Yin et al. Journal of Palaeogeography (2020) 9:22
https://doi.org/10.1186/s42501-020-00071-z

Journal of Palaeogeography

ORIGINAL ARTICLE Open Access

Early-Middle Permian palynoflora of Shandong Province, eastern North China

Tian-Tao Yin[1,2], Shou-Jun Li[1*], Xiang-Yu Zhang[1] and Xiu-Li Zhao[1]

Abstract

The Permian Taiyuan and Shanxi formations exposed in Shandong Province, eastern North China, contain abundant spores and pollen. In this study, a total of 42 genera and 146 species of spores and pollen from these Permian formations, native to northern China, are identified and related to the three epochs of the Permian Period (Cisuralian, Guadalupian, and Lopingian Epochs) as two assemblages: Assemblage I — the *Laevigatosporites*–*Granulatisporites* assemblage, inferred as the Cisuralian (~ 298.9–272.9 Ma); and, Assemblage II — the *Gulisporites*–*Sinulatisporites* assemblage, inferred as the Guadalupian (~ 272.9–259.1 Ma). Assemblage I represents growing ferns, whereas Assemblage II represents gymnosperms. The assemblage division and analysis indicated that the palaeoclimate of the study area during Early-Middle Permian time was dominated by warm and humid conditions, and later in the Middle Permian changed into moderately dry conditions.

Keywords: Permian, Spores and pollen, Vegetation succession, Paleoclimate, Environmental change, Taiyuan Formation, Shanxi Formation

1 Introduction

In recent decades, Carboniferous to Permian floras of China have been studied by many scientists (Gao 1984; Cheng 2000; Shi and Chen 2003; Hilton and Cleal 2007; Wang 2010; Spencer et al. 2013), and global terrestrial vegetation has also been widely studied (Phillips and DiMichele 1992; Peppers 1996; Cleal and Wang 2002; DiMichele et al. 2006, 2009, 2011). The evolution of plants during the Carboniferous and Permian Periods is commonly ascribed to their development, climatic zoning, and environmental change. Four distinct floras developed worldwide during the Pennsylvanian-Cisuralian Epochs were recognized respectively as the Cathaysian flora, the Euramerican flora, the Angaran flora, and the Gondwanan flora (Sun 1997; DiMichele et al. 2001; Hilton and Cleal 2007). These floras evolved under dissimilar environmental conditions. The Gondwanan and Angaran floras, different from the Euramerican and Cathaysian floras of low palaeolatitude and tropical area, were prevalent in middle and high palaeolatitudes (Meyen 1997; Vega and Archangelsky 1997; DiMichele et al. 2001; Naugolnykh 2002; Hilton and Cleal 2007).

Despite their location in low palaeolatitudes, research on the Euramerican and Cathaysian floras indicated some distinctions between the two floras. Sun (1996, 2001) discovered that the Cathaysian flora evolved from the Mississippian "global" *Lepidodendropis* flora. In addition, it is different from the Euramerican flora with the characteristics of endemic genera and species such as *Cathysiodendron*, *Gigantopteris*, *Gigantonoclea*, *Cathaysiopteris*, etc. (Sun 2006). Wang and Pfefferkorn (2013) also supported this viewpoint, suggesting that the Cathaysia flora has its own genera and species, which are different from the Euramerican flora. Furthermore, Hilton and Cleal (2007) inferred that the extinction time of the ecosystems of Euramerican and Cathaysia floras were inconsistent, which might be caused by climatic and environmental changes. Therefore further analysis is needed to improve understanding of the distinctions between Euramerican and Cathaysian floras.

Evolution of the Permian floras in China has been investigated in numerous researches regarding plant fossil

* Correspondence: lishoujun@126.com
[1]College of Earth Science and Engineering, Shandong University of Science and Technology, Qingdao 266590, Shandong Province, China
Full list of author information is available at the end of the article

assemblages (e.g., Tian et al. 1996, 2000; Sun 2001; Cleal and Wang 2002; Hilton and Cleal 2007; Wang 2010; DiMichele et al. 2011), such as the Cathaysian tropical flora reported in North China (Li 1997; Ouyang and Hou 1999; Hilton and Cleal 2007), the Cisuralian coal-forming flora originated from the Wuda District of Inner Mongolia (Pfefferkorn and Wang 2007), and, the macrofloral assemblages from Weibei coalfield of North China (Wang 2010); these previous researches provide a basis for this study.

Permian stratigraphy in South China was divided into three epochs based on marine setting data (Shen et al. 2005; Zhang et al. 2009), through comparisons of conodont-bearing stratigraphic sections with those in other areas of the world (Mei et al. 2004; Shen and Mei 2010; Shen et al. 2019). In contrast, the Permian strata in North China were continental and lacked international correlatives for comparison.

Shandong Province of eastern North China deposited a large number of coal resources during the Carboniferous-Permian. There were abundant spores and pollen in these sediments. A number of studies have been conducted on the Permian palynological fossils in different areas of Shandong Province, including the Jining coalfield (Ouyang and Hou 1999), Xinwen coalfield (Song et al. 2005), Yanzhou coalfield (Zhu et al. 2005), Tengxian coalfield (Su et al. 2007), and Echeng coalfield (Song et al. 2009). However, these studies used the older stratigraphy of the two-fold division scheme of the Lower and Upper Permian.

In contrast to the foregoing studies, this study puts forward some innovative results of the Permian palynological fossils in Shandong Province based on the current three-fold division of the Permian System. The aim of this study is to develop a more detailed understanding of Permian paleontology and stratigraphy in the study area and to provide evidence for the boundary identification between the Lower and Middle Permian in North China.

2 Geological setting

Shandong Province is located in the east of the North China Block (NCB; Fig. 1a), which is about 320 km from north to south and 280 km from east to west (Fig. 1b). Our study area is bounded by the Liaocheng-Lankao Fault in the west, Qihe-Guangrao Fault in the north,

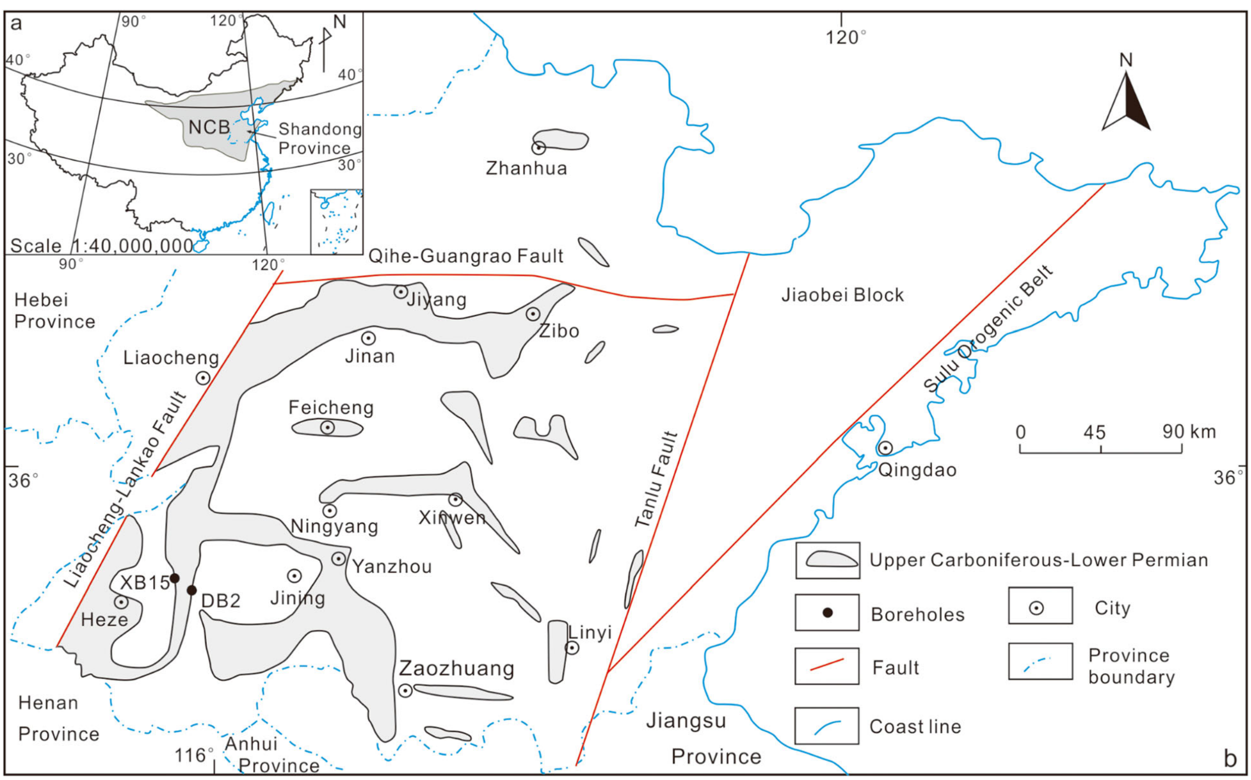

Fig. 1 a Location of the Shandong Province in North China (the map of China is based on the standard map available on the official website of Ministry of Natural Resources of China: http://bzdt.ch.mnr.gov.cn/); **b** The Upper Carboniferous to Lower Permian strata distribution in Shandong Province and locations of the studied boreholes (XB15 and DB2)

Tanlu Fault in the east (Fig. 1b). The two boreholes (XB15 and DB2) selected in this study are located in the Heze area of Shandong Province.

Upper Carboniferous to Lower Permian strata in Shandong Province are composed mainly of the Taiyuan and Shanxi formations in ascending order (Fig. 2). The Taiyuan Formation consists mostly of limestone, mudstone, sandstone and coal seams. The Shanxi Formation is characterized by thick sandstone, silty mudstone, and a small amount of coal. The upper Taiyuan Formation is of the marine/continental setting, and the Shanxi Formation indicates a continental environment.

Research on the Cathaysian flora has a long history. The term "Cathaysian flora" was proposed by Halle (1935) and is derived from the ancient microcontinent Cathaysia that constituted the easternmost part of Pangea. The Pennsylvanian to Permian Cathaysian flora contains true ferns, seed ferns, sphenopsids, and other plants (Sun 1996; Zhao et al. 2006; Yin et al. 2016), indicating tropical rainforest conditions. This flora was prevalent in areas corresponding to present-day Asia, including China, Korea, Japan, and other low-latitude countries. Additionally Li (1997) established two floras

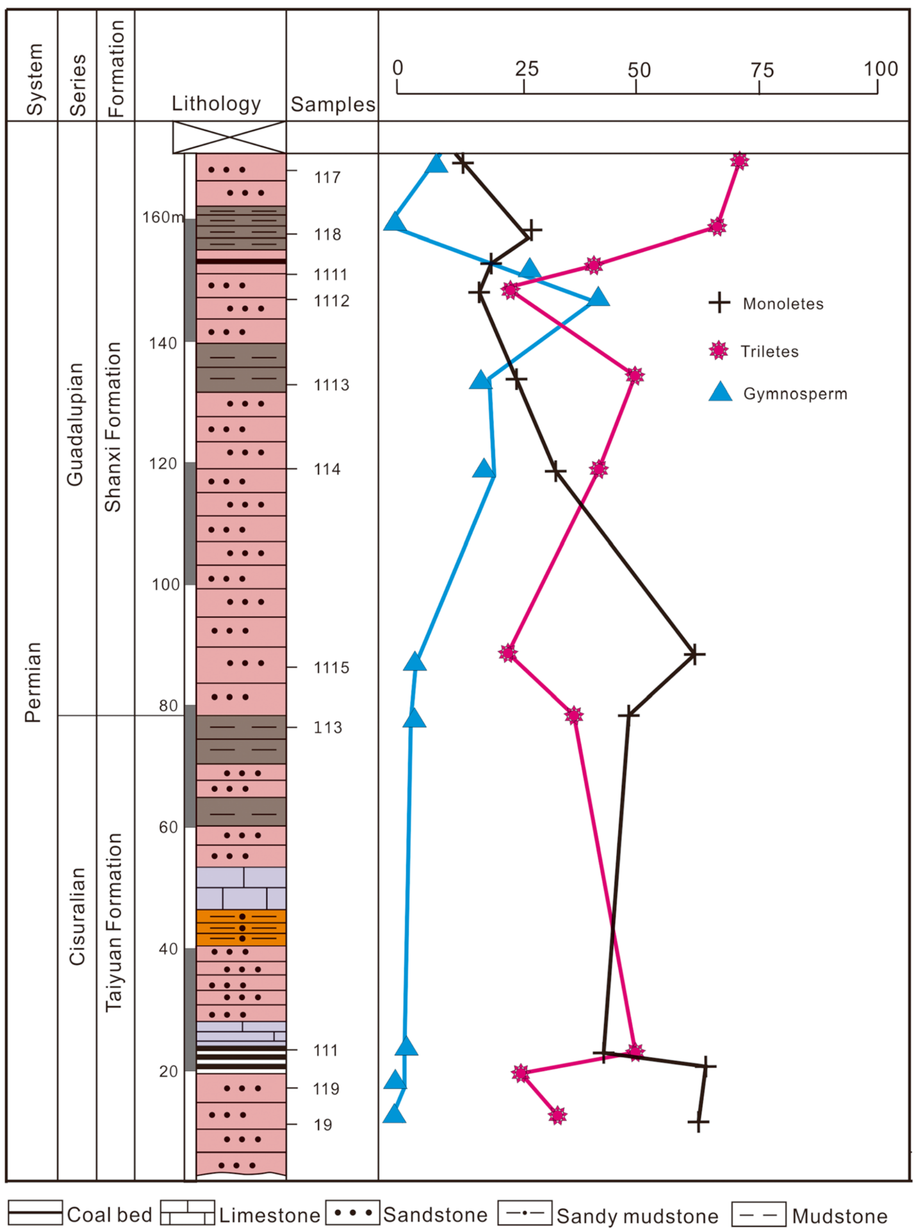

Fig. 2 The major stratigraphy, lithology, and fossil contents/variations of the Permian in Shandong Province, eastern North China (modified after Lü 2015)

in the Taiyuan and Shanxi formations in North China, namely, *Neuropteris ovata–Lepidodendron posthumii* and *Emplectopteridium alatum–Taeniopteris mucronata–Lobatannularia sinensis* plant assemblages, both belonging to the Cathaysian flora.

The Euramerican flora also attracted the interest of many scholars. Two main biomes are recognized in Europe and America continents in wetlands and seasonally dry environments during the Pennsylvanian to Permian (e.g., DiMichele and Aronson 1992; Falcon-Lang and Scott 2000). The wetland biomes are the best known and can be broadly subdivided into peat-forming-swamp and flood-basin floras (e.g., Gastaldo 1987; Gastaldo et al. 1996). Evidence for seasonally-dry communities is indicated by the presence of conifers during Middle Pennsylvanian (Scott 1974). Until the latest Carboniferous (of the older-named Stephanian Epoch), both the peat-forming-swamp and flood-basin floras occurred as well-developed, mainly seed-plant-dominated assemblages (Winston 1983; DiMichele and Aronson 1992; DiMichele et al. 2001).

In recent years, some Chinese scholars conducted extensive research on Permian palynological fossils in Shandong Province (e.g., Ouyang and Hou 1999; Jiang et al. 2002; Song et al. 2005, 2009; Su et al. 2007). They established different spore and pollen assemblages in the Taiyuan and Shanxi formations and discussed their characteristics and geological age. But these studies were based mainly on the traditional two-fold division scheme of the Permian (Lower and Upper). After division of Permian strata into three series/epochs (i.e., the Lower/Early, Middle/Middle, and Upper/Late Permian), Li et al. (2013) established two spore and pollen assemblages in the Taiyuan and Shanxi formations of Pengzhuang coalfield, discussed their characteristics and tried to solve the problem of their age attribution. However, the affinities of spores and pollen need further studies.

This study is based on analyses in relation to the three series/epochs of Permian in eastern North China and investigation of spores and pollen within the two studied boreholes. It attempts to explain the affinities of spores and pollen, discuss the palaeoclimate reflected by them, and compare them with the Euramerican flora. This study is significant to understand the characteristics of the Early-Middle Permian flora in Shandong Province, to enrich the Late Paleozoic flora in North China, and to further rectify the boundary of the Permian internal series in North China Block.

3 Material and methods

Eleven core samples were collected from each of the two studied boreholes (XB15 and DB2). Sediments most likely to yield palynomorphs (e.g., silt) were preferentially sampled. All of the samples contained abundant spore and pollen fossils. In the Spore and Pollen Laboratory of Shandong University of Science and Technology, Qingdao, sludge on the sample surface was removed and then clean samples were crushed for sieving with 0.3 mm pore diameter. After drying, 30 g of dried sediment from each sample was weighed and placed in a 1000 ml beaker, to which heavy liquid comprising hydrochloric acid, hydrofluoric acid, hydroiodic acid, and potassium iodide was added to macerate, fully dispersing the sample in the solvent and allowing organic material to be separated. Samples were repeatedly washed with tap water for about 2 weeks and the water was changed every 8 hours day by day. Sieve residues were dried to

Table 1 Authoritative name and corresponding representative illustration of Assemblage I taxa identified from the Permian spore and pollen fossils of boreholes XB15 and DB2 in Shandong Province

Taxa	Literature	Illustration
Calamospora breviradiata	Kosanke 1950	Fig. 3a
Calamospora sp.	Schopf et al. 1944	Fig. 3b
Calamospora hartungiana	Gao 1984	Fig. 3c
Calamospora minuta	Bharadwaj 1957	Fig. 3d
Convolutispora cerebra	Smith and Butterworth 1967	Fig. 3e
Convolutispora tessellata	Hoffmeister et al. 1955	Fig. 3f
Crassispora adornata	Ouyang 1962	Fig. 3g
Cyclogranisporites aureus	Potonié and Kremp 1955	Fig. 3h
Cyclogranisporites micaceus	Imgrund 1952	Fig. 3i
Densosporites annulatus	Smith and Butterworth 1967	Fig. 3j
Florinites minutus	Bharadwaj 1954	Fig. 3k
Foveolatisporites junior	Bharadwaj 1957	Fig. 3l
Granulatisporites minutus	Potonié and Kremp 1955	Fig. 3m
Gulisporites cereris	Gao 1984	Fig. 3n
Gulisporites cochlearius	Imgrund 1960	Fig. 3o
Laevigatosporites minimus	Schopf et al. 1944	Fig. 3p
Laevigatosporites maximus	Potonié and Kremp 1956	Fig. 4a
Laevigatosporites vulgaris	Ibrahim 1933	Fig. 4b
Laevigatosporites perminutus	Alpern 1958	Fig. 4c
Leiotriletes adnatus	Potonié and Kremp 1955	Fig. 4d
Leiotriletes sphaerotriangulus	Potonié and Kremp 1954	Fig. 4e
Leiotriletes sp.	Potonié and Kremp 1954	Fig. 4f
Lycospora pusilla	Schopf et al. 1944	Fig. 4g
Microreticulatisporites sp.	Potonié and Kremp 1954	Fig. 4h
Punctatisporites sp.	Potonié and Kremp 1954	Fig. 4i
Punctatosporites granifer	Potonié and Kremp 1956	Fig. 4j
Punctatosporites minutus	Ibrahim 1933	Fig. 4k
Striolatospora sp.	Zhou 1980	Fig. 4l
Spinosporites spinosus	Alpern 1956	Fig. 4m
Thymospora pseudothiessenii	Kosanke 1950	Fig. 4n
Verrucosisporites verrucosus	Ibrahim 1933	Fig. 4o

make specimens with glycerol. A Nikon microscope and camera were used for microexamination and imaging. All the imaged specimens are housed in the School of Earth Sciences and Engineering, Shandong University of Science and Technology. The grains shown in the plates were located with an England Finder, and the coordinates are held in the same facility as where the specimens are housed.

4 Results

A total of 42 genera and 146 species were identified from spore and pollen fossils in sediment samples from the boreholes XB15 and DB2. According to content changes in the spore and pollen fossils (Fig. 2), two assemblages were recognized: Assemblage I, *Laevigatosporites–Granulatisporites* assemblage; and Assemblage II, *Gulisporites–Sinulatisporites* assemblage. The authoritative names and corresponding representative images of Assemblage I taxa are listed in Table 1, and those of Assemblage II taxa are listed in Table 2. In addition, there are other less abundant genera and species that were identified. We speculate that they likely migrated to the study area with rare spores and low content by means of external forces, which are not representative and meaningless to indicate the palaeoclimate of the study area. Therefore, the focus of this study is to discuss the palaeoclimate change reflected by the dominant genera and species in the studied spore and pollen assemblages, which may be more typical.

Prior to the palynology analysis, species data were transformed to relative abundances (percentage) of the

Table 2 Authoritative name and corresponding representative illustration of Assemblage II taxa identified from the Permian spore and pollen fossils of boreholes XB15 and DB2 in Shandong Province

Taxa	Literature	Illustration
Calamospora pedata	Kosanke 1950	Fig. 5a
Converrucosisporites minutus	Gao 1984	Fig. 5b
Converrucosisporites sp.	Potonié and Kremp 1954	Fig. 5c
Cyclogranisporites aureus	Potonié and Kremp 1955	Fig. 3h
Cyclogranisporites micaceus	Potonié and Kremp 1955	Fig. 3i
Cyclogranisporites microgranus	Bharadwaj 1954	Fig. 5d
Cyclogranisporites pseudozonatus	Ouyang 1986	Fig. 5e
Densosporites annulatus	Smith and Butterworth 1967	Fig. 3j
Florinites antiquus	Schopf et al. 1944	Fig. 5f
Florinites minutus	Bharadwaj 1954	Fig. 3k
Gulisporites cereris	Gao 1984	Fig. 3n
Gulisporites cerevus	Imgrund 1960	Fig. 5g
Gulisporites cochlearius	Imgrund 1960	Fig. 3o
Gulisporites curvatus	Gao 1984	Fig. 5h
Gulisporites laevigatus	Imgrund 1960	Fig. 5i
Gulisporites sp.	Imgrund 1960	Fig. 6a
Laevigatosporites minimus	Schopf et al. 1944	Fig. 3p
Leiotriletes adnatus	Potonié and Kremp 1955	Fig. 4d
Leiotriletes sphaerotriangulus	Potonié and Kremp 1954	Fig. 4e
Leiotriletes tangyiensis	Zhou 1980	Fig. 6b
Lophotriletes cf. *communis*	Naumova 1953	Fig. 6c
Lophotriletes humilus	Hou and Wang 1986	Fig. 6d
Lycospora pusilla	Schopf et al. 1944	Fig. 4g
Punctatisporites gigantus	Ouyang 1986	Fig. 6e
Punctatisporites incomptus	Felix and Burbridge 1967	Fig. 6f
Sinulatisporites cf. *shanxiensis*	Gao 1984	Fig. 6g
Sinulatisporites cf. *sinensis*	Gao 1984	Fig. 6h
Stenozonotriletes marginellus	Gao 1984	Fig. 6i
Stenozonotriletes sp.	Hacquebard 1957	Fig. 6j
Triquitrites sp.	Potonié and Kremp 1954	Fig. 6k

total spore and pollen fossils in the established assemblages; and the spore and pollen fossil content variations were shown in Fig. 2. Diversities of the identified spore and pollen assemblages are illustrated as photomicrographs in Figs. 3, 4, 5 and 6.

4.1 Characteristics of Assemblage I

Relative abundance of major taxa in Assemblage I, the *Laevigatosporites–Granulatisporites* assemblage, identified in the Permian Taiyuan Formation, are provided in Table 3. The main genera and species of monolete spores are *Spinosporites spinosus*, *Laevigatosporites minimus*, *L. maximus*, *L. vulgaris*, *L. perminutus*, *Thymospora pseudothiessenii*, *Punctatosporites granifer*, *P. minutus*, *and Striolatospora* sp.

The main genera and species of Azonotriletes are *Granulatisporites minutus*, *Calamospora breviradiata*, *C. minuta*, *C. glaber*, *C. hartungiana*, *Verrucosisporites verrucosus*, *Cyclogranisporites micaceus*, *Leiotriletes sphaerotriangulus*, *L. adnatus*, *L. tangyiensis*, *Raistrickia saetosa*, *Cyclogranisporites microgranus*, *C. aureus*, *Convolutispora cerebra*, *C. tessellata*, *Crassispora adornata*, *Foveolatisporites junior*, and *Microreticulatisporites* sp. The Zonotriletes mainly include *Densosporites annulatus*, *Gulisporites cereris*, *G. cochlearius*, and *Lycospora pusilla*.

Gymnosperm pollen is principally *Florinites minutus*.

4.2 Characteristics of Assemblage II

Relative abundance of major taxa in Assemblage II, the *Gulisporites–Sinulatisporites* assemblage, identified in the Permian Shanxi Formation of Shandong Province, are reported in Table 4.

Azonotriletes include *Cyclogranisporites aureus*, *C. micaceus*, *C. microgranus*, *Converrucosisporites minutus*, *C.* sp., *Punctatisporites incomptus*, *P. gigantus*, *Leiotriletes tangyiensis*, *L. sphaerotriangulus*, *L. adnatus*, *Verrucosisporites kaipingiensis*, *Crassispora mucronata*, *Calamospora pedata*, *Lophotriletes* cf. *communis*, and *L. humilus.*

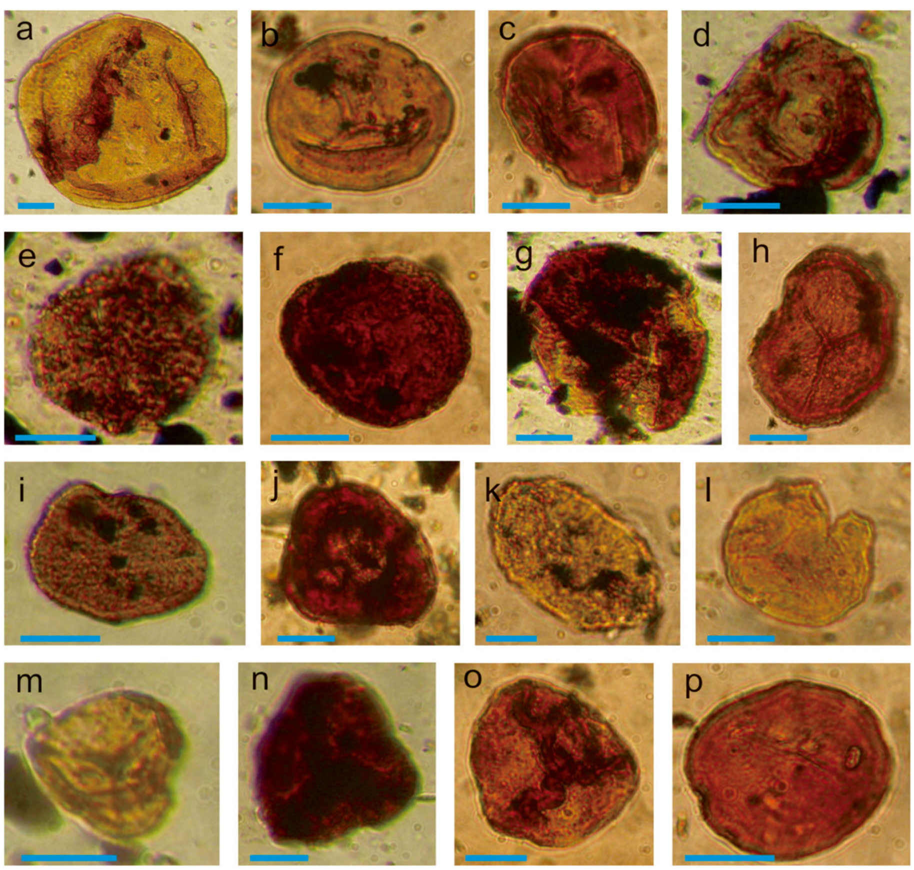

Fig. 3 Photomicrographs of a selection of spore and pollen fossils identified in samples from boreholes XB15 and DB2 in Shandong Province. **a** *Calamospora breviradiata*; **b** *Calamospora* sp.; **c** *Calamospora hartungiana*; **d** *Calamospora minuta*; **e** *Convolutispora cerebra*; **f** *Convolutispora tessellata*; **g** *Crassispora adornata*; **h** *Cyclogranisporites aureus*; **i** *Cyclogranisporites micaceus*; **j** *Densosporites annulatus*; **k** *Florinites minutus*; **l** *Foveolatisporites junior*; **m** *Granulatisporites minutus*; **n** *Gulisporites cereris*; **o** *Gulisporites cochlearius*; **p** *Laevigatosporites minimus*. Scale bars (in each) = 20 μm

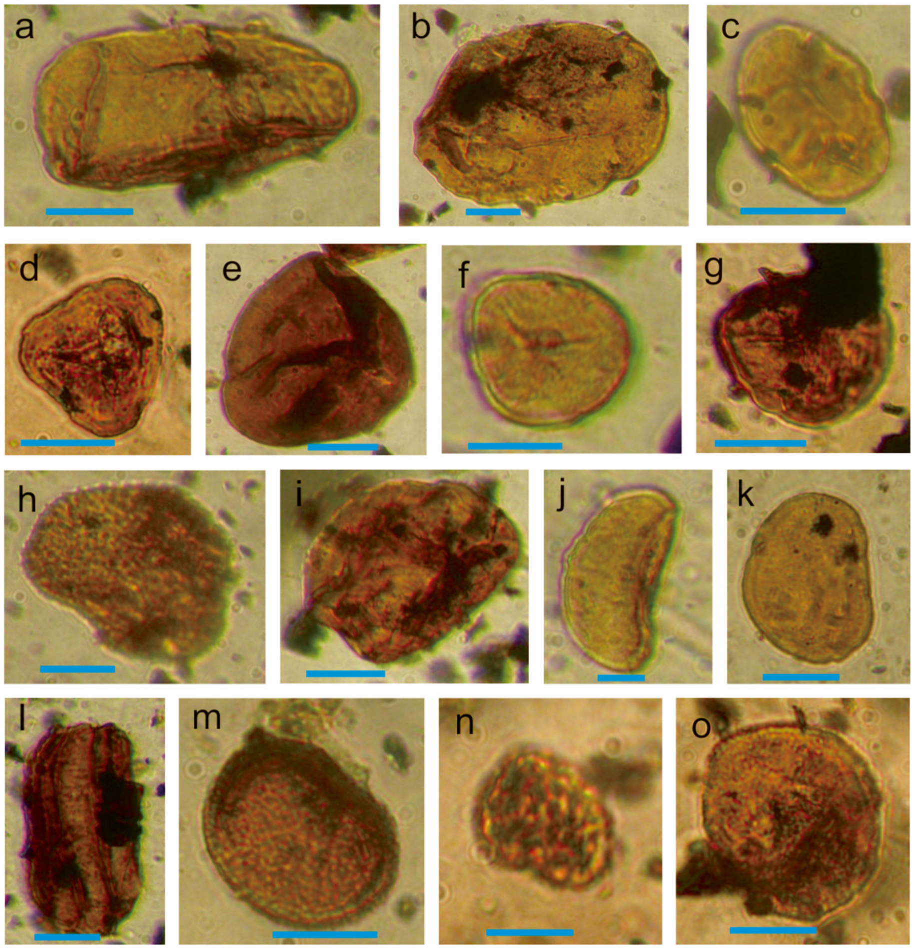

Fig. 4 Photomicrographs of a selection of spore and pollen fossils identified in samples from boreholes XB15 and DB2 in Shandong Province. **a** *Laevigatosporites maximus*; **b** *Laevigatosporites vulgaris*; **c** *Laevigatosporites perminutus*; **d** *Leiotriletes adnatus*; **e** *Leiotriletes sphaerotriangulus*; **f** *Leiotriletes* sp.; **g** *Lycospora pusilla*; **h** *Microreticulatisporites* sp.; **i** *Punctatisporites* sp.; **j** *Punctatosporites granifer*; **k** *Punctatosporites minutus*; **l** *Striolatospora* sp.; **m** *Spinosporites spinosus*; **n** *Thymospora pseudothiessenii*; **o** *Verrucosisporites verrucosus*. Scale bars (in **a-e**, **g-i** and **k-o**) = 20 μm; Scale bars (in **f** and **j**) = 10 μm

Zonotriletes include *Gulisporites cochlearius*, *G. cereris*, *G. laevigatus*, *G. cerevus*, *G. curvatus*, *G.* sp., *Sinulatisporites* cf. *shanxiensis*, *S.* cf. *sinensis*, *Stenozonotriletes marginellus*, *S.* sp., *Densosporites anulatus*, and *Lycospora pusilla*.

Monoletes include *Punctatosporites minutus* and *Laevigatosporites minimus.*

The principal species of gymnosperm pollen are *Florinites antiquus* and *F. minutus*.

4.3 Difference between Assemblage I and Assemblage II

In Assemblage I (the *Laevigatosporites*–*Granulatisporites* assemblage), the genera representing Calamitales (*Calamospora*), Filicanae (*Punctatisporites*, *Leiotriletes*, *Granulatisporites*) and Sphenopsida (*Laevigatoporites*) are relatively significant, while the gymnosperms (*Florinites*) are relatively limited.

In Assemblage II (the *Gulisporites*–*Sinulatisporites* assemblage), the genera representing Lycopsida (*Crassispora*, *Densosporites*) are scarce, which indicates that the Lycopsida content has shown signs of decline while the gymnosperm content increased in this assemblage compared with Assemblage I. This result proves the further prosperity of Cordaitales.

By comparing the two assemblages, we identified the genera and species that first appeared in Assemblage II or increased significantly compared with Assemblage I include *Gulisporites cereris*, *G. laevigatus*, *Sinulatisporites* cf. *sinensis*, *Stenozonotriletes marginellus*, *Punctatisporites incomptus*, *Florinites antiquus*, *F. minutus*, *Triquitrites sp.*, *Cyclogranisporites pseudozonatus*, *C. micaceus*, and *Lycospora pusilla.* Note that abundant *Sinulatisporites* were found in Assemblage II. This genus has a wide geographical distribution, as well as a stable stratigraphic distribution, mainly in the Shanxi Formation (Ouyang and Hou 1999; Zhang et al. 2005).

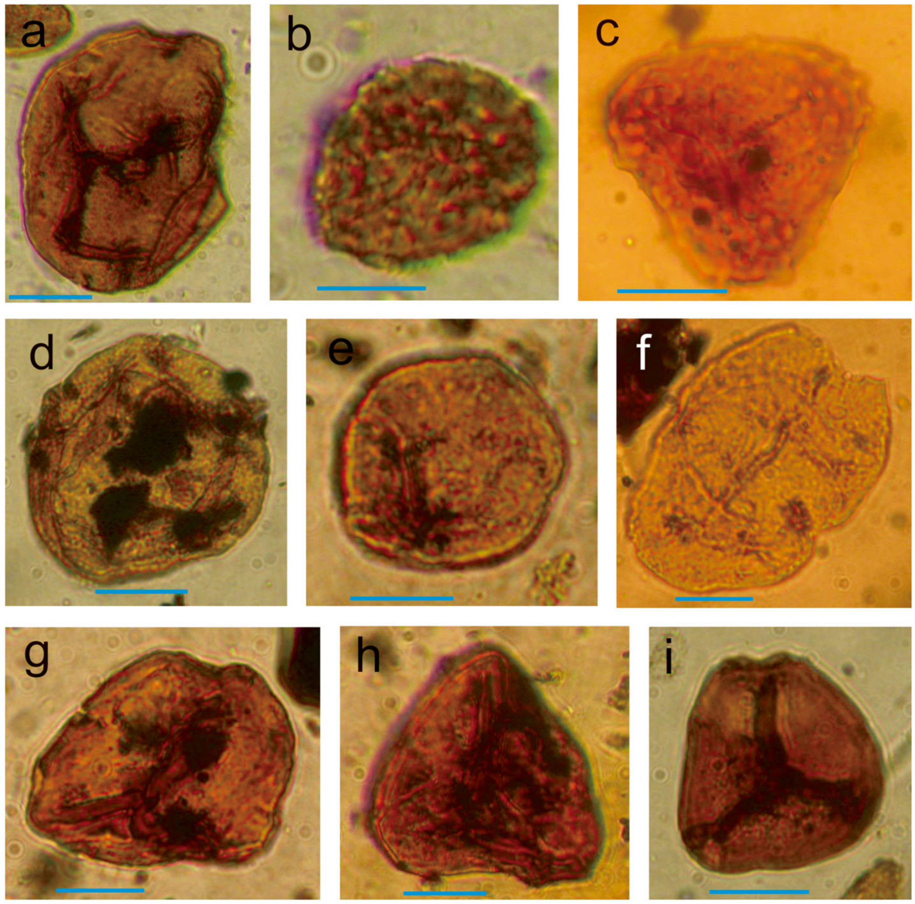

Fig. 5 Photomicrographs of a selection of spore and pollen fossils identified in samples from boreholes XB15 and DB2 in Shandong Province. **a** *Calamospora pedata*; **b** *Converrucosisporites minutus*; **c** *Converrucosisporites* sp.; **d** *Cyclogranisporites microgranus*; **e** *Cyclogranisporites pseudozonatus*; **f** *Florinites antiquus*; **g** *Gulisporites cerevus*; **h** *Gulisporites curvatus*; **i** *Gulisporites laevigatus*. Scale bars (in each) = 20 μm

5 Discussion

5.1 The geological age of spores and pollen assemblages

In the spores and pollen assemblage established in the upper Taiyuan Formation in western Shandong (Li et al. 2013), pteridophyte spores with main genera and species as *Punctatisporites minutus*, *P. punctatus*, *Leiotriletes adnatus*, and *Laevigatosporites perminutus* were dominant, and thus the geological age of this assemblage was interpreted as late Cisuralian by Li et al. (2013). Additionally, the stratigraphically highest conodont belt in the Taiyuan Formation of North China was the *Sweetognathus whitei* belt, corresponding to the late Cisuralian (Gao et al. 2005; Shen et al. 2019).

The Assemblage I established in this study and the spores and pollen assemblage established by Li et al. (2013) were both from the Taiyuan Formation of Shandong and contained common genera and species like *Laevigatosporites perminutus*, *Granulatisporites granulatus*, and *G. minutus*; therefore, these two assemblages can be compared, and the geological age of Assemblage I of this study can also be inferred as late Cisuralian.

The *Gulisporites cochlearius*–*Leiotriletes adnatus*–*Sinulatisporites sinensis* assemblage established in the Shanxi Formation of western Shandong by Tian et al. (2015) and the Assemblage II established in the Shanxi Formation in this study were both characterized by *Gulisporites* and *Sinulatisporites*, as well as an abundance of *Sinulatisporites*. Thus, we adopt the geological age of the assemblage identified by Tian et al. (2015), i.e., early Guadalupian, as the inferred age of Assemblage II of this study.

5.2 Flora and environmental change

The original diversity of a fossil flora can be reconstructed by a statistical analysis of spores and pollen (e.g., Pfefferkorn and Thomson 1982; Li et al. 2003;

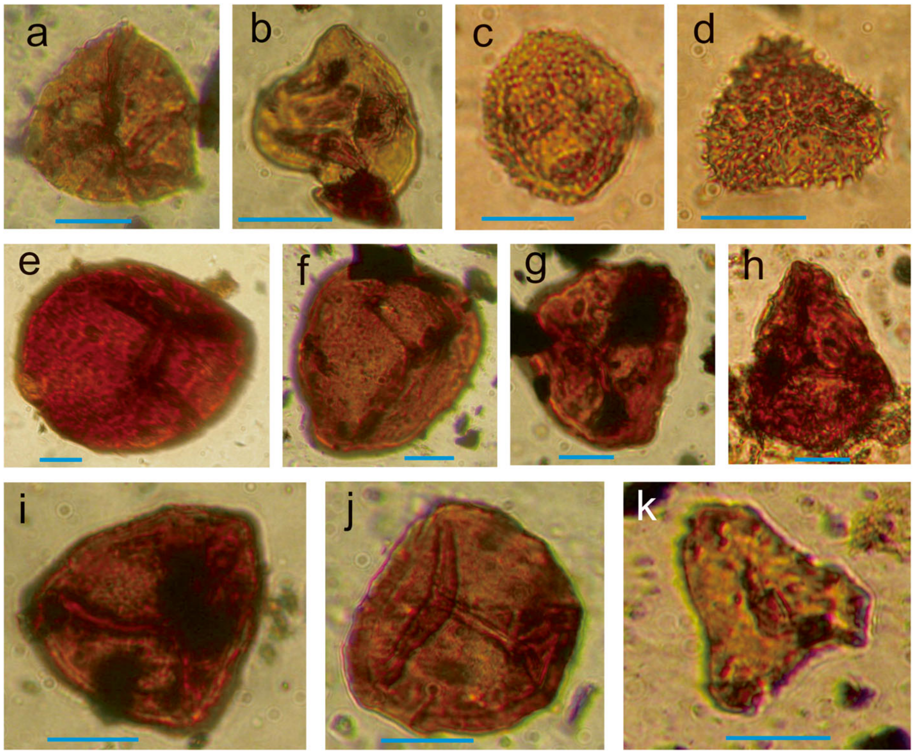

Fig. 6 Photomicrographs of a selection of spore and pollen fossils identified in samples from boreholes XB15 and DB2 in Shandong Province. **a** *Gulisporites* sp.; **b** *Leiotriletes tangyiensis*; **c** *Lophotriletes* cf. *communis*; **d** *Lophotriletes humilus*; **e** *Punctatisporites gigantus*; **f** *Punctatisporites incomptus*; **g** *Sinulatisporites* cf. *shanxiensis*; **h** *Sinulatisporites* cf. *sinensis*; **i** *Stenozonotriletes marginellus*; **j** *Stenozonotriletes* sp.; **k** *Triquitrites* sp. Scale bars (in each) = 20 μm

Wang 2010; Barbolini and Bamford 2014). We therefore attempted to establish the affinities of the primary spores and pollen taxa before analyzing vegetation succession and environmental changes, although this work has proved challenging in the past. We constructed Table 5 based on some results of previous studies. This compilation allowed the trends of the flora and environmental changes to be identified more easily.

According to Table 5, the flora of Assemblage I were composed mainly of the filicalean group,

Table 3 Comparison of spores and pollen contents (relative abundance) of Assemblage I from the Permian Taiyuan Formation in Shandong Province, North China

Location (see Fig. 1b for reference)	Spores and pollen assemblage	Relative abundance of Azonotriletes (%)	Relative abundance of Zonotriletes (%)	Relative abundance of Monoletes (%)	Relative abundance of Gymnosperm pollen (%)
Northern Shandong Province	*Kaipingispora–Densosporites–Crassispora*	87.1	8.5	7.0–24.6	9.0
Feicheng coalfield, Shandong Province	*Thymospra thiessenii–Densosporites*	35.8–60.9	10.0	20.0	5.0
Xinwen coalfield, Shandong Province	*Laevigatosporites–Thymospora*	62.6	8.6	23.0	6.2
Jining coalfield, Shandong Province	*Thymospora pseudothiessenii–thiessenii*	25.7	11.6	55.2	7.2
Boreholes XB15 and DB2 (This study)	*Laevigatosporites–Granulatisporites*	73.2	3.6	21.2	2.0

Note: Data of the northern Shandong Province, Feicheng, Xinwen, and Jining coalfields are from Li et al. (2013)

Table 4 Comparison of spores and pollen contents (relative abundance) of Assemblage II from the Permian Shanxi Formation in Shandong Province, North China

Location (see Fig. 1b for reference)	Spores and pollen assemblage	Relative abundance of Azonotriletes (%)	Relative abundance of Zonotriletes (%)	Relative abundance of Monoletes (%)	Relative abundance of Gymnosperm pollen (%)
Jiyang coalfield, Shandong Province	*Cyclogranisporites–Granulatisporites–Laevigatosporites*	45.6	10.2	24.7	12.7–30.5
Liaocheng coalfield, Shandong Province	*Gulisporites cochlearius–Sinulatisporites sinensis*	54.4	19.7	17.3	1.7–26.6
Feicheng coalfield, Shandong Province	*Gulisporites cochlearius–Sinulatisporites sinensis*	57.2–78.4	2.1	20.0	24.4–38.8
Xinwen coalfield, Shandong Province	*Gulisporites cochlearius–Sinulatisporites sinensis*	55.0–68.9	7.0	14.0	16.4
Boreholes XB15 and DB2 (This study)	*Gulisporites–Sinulatisporites*	59.8	13.6	20.7	5.9

Note: Data of Jiyang, Liaocheng, Feicheng, and Xinwen coalfields are from Zhao et al. (2006)

marattialean ferns, and gymnospermous Pteridosperms. The Cordaitales began to expand in importance with a synchronous decline of the isoetalean lycopsids, which is a typical pattern for the Cathaysian flora during the late Cisuralian. The composition of the Assemblage I revealed that the palaeoclimate was warm, humid, and seasonally dry or semi-arid. There might be an alternation of warm and humid conditions with drier conditions. The flora of Assemblage II showed a predominance of Filicales and Pteridosperms, and a further development of Sphenophyllales and Cordaitales, especially *Sinulatisporites*, which speculated that the plant produced *Sinulatisporites* was a fern or seed fern that preferred a wet and hot climate (Zhang et al. 2005). A warm and humid climate was still dominant during early Guadalupian time. However, the genus *Denosporites*, which represents Lycopsida, appeared sporadically, reflecting a further decline of isoetalean lycopsids in the Assemblage II. The increase in abundance of *Florinites* likely indicated a change to semi-arid climatic conditions.

In addition, from field observations, there is no obvious stratigraphic hiatus and lithological change between the top of the Taiyuan Formation and the bottom of the Shanxi Formation in the study area. However, from the flora represented by spore and pollen assemblages, we can distinguish the stratigraphic boundary of the Taiyuan and Shanxi formations. The flora belonging to the Shanxi Formation (Assemblage II of this study) can be distinguished from those of the Taiyuan Formation (Assemblage I of this study) by the sudden decline of Lepidodendrales and the emergence of new elements of true ferns and seed ferns.

5.3 A preliminary comparison between Cathaysian and Euramerican floras

The above analysis provides evidence that the Cathaysian flora consisted of plants that preferred a humid and warm (tropical) climate, including Lycopsida, Pteridopsida, and Cordaitales. However, the Euramerican habitat was characterized by a dry climate during the Cisuralian (DiMichele and Aronson 1992; Sun et al. 2000; DiMichele et al. 2001, 2009), where the plants requiring humid and warm conditions disappeared.

In summary, through a preliminary climatic comparison analysis, the principal outcome of this study is that plants which grew vigorously as the Cathaysian flora during the Early-Middle Permian Period were mainly developed in Late Pennsylvanian time in Euramerica. Further study will help to test and refine these results towards a better understanding and clearer comparison analysis.

6 Conclusions

1) This study recognized two assemblages, the *Laevigatosporites–Granulatisporites* assemblage (Assemblage I) and the *Gulisporites–Sinulatisporites* assemblage (Assemblage II), from an Early-Middle Permian sequence (Taiyuan and Shanxi formations) of Shandong Province, eastern North China, and established the affinities of spores and pollen taxa of the two assemblages.
2) The two assemblages had typical characteristics of the Cathaysian flora, which is widely distributed in North China during the Late Paleozoic Era. Abundant Marattiales were found in Assemblage I. The sudden decline of

Table 5 Affinities of the main spores and pollen taxa in the identified *Laevigatosporites–Granulatisporites* and *Gulisporites–Sinulatisporites* assemblages in the present study

Genera	Affinities	Literature	Assemblage	Formation	Palaeoclimate type
Leiotriletes	Filicinae, leicheniaceae, Pteridosperms	Su et al. 2007	Assemblage I	Taiyuan	Warm and humid
Punctatisporites	Filicales, Marattiales, Gleicheniaceae	Tian et al. 2015	Assemblage I	Taiyuan	Warm and humid
Granulatisporites	Filicinae	Su et al. 2007	Assemblage I	Taiyuan	Warm and humid
Calamospora	Calamitales, Sphenopsida	Ouyang et al. 2017	Assemblage I	Taiyuan	Seasonally dry
Verrucosisporites	Marattiales, Pteridosperms	Su et al. 2007; Ouyang et al. 2017	Assemblage I	Taiyuan	Warm and humid
Punctatosporites	Marattiales	Ouyang et al. 2017	Assemblage I	Taiyuan	Warm and humid
Laevigatosporites	Sphenopsida (large size), Filicales (small size)	Balme 1995; Su et al. 2007; Ouyang et al. 2017	Assemblage I	Taiyuan	Semi-arid
Thymospora	Marattiales	Ouyang et al. 2017	Assemblage I	Taiyuan	Warm and humid
Convolutispora	Marattiales	Su et al. 2007	Assemblage I	Taiyuan	Warm and humid
Lycospora	Lepidodendrales	Ouyang et al. 2017	Assemblage I	Taiyuan	Warm and humid
Gulisporites	Filicinae	Su et al. 2007	Assemblage II	Shanxi	Warm and humid
Sinulatisporites	Filicinae, Pteridosperms	Zhang et al. 2005	Assemblage II	Shanxi	Warm and humid
Crassispora	Lycopsida	Ouyang et al. 2017	Assemblage II	Shanxi	Semi-arid
Densosporites	Lycopsida	Wang et al. 2003	Assemblage II	Shanxi	Semi-arid
Lophotriletes	Filicinae	Su et al. 2007	Assemblage II	Shanxi	Warm and humid
Cyclogranisporites	Filicales, Pteridosperms	Ouyang et al. 2017	Assemblage II	Shanxi	Warm and humid
Triquitrites	Lycopsida	Su et al. 2007	Assemblage II	Shanxi	Semi-arid
Stenozonotriletes	Lycopsida	Su et al. 2007	Assemblage II	Shanxi	Semi-arid
Florinites	Cordaitales	Zhao et al. 2006	Assemblage II	Shanxi	Semi-arid

Lepidodendrales marks the distinction of Assemblage II.

3) Similar components, such as pteridophytes, existed between Euramerican and Cathaysian floras. Moreover, pteridophytes of the Euramerican flora representing a warm and humid climate were mainly developed in the Late Pennsylvanian, while pteridophytes of the Cathaysian flora lasted until the Early-Middle Permian.

Acknowledgements

The authors thank Prof. W.A. DiMichele from Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, USA for his suggestions on an earlier version of this paper. Thanks are also given to Prof. Zeng-Zhao Feng, Prof. Stephen Kershaw, other anonymous reviewers and editors for their very helpful comments.

Authors' contributions

TTY was the main contributor of the manuscript; SJL was the director, writer and appraiser of experimental results; XYZ was in charge of the drawing making and data analysis; XLZ was in charge of the experimental analysis and data arrangement. All authors read and approved the final manuscript.

Funding

This study was supported by the Open Foundation for the Modern Key Laboratory of Paleontology and Stratigraphy, Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences (Grant No. 123104).

Availability of data and materials
The datasets generated and/or analysed during the current study are available in the [College of Earth Science and Engineering, Shandong University of Science and Technology] Repository.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]College of Earth Science and Engineering, Shandong University of Science and Technology, Qingdao 266590, Shandong Province, China. [2]China Chemical Geology and Mine Bureau Shandong Geological Prospecting Institute, Ji'nan 250013, Shandong Province, China.

Received: 11 December 2019 Accepted: 2 August 2020
Published online: 19 August 2020

References
Alpern, B. 1956. Succinct description of the principal genera and species of pollen and spores found in the coals of central and eastern France. In *Entred'Etudes et Recherches des Charbonnages de France 56-9-052*, 23 3 pls.

Alpern, B. 1958. Description de Quelques Microspores du Permo-carbonifere Francais. *Review Micropaleontology* 1: 75–86.

Balme, B.E. 1995. Fossil in situ spores and pollen grains: An annotated catalogue. *Review of Palaeobotany and Palynology* 87: 81–323.

Barbolini, N., and M.K. Bamford. 2014. Palynology of an early Permian coal seam from the Karoo Supergroup of Botswana. *Journal of African Earth Sciences* 100: 136–144.

Bharadwaj, D.C. 1954. Einige neue Sporengattungen des Saarkarbons. Neues Jahrbuch fur Mineralogie. *Geologie und Palaontologie* 11: 512–525.

Bharadwaj, D.C. 1957. The palynological investigations of the Saar coals (part 1-Morphography of Sporae dispersae). *Palaeontographica* 101B: 73–125.

Cheng, Y.Q. 2000. *China stratigraphy of Permian*, 149. Beijing: Geological Publishing House (in Chinese).

Cleal, C.J., and Z.Q. Wang. 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.

DiMichele, W.A., and R.B. Aronson. 1992. The Pennsylvanian-Permian vegetational transition: A terrestrial analogue to the onshore–offshore hypothesis. *Evolution* 46: 807–824.

DiMichele, W.A., C.V. Looy, and D.S. Chaney. 2011. A new genus of gigantopterid from the middle Permian of the United States and China and its relevance to the gigantopterid concept. *International Journal of Plant Sciences* 172: 107–119.

DiMichele, W.A., I.P. Montanez, C.J. Poulsen, and N.J. Tabor. 2009. Climate and vegetational regime shifts in the late Paleozoic ice age earth. *Geobiology* 7: 200–226.

DiMichele, W.A., H.W. Pfefferkorn, and R.A. Gastaldo. 2001. Response of late carboniferous and early Permian plant communities to climate change. *Annual Review of Earth and Planetary Sciences* 29: 461–487.

DiMichele, W.A., T.L. Phillips, and H.W. Pfefferkorn. 2006. Paleoecology of late Palaeozoic pteridosperms from tropical Euramerica. *Journal of the Torrey Botanical Society* 133: 83–118.

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

Felix, C.J., and P.P. Burbridge. 1967. Palynology of the springer formation of southern Oklahoma, USA. *Palaeontology* 10: 349–435 14 pls.

Gao, L.D. 1984. Carboniferous and Permian spores and pollen. In *Paleontological Atlas of North China, v. 3, Micropalaeontologica*, ed. Tianjin Institute of Geology and Mineral Resource. (Ed.), 440. Beijing: Geological Publishing House (in Chinese).

Gao, L.F., H. Ding, and X.Q. Wan. 2005. Taxonomic revision of conodont *Sweetognathus* species in the uppermost Taiyuan formation, Yuhuai Basin and its significance. *Acta Micropalaeontologica Sinica* 22 (4): 370–382 (in Chinese with English abstract).

Gastaldo, R.A. 1987. Confirmation of carboniferous clastic swamp communities. *Nature* 326: 869–871.

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

Hacquebard, P.A. 1957. Plant spores in coal from the Horton group (Mississippian) of Nova Scotia. *Micropaleontology* 3: 301–324 3pls.

Halle, T.G. 1935. On the distribution of the late Palaeozoic flora in Asia. *Geografiska Annaler* 17: 106–111.

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

Hoffmeister, W.S., F.L. Staplin, and R.E. Malloy. 1955. Mississippian plant spores from the Hardinsburg formation of Illinois and Kentucky. *Journal of Paleontology* 29: 372–399.

Hou, J.-P., and Z. Wang. 1986. Late Permian sporo-pollen assemblages. In *Permian and Triassic strata and fossil assemblages in the Dalongkou area of Jimsar, Xinjiang, Geological Memoir Series*, 70–110. Beijing: Geological Publishing House (in Chinese with English summary).

Ibrahim, A.C. 1933. *Sporenformen des Aegirhorizonts des Ruhr-Reviers*, 47. Wurzburg: Berlin Dissertation privately publishing. 8 pls.

Imgrund, R. 1952. *The Sporites of the Kaiping Basin*, 1–96. Aachen: Rheinland-Westfalen Tech. Hochschule PhD Dissertation.

Imgrund, R. 1960. Sporae dispersae des Kaipingbeckens,ihre palaontologische und stratigraphische beareitung im Hinblick auf eine Parallelisierung mit dem Ruhrkarbon und dem Pennsylvanian von Illinois. *Geologisches Jahruch* 77: 143–204.

Jiang, H.C., M.Z. Wang, X.Q. Zhang, and Z.X. Li. 2002. Study on late Paleozoic sporopollen assemblages in east part of Jining coalfield, Shandong province. *Chinese Journal of Geology* 37 (1): 47–61 (in Chinese with English abstract).

Kosanke, R.M. 1950. Pennsylvanian spores of Illinois and their use in correlation. *Illinois Geological Survey Bulletin* 74: 1–128.

Li, S.J., M.Z. Wang, D.S. Zheng, and X.L. Zhao. 2003. Recovery of climate of Paleogene in Jiyang depression of Shandong. *Journal of Shandong University of Science and Technology (Natural Science)* 22 (3): 6–9 (in Chinese with English abstract).

Li, S.J., X.L. Zhao, T.T. Yin, L.Y. Yuan, M. He, F.L. Xu, R. Chen, and P.P. Huang. 2013. The characteristics of early to middle Permian sporopollen assemblages in Pengzhuang, Shandong Province. *Acta Geologica Sinica* 87 (12): 1819–1825 (in Chinese with English abstract).

Li, X.X. 1997. The origin, evolution and distribution of the Cathaysian Flora in East Asia. *Acta Palaeontologica Sinica* 36 (4): 411–422 (in Chinese with English abstract).

Lü, D.W. 2015. Discussion on micro-characteristics of transgressive event deposition and its coal-forming mechanism in the late Paleozoic epicontinental sea basin of North China. *Acta Sedimentologica Sinica* 33 (4): 633–640 (in Chinese with English abstract).

Mei, S.L., C.M. Henderson, and C.Q. Cao. 2004. Conodont sample-population approach to defining the base of the Changhsingian stage, Lopingian series, upper Permian. The palynology and micropalaeontology of boundaries. *The Geological Society of London, Special Publication* 230: 105–121.

Meyen, S.V. 1997. Permian conifers of Western Angaraland. *Review of Palaeobotany and Palynology* 96: 351–447.

Naugolnykh, S.V. 2002. Paracalamitina striata — A newly reconstructed equisetophyte from the Permian of Angaraland. *Journal of Paleontology* 76 (2): 377–385.

Naumova, S.N. 1953. Spore-Pollen assemblages of the Upper Devonian of the Russian Platform and their stratigraphic significance. *Transactions of the Institute of Geological Sciences, Academy of Science, SSSR* 143 (Geol. Ser.60): 1–204 (in Russian).

Ouyang, S. 1962. The microspore assemblage from the Longtan series of Changxing, Chekiang. *Acta Palaeontologica Sinica* 10 (1): 76–119 (in Chinese with English abstract).

Ouyang, S. 1986. Palynology of upper Permian and lower Triassic of Fuyuan district, eastern Yunnan, China. *Palaeontologia Sinica, NSA* 9: 1–122 (in Chinese).

Ouyang, S., and J.P. Hou. 1999. On characteristics of the Cathaysian palynoflora. *Acta Palaeontologica Sinica* 38 (3): 261–281 (in Chinese with English abstract).

Ouyang, S., L.C. Lu, H.C. Zhu, and F. Liu. 2017. *The late Paleozoic spores and pollen of China*, 36–613. Hefei: Press of University of Science and Technology of China (in Chinese).

Peppers, R.A. 1996. Palynological correlation of major Pennsylvanian (middle and upper carboniferous) chronostratigraphic boundaries in the Illinois and other coal basins. *Geological Society of America Memoirs* 188: 1–111.

Pfefferkorn, H.W., and M.C. Thomson. 1982. Changes in dominance patterns in upper carboniferous plant-fossil assemblages. *Geology* 10: 641–644.

Pfefferkorn, H.W., and J. Wang. 2007. Early Permian coal-forming floras preserved as compressions from the Wuda District (Inner Mongolia, China). *International Journal of Coal Geology* 69: 90–102.

Phillips, T.L., and W.A. DiMichele. 1992. Comparative ecology and life-history biology of arborescent lycopsids in late carboniferous swamps of Euramerica. *Annals of the Missouri Botanical Garden* 79: 560–588.

Potonié, R., and G. Kremp. 1954. Die Gattungen der palaozoischen Sporae dispersae und ihre Stratigraphie. *Geologisches Jahruch* 69: 111–194.

Potonié, R., and G. Kremp. 1955. Die sporae dispersae des Ruhrkarbons ihr Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte. *Palaeontographica* 98 (B): 1–136.

Potonié, R., and G. Kremp. 1956. Die sporae dispersae des Ruhrkarbons ihre morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte. *Palaeontographica* 99 (B): 85–191.

Schopf, J.M., L.R. Wilson, and R. Bentall. 1944. An annotated synopsis of Palaeozoic fossil spores and the definition of generic groups: Illinois state geological survey. *Report of Investigations* 92: 1–72.

Scott, A.C. 1974. The earliest conifer. *Nature* 251: 707–708.

Shen, S.Z., and S.L. Mei. 2010. Lopingian (late Permian) high-resolution conodont biostratigraphy in Iran with comparison to South China zonation. *Geological Journal* 45: 135–161.

Shen, S.Z., Y. Wang, and Y.G. Jin. 2005. Progress report on the global stratotype sections and points (GSSP) of the Permian in system. *Journal of Stratigraphy* 29 (2): 138–146 (in Chinese with English abstract).

Shen, S.Z., H. Zhang, Y.C. Zhang, D.X. Yuan, B. Chen, W.H. He, L. Mu, W. Lin, W.Q. Wang, J. Chen, Q. Wu, C.Q. Cao, Y. Wang, and X.D. Wang. 2019. Permian integrative stratigraphy and timescale of China. *Science China Earth Sciences* 62: 154–188.

Shi, G.R., and Z.Q. Chen. 2003. Global review of Permian Tyloplecta Muir-wood and Cooper, 1960 (Brachiopoda): Morphology, palaeobiogeographical and palaeogeographical implications. *Gondwana Research* 6: 777–790.

Smith, A.H.V., and M.A. Butterworth. 1967. Miospores in coal seams of the Great Britain. *Special Papers in Palaeontology* 1: 1–321 29pls.

Song, X.S., K.F. Wang, M.Z. Wang, and Q. Jia. 2009. Permian sporo-pollen assemblages of the Echeng town coalfield, Liaocheng, Shandong Province. *Acta Micropalaeontologica Sinica* 26 (3): 271–282 (in Chinese with English abstract).

Song, X.S., X.Q. Zhang, and M.Z. Wang. 2005. The Foraminiferal fauna and the carboniferous-Permian boundary in the Taiyuan formation of the Xinwen coalfield, Shandong province. *Acta Micropalaeontologica Sinica* 22 (1): 47–58 (in Chinese with English abstract).

Spencer, A.R., S. Wang, M.T. Dunn, and J. Hilton. 2013. Species of the medullosan ovule Stephanospermum from the Lopingian (late Permian) floras of China. *Journal of Asian Earth Sciences* 76: 59–69.

Su, W., X.L. Huang, M.Z. Wang, and X.Q. Zhang. 2007. Carboniferous-Permian Palynoflora and Paleoclimate of the Tengxian coalfield, Shandong. *Acta Micropalaeontologica Sinica* 24 (1): 98–104 (in Chinese with English abstract).

Sun, K.Q. 1996. Origin of the Cathaysia flora in Asia. *Palaeobotanist* 43: 59–62.

Sun, K.Q. 1997. Characteristics of the evolution and distribution of the global carboniferous and Permian floras. *Earth Science Frontiers* 4: 129–138 (in Chinese with English abstract).

Sun, K.Q. 2001. Carboniferous and Permian floras in China. *Chinese Bulletin of Botany* 18 (6): 691–706 (in Chinese with English abstract).

Sun, K.Q. 2006. The Cathaysia Flora and the mixed late Permian Cathaysian–Angaran floras in East Asia. *Journal of Integrative Plant Biology* 48: 381–389.

Sun, K.Q., X.Y. Shi, and J.Z. Cui. 2000. Phytogeographical provinces of the carboniferous and Permian in the world. *Chinese Bulletin of Botany* 17 (3): 193–203 (in Chinese with English abstract).

Tian, B.L., S.J. Wang, Y.T. Guo, G.R. Chen, and H. Zhao. 1996. Flora of Palaeozoic coal balls of China. *Palaeobotanist* 45: 247–254.

Tian, B.L., S.J. Wang, C.S. Li, and G.R. Chen. 2000. An approach on the origin Centre and the mechanics of evolution and extinction of the late Palaeozoic Cathaysian flora. *Chinese Bulletin of Botany* 17: 21–33 (in Chinese with English abstract).

Tian, C.L., S.J. Li, F.L. Xu, and X.L. Zhao. 2015. Carboniferous and Permian palynological assemblages and the coal forming environment in Pengzhuang coal mine of Shandong Province. *Coal Geology & Exploration* 43 (6): 12–22 (in Chinese with English abstract).

Vega, J.C., and S. Archangelsky. 1997. The first Gondwana carboniferous compound cupules and associated seeds. A preliminary note. *Review of Palaeobotany and Palynology* 99: 55–59.

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., and H.W. Pfefferkorn. 2013. The carboniferous–Permian transition on the North China microcontinent–oceanic climate in the tropics. *International Journal of Coal Geology* 119: 106–113.

Wang, M.Z., X.Q. Zhang, and X.L. Zhao. 2003. Permian spore-pollen assemblage of early and middle period of early Permian in Western Shandong. *Journal of Shandong University of Science and Technology* 22: 1–6.

Winston, R.B. 1983. A late Pennsylvanian upland flora in Kansas: Systematics and environmental implications. *Review of Palaeobotany and Palynology* 40: 5–31.

Yin, T.T., S.J. Li, and X.L. Zhao. 2016. Sequence stratigraphic and characteristics of carboniferous and Permian coal accumulation in Pengzhuang area of Shandong province. *Land and Resources in Shandong* 32 (12): 25–29 (in Chinese with English abstract).

Zhang, S.G., Y.B. Zhang, and H.J. Yan. 2009. A brief introduction to the "international stratigraphic chart" (2008). *Journal of Stratigraphy* 33 (1): 1–10 (in Chinese with English abstract).

Zhang, X.Q., M.Z. Wang, and X.L. Zhao. 2005. Temporal-spatial distribution of *Sinulatisporites* in North China and its stratigraphic significance. *Acta Palaeontologica Sinica* 44 (2): 306–313 (in Chinese with English abstract).

Zhao, X.L., S.J. Li, and X.Q. Zhang. 2006. Permian sporo-pollen assemblages of the Jiyang depression, Shandong province. *Acta Micropalaeontologica Sinica* 23 (2): 165–174 (in Chinese with English abstract).

Zhou, H.Y. 1980. The sporopollen assemblage from the Upper Paleozoic in northern Shandong Province. In *Symposium on Stratigraphy and Palaeontology oil and gas bearing areas in China (I)*, 1–17. Beijing: Petroleum Industry Press (in Chinese).

Zhu, Y.Y., J.S. Zhang, Q. Jia, X.Q. Zhang, and M.Z. Wang. 2005. Study on the Fusulinida fauna and the carboniferous-Permian boundary in the Taiyuan formation from the Yanzhou coalfield, Shandong Province. *Acta Micropalaeontologica Sinica* 22 (4): 400–411 (in Chinese with English abstract).

Publisher's Note