Cuticles and Spores in Situ of *Coniopteris hymenophylloides* from the Middle Jurassic in Gansu, Northwestern China

XIN Cunlin[1, 2, *], WANG Luhan[1], DU Baoxia[2], ZHANG Yamei[1] and WANG Jingjing[1]

1 *College of Geography and Environmental Science*, *Northwest Normal University*, *Lanzhou 730070*, *China*
2 *College of Earth and Environmental Sciences*, *Lanzhou University*, *Lanzhou 730070*, *China*

Abstract: *Coniopteris* was a ubiquitous plant of the Jurassic and Cretaceous periods and played an important role in the flora of the time. However, its anatomical structure is relatively poorly known. The specimens of *Coniopteris hymenophylloides* (Brongniart) Seward described here were collected from the Yaojie Formation in Gansu Province, northwestern China. The sterile fronds are characterized as being at least bipinnate with alternate arranged linear pinnae covered by thin cuticles. Fertile fronds are linear-lanceolate, with single sorus at the margin of each fertile pinnule. In situ spores are typically trilete, triangle to subcircular in polar view, cap-shaped in equatorial view, and 37 μm in average diameter. The trilete marking is straight and narrow, generally extends to 4/5 of the spore radius. The spore surface is smooth, and parts of the exine are granulated. The epidermal cells of cuticles are irregular in shape, approximately 40–60 μm long and 10–20 μm wide. The elliptical stomatal complexes are paracytic, approximately 30 μm long and 19 μm wide, and irregularly distributed. On the basis of its epidermal structures and comparisons with extant ferns, we consider that *Coniopteris* displays combined features of the related extant genera.

Key words: *Coniopteris hymenophylloides*, spore in situ, cuticle, Middle Jurassic, Yaojie Formation, Gansu, China

1 Introduction

It is generally thought that the Dicksoniaceae first appeared in the Early Jurassic, flourished in the Middle Jurassic and ended in the Early Cretaceous. The Dicksoniaceae was formerly considered a subfamily of Cyatheaceae and became independent due to the different position of its sori. *Coniopteris* from the Early Jurassic of England might be the oldest known Dicksoniaceous fern. Up to now, over 60 species of *Coniopteris* have been identified globally (Harris, 1961; Van Konijnenburg-van Citter, 1981, 2008; Deng Shenghui, 2002; Cantrill et al., 2005; Kostina et al., 2013; Scanu et al., 2015; Barbacka et al., 2016; Huang Min et al., 2016; Liu Gang et al., 2016; Guo Caiqing et al., 2017; Shi Qiuyuan et al., 2017) in temperate, subtropical and tropical zones. It likely preferred a warm, moist habitat (Vakhrameev, 1991; Wang Yongdong et al., 2009; Li Qijia et al., 2016; Herman et al., 2017; Li Gang, 2017; Li Zhenyu et al., 2017; Na Yulin et al., 2017; Zhang Yanzhen et al., 2017). *Coniopteris hymenophylloides* Seward is the most common Dicksoniaceae species in the Early and Middle Jurassic time. Although a series of studies of the sterile fronds and in situ spores of this species have been conducted (Harris, 1961; Vakrameev et al., 1961; Kilpper, 1964; Taylor et al., 1993; Li Houxin et al., 2015; Césari et al., 2016; Huang Wei et al., 2016; Sun Yuewu et al., 2016; Lara et al., 2017; Miao Huixin et al., 2018), it is still uncertain whether the spores of *Coniopteris hymenophylloides* are of the *Cyathidites* type or of the *Deltoidospora* type.

In China, around 40 species of *Coniopteris* have been recorded. *Coniopteris* is considered as a kind of small to large creeping rhizomatous ferns; and its habit, habitat, phytogeography and climatic setting were discussed by Deng Shenghui (2002). Wang Yongdong et al. (2009) found fossils of *Coniopteris hymenophylloides* with both sterile and fertile pinnae in the Lower Jurassic Hsiangchi Formation in western Hubei, China. He noted that this species is very small and slender in growth form, less than 20 cm tall. Although *C. hymenophylloides* has been recorded from a variety of localities (e.g., Chen Fen et al., 1984; Wu Shunqing and Zhou Hanzhong , 1986; Cao

* Corresponding author. E-mail: xincunling@163.com

Zhengyao and Zhang Yaling , 1996; Duan Ye et al., 2009; Zhang Fade and Tong Haikui , 2012; Huang Min et al., 2016; Zhao Miao et al., 2016; Han Gang et al., 2016, 2017; Wang Zixi et al., 2017), few of the specimens found at these locations involved microstructure features. And this is important to identification, phylogeny of *Coniopteris* and reconstruction of paleoclimate. So far only Li Qijia (2016) made cuticular analyses of *C. hymenophylloides* from the Middle Jurassic Yan'an Formation in Huating, Gansu. She found the upper and lower epidermis of *C. hymenophylloides*, but she didn't provide the details of stomatal complexes.

In the present study, well-preserved materials including sterile and fertile pinnae, sporangia and in situ spores, epidermal cuticles, as well as stomatal complexes of *C. hymenophylloides* from the Middle Jurassic Yaojie Formation in Gansu Province, northwestern China are investigated. They might be valuable in the systematics and phylogeny of *Coniopteris*.

2 Geological Setting

The Yaojie Basin is located in Gansu Province, northwest China. The basin belongs to the Middle Qilian uplift zone and lies at the transfer site of the Qilian folded mountains and the Lanzhou block. As an inland basin, it was formed in the Mesozoic and developed in the Cenozoic . It is a long and narrow basin extending north-southward; the average elevation is approximately 1520 meters (Fig. 1).

The Yaojie Formation is coal-bearing, formed in the fluvial-lacustrine depositional system with a total thickness of 235 meters (Fig. 2). The geological age of the Yaojie Formation has been dated as Aalenian to Bajocian based on plant fossil assemblages (Sun Bainian, 1986; Sun Bainian et al., 2007; Yan Defei et al., 2009). According to its lithologic characteristics, the sequence of strata of the formation (from bottom to top) is: conglomeratic sandstone Member (J_2y^1), coal-bearing Member (J_2y^2), mudstone Member (J_2y^3), oil shale Member (J_2y^4), and muddy siltstone Member (J_2y^5) (Gansu Geology and Mineral Bureau, 1989; Xie Sanping et al., 2006). The fossils were collected from the muddy siltstone Member (J_2y^5) which consists of gray, grayish-green, grayish-yellow sandstones, siltstones, grayish-black mudstones and coal seams. The thickness of the member is around 70 meters. The studied fossils at present were associated with other plant taxa, including *Equisetites lateralis* (Phillips), *Coniopteris burejensis* (Zalessky) Seward, *Coniopteris simplex* (L. et H.) Harris, *Cladophlebis whitbiensis* (Brongniart), *Pterophyllum subaequale* Hartz, *Ginkgoites digitata* (Brongniart) Heer, *Ginkgo huttoni* (Sternberg) Heer, *Phoenicopsis angustifolia* Heer, *Pozodamites lanceolatus* (L. et H.) Heer, indicating a kind of the *Coniopteris-Phoenicopsis* flora in North China.

3 Materials and Methods

The specimens used in this study and their sterile and fertile fronds were collected from coal-bearing members (J_2y^2), oil shale members (J_2y^4), and muddy siltstone members (J_2y^5) of the Yaojie Formation.

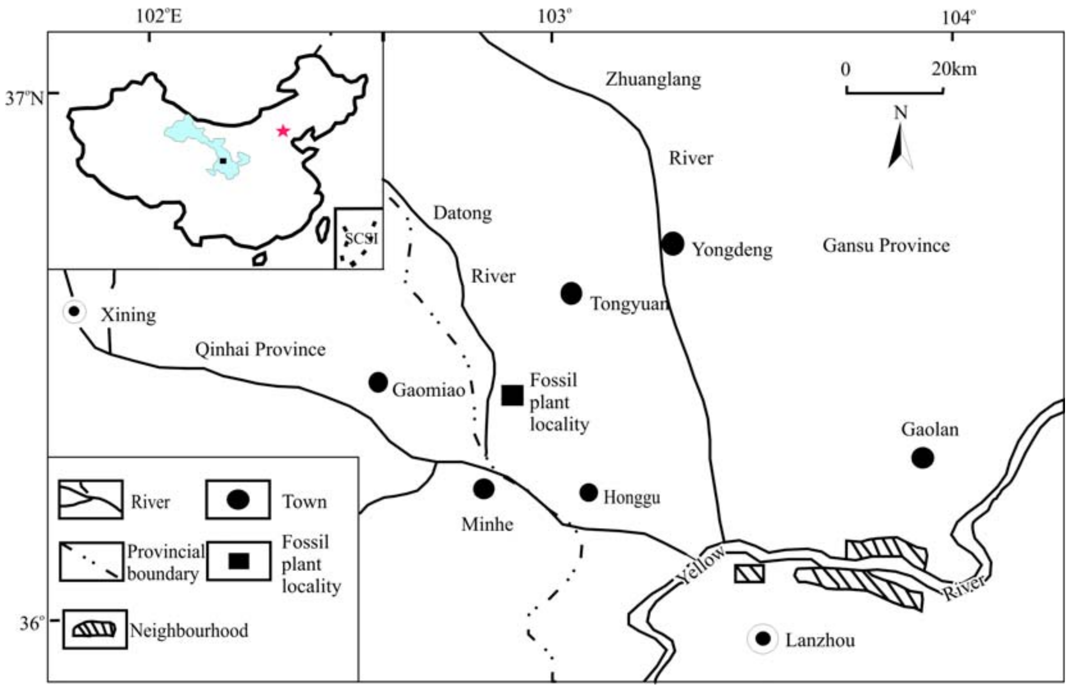

Fig. 1. Sketch map showing the fossil plants'location in Yaojie Basin, Gansu Province, China.

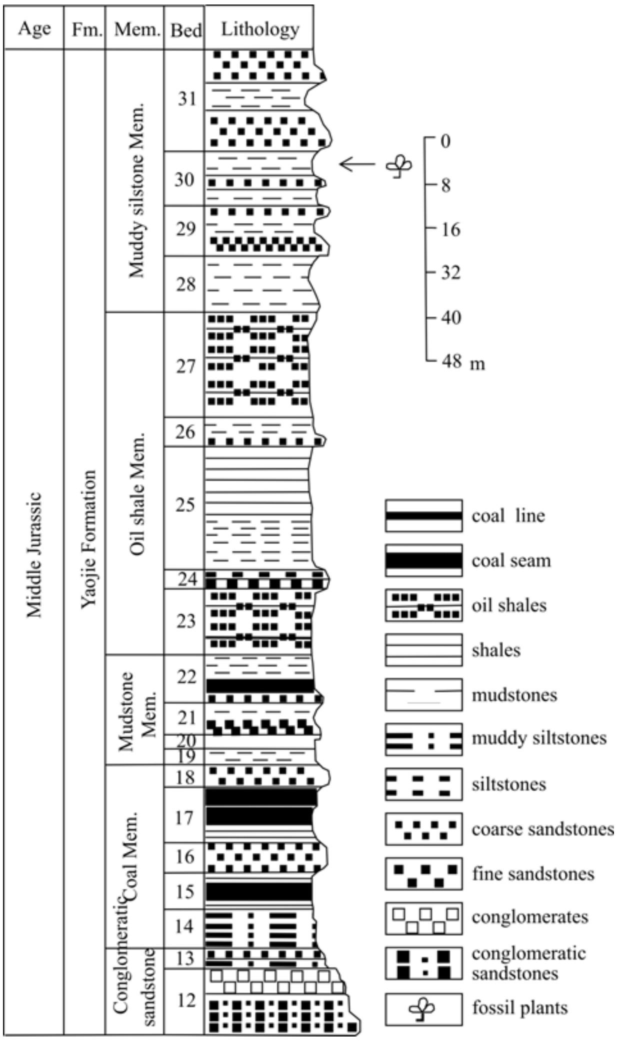

Fig. 2. Stratigraphic section through the Yaojie Formation, Gansu Province, China.

Treatment of spores: The sori were extracted from fertile pinnules using the peel method or a small knife and treated with HCl to remove calcium. The samples were then dissolved in 39% HF to remove siliceous and clay material, followed by cold treatment for 24 hours or boiling for 15–20 minutes. The samples were then treated with 5% HNO_3 and neutralized with 5%–10% KOH until their color changed to light brown. The samples were divided into two parts: one part was mounted for observation under the light microscope, and the other part was used as a standby.

Treatment of fossil cuticles (Lei Xiangtong et al., 2018): First, the black membranes were stripped from the middle parts of the fossil fronds, and the fronds were washed with distilled water and placed in an HCl solution to remove calcium. The samples were then placed in 39% HF to remove siliceous impurities, followed by maceration with Schulze's solution for 30 minutes. When the color became brown to red, the samples were neutralized with distilled water. After a short treatment (approximately 30 mins) with 5% ammonia, the samples were stained with Safranin T and mounted for observation (Kerp et al., 1999).

All specimens, megafossils and slides for LM are stored at the Northwest Normal University, Gansu Province, China.

4 Description

Order Filices

Family Dicksoniaceae

Genus *Coniopteris* Brongnart, 1948

Coniopteris hymenophylloides (Brongniart) Seward 1900 (Figs. 3, 4a-d)

1828 *Coniopteris hymenophylloides*, Brongniart, P. 589, pl. 122, fig. 3, 4.

1875 *Sphenopteris hymenophylloides*, Brongniart, P. 215, pl. 10, fig. 8.

1900 *Coniopteris hymenophylloides*, Seward, P. 99, pl.16, fig. 4, 6.

1988 *Coniopteris hymenophylloides*, Li, P.52, pl.23, fig. 4, 5.

Age and horizon: Middle Jurassic, Yaojie Formation

Type locality: Yaojie Basin in Gansu province, northwestern China (36°25′N, 102°50′ E)

Stratigraphy: Yaojie Formation, Aalenian to Bajocian

4.1 Megafossils

Leaf usually are entirely sterile or almost entirely fertile, and few borne together (Fig. 3d). The preserved fronds are bipinnate, measured over 40 mm long and 25 mm wide (Fig. 3a). The main rachis is straight, up to 2 mm. Sterile pinnae are linear, 20 mm long and 3 mm wide. Basal pinnules nearly opposite, later ones becoming alternate in katadromic order. Pinnules from lower parts of pinnae are mainly rhombic with shallowly lobed margins. The lobes are acuminate. And the first basiscopic lobe developed as filiform lying over the rachis. Upper pinnules are ovate and entire, about 3 mm long and 1 mm wide, with decurrent leaf bases (Fig. 3c). In particular, almost every first basiscopic pinnae turn to filiform, which differs from other ones (Fig. 3b).

Fertile pinnae are linear-lanceolate, 15 mm long and 3 mm wide, as wide as sterile ones (Fig. 3e). Fertile pinnules are strongly shrunk to thin rod shapes while always retaining a certain leaf membrane with marginal sori. In addition, there are some basiscopic lobe also developed as filiform which is similar to the sterile ones (Fig. 3f).

4.2 Sori and sporangia

Each fertile pinnule usually bearing a single sorus; sorus oval to rounded with a suspensor, about 1 mm in diameter.

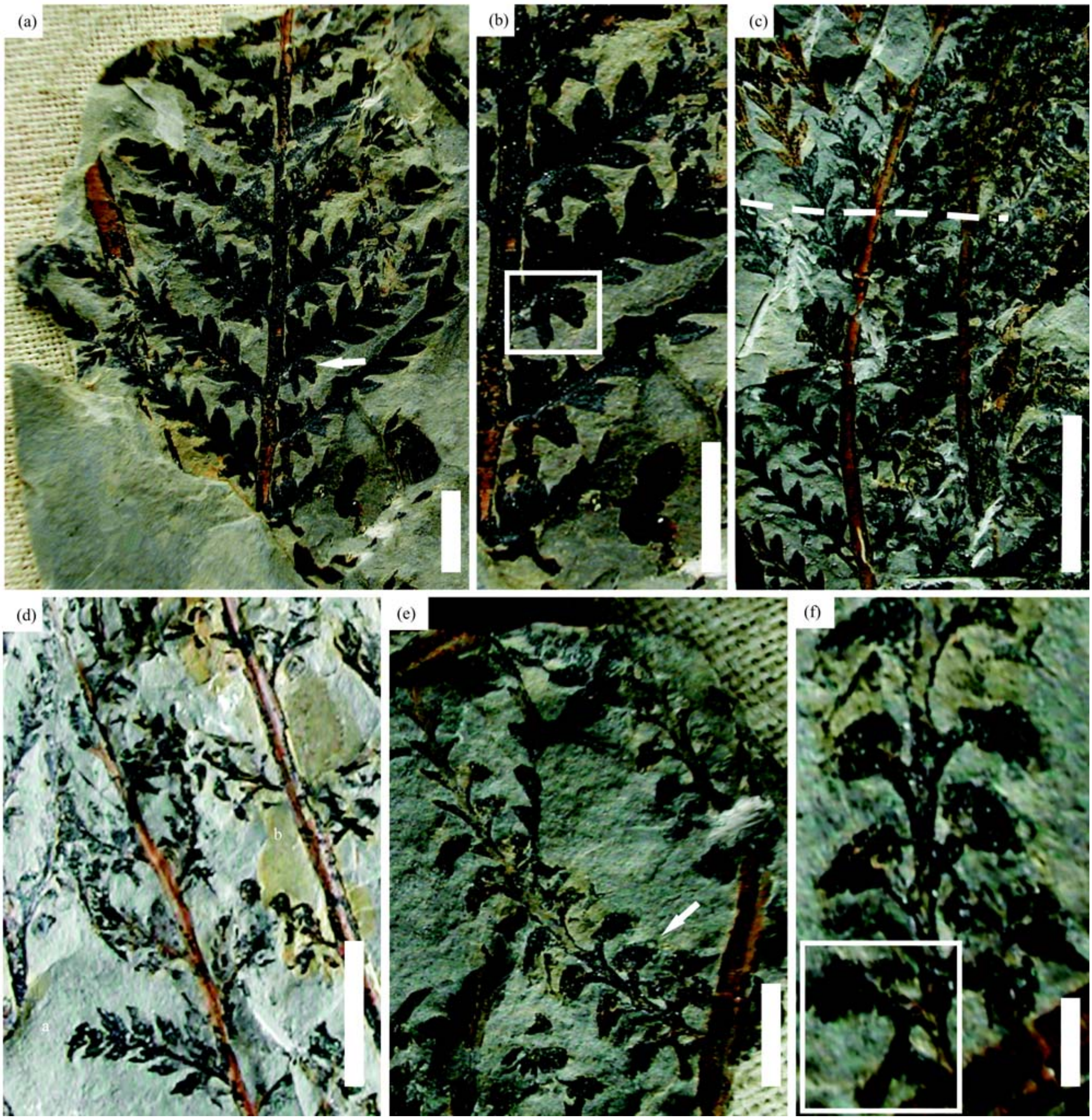

Fig. 3. Leaves, sporangia and in situ spores of *Coniopteris hymenophylloides.*

The sporangium is globate or ellipsoidal, approximately 400 μm long and 250 μm wide. Each sporangium contains spore masses (Fig. 4a).

4.3 In situ spores

Spores are typically trilete, yellow or brown, tetrahedral, mainly triangular in polar view, and some are subcircular. The three sides are of equal length and slightly convex, and several are slightly concave with round or obtuse apices (Fig. 4b–c). The spores are semicircular or cap-shaped in equatorial outline (Fig. 3d). The spore diameter ranges from 27.5 to 46 μm in polar view (37 μm on average). The radius is straight and narrow, sometimes cracked or even triangular; a few are slightly curved or undulate, and the young spores have an elevated radius, unlike the mature ones. The radius generally extends to 4/5 of the spore radius, approaching the edge of the spore, and the spore edges are not lipped. The spore surface is smooth, although parts of the exine are granulate.

4.4 Epidermal structures

Fronds are hypostomatic with thin cuticle. The upper epidermal cells are irregular in shape but usually rectangular, 40–60 μm long and 10–20 μm wide. The anticlinal walls are straight or slightly undulate (Fig. 4e). The lower epidermal cells are similar to the upper ones (Fig. 4f). The elliptical stomatal complexes are paracytic and irregularly distributed, about 30 μm long and 19 μm wide, and the stomatal density is small (Fig. 4g). The stomatal aperture is an elongated oval, a few microns in length. The guard cells are large and clear, and each pair of guard cells is completely surrounded by two subsidiary cells whose long axes are parallel to those of the guard cells (Fig. 4h).

5 Discussion and Comparisons

5.1 Comparisons

The sori of the present specimens grew at the margin of each fertile pinnule; this feature is only recorded in the Family Dicksoniaceae of the Order Filices (Sun Keqin et al., 2010). The fossil Dicksoniaceae comprises five genera. The present specimens is very similar to *Coniopteris hymenophylloides* (Harris, 1961), the type species of *Coniopteris*: both have a rachis that is 2 mm wide, linear to lanceolate pinnae, and rhombic to lanceolate pinnules with acute lobes. The angle between the pinna and the axis is approximately 40°–50° (Si Xingjian and Li Xingxue , 1963). These features separate the present specimen from other genera. Consequently, we assign the present specimens to *Coniopteris*.

The specimens have two obvious features. The first is the divisions of pinnules, which is an important basis for the identification of *Coniopteris.* Pinnules of the present specimens are slightly lobed to entire from lower to upper part, and the lobes all are acuminate. Besides the first basiscopic lobe of the present specimens always developed as filiform. There are 5 species from the

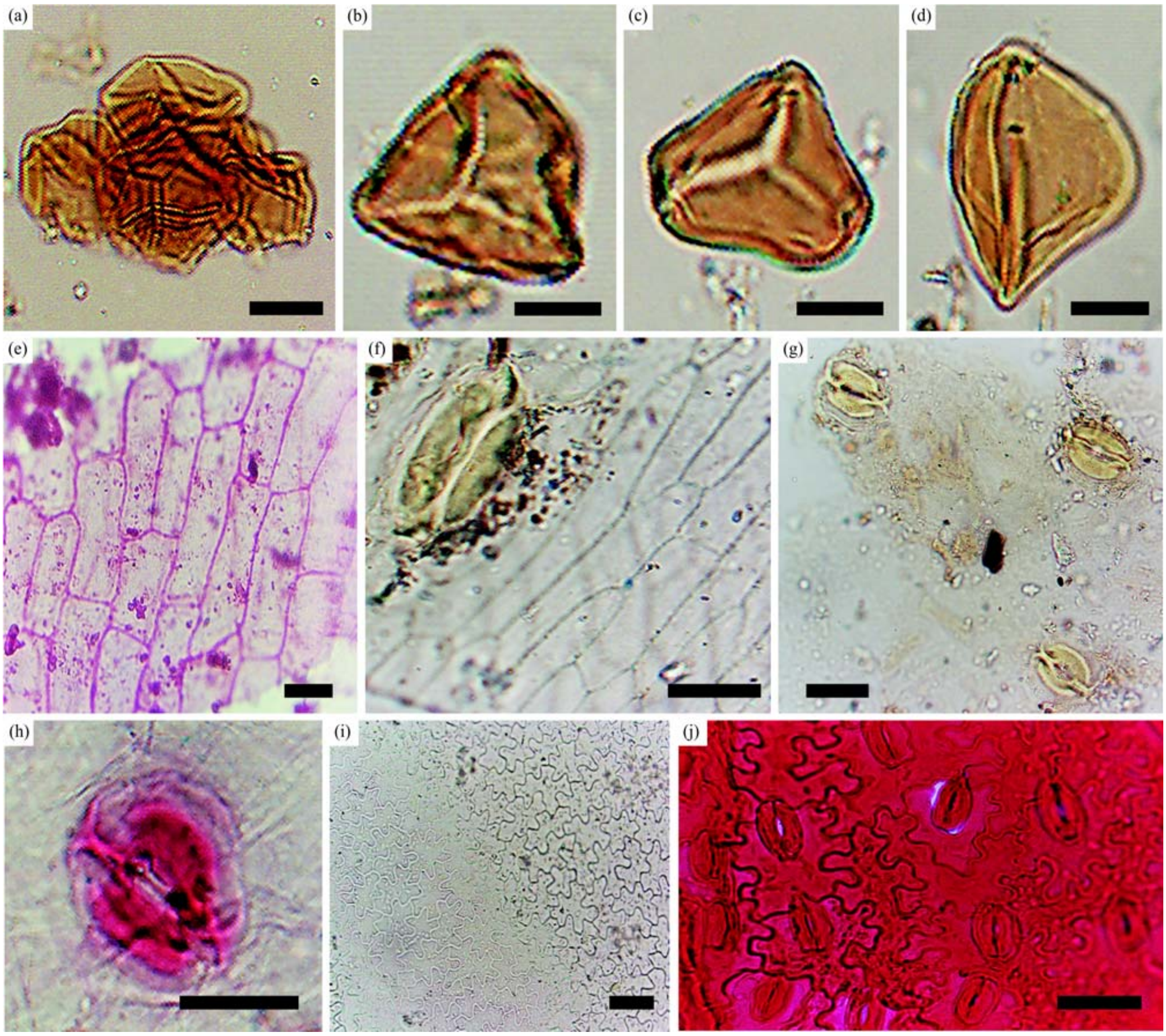

Fig. 4. Spores and cuticles of *Coniopteris hymenophylloides* and cuticles of the extant species *Cyathea spinulosa.*

Jurassic that have abnormal leaves. However as for *Coniopteris qinghaiensis*(Li Peijuan, 1988), pinnules in the middle and upper portions have 5–7 lobes, more than are found in the present specimens. *C. beijingensis*(Chen Fen et al., 1984) has a thinner rachis, less than 2 mm wide and its fertile pinnules are not shrunken. And *C. tiehshanensisi*, has lobes bear rounded apexes (Ye Meina et al., 1986). In *C. murrayana*(Sun Keqin et al., 2010), the first pinnule above the rachis at the base of the pinna is slightly larger than the one below it; the rachis is approximately 1 mm wide, and the pinnules are divided into 2-3 pairs of lobes with obtuse apexes (Li Peijuan, 1988). These features all differ from those of the present specimens, whereas in *C. hymenophylloides* (Harris,1961), basal pinnule with its first basiscopic lobe developed as filiform processes lying over the rachis, same to the present specimens. Besides the upper epidermal cells of the present specimens are enlonged cells about 20 long and 70 long, similar with the *C. hymenophylloides*. Meanwhile we also make comparisons between the present specimens and other similar species in *Coniopteris* (Table 1). Therefore, based on the foregoing analysis, we assign the present specimens to *C. hymenophylloides*.

5.2 Comparison with other cuticles of fossil ferns

The fern cuticles are very rarely studied because their preservation usually is very poor and fern cuticles are very thin. Up to date, the anatomical research of the fern was mainly on Pteridosperm (Barbacka et al., 1998; Retallack, 2001). The study on cuticles of *Pachypteris* (fern) from late Jurassic (Doludenko, 1971; Barbacka et al., 1998; Retallack, 2001; Guignard et al., 2009) is a typical research which showed details in epidermal structures. The fronds of *Pachypteris* are hypostomatic. And upper epidermis is composed of cells with thick walls, arranging disorderly. The stomatal apparatus distributed in the lower epidermis, arrange disorderly. The density of stomata usually increases from the edge of the pinnule to the center. The subsidiary cells are well developed, usually 5 to 6 ,with irregular shape, arranged around stoma. The main difference between the cuticles of *Coniopteris hymenophylloides* and *Pachypteris* is the guard cells and subsidiary cells. The former ones have well developed guard cells, conversely, the latter has developed subsidiary cell. But they have similarities in the shape and size of stomata apparatus. Thus this could also explain that the affinity of *Pachypteris* and *Coniopteris* is relatively far, but they all are ferns.

Harris (1961) made a preliminary study of several cuticles of *Coniopteris* from the Yorkshire Flora. The cuticles of *C. murrayana* are similar to *C. hymenophylloides*, but its upper epidermis cells could reach 250 μm long. And Li Qijia (2016) studied the cuticles of *C. hymenophylloides* and *Sphenopteris chowkiawanensis*, found that they both characterized as being thin, no tubers and flat.

5.3 Comparison with extant related genera

Coniopteris in the Middle Jurassic is an herbaceous plant that is short with creeping rhizomes. The pinnules are ovate, rhomboid and lanceolate. A single sorus (seldom double) inserts at the top of the vein; the margin of the pinnule is usually fully or partly surrounded by a cup-like indusium. The spores are typically trilete with granular or rugulate elements on the surface. These characteristics also occur in some extant genera in the Dicksoniaceae, Cibotiaceae, Culcitaceae, Thyrsopteridaceae and Cyatheaceae. In this paper, we compared the morphological characters of *Coniopteris* with those of related extant genera in these families to determine the similarities between *Coniopteris* and extant plants, then the affinity and systematics of *Coniopteris* (Table 2).

The extant dicksoniaceous plants are tree ferns, generally marked by pinnules with vein ends terminating in submarginal sori that are similar to those of *Coniopteris.* The Dicksoniaceae used to include 6 extant genera, of which now only 3, *Dicksonia*, *Calochlaena* and *Lophosoria*, remain. These ferns are mostly arborescent or with erect or ascending rhizomes; the pinnae are linear or lanceolate, as are the pinnules, and the spores are globose or tetrahedral. However, the spore surface is psilate. Although *Dicksonia* and *Calochlaena* possess bivalved indusia, *Lophosoria* even lacks indusia (Smith et al., 2006). Moreover, the stomatal complexes of *Dicksonia* are paracytic, approximately 30 μm long and 20 μm wide, similar to those of *Coniopteris.* However, the anticlinal walls are obviously deeply wavy (Volkova et al., 2011).

The Cibotiaceae, Culcitaceae, and Thyrsopteridaceae were formerly considered genera in Dicksoniaceae. In the Culcitaceae, there is only one genus, *Culcita*, with two species. The rhizomes are creeping or ascending, similar to *Coniopteris*; the sori are approximately 3 mm wide and terminate on veins with bivalved indusia, and the spore surface is psilate (Deng Shenghui and Chen Fen, 2001). These features differ from those of *Coniopteris.* In the Cibotiaceae, there is only one genus, *Cibotium*, with 11 species. The pinnules of *Cibotium* are falcate with serrulate marginals; the sori terminate on veins with bivalved indusia, and the stomata have 3 subsidiary cells (Smith et al., 2006), whereas there are 2 subsidiary cells in *Coniopteris.*

In the Thyrsopteridaceae, there is one genus, *Thyrsopteris*, with a single species, *T. elegans.* The

Table 1 Comparison of the megafossils of *Coniopteris hymenophylloides* with other similar species

Species	Fronds (mm)	Pinnae	Sterile pinnule		Fertile pinnule			Reference
			Margins	Shape	Abnormal	Type	Shape	
C. kuandianensis	Unknown	Lanceolate L=20, W=15–20	Lobed, undulate	Rhombic, ovoid with acute apexes, L=10–20, W=3	Possess	All fertile pinnules	Shrunken to stipiform	Zhang, 1980
C. microlepioides	R<1	Linear, A=20°–30°,	Entire	Fusiform to lanceolate with acute apexes	-	Unknown	Not shrunken	Zhou, 1984
C. beijingensis	L=85, W=60, R < 2	Lanceolate to long-triangular A=40°–60°, L=30, W=5	Entire to lobed	Rhombic with acute apexes, L=6, W=2	Possess	Together with sterile pinnules	Not shrunken	Chen, 1984
C. saportana	Unknown	Linear L=70, W=5–10	Entire	Long ovoid with acute apexes, L=10, W=3	-	Unknown	Unknown	Zhang,1980
C. sewardii	Unknown	Linear L=7–10, W=3	Entire or lobed	Obovate with acute apexes, L<2.5, W=1	Possess	Unknown	Unknown	Zhang, 1980
C. silapensis	R=1–3	Lanceolate, L>30, W=15	Entire or lobed	Long ovoid to triangular with acute apexes, L=3, W=1	Possess	Unknown	Unknown	Zhang,1980
C. simplex	W=18, R=1	Long ovoid, A=50°–60° L=8, W=4	Lobed	Ovoid to long ovoid, L=1–1.5, W=1	-	Together with sterile pinnules	Shrunken	Harris, 1961
C. tyrmica	R=1	Linear to lanceolate, A=70°–80° L=10-30, W=3	Entire	Long ovoid with obtuse apexes	-	Unknown	Shrunken	Zhang, 1980
C. xipoensis	L=15–25, W=3, R=1	Lanceolate L>30, W<10	Undulate, lobed	Ovoid with obtuse apexes, L=5, W=2	-	All fertile pinnules	Shrunken to short stipiform	Liu, 1982
C. zindanensis	R<1	Linear, A=nearly 90° L=30-40, W=7	Lobed	Rhombic with acute apexes, L=4, W=3	Possess	Together with sterile pinnules	Shrunk to stipiform	Zhang, 1980
C. hymenophylloides	L=40, W=20, R=1.5	Linear to lanceolate L=25, W=10	Parted, lobed, entire	Ovate, triangular with acute apexes, L=5, W=3	Possess	All fertile pinnules or together with sterile pinnules	Shrunk to thin-rod shaped	Harris, 1961
C. arctica	R=1	Lanceolate L=10–25, W=5–12	Lobed	Long ovate, rhombic with acute apexes; L=10, W=3	-	Together with sterile pinnules	Shrunken to virgate	Deng, 2001
C. gansuensis	R<1	Linear to lanceolate	Parted	Ovoid, L=7–10, W=4-–5	Possess	Unknown	Shrunken to stipiform or a little	Cao, 1996
C. qinghaiensis	R<1	Long lanceolate,70° L=40–50, W=7–8	Parted, lobed, entire	Rhombic, L=6-7, W=2.5	Possess	Together with sterile pinnules	Somewhat shrunken	Li, 1988
C. nikaensis	L>200， W=120–150, R=2	Linear, A=45°–50° L=100, W=15–20	Parted, lobed, entire	Rhombic, L=10, W=5–7	-	Unknown	Unknown	Zhang, 1998
C. burejensis	R=1	Linear to lanceolate, A=45°–60°, L=60,W= 50	Parted, lobed, undulate	Long-ovate, L=4,W=2	-	All fertile pinnules	Slightly shrunken	Li, 1988
Present specimens	L=45, W=25, R=2	Linear L=20, w=3	Lobed, entire	Rhombic ovate with acute apexes, L=3, W=2	Possess	All fertile pinnules or together with sterile pinnules	Shrunk to thin-rod shaped	Present paper

Note: R: rachis width; L: length; W: width; A: angles of rachis to pinnae.

Table 2 Cuticular structures of several extant genera and *Coniopteris*

Family	Genus	Pinnules		Sori position	Indusia	Spore	Anticlinal	Stomata	Reference
		shape	margin			ornamentation	walls		
Dicksoniaceae	*Dicksonia*	Ovate or linear	Lobate or parted	Edge of the lobe	Bivalved	Psilate or lophlate	Deeply -wavy	Long elliptical	Smith, 2006
	Calochlaena	Linear or lanceolate	Parted	Edge of the lobe	Bivalved	Verrucate or tuberculate	-	-	
	Lophosoria	Linear	Entire	Edge of the lobe	Lacks		-	-	
Cibotiaceae	*Cibotium*	Falcate	Serrulate	Edge of the lobe	Bivalved	Granulate	-	-	Smith, 2006
Culcitaceae	*Culcita*			Edge of the lobe	Bivalved	Psilate	-	-	Deng, 2001
Thyrsopteridaceae	*Thyrsopteris*	Rhomb or lanceolate	Lobate or entire	Edge of the lobe	Cup-shaped	Tuberculate, lamellate or rugulate	-	-	Pérez, 1997
Cyatheaceae	*Sphaeropteris*	Linear to lanceolate	Parted or divided	Near the pinnule midvein	Lacks	Granulate or verrucate	Deeply -wavy	Elliptical to long elliptical	Fishbein, 2008
	Alsophila	Falcate	Entire or sinuous	Near the pinnule midvein	Cup-shaped, scale-shaped or lacks	Stiate or granulate	Deeply -wavy	Elliptical to long elliptical	
	Cyathea	Lanceolate or falcate	Entire or serrulate	Each side of the pinnule midvein	Globose	-	-	-	
-	*Coniopteris*	Ovate, rhomb, lanceolate or triangle	Entire, lobate or parted	Edge of the lobe	Cup-shaped	Granulate, rugulate or plicate	Straight, slightly undulate	Elliptical	

pinnules are rhomboid or lanceolate, and the sori are borne at the edge of the lobe. The indusia are cup-shaped. Moreover, the spores are globose-tetrahedral with prominent angles, approximately 50 μm long. The spore surface is tuberculate, lamellate or rugulate (Pérez García et al., 1997). These features are similar to those of *Coniopteris*. However, the epidermal anatomy of this species is unknown.

The classification of the Cyatheaceae has had a long and controversial history, and three tentative 'clades', *Alsophila*, *Cyathea* and *Sphaeropteris*, have been developed (Korall et al., 2006). *Sphaeropteris* and *Cyathea* have linear or lanceolate pinnules. However, the sori of these clades differ from those of *Coniopteris*. The sori of *Sphaeropteris* are borne halfway between the pinnule midvein and the edge of the lobe and lack indusia. The sori of *Cyathea* are borne at each side of the pinnule midvein and are globose. Some species of *Alsophila* have sori with cup-shaped indusia, similar to *Coniopteris*, but these sori are borne near the pinnule midvein (Fishbein, 2008). The stomatal complexes of *Sphaeropteris* and *Alsophila* are paracytic. Both have two guard cells and two subsidiary cells. The stomatal complexes of *Sphaeropteris* are approximately 30-40 μm long and 15-20 μm wide. In *Alsophila spinulosa*, the typical representative of *Alsophila*, the upper and lower epidermal cells are almost the same shape and size, approximately 50-80 μm in diameter, and the lower epidermis is relatively better developed. The stomata are arranged on each side of the veins. The stomatal apparatus is oval or ovate, approximately 28 μm long and 20 μm wide (Fig. 4E-F). However, the anticlinal walls of *Sphaeropteris* and *Alsophila* are mainly deeply wavy (Liu Houxin et al., 2015).

In conclusion, the pinnae, pinnules, sori and indusia of *Thyrsopteris* are more similar to those of *Coniopteris* than to those of any other genus. With respect to epidermal anatomy, the stomatal complexes of *Dicksonia*, *Sphaeropteris* and *Alsophila* are all paracytic, and the sizes and shapes of their stomatal complexes are also similar. Thus, the comparison with extant related genera shows that *Coniopteris* has the combined features of these genera.

5.4 Paleoclimate

The Yaojie Formation contains flora of the Middle Jurassic and a part of the late *Coniopteris*-*Phoenicopsis* flora (Sun Bainian, 1986). True ferns, including *Coniopteris*, *Rhizomopteris*, *Eboracia*, *Clathropteris*, *Hausmannia*, and *Cladophlebis*, are one of the dominant plant components of the Yaojie Formation. *Coniopteris* is by far the dominant genus, representing 42.6% of the total fern specimens and 7 species. Among these, *Coniopteris hymenophylloides* is very common, being found almost all over the world. On the basis of its distribution, it can be concluded that *C. hymenophylloides* lived under warm and humid climatic conditions (Deng Shenghui, 2002). The dominant elements associated with *C. hymenophylloides* in the fossil assemblage of the Yaojie Formation include *Ginkgoites*, *Phoenicopsis*, *Elatocladus*, *Podozamitales*, and others. These genera mainly lived in tropical or subtropical zones. In addition, the cuticles of *C. hymenophylloides* are thin, and the epapillate and stomatal complexes of the megafossils are not sunken; these features of *C. hymenophylloides* also indicate a more humid environment. Based on the above, the Middle Jurassic of Yaojie in Gansu presented a warm and humid subtropical climate.

6 Conclusions

Based on study and analysis of the features of the megafossils described in this work, we confirm that the specimen is *Coniopteris hymenophylloides* (Brongniart) Seward.

The discovery of *C. hymenophylloides* in the Yaojie Formation adds new evidence that dates the geological age of the Yaojie Formation as Aalenian to Bajocian and indicates that the Yaojie Formation experienced a warm and humid climate during the Middle Jurassic period preliminarily.

We extracted well-preserved in situ spores from the present specimens and studied. The comparison of *Coniopteris* with extant species shows that *Coniopteris* combines the features of its related extant genera.

Moreover, a detailed studied has made. The ultrastructural research on *C. hymenophylloides* has a certain guiding significance for the identification and classification of fern fossil plants and the found of stomatal apparatus could use to reconstruct the paleoclimate quantificationally.

Acknowledgements

This project received financial support from the National Natural Science Foundation of China (No. 41262001) and the Science and Technology Support Fund of Gansu Province (No. 1104FKCA116).

Manuscript received Nov. 3, 2017
accepted Apr. 11, 2018
edited by Fei Hongcai

References:

Barbacka, M., Popa, M.E., Mitka, J., Bodor, E., Püspöki, Z., and Mcintosh, R.W., 2016. A quantitative approach for identifying plant ecogroups in the romanian early jurassic terrestrial vegetation. *Palaeogeography Palaeoclimatology Palaeoecology*, 446: 44–54.

Barbacka, M., and Van Konijnenburg-van Citter, J.H.A., 1998. Sun and shade leaves in two Jurassic species of Pteridosperms. *Review of Palaeobotany and Palynology*, 103 : 209–221.

Cantrill, D.J., Nagalingum, N.S., 2005. Ferns from the Cretaceous of Alexander Island, Antarctica: implications for Cretaceous phytogeography of the Southern hemisphere. *Review of Palaeobotany and Palynology*, 137: 83–103.

Cao Zhengyao and Zhang Yaling, 1996. A new spcies of *Coniopteris* From Jurassic of Gansu. *Acta Palaeontologica Sinica*, 35(2): 241–247 (in Chinese with English abstract).

Césari, S.N., and Colombi, C., 2016 Palynology of the late Triassic ischigualasto formation, Argentina: Paleoecological and paleogeographic implications. *Palaeogeography Palaeoclimatology Palaeoecology*, 449: 365–384.

Chen Fen, Dou Yawei and Huang Qisheng, 1984. *Beijing Xishan Jurassic Flora*. Beijing: Geological Publishing House, 36–40 (in Chinese).

Deng Shenghui and Chen Fen, 2001. *The Early Cretaceous Filicopsida from northwest China*. Beijing: Geological Publishing House, 76–108 (in Chinese).

Deng Shenghui, 2002. Ecology of the Early Cretaceous ferns of Northeast China. *Review of Palaeobotany and Palynology*, 119: 93–112.

Doludenko, M.P., 1971. Thinnfeldia, a junior synonym of *Pachypteris*. *Paleontological Journal*, 2: 99–104.

Duan Ye, Zheng Shaolin, Hu Dongyu, Zhang Lijun and Wang Wuli, 2009. Preliminary report on Middle Jurassic strata and fossils Linglongta area of Jianchang, Liaoning. *Global Geology*, 28(2): 143–147 (in Chinese with English abstract).

Fishbein, M., 2008. Plant Systematics: A Phylogenetic Approach. *Quarterly Review of Biology*, 83(3): 317–318.

Gansu Geology and Mineral Bureau Exploration and Mineral Development, 1989. *Regional Geology of Gansu Province*. Beijing: Geological Publishing House, 1–692 (in Chinese).

Guignard, G.,Wang Yongdong, Ni Qing, Tian Ning and Jiang Zikun, 2009. A dipteridaceous fern with *in situ* spores from the Lower Jurassic in Hubei, China. *Review of Palaeobotany and Palynology*, 156: 104–115.

Guo Caiqing, Yao Jianxin, Zhang Jianwei, Wu Pengcheng and Li Chengsen, 2017. New Fossil Liverworts from the Lower Cretaceous of Western Liaoning, China. *Acta Geologica Sinica* (English Edition), 91(5): 1542–1552.

Han Gang, Liu Zhongjian and Wang Xin, 2017. A Dichocarpum-like Angiosperm from the Early Cretaceous of China. *Acta Geologica Sinica* (English Edition), 91(1): 1–8.

Han Gang, Liu Zhongjian, Liu Xueling, Mao Limi, Jacques, F.M.B., and Wang Xin, 2016. A Whole Plant Herbaceous Angiosperm from the Middle Jurassic of China. *Acta Geologica Sinica* (English Edition), 90(1): 19–29.

Harris, T.M., 1961. *The Yorkshire Jussic Flora.1Thallophyta-Pteridophyta*. London: British Museum (Natural History), 1–204.

Herman, A.B., and Sokolova, A.B., 2016. Late Cretaceous Kholokhovchan flora of northeastern Asia: Composition, age and fossil plant descriptions. *Cretaceous Research*, 59: 249–271.

Huang Min, Zhu Huaicheng, Liu Feng and Peng Huiping, 2016. Lower and middle Devonian spore assemblages from Longmen Mountains, Sichuan Province. *Geology Review*, 62 (6): 1533–1548 (in Chinese with English abstract).

Huang Wei, Dilcher, D.L., Wang Hongshan, Na Yuling, Li Yun feng, Li Tao and Sun Chunlin, 2016. First record of Sphenarion, (Czekanowskiales) with epidermal structures from the Middle Jurassic of Inner Mongolia, China. *Palaeoworld*, 26(3): 510–518.

Kilpper, K., 1964. Über eine Rät/Lias Flora aus dem Nördlichen Abfall des Alburs-Gebirges in Nordiran. *Palaeontographica Abteilung B -Stuttgart-*, 114: 1–78.

Korall, P., Pryer, K.M., Metzgar, J.S., Schneider, H., and Conant, D.S., 2006. Tree ferns: Monophyletic groups and their relationships as revealed by four protein-coding plastid loci. *Molecular Phylogenetics and Evolution*, 39(3): 830–845.

Kostina, E.I., and Herman, A.B., 2013. Middle Jurassic flora of

South Mongolia: Composition, age and phytogeographic position. *Paleontological Journal*, 193(12): 82–98.

Kerp, J.H.F., and Krings, M., 1999. Light microscopy of cuticles. In: Jones, T., and Rowe, N. (eds.), *Fossil plants and spores. Modern techniques*. London: The Geological Society, 52–56.

Lara, M.B., Cariglino, B., and Zavattieri, A.M., 2017. Palaeoenvironmental interpretation of an Upper Triassic deposit in southwestern Gondwana (Argentina) based on an insect fauna, plant assemblage, and their interactions. *Palaeogeography Palaeoclimatology Palaeoecology*, 476: 163–180.

Lei XiangTong, Du Zhen., Du BaoXia, Zhang Mingzhen and Sun Bainian, 2018. Middle Cretaceous pCO_2 variation in Yumen, Gansu Province and its response to the climate events. *Acta Geologica Sinica* (English Edition), 92(2): 801–813.

Li Gang, 2017. SEM morphological study of the type species of Ordosestheria, Wang, 1984 (Spinicaudata) from Ordos Basin of mid-west China. *Cretaceous Research*, 75: 1–6.

Li Peijuan, 1988. *Early and Middle Jurassic strata and their floras from northwestern border of Qaidam Basin, Qinghai*. Nanjing: Nanjing University Press (in Chinese).

Li Qijia, 2016. *Plant composition and palaeoenvironmental analysis of Middle Jurassic flora in Huating, Gansu province*. Lanzhou University.

Li Qijia, An Pengcheng, Li Jun, Zhao Zhenrui, Wu Jingyu, Wang Yongdong, Zhu Yuting and Ding Suting, 2016. Cuticular structure of Storgaardia, Harris from the Middle Jurassic of Northwest China and its systematic and biogeographical significances. *Palaeoworld*, 26(1): 149–158.

Li Zhenyu, Ding Lin, Song Peiping, Fu Jiajun and Yue Yahui, 2017. Paleomagnetic constraints on the paleolatitude of the Lhasa block during the Early Cretaceous: Implications for the onset of India–Asia collision and latitudinal shortening estimates across Tibet and stable Asia. *Gondwana Research*, 41: 352–272.

Liu Gang, Mou Quanhai and Yao Haitao, 2016. Features of mammalian fossil geoheritage in Hezheng, Gansu and their scientific significances. *Acta Geologica Sinica*, 90 (8): 1679–1691(in Chinese with English abstract).

Liu Houxin, Wei Xuezhi and Yang Ruilin, 2015. The Leaf Epidermis Micromorphological Observation and its Taxonomic Significance of Six Species of Two Genera in Cyatheaceae in China. *Chinese Journal of Tropical Crops*, 36 (10): 1808–1813(in Chinese with English abstract).

Miao Huixin, Zhang Jiaodong, Zhou Xingui, Liu Deliang, Li Zhengsheng, Song Licai, Zeng Qinan, Liu Xufeng, Bi Caiqin and Sun Fuli, 2018. Characteristics and age assignment of the sporo-pollen assemblages of Pre-Jurassic basement starta in Well Ancan-1, Hefei Basin. *Acta Geologica Sinica*, 92(3): 466–481 (in Chinese with English abstract).

Na Yulin, Sun Chunlin, Wang Hongshan, Dilcher, D.L., Li Yufeng and Li Tao, 2017. A brief introduction to the Middle Jurassic Daohugou Flora from Inner Mongolia, China. *Review of Palaeobotany and Palynology*, 247: 53–67.

Pérez García, B., Mendoza, A., Riba, R., and Ricci, M., 1997. Morfogénesis del gametotito del helecho, *Thyrsopteris elegans*, (Filicales: Thyrsopteridaceae). *Revista de Biologia Tropical*, 44(3)/45(1): 59–65.

Retallack, G.J.A., 2001. 300-million-year record of atmospheric carbon dioxide from fossil plant cuticles. *Nature*, 411: 287–290.

Shi Qiuyuan, Ji Zhansheng, Wu guichun, Li Hao, He Jifu and Zhong Zhao, 2017. Discovery of the Middle Permian coral fossils in the north of Geren Lake, Xizang (Tibet). *Geology Review*, (b04): 319–320 (in Chinese).

Scanu, G.G., Kustatscher, E., and Pittau, P., 2015. The Jurassic flora of Sardinia-A new piece in the palaeobiogeographic puzzle of the Middle Jurassic. *Review of Palaeobotany and Palynology*, 218: 80–105.

Si Xingjian and Li Xingxue, 1963. *Fossil Flora of China* (Volume 2): *Chinese Mesozoic plants*. Beijing: Science press (in Chinese).

Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., and Wolf, P.G., 2006. A classification for extant ferns. *Taxon*, 55(3): 705–731.

Sun Bainian, 1986. A preliminary study of Middle Jurassic fossil plants from Yaojie coal-field of Lanzhou. *Journal of Lanzhou University* (Natural Science), 22(1): 18–23 (in Chinese with English abstract).

Sun, Bainian., Xiao Liang., Xie Sanping, Deng Shenghui, Wang Y.ongdong., Jia Hui and Turner, S., 2007. Quantitative analysis of paleoatmospheric CO_2 level based on stomatal characters of fossil Ginkgo from Jurassic to Cretaceous in China. *Acta Geologica Sinica* (English edition), 81(6): 931–939.

Sun Keqin, Cui Zhongshu and Wang Shijun, 2010. *Fossil Flora of China* (Volume 2): *Fossil Pteridophytes in China*. Higher Education Press, 235 (in Chinese).

Sun Yuewu, Li Xiang, Zhao Guowei, Liu Huan and Zhang Yanlong, 2016. Aptian and Albian atmospheric CO_2, changes during oceanic anoxic events: Evidence from fossil Ginkgo, cuticles in Jilin Province, Northeast China. *Cretaceous Research*, 62: 130–141.

Taylor, T.N., and Taylor, E.L., 1993. The biology and evolution of fossil plants. *Taxon*, 42(1): 44–45.

Vakhrameev, V.A., and Doludenko, M., 1961. Late Jurassic and Early Cretaceous floras from Bureja Basin and its significance for stratigraphy. *Transaction of the Geological Institute of the Academy of Sciences of USSR*, 54: 1–135 (In Russian).

Vakhrameev, V.A., 1991. *Jurassic and Cretaceous Floras and Climates of the Earth*. Cambridge University Press, Cambridge, 318.

Van Konijnenburg-van Citter, J.H.A., 1981. Dicksoniaceous spores in situ from the Jurassic of Yorkshire England.*Review of Palaeobotany and Palynology*, 61(3): 273–301.

Van Konijnenburg-van Citter, J.H.A., 2008. The Jurassic fossil plant record of the UK area. *Proceedings of the Geologists Association*, 119(1): 59–72.

Volkova, L., Bennett, L.T., and Tausz, M., 2011. Diurnal and seasonal variations in photosynthetic and morphological traits of the tree ferns *Dicksonia antarctica* (Dicksoniaceae) and *Cyathea australis* (Cyatheaceae) in wet sclerophyll forests of Australia. *Environmental and Experimental Botany*, 70(1): 11–19.

Wang Yongdong, Tian Ning, Jiang Zikun and Mei Shengwu, 2009. Recent progresses on the studies of fossil ferns from the early Jurassic Hsiangchi flora in northwest Hubei, China. *Acta Palaeontologica Sinica*, 48(3): 527–540 (in Chinese with English abstract).

Wang Zixi, Sun Fankai, Jin Peihong, Chen Yingquan, Chen Jingwei, Deng Peng, Yang Guolin and Sun Bainian, 2017. A new species of *Ginkgo* with male cones and pollen grains in situ from the Middle Jurassic of Eastern Xinjiang, China. *Acta Geologica Sinica* (English Edition), 91(1): 9–21.

Wu Shunqing and Zhou Hanzhong,1986. Early Liassic plants from east Tianshan mountain. *Acta Palaeontologica Sinica*, 25(6): 636–647 (in Chinese with English abstract).

Xie Sanping, Sun Bainian, Yan Defei, Xiao Liang and Wei Lijie, 2006. Leaf cuticular characters of Ginkgo and implications for paleoatmospheric CO_2 in the Jurassic. *Progress in Natural Science*, 16(Special Issue): 258–263.

Yan Defei., Sun Bainian, Xie Sanping, Li Xiangchuan, Wen Wenwen, 2009. Response to paleoatmospheric CO_2 concentration of Solenites vimineus (Phillips) Harris (Ginkgophyta) from the Middle Jurassic of the Yaojie Basin, Gansu Province, China. *Science in China Series D: Earth Sciences*, 52(12): 2029–2039.

Ye Meina, Liu Xingyi and Huang Guoqing, 1986. *Late Triassic and Early-Middle Jurassic fossil plants from northeastern Sichuan*. Heifei: Anhui Science and Technology Press, 30–33 (in Chinese).

Zhang Fade and Tong Haikui, 2012. Discussion of plants fossils and its geological ages of the Lower-Middle Jurassic in Mangya area, Qinghai province. *Northwest Geology*, 45(1): 86–93 (in Chinese with English abstract).

Zhang Yanzhen, Li Gang, Teng Xiao, Wang Lihong and Cheng Shengxian, 2017. New Jurassic spinicaudatans from Xinjiang Uygur Autonomous Region of northwestern China and their evolutionary implications. *Palaeoworld*, 26(4): 663–671.

Zhao Miao, Sun Chunlin , Dilcher D.L., Na Yuling and Xing Dehe, 2016. A new species of Baiera, from the Early Cretaceous Jehol Biota of southeastern Jilin, China. *Palaeoworld*, 25(2): 251–262.

About the first author

XIN Cunlin, male; born in 1967 in the city of Qing'an, Gansu Province; Ph.D.; Professor of Northwest Normal University, master graduate tutor; mainly engaged in the study of paleobotany and environmental evolution. E-mail: xincunling@163.com.