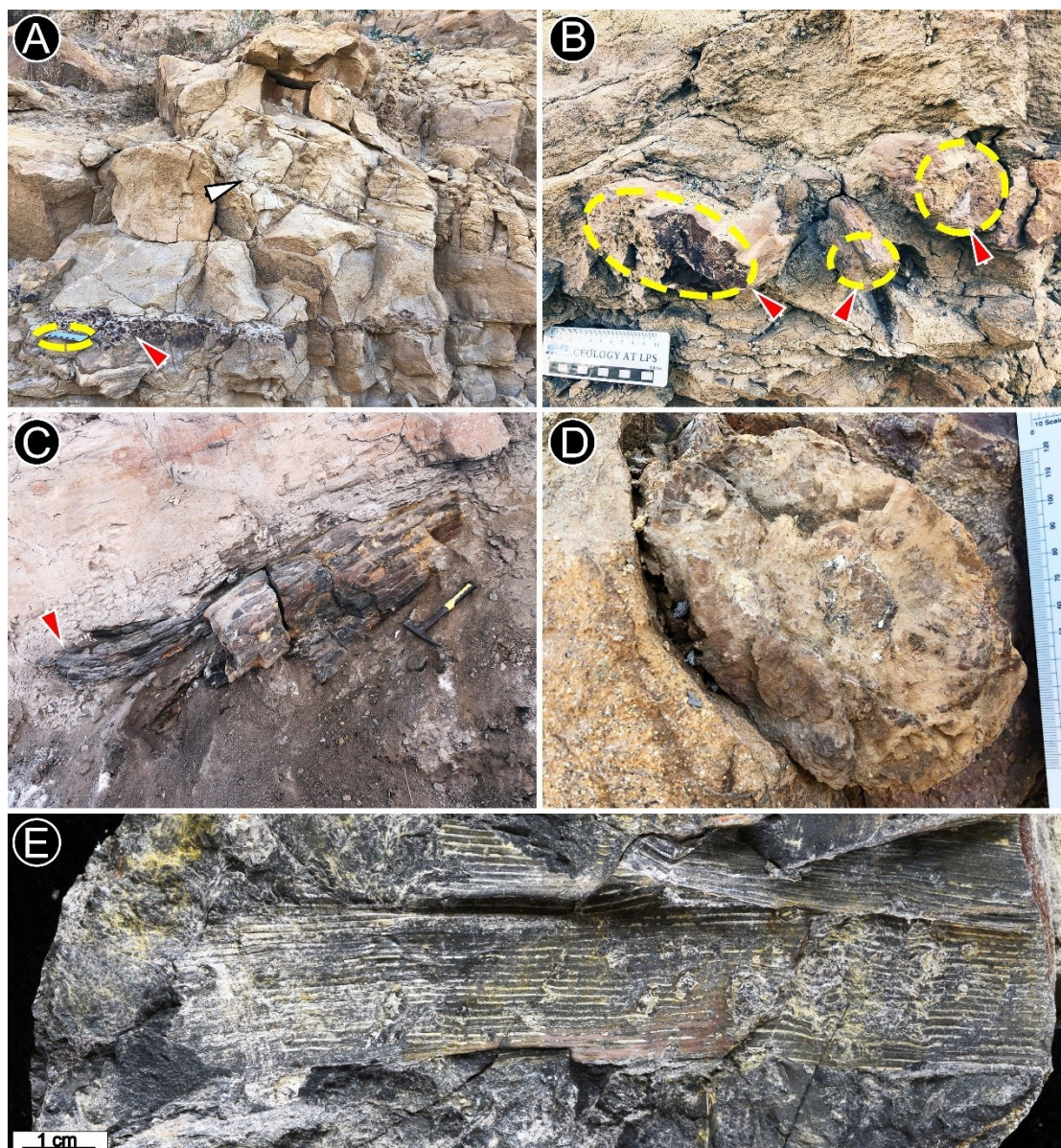
**Abstract:** Fifty-six cordaitalean trunks with anatomical features are discovered and described from the Moscovian (Pennsylvanian) Benxi Formation in Yangquan City, Shanxi Province, North China. They are allochthonously preserved in fluvial channel deposits and classified into two types based on the anatomy. The first type is characterized by a solid and heterocellular pith, endarch primary xylem and pycnoxylic secondary xylem with araucarian radial tracheidal pits and araucaroid cross-field pitting. The second type contains a septate pith and a pycnoxylic secondary xylem which is comparable to that of the first type. Primary xylem is absent in the second type. The diameter of these trunks ranges from 0.11 to 0.55 m. The largest tree is estimated to be 29.96 meters high using an allometric approach. The trunks represent the oldest and largest trees from the North China Craton during the Pennsylvanian due to the absence of Silurian, Devonian, and Mississippian there. The fossil evidence shows that cordaitaleans were large arborescent trees growing on clastic substrates in the Cathaysia during the Pennsylvanian. Their occurrence from the upper Pennsylvanian in North China Craton suggests that the previously reported diversity of cordaitaleans, which were estimated based on impressions, is a gross underestimate. The absence of growth rings in the trunks and co-occurrence of arborescent lycopsids in the same interval, together with coal seams and bauxite around the fossil-bearing horizons, indicate that the trees grew under perhumid tropical conditions.

**Keywords:** Fossil wood; Anatomy; Carboniferous; Cathaysia; Palaeoecology

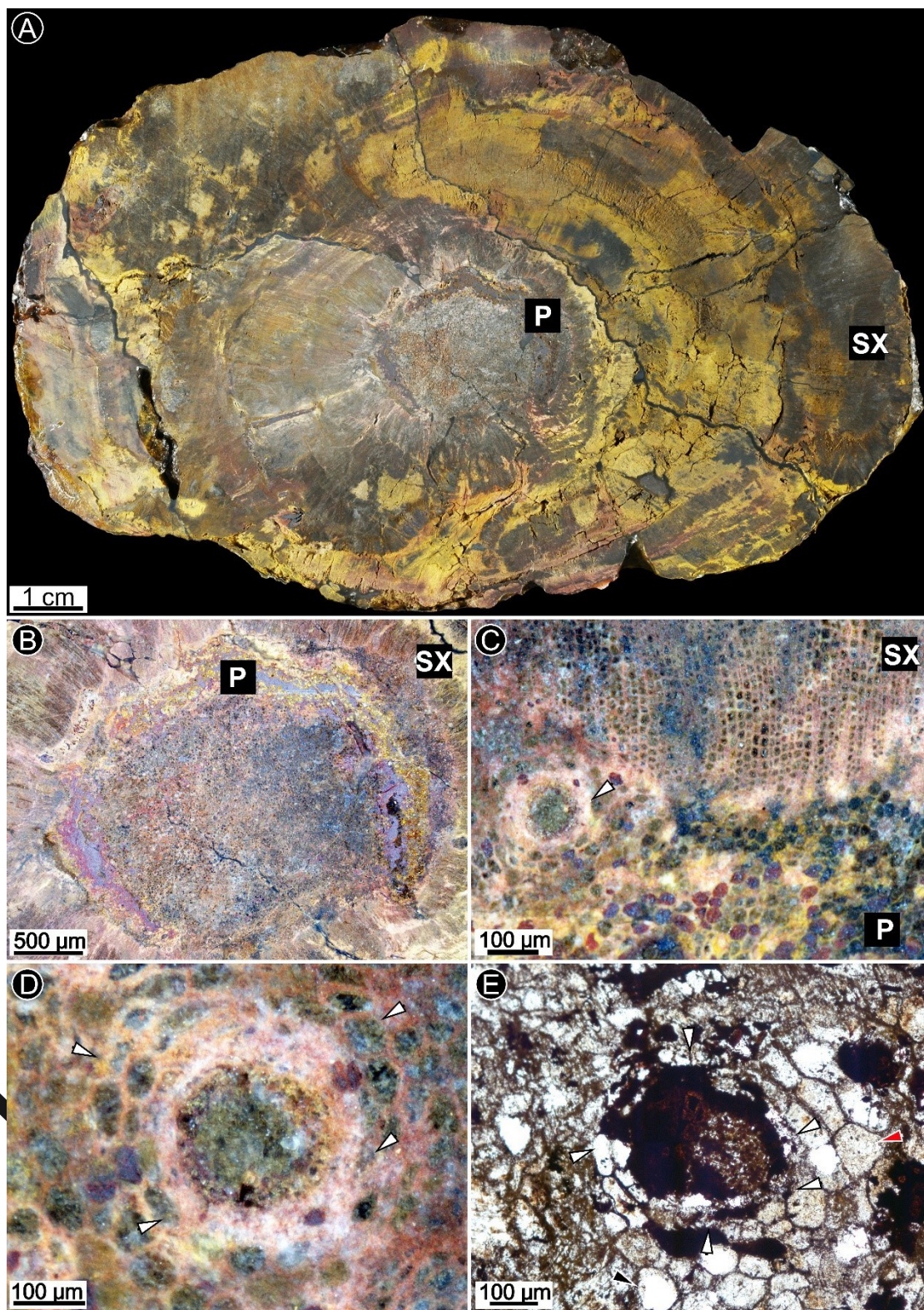




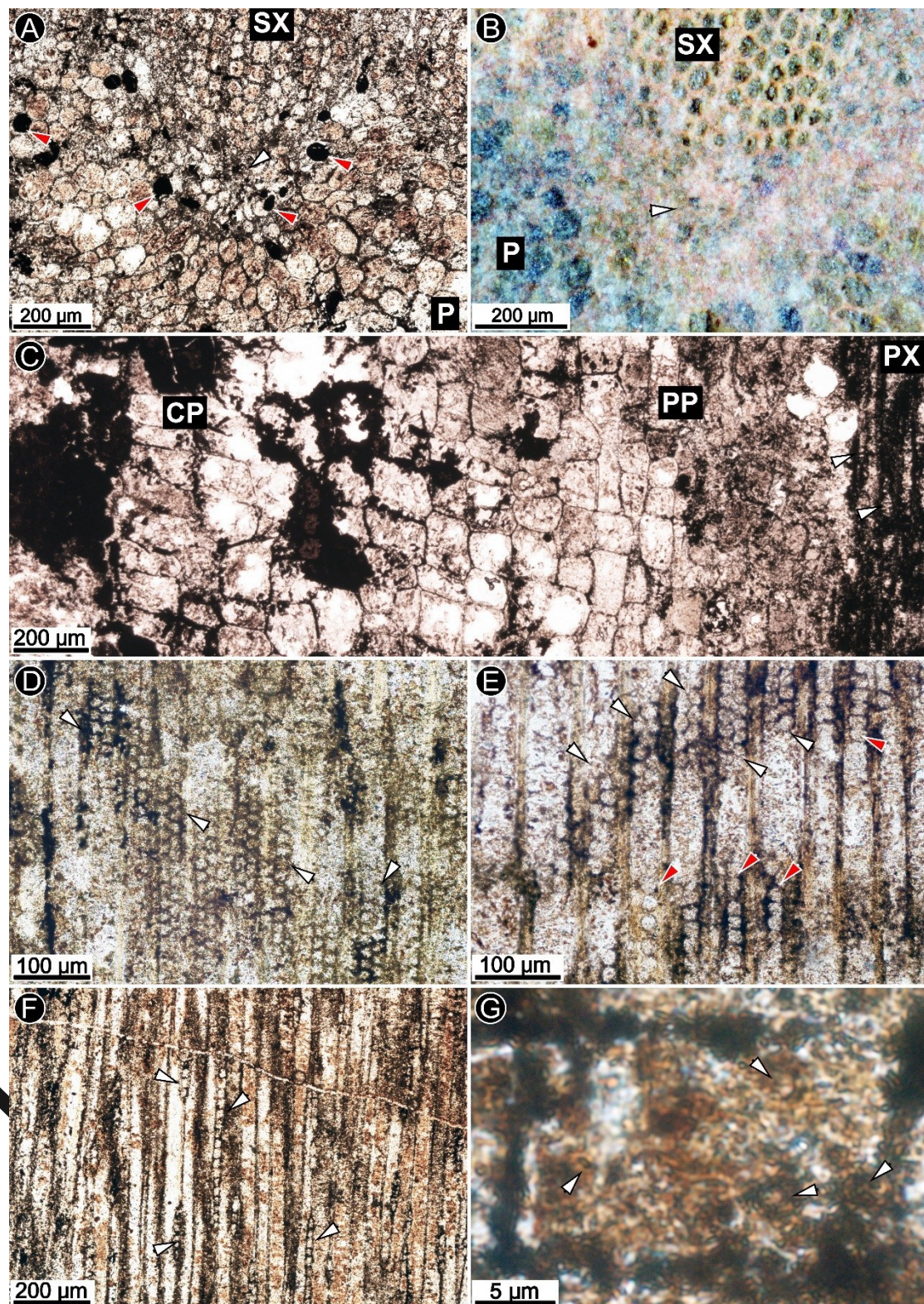














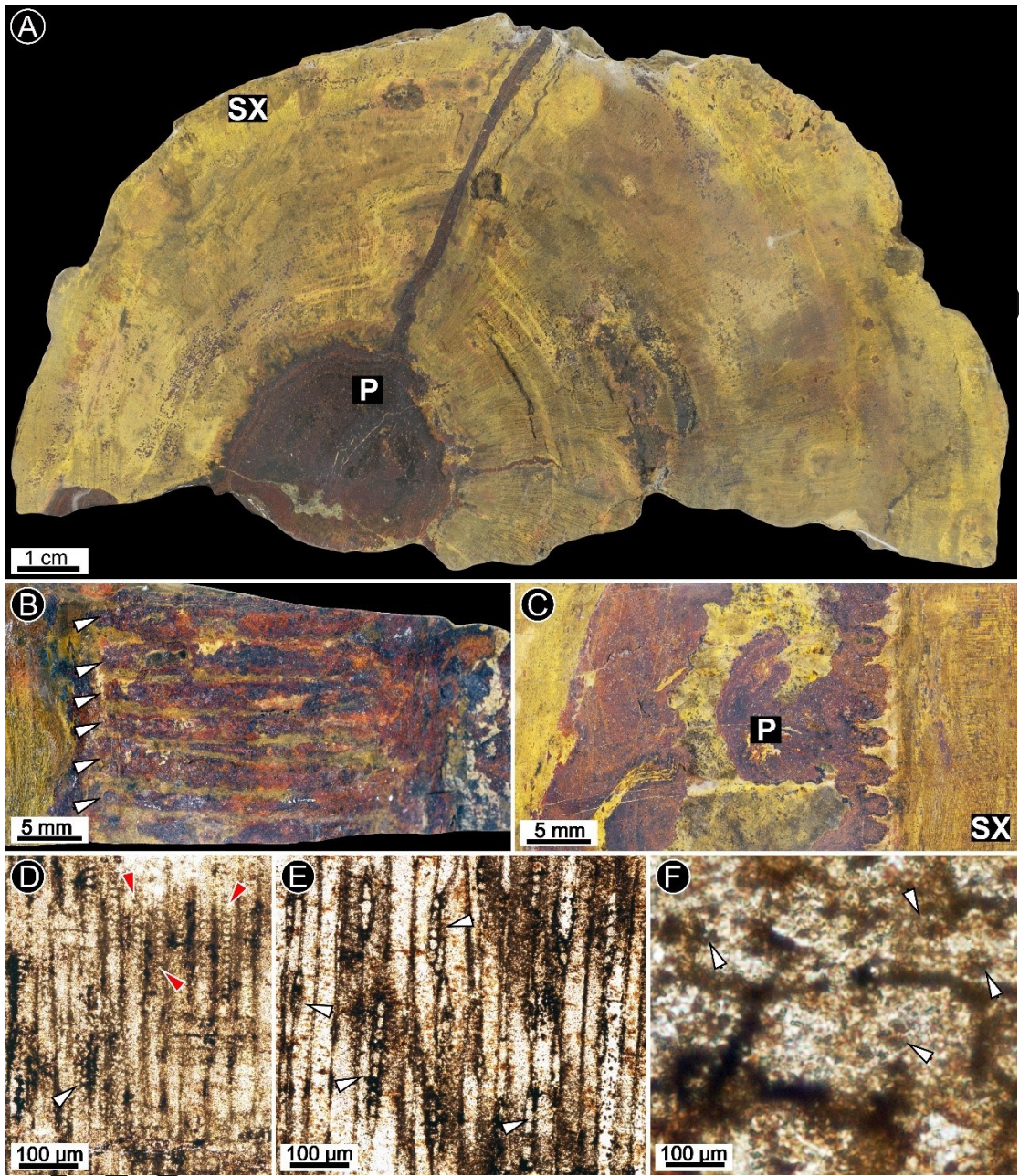


Table 1. Comparative features of the species of *Damudoxylon* Maheshwari, 1967.

Species	Pith	Primary xylem	Secondary xylem			Reference
			Pits on radial walls	Xylem rays	Cross-field pits	
<i>Damudoxylon meii</i> n. sp.	Circular, heterogeneous, with parenchymatous cells and secretory cavities pits alternatively distributed	Endarch	Mostly biseriate, rarely uniseriate, uniseriate pits continuously arranged, biseriate	Uniseriate, 2–27 cells high	Small, dispersed bordered pits with circular apertures present	The present paper

<i>D. adbariense</i> (Prasad) Pant and Singh	Small, wedge-shaped, heterogeneous with resin cells	Endarch	Uni- to tetraseriate, hexagonal, alternate, contiguous pits	Uni- to biseriate, 1–17 cells high	Araucarioid, 3–5 pits	Prasad, 1982
<i>D. arberi</i> Walton	Heterogeneous, with a specialized layer of cells lining inner margins of primary xylem	Undescribed	Uni- to triseriate, occasionally tetraseriate	Uniseriate, 1–20 cells high	1–9 pits in the cross field	Maheshwari, 1967, 1972
<i>D. buritiranaense</i> Kurzawe et al.	Heterocellular, with secretory cells	Endarch	Uniseriate, rarely biseriate	Uniseriate, up to 10 cells high	up to 8 pits	Kurzawe et al., 2013
<i>D. chandrapuraensis</i> (Prasad) Pant and Singh	Heterogeneous, wedge-shaped, with five bays of parenchymatous cell distributed in dark ground tissue	Endarch	Uni- to biseriate	Uni- to biseriate, 1–30 cells high	5–6 pits, bordered, contiguous, rarely serrate, alternate with circular pit pores	Prasad, 1982
<i>D. humile</i> Kurzawe et al.	Homocellular	Endarch	Uniseriate, tangential walls pitted	Uniseriate, up to 3 cells high	Up to 8 pits	Kurzawe et al., 2013
<i>D. indicum</i> (Holden) Pant and Singh	Heterogeneous, with parenchyma and secretory regions, separated by a transfusion sheath	Undescribed	Uni- to biseriate	Uniseriate, 2–7 cells high	1–4 pits in the cross field	Maheshwari, 1967, 1972
<i>D. maharashtraensis</i> (Prasad) Pant and Singh	Heterogeneous with secretory cells, disturbed in the parenchymatous ground tissue	Endarch	Uni- to triseriate, mostly biseriate	Mostly uniseriate, rarely biseriate, 1–16 cells high	Circular, bordered, 5–6 pits in the cross field	Prasad, 1982
<i>D. rossleri</i> Kurzawe et al.	Homocellular	Endarch	Uni- to triseriate	Uniseriate, rarely biseriate, up to 16 cells high	5–6 pits	Kurzawe et al., 2013
<i>D. waltonii</i> Maheshwari	Homocellular, 1 cm or less in diameter with secretory cells and parenchyma	Undescribed	Uni- to triseriate pitting, occasionally tetraseriate	1–14 cells high, mostly 2–3 cells	1–9 pits in the cross field	Maheshwari, 1967, 1972
<i>D. zhoui</i> Zhang and Zheng	Circular, heterogeneous, with parenchymatous and secretory cells	Endarch	Uni- to triseriate, tangential pits present	Mostly uniseriate, rarely biseriate	Undescribed	Zheng et al., 2008