A New Species of *Ginkgo* with Male Cones and Pollen Grains in situ from the Middle Jurassic of Eastern Xinjiang, China

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Abstract: Well-preserved Ginkgo pollen organs are analyzed from the Middle Jurassic Xishanyao Formation of the Turpan–Hami Basin, Xinjiang Uygur Autonomous Region, northwestern China, and are described as a new species, Ginkgo hamiensis Z.X. Wang et B.N. Sun sp. nov. The immature male cones are cylindrical and catkin-like, with two longitudinal stripes on the stalk. The pollen sacs are shaped like a long oval with two pollen sacs fused together for each microsporophyll, and the microsporophyll tip is a triangular cystidium. The pollen grains are oblong or fusiform and monocolpate; both ends are blunt or sharp. By comparison with previously reported fossil records of Ginkgo plants, we determined that the current fossils are different from all other reported species; thus, the present fossil is referred to as a new species of Ginkgo. The reproductive organs of the Ginkgo fossils described herein can provide valuable information for the study of Ginkgo plants. Further, there are two probable evolutionary trends in the *Ginkgo* pollen cones. One trend is that the number of pollen sacs changed from three or four during the Jurassic and Cretaceous to two at the present day; the other is that the number of pollen sacs has remained two from the Middle Jurassic to the present day. In addition, the pollen cones described herein are similar to the pollen cones of the extant Ginkgo, which strongly indicates that the morphology of Ginkgo plants may have remained highly conserved over millions of years.

Key words: *Ginkgo hamiensis*, Pollen cones, Middle Jurassic, Xinjiang Uygur Autonomous Region, Systematic evolution

1 Introduction

The Turpan–Hami Basin is located in the eastern part of Xinjiang Uygur Autonomous Region, northwestern China, where an almost complete, well-exposed sequence of terrestrial Jurassic strata is developed. This region has yielded abundant fossils of various taxa and is one of the best regions for terrestrial Jurassic strata in China and globally (Deng Shenghui et al., 2010). Thus, this area can provide abundant fossil materials for our research.

Ginkgoalean plants were very abundant and widespread in the Mesozoic (Dong Ma et al., 2012; Zhou Zhiyan et al., 2006a). The Late Jurassic to the Early Cretaceous was the acme of ginkgoalean plants, but they subsequently experienced a rapid decline. According to the fossil records, the earliest ginkgoalean plants appeared in the Permian (Florin, 1949). The evolution of ginkgoalean plants was slow during the Permian and Triassic, and the genera and species showed few changes. In the Late Triassic, Ginkgoalean distribution expanded further to include the entire Northern Hemisphere, Australia, Argentina, and South Africa (Sze et al., 1963). The most important stage of the evolution of ginkgoalean plants was during the Middle Jurassic. The Late Jurassic to the Late Cretaceous saw the flourishing of ginkgoalean evolution, with the distribution being wider than that during the Late Triassic. Ginkgoalean remains of this age have been recovered from the Arctic Circle and countries in the Southern Hemisphere such as Australia and New Zealand (Liu, 2005). In fact, ginkgoalean plant fossils are found widely, except at the Equator and in Antarctica (Sze et al., 1963). After the Cretaceous, ginkgoalean plants began to

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decline rapidly, their abundance was reduced, and their distribution narrowed to only temperate forests (Sze et al., 1963). From the Oligocene to the present, only *Ginkgo* have persisted. At the end of the Miocene, Ginkgoalean plants disappeared from the North American forest. The plant group had also vanished by the end of the Pliocene in Europe. The genus *Ginkgo* has a fossil record of well-preserved leaf cuticles at least back to the Late Triassic Epoch (Anderson et al., 1989), and its abundance reduced rapidly in the Late Cretaceous and the Paleogene. The genus has a circumpolar distribution in the high latitudes of the Northern Hemisphere because of the decrease in its range (Tralau, 1968; Zhou Zhiyan et al., 2006b). At present, only one species of *Ginkgo* survives in East Asia (Sze et al., 1963).

Most classifications of ginkgoalean plants have been based on vegetative organs due to the lack of reproductive organ fossils, even though ginkgoalean leaf fossils are abundant (Sze et al., 1963). This has made the classification system of Ginkgoalean and Czekanowskiales chaotic and affected understanding of Ginkgoalean evolution (Zhou, 2003). Fossil reproductive organs of ginkgoalean plants are very scarce and are mostly female cones with ovules (Deng Shenghui et al., 2004; Harris, 1961; Heer, 1876; Kräusel, 1943; Van Konijnenburg-van Cittert, 2010; Zhou Zhiyan et al., 1988; Zhou Zhiyan et al., 1992). Of the male ginkgoalean reproductive organs, Sorosaccus (Harris, 1935), Ginkgo (Nathorst, 1899), Antholithus (Zhou Zhiyan, 1997), and Stachyopitys (Schenk, 1867) have been described. Pollen organs of ginkgoales are also rare in the fossil record (Zhou Zhiyan, 2009). Only three species of Ginkgo male cones have been reported: Ginkgo huttoni (Heer, 1876; Harris et al., 1974; Kräusel, 1943), a Ginkgo male cone from Alberta (Rothwell et al., 1997; Serbet, 1996), and Ginkgo liaoningensis from western Liaoning (Liu et al., 2006).

In the Sandaoling coal mine of Hami, Xinjiang, we discovered well-preserved male cones and leaf fossils of Ginkgo from the Middle Jurassic Xishanyao Formation. Herein we describe a new species for the male cone, Ginkgo hamiensis sp. nov. The leaves were identified as Ginkgo obrutschewii Seward. By comparison of the new fossil specimens with modern plants and previously known fossil species of Ginkgo, we discuss the significance of the male cone of *Ginkgo* for the evolution of the group. Although there is a history of research on plant fossils from the Middle Jurassic of the Turpan-Hami Basin, most established taxa still lack a detailed description or have been named only with an illustration (Gothan et al., 1931; Li et al., 2016; Seward, 1911; Sze, 1956; Shang Ping., 1999; Wang Shijun et al., 1994; Wang Zixi et al., 2015). Thus, research on the macroscopic characteristics and microscopic structures of these plant fossils is required.

2 Geological Background

The Turpan–Hami Basin, located in the eastern part of Xinjiang Uygur Autonomous Region, is the joint name of several terrestrial basins. The basin extends from west to east, covering an area of approximately 53,000 km², and is surrounded by mountains. The Sandaoling Coal Mine section lies approximately 90 km west of Hami City (Fig. 1) in an open-cut coal mine (Deng Shenghui et al., 2010). The present mine area is located in the north of the Turpan–Hami Basin. The basin is located in the Tianshan orogenic belt. The basin formed during the late Paleozoic and developed into a large inland–intermountain basin during the Mesozoic and Cenozoic. The basin is also located in the East Tianshan mountain range. The Jueluotage orogenic belt lies to the south of the basin; to the north is the Bogda–Harlik orogenic belt (Tao Mingxin,



Fig. 1. Map showing the fossil locality.

1994). The Sandaoling open coal mine, from which the material studied in this article was collected, is located in the south of Bogda–Harlik Mountain.

The formation and evolution of the Turpan–Hami Basin was controlled by tectonic movements during different periods. From the Permian to the Early-Middle Jurassic, the Turpan-Hami Basin was a foreland basin; from the Late Jurassic until the present day, it has been an umbilicate-type basin (Wu Tao et al., 1993). The basin is composed of rivers, lakes, and swamps. On the basis of the lithofacies and paleontological characteristics, the Jurassic sequence can be divided into the Lower Jurassic Badaowan and Sangonghe Formations; the Middle Jurassic Xishanyao, Sanjianfang, and Qiketai Formations; and the Upper Jurassic Qigu and Kalazha Formations. The Xishanyao Formation is mainly composed of a set of coalbearing strata and is widely distributed in the basin (Hong Youchong et al., 1995). The upper part of the Middle Jurassic and the Upper Jurassic strata of the Hami Depression in the east of the Turpan-Hami Basin have been strongly eroded as a result of tectonic movements, and only the Badaowan and Sangonghe Formations and part of the Xishanyao Formation remain (Deng Shenghui et al., 2010).

The Xishanyao Formation, which was formed during the early part of the Middle Jurassic, is mainly composed of lake, swamp, and coal deposits (Zhang et al., 2002). The Xishanyao Formation is characterized by thick sandstone and mudstone with interbedded coal seams that mainly formed in a lake delta environment (Shao Longyi et al., 2003). The fossil material described in this paper was obtained from the Xishanyao Formation.

3 Materials and Methods

The fossils described in this study were collected from the silty mudstone (Fig. 2) of the Middle Jurassic Xishanyao Formation and are housed in the Paleontology Laboratory of the School of Earth Sciences, Lanzhou University. The ginkgo fossils include two pollen cones and unattached leaves.

Fossil cuticle preparation: Specimens with carbonaceous membranes were removed from the matrix using dissecting needles. The material was placed in 30% hydrofluoric acid for 4 or 5 h, then removed and washed with distilled water until neutral pH was achieved. The washed membranes Ewere macerated in a plastic test tube with 50% hydrofluoric acid and washed with distilled water until the pH was neutral, followed by maceration with Schulze's solution. When the color of the carbonaceous membrane had changed from black to light yellow or transparent, the membrane was removed from



Fig. 2. Stratigraphic column of the Xishanyao Formation, Turpan–Hami Basin.

the solution. After that, the material was washed with distilled water and treated briefly with 25% ammonia. The upper and lower epidermis was separated using dissecting needles. Finally, the processed samples were removed and divided into two parts for different microscopic observations. One part was mounted on standard slides for observation under a light microscope (LM); the other was mounted on stubs for scanning electron microscopy (SEM) (Dao Kequn et al., 2013; He Yuli et al., 2014; Ma Fujun et al., 2015; Wang Qiujun et al., 2014; Xu Xiaohui et al., 2013).

Pollen grain preparation: Fragments of the preserved pollen cones were removed with a scalpel, macerated in 10% hydrochloric acid for 3 or 4 h, washed with distilled water, then placed in a plastic test tube with 50% hydrofluoric acid and heated in a water bath till boiling, until all impurities were removed. After removal of impurities, the test tube was centrifuged at 1900 r/sin for 5 min. Then, the bulk maceration was washed following the

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same procedure until the solution was neutralized. Finally, the samples were moved to thumb tubes, and 95% ethanol was added. After evaporation, one or two drops of glycerin were added to the thumb tube, which was then sliced. The slices were sealed using nail polish.

4 Fossil Description

Class Ginkgopsida Order Ginkgoales Family Ginkgoaceae Genus *Ginkgo* L. 1771

Species *Ginkgo hamiensis* Z.X. Wang et B.N. Sun sp. nov.

Derivation of name: The epithet *hamiensis* refers to Hami City, where the specimens were collected.

Holotype: Specimen no. HMSDL-LDGSW-2013-401 (Fig. 3: 1).

Type locality: Sandaoling coal mine, Hami prefecture, Xinjiang Uygur Autonomous Region, northwestern China.

Stratigraphic horizon: Xishanyao Formation, Middle Jurassic.

Repository: Institute of Paleontology and Stratigraphy, School of Earth Sciences, Lanzhou University, China.

Diagnosis: The pollen cones are cylindrical. The top part of the cone is round and slightly shrunken and approximately 17.54–20.74 mm long and 5.19–6.3 mm wide. The pollen cones contain numerous helical to catkin-like and imbricately arranged microsporophylls. The microsporophylls diverge from the axis at an angle of approximately 45°. There are usually two basally fused pollen sacs on every microsporophyll. The pollen sac wall is thin and smooth, and the cells are rectangular. The pollen grain is oblong or fusiform and monocolpate, both ends are blunt or sharp, and the monocolpate is parallel to and the same length as the axis. The pollen grain surface is smooth and unornamented. The pollen grains are 25.57–43.01 µm long and 14.28–21.11 µm wide.

Description: The specimen consists of leaves and two immature pollen cones (Fig. 3: 1). The pollen cones are preserved separately and not attached to the leaves. The pollen cones are cylindrical. The top part of the cone is round and slightly shrunken, and approximately 17.54–20.74 mm long and 5.19–6.3 mm wide; the top is approximately 1.3–2.78 mm wide (Fig. 3: 2, 3). There are two longitudinal stripes on the stalk (Fig. 3: 3; Fig. 4: 2, 5), 1.83 mm long and 0.46 mm wide. The pollen cones possess numerous helical to catkin-like and imbricately arranged microsporophylls (Fig. 4: 2; due to the preservation of the material, it is not possible to ascertain the number of microsporophylls). The tops of the microsporophylls are slightly bent toward the middle axis (Fig. 4: 4, 7). There are mostly two or three (usually two)

basally fused pollen sacs on every microsporophyll (Fig. 4: 4, 7); the top part is a triangular cystic structure (Fig. 4: 8, 9; Fig. 5), approximately 0.514 mm long and 0.41 mm wide. The pollen sacs are oblong or cymbaeform, measuring 0.822–1.35 mm in length and 0.539–0.78 mm in width at the base, and split longitudinally (Fig. 4: 4, 7, 8). The microsporophylls diverge from the axis at an angle of approximately 45° (Fig. 4: 2), and the stalk linking the microsporophylls and the middle axis is invisible. The leaf is fan-shaped: it is initially deeply divided into two and then each half splits into two parts. The leaves are approximately 2.01 cm long and 0.46 cm wide, apex obtuse, and without a petiole (Fig. 3: 5, 6). We identified these leaves as *Ginkgo obrutschewii* Seward.

The pollen sac wall is thin and smooth. The cells are rectangular, 800 μ m long and 280 μ m wide, and the anticlinal walls are thick and undulate on their adaxial surfaces (Fig. 6: 1, 2). As some pollen grains may have dropped out during fossilization and/or during preparation, some pollen grains attached to the pollen sac are visible. The pollen grains are oblong or fusiform and monocolpate, both ends are blunt or sharp, and the monocolpate is parallel to and the same length as the axis. The surface of the pollen grain is smooth and unornamented (Fig. 6: 2–9). The pollen grains are 25.57–43.01 μ m long and 14.28–21.11 μ m wide (Fig. 6: 5–9).

5 Comparisons

The pollen cones described herein are cylindrical, with numerous helical to catkin-like and imbricately arranged microsporophylls. The pollen grains are oblong or fusiform and monocolpate, both ends are blunt or sharp, and the monocolpate is parallel to the axis and of the same length. The combination of characteristics indicates that the present fossil can be clearly assigned to Ginkgoaceae.

5.1 Comparison with Ginkgo biloba L.

Ginkgo biloba L., which is famous as a living fossil, is the unique extant species of the order ginkgoales and a native species in China (Gifford et al., 1989). *Ginkgo biloba* L. is a deciduous tree and the branch is very prosperous with long and short ones. The leaves are fanshaped with a long petiole and clusters in short branches. The cone is unisexual and dioecious, forming clusters on short branches. The male cones, which have a short stalk, are cylindrical with numerous helical to catkin-like and imbricately arranged microsporophylls (Fig. 7: 6–8). Each microsporophyll usually has two (occasionally three or four) basally fused pollen sacs (Fig. 7: 9–10) (Zheng Wangjun et al., 1978). The pollen grains are oblong or fusiform with monocolpate, and both ends are blunt or



Fig. 3. Morphology of *Ginkgo hamiensis* sp. nov., specimen no. HMSDL-LDGSW-2013-401. (1), Pollen cones of *Ginkgo hamiensis* sp. nov. (arrows). Scale bar = 1 cm. (2–3), Pollen cones of *Ginkgo hamiensis* sp. nov. Scale bar = 0.5 cm. (3), The white arrows indicate the two longitudinal ridges on the stalk. (4), Reconstruction of the pollen cone. Scale bar = 0.5 cm. (5), *Ginkgo obrutschewii*. Scale bar = 1 cm. (6), Reconstruction of *Ginkgo obrutschewii*. Scale bar = 1 cm.

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Fig. 4. Present-day Ginkgo specimens and microsporophylls of Ginkgo hamiensis sp. nov.

(1), Modern *Ginkgo* plant specimens: https://en.wikipedia.org/wiki/Ginkgo_biloba. The arrows indicate the pollen cones of *Ginkgo biloba*. Scale bar = 1 cm. (2), A visible small sporophyll pattern, with the white arrows pointing to the two longitudinal stripes on the handle. Specimen no. HMSDL-LDGSW-2013-401. Scale bar =1000 μ m. (3), There are two longitudinal stripes on the handle. The black arrows indicate the longitudinal stripes. Specimen no. LDGSW-*Ginkgo*-02. Scale bar = 2.5 mm. (4), There are two or three (usually two) pollen sacs attached to each microsporophyll. White arrows indicate the pollen sacs. Specimen no. HMSDL-LDGSW-2013-401. Scale bar = 500 μ m. (5), The stalk of the pollen cone, with arrows pointing to the two longitudinal stripes on the handle. Scale bar = 250 μ m. (6), There are two pollen sacs attached to each microsporophyll (microsporophylls indicated by red arrows). Specimen no. LDGSW-*Ginkgo*-01. Scale bar = 2.5 mm. (7), The white arrows indicate the microsporophyll. Scale bar = 250 μ m. (8–9), The microsporophyll. (8), The red arrows indicate the pollen sacs and the white arrow indicates the triangular cystidium. Scale bar = 250 μ m. (9), Reconstruction of the microsporophyll. Scale bar = 250 μ m.

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Fig. 5. Line drawing of the microsporophyll of *Ginkgo* hamiensis sp. nov. Scale bar = $250 \mu m$.

sharp. The monocolpate is parallel to and the same length as the axis. These characteristics are the same as those of the current fossil (Fig. 8). We infer that the leaves of *Ginkgo obrutschewii* collected by us might belong to the present pollen cone on the basis of the fact that both the leaves and the cones were recovered from the same stratum.

5.2 Comparison with fossil species of Ginkgo

Ginkgo liaoningensis, described by Liu et al. (2006), from the Lower Cretaceous of Liaoning Province, China, has numerous helical to catkin-like and imbricately arranged microsporophylls. The pollen sacs are oblong or cymbaeform. The single pollen grain is oblong or fusiform with monocolpate, and both ends are blunt or sharp. The monocolpate is parallel to and the same length as the axis. These characteristics are similar to those of the new material described herein, although *Ginkgo liaoningensis* has two or four (usually four) basally fused pollen sacs on



Fig. 6. Pollen sacs and pollen grains of *Ginkgo hamiensis* sp. nov. Specimen no. HMSDL-LDGSW-2013-401. (1–2), Pollen sacs and pollen grains. (1), Scale bar = 100 μ m. (2), Scale bar = 40 μ m. (3), Pollen grains. Scale bar = 20 μ m. (4–9), Single pollen grains. Scale bar = 20 μ m.



Fig. 7. Ginkgophyte leaves from the Middle Jurassic Xishanyao Formation, Hami, and modern *Ginkgo* specimens (*Ginkgo biloba* L.). (1–5), *Ginkgo obrutschewii* from the Middle Jurassic Xishanyao Formation, Hami. Scale bar = 1 cm. (1), Specimen no. HMSDL-LDGSW-2013-380. (2), Specimen no. HMSDL-LDGSW-2013-381. (3), Specimen no. HMSDL-LDGSW-2013-382. (4), Specimen no. HMSDL-LDGSW-2013-383. (5), Specimen no. HMSDL-LDGSW-2013-384. (6–8), Pollen cone of *Ginkgo biloba* L. Scale bar = 1 cm. (6), Specimen no. LDGSW-*Ginkgo*-03. (7), Specimen no. LDGSW-*Ginkgo*-05. (9–10), Sporophylls bearing sporangia of *Ginkgo biloba* L. Scale bar = 1 mm.



Fig. 8. Reconstruction of *Ginkgo hamiensis* sp. nov. Scale bar = 1 cm.

every microsporophyll. The pollen sacs are 1-3 mm long and 0.5-3.5 mm wide, larger than those of the present material. The pollen cone is 20–45 mm long and 5–8 mm wide, longer than that of the present material. The microsporophyll arrangement is looser than the current fossil. These characteristics are different from those of the fossil material described in the present paper.

Ginkgo huttoni (Harris et al., 1974; Heer, 1876; Van Konijnenburg-van Cittert, 1971), from the Middle Jurassic of Yorkshire, has incompletely preserved pollen cones. The cones are 6 mm long and 3 mm wide, smaller than those of the Xishanyao Formation specimens. The pollen sacs are 0.5 mm long and 0.15 mm wide, smaller than those of the material described herein, although there are two basally fused pollen sacs on every microsporophyll. In addition, the microsporophyll arrangement of *G. huttoni* is looser than that of the current fossil. All these features clearly separate *G. huttoni* from *G. hamiensis* sp. nov.

The pollen cone of *Ginkgo* (Rothwell et al., 1997; Serbet, 1996) that was collected from the Upper Cretaceous of Canada has incompletely preserved pollen cones and some microsporophylls, with two basally fused pollen sacs on every microsporophyll. The cone axis is 4 mm wide, wider than the material described in the present study. The pollen sacs are 6 mm long and 4 mm wide, larger than the current fossil specimens. This combination of features is very different from that of the new material.

Sorosaccus Harris, described by Harris (1935), from the

Upper Triassic of Greenland, UK, is 35-45 mm in length and 6-10 mm in diameter, larger than the current fossil specimen. The cone axis is 1-2 mm in diameter, wider than the present fossil. Each microsporophyll consists of a distal laminar portion and a microsporangium, and there are six or eight basally fused pollen sacs on every microsporophyll. Each microsporangium is 1-1.5 mm long and 0.5-1 mm wide, larger than that of the new material. These features mean that *Sorosaccus* is distinct from the current fossil specimen.

In conclusion, the new species is different from all previously published material, as demonstrated by comparison of the present fossil species and previously published fossil species of *Ginkgo* (Table 1). The new material from the Middle Jurassic Xishanyao Formation in Xinjiang Uygur Autonomous Region can be confidently identified as a new species—*Ginkgo hamiensis* Z.X. Wang et B.N. Sun sp. nov.

6 Discussion

6.1 Taphonomy of plant fossils

Researching paleoenvironments using plant fossils is more difficult than studying present-day environments using modern plants. Fossil plants may have been buried in a different place from where they lived: they may have been moved to a distant location, which would affect our reconstruction of the paleoenvironment and paleoclimate in the geologic past. This transport phenomenon is relatively obvious in the preservation of plant fossils. Plants are more fragile than animal bones; in addition, the entire plant is very large in some special cases. Therefore, complete plants are very difficult to preserve as fossils, and some plant body organs (nutritional leaves, stems, roots, fruits, flowers, seeds, and pollen) are often preserved as scattered remains (Jin Jianhua, 1999). In general, the damage resistance of thin-textured leaves and propagative organs is poor. If plant fossils are well-preserved, we can presume that there was no long-distance transportation, and the burial would have been autochthonous or hypautochthonous (Zhang Yingfang, 2006).

The new material is of some phenological significance. Comparing with *Ginkgo biloba*, the young male cones containing pollen grains in pollen sacs indicate that they were preserved in the growing season. We infer that storms or other violent events may have removed these structures from the parent plant when they were still immature. Given the good preservation of the pollen cones, the *in situ* pollen sac, and the pollen grains, we inferred that they had not been transported or transported over only a short distance prior to rapid burial, and burial was basically autochthonous.

6.2 Evolution of *Ginkgo* pollen cones

During the Mesozoic, the quantity and variety of ginkgophyte nutritional organs was very high; most of the nutritional leaves were classified and identified on the basis of their morphology (Harris et al., 1974; Krassilov, 1970, 1972; Tralau, 1968). However, some fossils of plants that possess the same propagative organs include the nutritional organs and reproductive organs, which are well-preserved and deeply studied; their nutritional leaves tend to be of a variety of types with some morphological transitions and overlaps between different leaf types (Fig. 9; Zhou Zhiyan, 1997, 2003). Most previous workers have systematically classified plant fossils based on their vegetative organs and have attributed doubtful records of Ginkgo provisionally to Ginkgoites because of the lack of fossil reproductive organs (Zhou Zhiyan, 2006b). This has led to both a lack of clarity and confusion between Ginkgo and Ginkgoites in plant phylogenetic systematics. Particularly in the Mesozoic, ginkgophyte fossils are relatively common and the numbers of species and genera are high. Some researchers have classified these fossil leaves as Ginkgo and Ginkgoites, which are similar to extant Ginkgo and the vegetative organs of Ginkgo found from the Jurassic (Zhou, 2003). Preserved reproductive organs are very important in the Mesozoic. A classification system using only the nutritional leaves is not reliable. The classification of Ginkgopsida of Zhou

(2003) is a preliminary scheme, and it is generally agreed that pollen cones are very important and significant in research on plant phylogeny. Ginkgophyte fossils have been found in the Xishanyao Formation, including *Ginkgo longifolius* Harris, *Ginkgo digitata* (Brongniart) Heer, and *Ginkgo yimaensis* Zhou, but reproductive organs have not been previously described. The discovery of the present *Ginkgo* male cone fossils has enriched the fossil record of the study area and could promote research on Mesozoic ginkgophyte fossils. This material provides a basis for future studies of *Ginkgo* or *Ginkgoites*.

Harris et al. (1974) described Ginkgo huttoni from the Middle Jurassic of Yorkshire and stated that there are two short diverging branches at the end of its microsporophyll, which were inferred to be microsporangia. The current fossil is also from the Middle Jurassic, and there are obviously two pollen sacs on each microsporophyll. Thus, we can confirm that the inference of Harris et al. (1974) is correct. The number of pollen sacs on each microsporophyll of male cone fossils of Ginkgo huttoni (Harris et al., 1974; Heer, 1876; Van Konijnenburg-van Cittert, 1971) collected from the Middle Jurassic of Yorkshire and Ginkgo hamiensis sp. nov. from the Middle Jurassic of Xinjiang is usually two. There is still a possibility that the number of pollen sacs on each microsporophyll of male cone fossils of Ginkgo during the Jurassic was three or four (supported by the reduction



Fig. 9. Diagrammatic drawing of the leaf polymorphism of Ginkgo biloba L. (redrawn from Zhou, 2003).

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hypothesis). The number of pollen sacs on each microsporophyll of male cone fossils of *Ginkgo liaoningensis* (Liu et al., 2006) from the Middle Jurassic of China and *Ginkgo* sp. (Rothwell et al., 1997; Serbet, 1996) from the Upper Cretaceous is usually three or four and two, respectively. In conclusion, there are two probable evolutionary trends in *Ginkgo* pollen cones (Fig. 10). One is that the number of pollen sacs was three or four during the Jurassic and Cretaceous, which has reduced to two at the present day. The other trend, based on the known fossil records (Table 2), is that the number of pollen sacs was two during the Middle Jurassic, the same as present-day *Ginkgo biloba* L., suggesting that there has been some morphological stasis in the reproductive organs of *Ginkgo*.

In addition, the leaf of Ginkgo biloba L. is pleiotypic (Fig. 9), with even the shape of some leaves (Fig. 9: 5) being very similar to that of Jurassic Ginkgo. To some extent, the shape of Ginkgo has been particularly conserved. Zhou Zhiyan et al. (2003) found that the Ginkgo reproductive structures in the Lower Cretaceous strata of Liaoning were similar to those of present-day Ginkgo biloba, indicating that their morphology has changed little for 100 Myr. Ginkgo is also well suited for paleoenvironmental reconstruction (Sun Bainian et al., 2007). Sun Bainian et al. (2007) obtained carbon isotope values for Ginkgo of 21‰ in the Jurassic, 22‰ in the Paleogene, and 21.6‰ at the present day by biology, plant physiology, organic geochemistry, and other methods (Sun Bainian et al., 2003). Thus, the carbon isotope discrimination of fossil leaves is similar to that of the present-day leaves of Ginkgo. From this, Sun Bainian et al. (2007) considered that the physiology of leaf carbon uptake and regulation of water loss in Ginkgo has remained highly conserved, despite the potential for evolutionary change, over millions of years. It is noteworthy that the pollen cones in the new material are



Fig. 10. Number of pollen sacs (based on the fossil record of *Ginkgo*) and their stratigraphic distribution.

similar to the present-day pollen cones of *Ginkgo* in terms of shape, arrangement of microsporophylls, number of pollen sacs on each microsporophyll, stalk, and pollen grains. All these features indicate that the morphology of *Ginkgo* plants may have remained highly conserved over millions of years.

7 Conclusions

(1) A new species, *Ginkgo hamiensis* sp. nov., was collected from the Middle Jurassic Xishanyao Formation of the Turpan–Hami Basin, Xinjiang Uygur Autonomous Region, northwestern China. The major characteristics of the new species are described in detail.

(2) There are two probable evolutionary trends in *Ginkgo* pollen cones based on the study of the current pollen cones.

(3) Based on the characteristics of the current pollen cones, it can be inferred that the morphology of *Ginkgo* plants may have remained highly conserved over millions of years.

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References

- Anderson, J.M. and Anderson, H.M., 1989. Palaeoflora of Southern Africa, Molteno Formation (Triassic) Vol. 2 Gymnosperms (excluding Dicroidium). Rotterdam: Balkema.
- Dao Kequn, Chen Junlin, Jin Peihong, Dong Chong, Yang Yi, Xu Xiaohui, Wu Jingyu, Xie Sanping, Lin Zhicheng, and Sun Bainian, 2013. A new material of *Lindera* (Lauraceae) of the Late Pliocene from Tengchong, Yunnan and the Genus' biogeography significance. *Acta Geologica Sinica* (English Edition), 87(3): 690–706.
- Deng Shenghui, Yang Xiaoju and Zhou Zhiyan, 2004. An Early Cretaceous Ginkgo ovule-bearing organ fossil from Liaoning, Northeast China and its evolutionary implications. *Chinese Science Bulletin* (English Edition), 49(16): 1774–1776.
- Deng Shenghui, Lu Yuanzheng, Fan ru, Pan Yanhong, Cheng

Xiansheng, Fu Guobin, Wang Qifei, Pan Huazhang, Shen Yanbin, Wang Yaqion, Zhang Haichun, Jia Chengkai, Duan Wenzhe and Fang Lin hao, 2010. *The Jurassic system of northern Xinjiang, China*. Hefei: University of Science and Technology of China Press.

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- Dong Man and Sun Ge, 2012. Ginkgo huolinhensis sp. nov. from the Lower Cretaceous of Huolinhe Coal Field, Inner Mongolia, China. Acta Geologica Sinica (English Edition), 86 (1): 11–19.
- Florin, R., 1949. The morphology of Trichopitys heteromorpha Saporta, a seed-plant of Palaeozoic age, and the evolution of the female flowers in the Ginkgooinae . *Acta Horti Bergiani*, 15: 79–109.
- Gifford, E.M. and Foster, A.S., 1989. Morphology and evolution of vascular plants W. Freeman: New York.
- Gothan, W. and Sze, H., 1931. Pflanzenreste aus dem Jura von Chinesisch Turkestan (Prov. Singkiang). *Contrib. fr. Nat. Res. Inst. Geol.*(Acad. Sinica), 1: 33–40.
- Harris, T.M., 1935. The fossil flora of Scoresby Sound, East Greenland. Part 4: Ginkgoales, Coniferales, Lycopodiales and isolated fructifications. Medd. Grønl. 112.
- Harris, T.M., Millington, W., and Miller, J., 1974. The Yorkshire Jurassic Flora. T. IV. Ginkgoales and Czekanowskiales. London: Brit. Mus. Nat. Hist.
- Harris, T.M., 1961. Yorkshire Jurassic flora, I. Thallophyte-Pteridophyta. London: Brit Mus (Nat Hist).
- He Yuli, Li Na, Wang Zixi, Wang Haofei, Yang Guolin, Xiao Liang, Wu Jingyu and Sun Bainian, 2014. Quercus yangyiensis sp.nov.from the Late Pliocene of Baoshan, Yunnan and its paleoclimatic significance. *Acta Geologica Sinica* (English Edition), 88(3): 738–747.
- Heer, O., 1876. *Beiträge zur Jura-flora Ostsibiriens und des Amurlandes Mémoires de L'Académie* Impériale des Sciences St.-Pétersbourg, Sér.
- Hong Youchong, Liang Shijun, Hu Ting and Hou Qichang, 1995. Study on geology and paleontological assemblage from Tuha Basin Of Xinjiang, China. *Geoscience*, 9: 426–440 (in Chinese with English abstract).
- Jin Jianhua, 1999. Reconstruction of plant life forms in geological period and recovery of palaeobotanic community. *Ecologic Science* 18, 40–46 (in Chinese with English abstract).
- Kräusel, R., 1943. Die Ginkgophyten der Trias von Lunz in Nieder-Österreich und von Neue Welt bei Basel. Untersuchungen zur mesozioschen Florengeschichte des alpinen und süddeutschen Raumes II. *Palaeontographica Abteilung B*, 87(2-6): 59–93.
- Krassilov, V., 1970. Approach to the classification of Mesozoic "Ginkgoalean" plants from Siberia. *Palaeobotanist*, 18: 12–19.
- Krassilov, V., 1972. Mesozoic flora of Bureya River. (Ginkgoales and Czekowskiales). Nauk, Moscow (in Russian).
- Li R.Y., Wang X.L., Chen J.W., Deng S.H., Wang Z.X., Dong J.L. and Sun B.N., 2016. A new thalloid liverwort: *Pallaviciniites sandaolingensis* sp. nov. from the Middle Jurassic of Turpan–Hami Basin, NW China. *Paläontologische Zeitschrift.* (In Press).
- Liu Xiuqun, 2005. Studies on the reproductive organs of ginkgoales and czekanowskiales from the Mesozoic of

Liaoning, China. Chinese Academy of Sciences (Laboratory of Systematic and Evolutionary Botany Institute of Botany) (Ph. D thesis): 1–77.

- Liu Xiuqun, Hueber, F.M., Li Chengsen and Wang Yufei, 2004. Emendation of *Sorosaccus gracilis* Harris, 1935. A gymnospermous pollen cone. *Acta Phytotaxonomica Sinica*, 43: 182–190.
- Liu X.Q., Li C.S. and Wang Y.F., 2006. The pollen cones of *Ginkgo* from the Early Cretaceous of China, and their bearing on the evolutionary significance. *Botanical Journal of the Linnean Society*, 152: 133–144.
- Ma Fujun, Wang Qiujun, Dong Junling, Yang Yi, Wang Wenjia, Yan Defei and Sun Bainian, 2015. *Buxus* leaves from the Oligocene of Guangxi, China and their biogeographical significance. *Acta Geological Sinica* (English Edition), 89(5): 1453–1469.
- Nathorst, A.G., 1899. Fossil plants from Franz Josef Land Longmans, Green.
- Rothwell, G.W. and Holt, B., 1997. Fossils and phenology in the evolution of *Ginkgo biloba*, *Ginkgo Biloba A Global Treasure Springer*, 223–230.
- Schenk, A., 1867. Die fossile Flora der Grenzschichten des Keupers und Lias Frankens: Hauptbd Kreidel.
- Serbet, R., 1996. A diverse assemblage of morphologically and anatomically preserved fossil plants from the Upper Cretaceous (Maastrichtian) of Alberta, Canada. International Organization of Paleobotany Conference V, Santa Barbara, 89.
- Seward, A.C., 1911. Jurassic plants from Chinese Dzungaria, collected by Prof. Obutschew. *Mem Com Geol St-Petersbourg*, NS, 75: 1–161.
- Shao Longyi, Zhang Pengfei., Hilton, J., Gayer, R., Wang Yabin, Zhao Changyi and Luo Zhong, 2003. Paleoenvironments and paleogeography of the Lower and lower Middle Jurassic coal measures in the Turpan-Hami oil-prone coal basin, northwestern China. *AAPG bulletin*, 87: 335–355.
- Shang Ping, Fu Guobin, Hou Quanzheng and Deng Shenghui, 1999. Middle Jurassic fossil plants from Turpan-Hami Basin, Xinjiang, Northwest China. *Geoscience — Journal of Graduate School* (China University of Geosciences), 13(4): 403–407 (in Chinese).
- Sun Bainian, Dilcher, D.L., Beerling, D.J., Zhang Chengjun, Yan Defei, and Kowalski, E., 2003. Variation in *Ginkgo biloba* L. leaf characters across a climatic gradient in China. *Proceedings of the National Academy of Sciences of the United States of America*, 100: 7141–7146.
- Sun Bainian, Xiao Liang, Xie Sanping, Deng Shenghui, Wang Yongdong, Jia Hui and Turner, S., 2007. Quantitative analysis of paleoatmospheric CO₂ level based on stomatal characters of fossil *Ginkgo* from Jurassic to Cretaceous in China. *Acta Geological Sinica* (English Edition), 81(6): 931–939.
- Sze, H.C.,1956. The fossil flora of the Mesozoic oil-bearing deposits of the Dzungaria-Basin, Northwestern Sinkiang. *Journal of Paleontology*, 4: 461–476.
- Sze H.C., Lee H.H. et al. (Editors), 1963 Mesozoic plants of China In Fossil Plants of China, 2 Scientific Press, Peking, 429 pp (in Chinese).
- Tao Mingxin, 1994. Tectonic environmental analysis of Turpan-Hami Basin on the Genetic Relationship Between Basin and

orogenic belt of continental inner plate. *Acta Secta Sedimentologica Sinica*, 12: 40–50 (in Chinese with English abstract).

- Tralau, H., 1968. Evolutionary trends in the genus *Ginkgo*. *Lethaia*, 1(1): 63–101.
- Van Konijnenburg-van Cittert, C., 2010. The Early Jurassic male ginkgoalean inflorescence *Stachyopitys preslii* Schenk and its *in situ* pollen. *Scripta Geologica*. Special Issue 7: 141–149.
- Van Konijnenburg-van Cittert, J.H., 1971. *In situ* gymnosperm pollen from the Middle Jurassic of Yorkshire. *Acta Bot Neer*.
- Wang Qiujun, Ma Fujun, Yang Yi, Dong Junling, Wang Haofei, Li Ruiyun, Xu Xiaohui, and Sun Bainian. 2014. Bamboo leaf and pollen fossils from the Late Miocene of eastern Zhejiang, China and their phytogeological significance. *Acta Geologica Sinica* (English Edition), 88(4): 1066–1083.
- Wang Shijun, Tang Xiuyi, Zhang Jing, Yu Bing, 1994. Some coal-forming plants of Jurassic in Hami, Xinjiang. *Xinjiang Geology*, 2: 172–174 (in Chinese).
- Wang Zixi, Wang Xuelian, Chen Jingwei, Deng Peng, Wang Tianzi, Li Ruiyun and Sun Bainian, 2015. *Elatides* sandaolingensis n. sp. (Cupressaceae sensu lato)—A new fossil conifer with cones from the Middle Jurassic of Xinjiang, northwestern China. *Palaeoworld* (In Press).
- Wu Tao, Yuan Mingsheng and Wang Wuhe, 1993. The tectonic evolution and oil-gas accumulation of Turpan-Hami Basin. *Oil Geology*, 9: 165–174 (in Chinese).
- Xu Xiaohui, Li Ruiyun, Dong Chong, Wang Qiujun, Jin Peihong and Sun Bainian, 2013. New Schizolepis fossils from the Early Cretaceous in Inner Mongolia, China and its Phylogenetic Position. *Acta Geological Sinica* (English Edition), 87(5): 1250–1263.
- Zhang D.S., Fu G.B., Qin E.P., Hou Q.Z. and Li X.L., 2002. Jurassic, palaeoclimate, paleovegetation and palaeoenvironment in the Turpan-Hami Basin in Xinjiang. *Geoscience*, 16: 147–152 (in Chinese with English abstract).
- Zhang Yingfang, 2006. Study on and palaeoecology the

phytogeography of Middle Jurassic flora in Western Hills of Beijing. China University of Geosciences (Beijing) (M.S. thesis): 1–64.

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- Zheng Wanjun and Fu Liguo, 1978. *The flora of China (vii)*. Beijing: Science Press, 285–310.
- Zhou Z.Y., 1997. Mesozoic ginkgoalean megafossils: a systematic review, Ginkgo Biloba A Global Treasure. Springer, 183–206.
- Zhou Zhiyan, 2003. Mesozoic Ginkgoaleans: phylogeny, classification and evolutionary Trends. Acta Botanica Yunnanica, 25(4): 377–396 (in Chinese with English abstract).
- Zhou Zhiyan and Zhang Bole, 1988. Female reproductive organs of two kinds of ginkgoales of Middle Jurassic Flora in Henan Yima. *Chinese Science Bulletin*, 33(3): 216–217 (in Chinese).
- Zhou Zhiyan and Zhang Bole, 1992. Baiera hallei Sze and associated ovule-bearing organs from the Middle Jurassic of Henan, China. *Palaeontographica Abteilung B*, 224(4-6): 151–169.
- Zhou Z.Y. and Zheng S.L., 2003. Palaeobiology: The missing link in *Ginkgo* evolution. *Nature*, 423: 821–822.
- Zhou Zhiyan and Wu Xiangwu, 2006a. Early Mesozoic radiation and diversification of ginkgoaleans. In: Rong Jiayu, et al. (eds.), Originations and Radiations—Evidences from South China. Science Press: Beijing. (in Chinese with English abstract).
- Zhou Zhiyan and Wu Xiangwu, 2006b. The rise of ginkgoalean plants in the early Mesozoic: a data analysis. *Geol. J.* 41 (3/4, Spec. issue): 363–375.
- Zhou Zhiyan, 2009. An overview of fossil Ginkgoales. *Palaeoworld*, 21: 1–22.

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