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

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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). The evolution of these floras was influenced by 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” Lepidodendron 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 Cathaysia floras.

Evolution of the Permian floras in China has been investigated in numerous researches regarding plant fossil
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,
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 Pangaea. 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.
in the Taiyuan and Shanxi formations in North China, namely, *Neuropteris ovata*–*Lepidodendron posthumii* and *Emplyctopteridium alatum–Taeniopteris mcroronata–Lobatanullaria 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 palynmorphs (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 breviadaita | Kosanke 1950                                  | Fig. 3a |
| Calamospora sp. | Schopf et al. 1944                             | Fig. 3b |
| Calamospora hartungiana | Gao 1984                                     | Fig. 3c |
| Calamospora minuta | Bharadvaj 1957                               | Fig. 3d |
| Convolulispora cerebra | Smith and Butterworth 1967                    | Fig. 3e |
| Convolulispora tessellata | Hoffmeister et al. 1955                     | Fig. 3f |
| Crassispora adomata | Ouyang 1962                                  | Fig. 3g |
| Cyclogranisporites aureus | Potonié and Kremp 1955                | Fig. 3h |
| Cyclogranisporites micaceus | Imgrind 1952                               | Fig. 3i |
| Densosporites annulatus | Smith and Butterworth 1967                  | Fig. 3j |
| Floinites minutus | Bharadvaj 1954                               | Fig. 3k |
| Foveolatisporites junior | Bharadvaj 1957                              | Fig. 3l |
| Granulatisporites minutus | Potonié and Kremp 1955              | Fig. 3m |
| Gulispores ceris | Gao 1984                                    | Fig. 3n |
| Gulispores cochlearis | Imgrind 1960                                 | Fig. 3o |
| Laevigatosporites minimus | Schopf et al. 1944                          | Fig. 3p |
| Laevigatosporites maximus | Potonié and Kremp 1956                  | Fig. 3q |
| Laevigatosporites vulgaris | Ibrahim 1933                               | Fig. 3r |
| Laevigatosporites perminutus | Alpern 1958                               | Fig. 3s |
| Leiotrilites adnatus | Potonié and Kremp 1955                      | Fig. 3t |
| Leiotrilites sphaerotriangulus | Potonié and Kremp 1954       | Fig. 3u |
| Leiotrilites sp. | Potonié and Kremp 1954                      | Fig. 3v |
| Lycospora pusilla | Schopf et al. 1944                           | Fig. 3w |
| Microcreticulosporites sp. | Potonié and Kremp 1954               | Fig. 3x |
| Punctatisporites sp. | Potonié and Kremp 1954                      | Fig. 3y |
| Punctatisporites granifer | Potonié and Kremp 1956                  | Fig. 3z |
| Punctatisporites minutus | Ibrahim 1933                               | Fig. 3a |
| Spinosporites spinosus | Alpern 1956                                | Fig. 3b |
| Thymospora pseudothiessenii | Kosanke 1950                               | Fig. 3c |
| Verrucosisporites verrucosus | Ibrahim 1933                             | Fig. 3d |
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                  | Kosaek 1950                 | Fig. 5a      |
| Converrucosporites minutus          | Gao 1984                    | Fig. 5b      |
| Converrucosporites 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 cereis                 | Gao 1984                    | Fig. 3n      |
| Gulisporites cereus                 | Imgrund 1960                | Fig. 5g      |
| Gulisporites cochlearius            | Imgrund 1960                | Fig. 3o      |
| Gulisporites curvatus               | Gao 1984                    | Fig. 5h      |
| Gulisporites laevidigatus           | Imgrund 1960                | Fig. 5i      |
| Gulisporites sp.                    | Imgrund 1960                | Fig. 6a      |
| Laevigatosporites minimus           | Schopf et al. 1944          | Fig. 3p      |
| Leiotrites adnatus                  | Potonié and Kremp 1955      | Fig. 4d      |
| Leiotrites sphaerotriangulus        | Potonié and Kremp 1954      | Fig. 4e      |
| Leiotrites tangyiensis              | Zhou 1980                   | Fig. 6b      |
| Lophotrites cf. communis            | Naumova 1953                | Fig. 6c      |
| Lophotrites humilis                 | Hou and Wang 1986           | Fig. 6d      |
| Lycospora pusilla                   | Schopf et al. 1944          | Fig. 4g      |
| Punctatisporites gigantus           | Ouyang 1986                 | Fig. 6e      |
| Punctatisporites incompitus         | Felix and Burbridge 1967    | Fig. 6f      |
| Sinulatisporites cf. shanxiensis    | Gao 1984                    | Fig. 6g      |
| Sinulatisporites cf. sinensis       | Gao 1984                    | Fig. 6h      |
| Stenazosporites marginellus         | Gao 1984                    | Fig. 6i      |
| Stenazosporites sp                  | Hacquebard 1957             | Fig. 6j      |
| Triquirites 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, Convoreticulatisporites minutus, C. sp., Punctatosporites incomptus, P. gigantus, Leiotriletes tangyiensis, L. sphaerotriangulus, L. adnatus, Verrucosisporites kaipingiensis, Crassispora mucronata, Calamospora pedata, Lophotriletes cf. communis, and L. humilus.
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*), Filicinaceae (*Punctatisporites, Leiotriletes, Granulatisporites*) and Sphenopsida (*Laevigatoporus*) 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).
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;...
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, based on some results of previous studies. This compilation allowed the trends of the flora and environmental changes to be identified more easily.

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 | Kaipingspora–Densasporites–Crassispora | 87.1 | 8.5 | 7.0–24.6 | 9.0 |
| Feicheng coalfield, Shandong Province | Thymospora thiessenii–Densasporites | 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)
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 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 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 | 127–305 |
| 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).

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, Pteridosida, 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.
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     |
| Vernucusporites | 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| Philicales (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          |
| Lophotrilites   | Filicinae                                                                   | Su et al. 2007                                                             | Assemblage II | Shanxi   | Warm and humid     |
| Cyclogranisporites| Filicales, Pteridosperms                                                   | Ouyang et al. 2017                                                         | Assemblage II | Shanxi   | Warm and humid     |
| Triquirittes    | Lycopsida                                                                  | Su et al. 2007                                                             | Assemblage II | Shanxi   | Semi-arid          |
| Stenazonotrilites| 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.

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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.

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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.

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