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He, Xue-Zhi; Wang, Shi-Jun; Wan, Ming-Li; Hilton, Jason; Wang, Jun

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***Gigantopteris* Schenk ex Yabe in the Lopingian (Late Permian) flora of central Shanxi in the North China Block: palaeobiogeographical and palaeoecological implications**

Xuezhi He ^{a,b}, Shijun Wang ^a, Mingli Wan ^b, Jason Hilton ^c, Jun Wang ^{b,*}

^a *State Key Laboratory of Systematic and Evolutionary Botany (LSB), Institute of Botany, Chinese Academy of Sciences, Beijing 100093, PR China.*

^b *State Key Laboratory of Palaeobiology and Stratigraphy (LPS) and Department of Palaeobotany and Palynology, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, PR China.*

^c *School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B 15 2TT, UK.*

* Corresponding author. Tel.: (0)25-8328-2227. E-mail address jun.wang@nigpas.ac.cn (Jun Wang)

ABSTRACT

The concept of the Cathaysian Flora was originally based on fossils from the Permian of central Shanxi Province in North China but is now considered representative of the flora of much of East Asia during the Carboniferous and Permian. Although *Gigantopteris* Schenck ex Yabe is characteristic and often distinctive of the Cathaysian Flora in general, it has previously not been recorded in Shanxi Province within the central part of the North China Block. Recent investigations on the Lopingian (Late Permian) flora of the Taiyuan East Hill Coalfield in Shanxi have yielded well-preserved specimens of *Gigantopteris dictyophylloides* Gu et Zhi within the Upper Shihhotse Formation, contained within continental red-beds interpreted as representing a floodplain environment. Discovery of *G. dictyophylloides* enlarges the palaeogeographic distribution of the genus and shows that the Permian flora of Shanxi is more typical of the Cathaysian flora than previously thought. Results also provide new information on the ecology of *G. dictyophylloides* based on assessments of its occurrence within depositional sedimentary facies from which we conclude that this species thrived in alluvial – fluvial sediments in the North China Block. We conclude that the red beds of the Upper Shihhotse Formation that yield gigantopterids most likely formed under a seasonally dry climate rather than under arid conditions as previously considered.

Keywords: Cathaysian flora, Permian, North China Block, Upper Shihhotse Formation, Palaeobotany, gigantopterids, leaf physiognomy, palaeoclimate

Highlights

- First discovery of *Gigantopteris* from central North China Block
- Palaeogeographic distribution of *Gigantopteris* enlarged to include central North China Block
- Permian regional flora of Shanxi typical of Cathaysian flora
- Evidence for seasonally dry Permian climates in the North China Block

1. Introduction

Although originally based on the late Palaeozoic flora of Shanxi Province in North China (Halle, 1927, 1935), the Cathaysian Flora is now considered representative of the Carboniferous-Permian flora of China and much of East Asia and includes the endemic taxa *Lepidodendron oculus-felis* (Abbado) Zeiller, *Lobatannularia* Kawasaki, *Conchophyllum* Schenk, *Tingia* Halle, *Gigantopteris* Schenk ex Yabe (Wang, 2009), *Gigantonoclea* Koidzumi; *Fascipteris* Gu et Zhi, *Emplectopteris* Halle, *Emplectopteridium* Kawasaki and *Taeniopteris* Brongn. (Shen, 1995; Wang, 2009). Since Halle's (1927) pioneering palaeobotanical research the Permian regional flora from Shanxi, the flora has been extensively investigated (e.g. Sze 1953a, b, 1954, 1955a, b; Lee 1955, 1963; Zhao et al., 1987; Kong et al., 1995, 1996; He et al., 1995; Wang, 1983a, b, 1992, 1999; Wang et al., 1996; Shen, 1995; Glasspool et al., 2003, 2004a, b) and is now recognized as including all of the genera considered characteristic of the Cathaysian Flora with the exception of *Gigantopteris*. The absence of *Gigantopteris* is unusual considering its seemingly ubiquitous occurrence elsewhere within Cathaysia, a fact that previously led to the Cathaysian

Flora being called the *Gigantopteris* flora (Halle 1935; Koidzumi 1936; Shen 1995; Wang 1996).

In the present article we investigate the Lopingian (Late Permian) flora of the upper part of the Upper Shihhotse Formation in Shanxi Province (Fig. 1) and document well-preserved specimens of *Gigantopteris dictyophylloides* Gu et Zhi. This represents the first identification of the genus from Shanxi Province and shows that the Shanxi regional flora was more typical of the Cathaysian flora in general and that the genus was palaeobiogeographically more cosmopolitan within Cathaysia than previously recognized. Our results also allow us to consider its spatial distribution and palaeoecological setting of Cathaysian gigantopterids within the North China Block during the Lopingian by analyzing their occurrences within sedimentary depositional environments.

2. Material and methods

Specimens were collected from Mengjiagou village in Shouyang district (Fig. 1) of the Taiyuan East Hill Coalfield in Shanxi Province, occurring in the upper part of the Upper Shihhotse Formation (Wang and Pfefferkorn, 2010). The sedimentary succession, shown in Figure 2a and is summarized in Table 1, is dominated by red-beds (arrows in Fig. 2a) that comprise sandstones, siltstones and claystones inter-bedded amongst paler colored sandstones, siltstones and claystones. The sedimentary succession is interpreted as being deposited under fluvial conditions (?reference) progressing from the bottom to the top from overbank to point bar deposits and above this alternating deposition of fluvial channel sandstones with occasional gravel bases and finer grained overbank (floodplain) deposits of siltstones and claystones (Table 1).

[Approximate position of Figures 1 and 2]

The specimens documented here were collected from bed 5 (Fig. 1b; Table 1) and is indicated by yellow lines in Figure 2b, occurring in a 0.5 m thick grayish colored claystone and siltstone between two red beds (Fig. 2a-b). The fossil plants constitute a leaf horizon in which the fossils are well preserved in fine grained sediment allowing detailed features of their morphology to be identified; the fossil plants are relatively complete suggesting that they have not been subjected to transportation and were growing in close proximity to the depositional location although a more detailed taphonomic analysis is not presently available.

Fossil plants associated with *Gigantopteris* in Bed 5 at Mengjiagou include the characteristic Cathaysian genera *Lobatannularia*, *Annularia*, *Tingia*, *Pecopteris*, *Cladophlebis*, *Sphenopteris*, *Fascipteris*, *Gigantonoclea*, *Neuropteridium*, *Taeniopteris* and *Nystroemia* (Wang and Pfefferkorn, 2010). *Gigantopteris* is a rare/common constituent of the assemblage in this horizon and to date approximately XX specimens have been identified/collected.

[Approximate position of Table 1]

Specimens were photographed by Nikon D800 digital camera with a 60 mm macro lens and are deposited at Nanjing Institute of Geology and Palaeontology (Chinese Academy of Sciences) under the registration number PB21949.

3. Results

A well preserved specimen is selected to display here showing the distinctive venation characters and leaf margin of the genus *Gigantopteris* (Fig. 3). The specimen preserves right half of a large leaf including part of primary vein, and measures approximately 80 mm long by 47 mm wide from its incomplete extremities. The

dentate margin bears at least two teeth. Each secondary vein stretches into one tooth, approaching the apex, fading away at the leaf margin. The primary vein is rather thick and straight. The secondary vein is moderately thin in comparison with the primary vein and arising from it at a cute angle of ca. 60° degrees, tapering upward. The tertiary vein is much thinner than secondary vein, departing from the secondary vein at an angle about 70–80°, with a slightly decurrent base, regularly spaced, and disposed in a sub-opposite pattern. Close inspection reveals the tertiary veins dichotomise at their apex and anastomose with adjacent tertiary veins arising from the same secondary vein and with those from opposite secondary vein forming larger polygonal venation meshwork. The quaternary vein is very thin, departing from the tertiary vein at an angle of ca. 80°, and anastomoses with adjacent quaternary veins from the same tertiary vein and those from opposite tertiary veins to form larger reticulate veins. The veinlets dichotomise and anastomose forming irregular venation meshwork within the larger meshes. Accessory meshes are not observed along the primary vein. The feature of the specimen shown in Figure 3 conforms to the circumscription of *Gigantopteris dictyophylloides* (Gu et Zhi, 1974; Glasspool et al., 2004a, b) allowing us to document its occurrence in the Permian flora of Shanxi Province for the first time.

[Approximate location of Figure 3]

4. Discussion

Within gigantopterids most of the leaf genera have reticulate venation including *Gigantopteris* Schenck ex Yabe (Gu et Zhi, 1974; Glasspool et al., 2004a; Wang, 2009), *Gigantonoclea* Koidzumi (Koidzumi, 1936), *Cathaysiopteris* Koidzumi (Koidzumi, 1936), *Cathaysiopteridium* Li (Huang et al., 1989), *Delnortea* Mamay et al. (Mamay, 1988), *Evolsonia* Mamay (Mamay, 1989), *Gigantopteridium* (White)

Koidzumi (Koidzumi, 1936), *Gothanopteris* Koidzumi (Koidzumi, 1936), *Lonesomia* Weber (Weber, 1997), *Neogigantopteridium* Yang (Yang, 2006), *Palaeogoniopteris* Koidzumi (Koidzumi, 1936), *Zeilleropteris* Koidzumi (Koidzumi, 1936) and *Euparyphoselis* DiMichele et al. (DiMichele et al., 2004). Although the evolutionary relationships between gigantopterid taxa remain uncertain from which it is unclear if they represent a single biological group (e.g. Glasspool et al., 2004a, b; DiMichele et al., 2011), most genera occur either exclusively in North–South America or in China – Southeast Asia suggesting a phytogeographical distinction occurs amongst them (DiMichele et al., 2011). They are well known for sharing morphological and anatomical features with both gymnosperms and angiosperms (Li et al., 1994, 1996; Li and Taylor, 1998; Glasspool et al., 2003, 2004a, 2004b) and may be vegetative analogues for angiosperm physiology (Glasspool et al., 2004b). Amongst gigantopterids, *Gigantopteris* has the most complex venation system with four orders of reticulate veins, and veinlet forming meshes in reticulate quaternary veins and is the most ‘angiosperm-like’.

The poorly preserved type specimens of *Gigantopteris* and the poorly circumscribed diagnosis proposed by Schenk (1883) led to many Palaeozoic fossil leaf taxa with reticulate venation being included within the genus historically (e.g. Halle, 1927; Jongmans and Gothman, 1935; Kawasaki, 1927-1931; Kawasaki, 1932-1934, et al.). The ensuing taxonomic inflation resulted in *Gigantopteris* being considered as a widely distributed genus within China. However, in 1974 the diagnosis of *Gigantopteris* was emended by Gu et Zhi to restrict it to veinlets forming small meshes within reticulate quaternary veins and as a consequence many of the previously included taxa were placed within other genera, such as *Gigantonoclea* (Gu et Zhi, 1974) et al. Gu et Zhi’s (1974) treatment was written in Chinese and was not

widely accessible outside China, and as their treatment did not compare the more recently discovered Chinese specimens with the type specimens of *Gigantopteris*, meaningful conclusions were tentative. Subsequently Glasspool et al. (2004a) reinvestigated the type specimens of *Gigantopteris nicotianaefolia* Schenk ex Yabe and provided a formal diagnosis and in doing so restricted the genus to include megaphylls with pinnate venation and lamina with at least four orders of venation, with penultimate vein orders forming large reticulate polygonal meshes within which finer ultimate order veinlets anastomose to form meshes and blind endings. According to the revised *Gigantopteris* concept of Glasspool et al. (2004a), within China the distribution of *Gigantopteris* is restricted to the Yangtze Block in southern China during the Wuchiapingian to Changhsingian stages of the Permian, and the southern corner of the North China Block during the Wordian to Wuchiapingian stages of the Permian (Zhang, 1991; Glasspool et al., 2004a; Yang et al., 2006).

The discovery of *Gigantopteris* within the Shanxi regional flora confirms the genus to be a typical member of the Cathaysia Flora in the North China Block. *Gigantopteris dictyophylloides* occurring within the central part of the North China Block (Fig. 4) in Shanxi Province extends the geographical range of the genus and also demonstrates that it lived in alluvial – fluvial sediments in this region as demonstrated by its occurrence in the Mengjiagou succession within floodplain deposits. This differs from its contemporaneous occurrences in the southern corner of the North China Block (Fig. 4) where it occurs in thick coal seams that have been used to suggest palaeoenvironmentally moist settings (Liu, 1990).

[Approximate location of figure 4]

Taphonomic and palaeoecological research on specimens from the Yangtze Block in South China suggests that the gigantopterids *Gigantonoclea* and *Gigantopteris*

occupied a liana-like growth habit where they are interpreted as forming the understory in tropical forests (Yao, 1983). In Cathaysia, gigantopterids occurred frequently in lowland floras and are absent in upland floras, and in many cases they co-occur with freshwater to brackish fauna including ostracoda and gastropods. The freshwater gastropod *Permoplanorboidea striatulus* Wang (Wang, 1984) is often found attached to *Gigantopteris dictyophylloides* leaves suggesting *Gigantopteris* grew near lakes or in peat swamps with standing shallow water (Yao, 1983). Such an interpretation would be consistent with environmental inferences from the leaf physiognomy of *Gigantopteris dictyophylloides* (e.g. Wolfe, 1995; Glasspool et al. 2004b).

Previously the climate of the central North China Block during the Loipian was interpreted as arid (Norrin, 1922; Li et al., 1995; Yang, 2006; Zhu et al. 2007) due to extensive continental red bed formation that either suggests hot and dry climates (Walker, 1976; Parrish, 1995) or warm climates with alternating wet-and-dry seasons (Parrish, 1998; Dubiel and Smoot, 1994). However, Sheldon (2005) considered that continental red beds can also form in warm, humid climates with good drainage and as such red color in itself does not indicate specific palaeoclimatic conditions. The available palaeobotanical evidence with luxuriant vegetation often with megaphyllous leaves such as *Gigantopteris dictyophylloides* in Shanxi Province supports this viewpoint (e.g. Li, 1980; Li, 1995; Wang, 1999) and leads us to conclude that the palaeoenvironment in which the present plant assemblage formed was probably humid. The flora assemblage documented here from Mengjiagou village within Shanxi Province lacks taxa indicative of drier climates such as ginkgopsida and conifers.

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Figure captions

Fig. 1. Locality of *Gigantopteris* in Shanxi. Geological map of central Shanxi province with red arrow indicating location of outcrops; €: Cambrian; O₁: Ordovician Liangjiashan Fm.; O₂: Ordovician Fengfeng Fm.; C₂: Carboniferous Taiyuan Fm.; P: Permian; P₃: Late Permian, Sunjiagou Fm.; T₁₋₂: Early and Middle Triassic; T₃: Late Triassic, Yanchang Fm.; N₂: Neogene; Q₁: Quaternary, loess deposit; Q₂: Quaternary, loess deposit; Q₃: Quaternary, loess deposit; Q₄: Quaternary, fluvial deposit.

Fig. 2. Stratigraphy and outcrop of *Gigantopteris* in Shanxi. (a) sedimentary log of the outcrop at Mengjiagou village; red-color indicates red beds. Sedimentary structures: 1. cross bedding; 2. parallel bedding; 3. roots and leaf fossils. Grain size scale: clay = clay; silt = silt sand; vf = very fine sand; f = fine sand; m = medium sand; c = coarse sand; vc = very coarse sand; gran = granules; peb = pebbles. (b) Photo of the outcrop at Mengjiagou village. The yellow arrow indicates position of fossil horizons, and white arrows position of red beds.

Fig. 3. *Gigantopteris dictyophylloides* from Taiyuan East Hill Coalfield. (a) shows the gross morphology of *G. dictyophylloides*, white arrow head directing the primary vein, scale bar is 10 mm; (b) enlargement of an area in (a), shows detail of the tertiary vein, quaternary vein and veinlet. White arrow head indicates quaternary vein and black arrow head directs veinlet, scale bar is 5 mm; (c) camera lucida draw of (a), showing the detail of venation system. Registration number PB21949.

Fig. 4. Palaeogeographic distribution of *Gigantonoclea* and *Gigantopteris* in the North China Block showing sedimentary lithofacies and isopachs of coal thickness for the Middle Permian and early Late Permian (Lower and Upper Shihhotse formations). Palaeogeographic map of modified from Liu (1990).

Table 1. Summary of sedimentary features of the Upper part of the Upper Shihhotse Formation at Mengjiagou village containing leaves of *Gigantopteris dictyophylloides*. Bedding thickness for thin bedded 1-10 cm, medium bedded 10-30 cm, and for thick bedded 30-100 cm. Bed 1 represents the bottom of the sedimentary succession.

Figure 1

Figure 2

Figure 3

Figure 4

Table 1

Bed	Thickness (m)	Description	Interpretation
17	4.4	Grayish w hite, thick bed, medium to coarse sandstone, containing pebbles at the bottom, cross-bedding, plant fossils absent	Fluvial channel deposit
16	0.7	Yellow , medium bed, siltstone containing clay, plant fossils absent	Overbank deposit
15	0.9	White, thick bed, medium sandstone, cross-bedding, plant fossils absent	Fluvial channel deposit
14	2.0	Red, thick bed, medium to fine sandstone, cross-bedding, plant fossils absent	
13	0.3	Yellow , medium bed, claystone, plant fossils absent	Overbank deposit
12	0.9	Red, medium bedded, siltstone to clay, parallel bedding, plant fossils absent	
11	1.5	Yellow , thick bedded, coarse sandstone containing pebbles at the bottom, cross-bedding, plant fossils absent	Fluvial channel deposit
10	1.8	Red, thick bedded, coarse sandstone, cross-bedding, plant fossils absent	Point bar deposit
9	0.6	Black, thin bedded, carbonaceous claystone, root fossils present	
8	0.7	Yellow , thick bedded, siltstone, plant fossils absent	
7	1.0	White, medium bedded, siltstone, plant fossils absent	
6	0.5	Yellow , medium bedded claystone, massive bedding structure, containing a large amount of plant fossils and root, including leaves of <i>Gigantopteris dictyophylloides</i>	Overbank deposit
5	0.6	Grayish, medium bedded, claystone and siltstone, at top part containing plant fossils including leaves of <i>Gigantopteris dictyophylloides</i>	
4	0.3	White to gray, medium bedded, siltstone, plant fossils absent	
3	0.7	Yellow , medium bedded, fine sandstone, plant fossils absent	
2	1.0	Red, medium bedded, fine sandstone	
1	unknown	Red, thick bedded, siltstone to claystone, bottom, plant fossils absent	