

Permineralized osmundaceous and gleicheniaceous ferns from the Jurassic of Inner Mongolia, NE China

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Abstract Structurally preserved fossil ferns are extremely significant for exploring the origin and evolution of this plant clade; however, they are quite scarce and limited in the Mesozoic. Here, we report some well-preserved fern rhizomes and rachides with anatomical details from the Upper Jurassic Manketouebo Formation in Inner Mongolia, NE China. Two taxa, including *Ashicaulis liaoningensis* (Zhang et Zheng) Tidwell referred to Osmundaceae and *Gleicheniorachis sinensis* sp. nov. referred to Gleicheniaceae, are recognized. Anatomically, *Ashicaulis liaoningensis* consists of a heterogeneous pith, an ectophloic dictyoxyllic siphonostele, a two-layered cortex, C-shaped leaf traces, and a mantle of petiole bases. The petiole base is characterized by a heterogeneous sclerotic ring with an abaxial thick-walled fiber arc.

Gleicheniorachis sinensis sp. nov. consists of a C-shaped vascular bundle with two incurved adaxial hooks, a distinct sclerenchyma sheath, an endodermis, and a heterogeneous cortex. In particular, the finding of *Gleicheniorachis sinensis* sp. nov. represents the first report of unequivocal Jurassic record of Gleicheniaceae in northern China, as well as the first record of a Jurassic permineralized gleicheniaceous fern in the Northern Hemisphere. This study provides new data and evidence for exploring the anatomical diversity and evolution of Mesozoic ferns, and contributes to further understanding the floral composition of Late Jurassic flora in Northeast China.

Keywords Osmundaceae · Gleicheniaceae · Permineralization · Jurassic · Inner Mongolia · China

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Introduction

Among extant land plants, ferns are a large and diverse group, second only to angiosperms in species number (Tryon and Tryon 1982; Gifford and Foster 1989; Rothwell 1999). In the geological past, ferns have undergone several major radiation events (Rothwell 1987). The Palaeozoic radiation created several families that became extinct at the end of the Permian, though some primitive groups of modern ferns including Marattiaceae, Osmundaceae, and Gleicheniaceae survived through the Palaeozoic and up to the present (Tidwell and Ash 1994; Pryer and Smith 1995). Then, the Mesozoic diversification is proposed to have initiated the evolution of series of modern filicalean families (Phipps et al. 2000). Variation in these long-lived families provides valuable information as to which characters are the most plastic and how each evolved (Phipps et al. 2000).

Compared to morphologically preserved leaves, structurally preserved fern remains not only provide more anatomical details, but also contribute to understanding the evolution and phylogeny of various fern taxa. Though reproductive characters have traditionally been heavily used in fern classification (Bower 1926; Smith 1995; Collinson 1996), anatomical characters of filicalean ferns are also correlated with relationships inferred from cladistic analyses of morphological and molecular data (Serbet and Rothwell 2003). These characters strongly support the hypothesis that internal anatomy is a valuable tool for identifying systematic relationships of fossil ferns (Hasebe et al. 1995; Pryer and Smith 1995; Smith 1995; Rothwell 1999) and provide a vehicle for assessing minimum dates for the origin of leptosporangiate fern clades (Serbet and Rothwell 2003).

Numerous Mesozoic fossil records have been documented worldwide referring to permineralized fern remains of Osmundaceae, Gleicheniaceae, Dennstaedtiaceae, Cyatheaceae, Matoniaceae, and Loxsomaceae (e.g., Skog 1976; Sharma and Bohra 1976, 1977; Bohra and Sharma 1979; Nishida and Nishida 1982; Millay and Taylor 1990; Tidwell 1986, 1994; Tidwell and Parker 1987; Tidwell and Ash 1994; Gandolfo et al. 1997; Herendeen and Skog 1998; Phipps et al. 1998, 2000; Tidwell and Skog 1999; Serbet and Rothwell 2003; Cheng and Yang 2017). Mesozoic ferns are well documented in both the northern and southern phytoprovinces of China with diverse and abundant fossil records (Sun et al. 1995a, b; Zhou 1995; Deng and Shang 2000; Wang et al. 2009; Sun et al. 2010; Zhou et al. 2016; Tian et al. 2016). However, almost all these fossil records are represented by leaf impressions/compressions, whereas structurally preserved fern remains are quite scarce in China. Though some permineralized fern rhizomes have been described from the Jurassic of western Liaoning and northern Hebei Provinces, they are all referred to Osmundaceae (Wang 1983; Zhang and Zheng 1991; Matsumoto et al. 2006; Cheng and Li 2007; Cheng et al. 2007; Cheng 2011; Tian et al. 2008, 2013, 2014a, b). Additionally, fern stems referable to Cyatheaceae were recently described from the Upper Cretaceous in the Keshan County of Heilongjiang Province (Cheng and Yang 2017). Other fern lineages have never been reported with structurally preserved fossils from the Mesozoic deposits in China, so far.

In this paper, we described well-preserved fern remains represented by permineralized rhizomes and rachides from the Upper Jurassic Manketouebo Formation in Inner Mongolia, NE China. These fern fossils are assigned to fern families Osmundaceae and Gleicheniaceae. This finding represents the first record of the Jurassic permineralized gleicheniaceous ferns with anatomical details in China, as well as in the Northern Hemisphere.

Material and methods

The fossil fern specimens were collected from the Upper Jurassic Manketouebo Formation on a small hill named Xiehesierde, northeast of the Baiyinbaoligao Village of Daiqintala Town, Horqin Right Wing Middle Banner, Inner Mongolia, NE China (45° 11' 50" N, 121° 35' 10" E) (Fig. 1). The Manketouebo Formation, represented by a suite of felsic lavas, tuffs, ignimbrites, and volcanoclastic rocks, is widely distributed across the Great Xing'an Range, NE China (Zhang et al. 2010). In the present fossil locality, the Manketouebo Formation unconformably overlies the Lower Permian Shoushangou Formation and comprises tuffaceous sandstone, pebbly sandstone, and crystal tuff (Fu et al. 2012). The outcropped sequence of the Manketouebo Formation is over 150 m in thickness and was divided into five lithological units (Fu et al. 2012) (Fig. 2). The fossil fern remains described here occur in the light gray-green tuff matrix of the Member 5. Besides fern remains, diverse permineralized coniferous wood and cones have also been reported from the same layer in the same locality (Fu et al. 2012; Zheng et al. 2013).

The petrified fern remains were cut transversely into several thin sections. These sections were prepared by standard methods, including cutting, grinding, and polishing preparations (Hass and Rowe 1999). These sections were then mounted on slides for microscopic examinations. Photographs were taken with OLYMPUS BX51 and YONGXIN BM2000 microscopes. All specimens and slides described in this paper are housed in Shenyang Institute of Geology and Mineral Resources, Shenyang, China with registration numbers BY-01(A-B) and BY-031(A-C).

Systematic palaeontology

Order Filicales

Family Osmundaceae Berchtold et Presl, 1820

Subfamily Osmundoideae Miller, 1971

Genus *Ashicaulis* Tidwell, 1994

Species *Ashicaulis liaoningensis* (Zhang et Zheng) Tidwell, 1994

(Fig. 3)

Specimen: BY-01 with two slides BY-01-(A-B)

Fossil locality: Baiyingbaoligao Village of Daiqintala Town, Horqin Right Wing Middle Banner, Inner Mongolia, NE China

Formation and age: Manketouebo Formation, Late Jurassic

Repository: The specimen and prepared slides are deposited in the Shenyang Institute of Geology and Mineral Resources, Shenyang, China

Description: This fossil specimen is represented by a petrified rhizome, composed of a stem and a mantle of adhering petiole

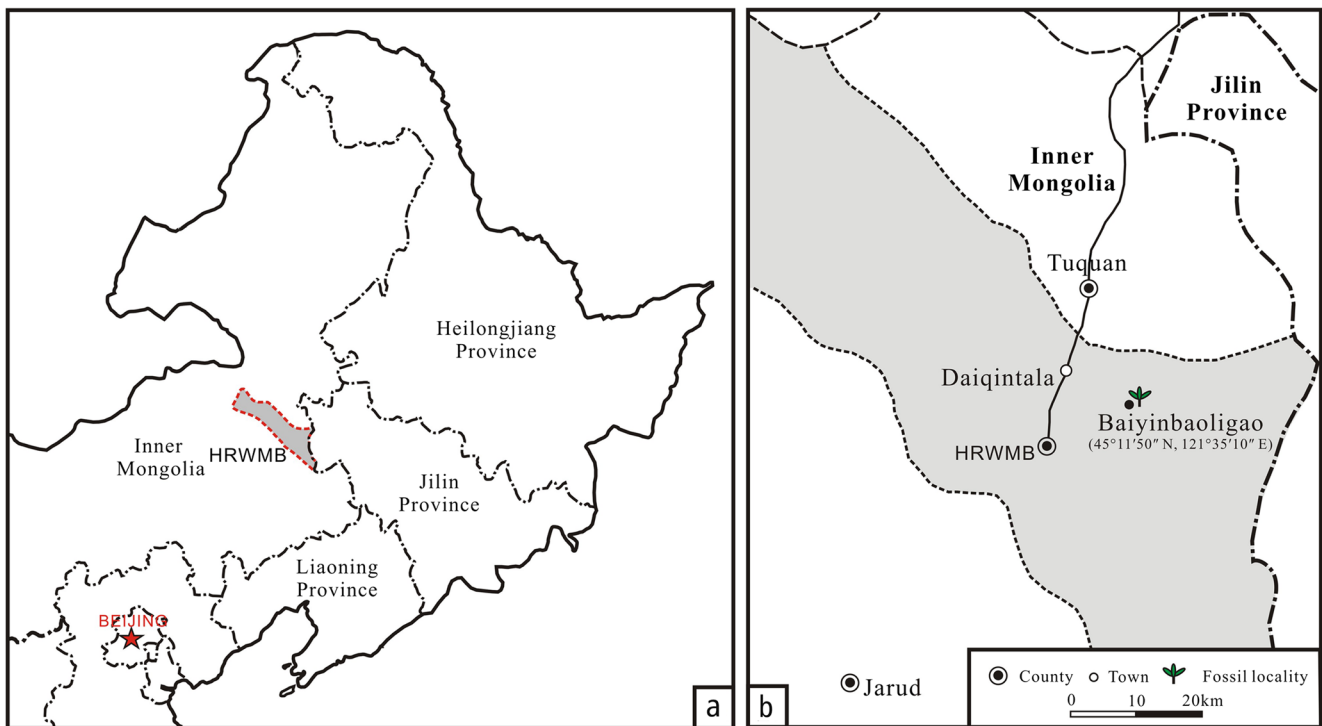


Fig. 1 Location map for the sources of the fossils. **a** Map showing the locality of the Horqin Right Wing Middle Banner (HRWMB) in Inner Mongolia, Northeast China. **b** Sketch map of fossil locality for

permineralized fern remains in Daiqintala Town of HRWMB, Inner Mongolia

bases and adventitious roots. Tissue preservation of the present fossil rhizome is generally fair, although some thin-walled cells (e.g., in the pith) are degraded, and sub-cellular details evident in some other fossil Osmundaceae (e.g., *Osmundastrum pulchellum*: Bomfleur et al. 2014, 2015) are not preserved. The stem is about 8.0 mm in diameter and consists of a pith, a xylem cylinder, and a two-layered cortex (Fig. 3a, b). The pith, 1.4–1.5 mm across, is heterogeneous and composed of isodiametric parenchymatous cells with scattered sclerenchymatous cells (Fig. 3c, d). The xylem cylinder consists of about eight xylem strands, each about 0.5–0.6 mm thick (7–9 tracheids) (Fig. 3c). The xylem strands with mesarch protoxylem elements are mainly composed of metaxylem tracheids surrounding the protoxylem points (Fig. 3c). The xylem cylinder is dissected mostly by definite leaf gaps, which are of intermediate type (Fig. 3c). The phloem is ectophloic, but poorly preserved with no anatomical details.

The cortex contains many helically arranged leaf traces. The whole cortex can be differentiated into two distinct layers, i.e., a 1–1.5 mm thick inner cortex and a 0.9–1.5 mm thick outer cortex (Fig. 3a). The inner cortex is parenchymatous and contains nine leaf traces, whereas the outer cortex is sclerenchymatous with eight leaf traces (Fig. 3a, b). The leaf trace is reniform in shape, with a single endarch protoxylem cluster when departing from the stele (Fig. 3c, e), and becomes C-shaped with two protoxylem strands when entering into the outer cortex (Fig. 3f). Upon departing from the stele, the leaf trace enters the petiolar zone. The petiole base bears two typical stipular wings (Fig. 3i, j). The

petiolar size, shape, and sclerenchyma arrangement varies at different levels. The sclerotic ring of the petiole base is heterogeneous, with an abaxial arch of thick-walled fibers in the semicircle (Fig. 3i, j). Only one large sclerenchyma mass occurs on each side of the stipular wing. Additionally, a meniscus sclerenchyma exists in the adaxial concavity of the vascular bundle (Fig. 3i, j). No sclerenchyma tissue occurs in other part of the petiolar cortical region (Fig. 3i, j). Adventitious roots bear typical diarch xylem (Fig. 3g) and always arise endogenously from the stele xylem cylinder (Fig. 3a).

Comparison and remarks: The fossil rhizome from Inner Mongolia is characterized by an ectophloic dictyoxylic siphonostele, a two-layered cortex, a mantle of petiole bases, and C-shaped leaf traces. Such a combination of anatomical characters strongly indicates an affinity of the fern family Osmundaceae. Generally, the anatomical characters of this fossil rhizome are consistent with those of the genus *Ashicaulis* Tidwell, which is featured by possessing ectophloic dictyoxylic siphonostele and complete leaf gaps (Tidwell 1994; Tidwell and Ash 1994; Tian et al. 2008). Vera (2008) proposed merging the form genus *Ashicaulis* Tidwell (with perforate steles) and *Millerocaulis* Erasmus ex Tidwell emend. Tidwell (with imperforate steles) into a single genus, the broadly defined *Millerocaulis* Tidwell emend. E.I. Vera. This was supported by phylogenetic network analysis of Osmundales by Bomfleur et al. (2017). Here, we retain the use of the fossil genus *Ashicaulis* in this study for *Millerocaulis*-like axes with perforate steles. To date, over 30 species

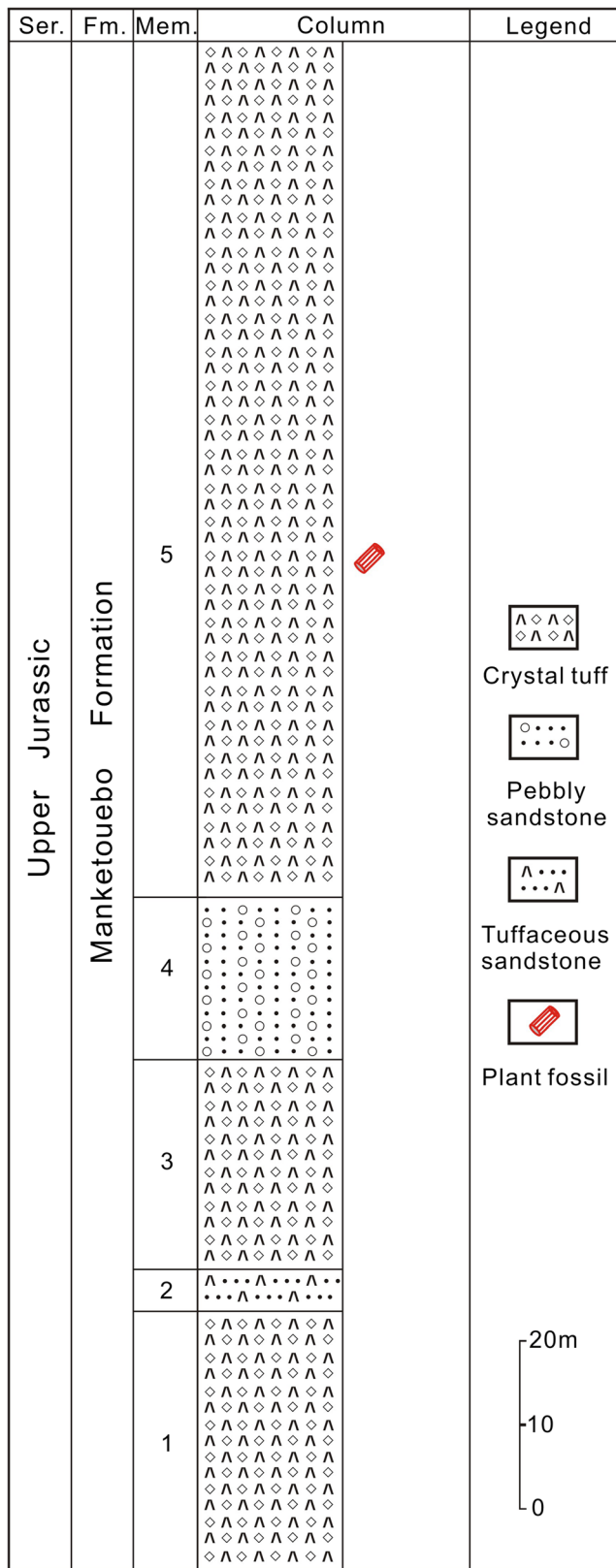
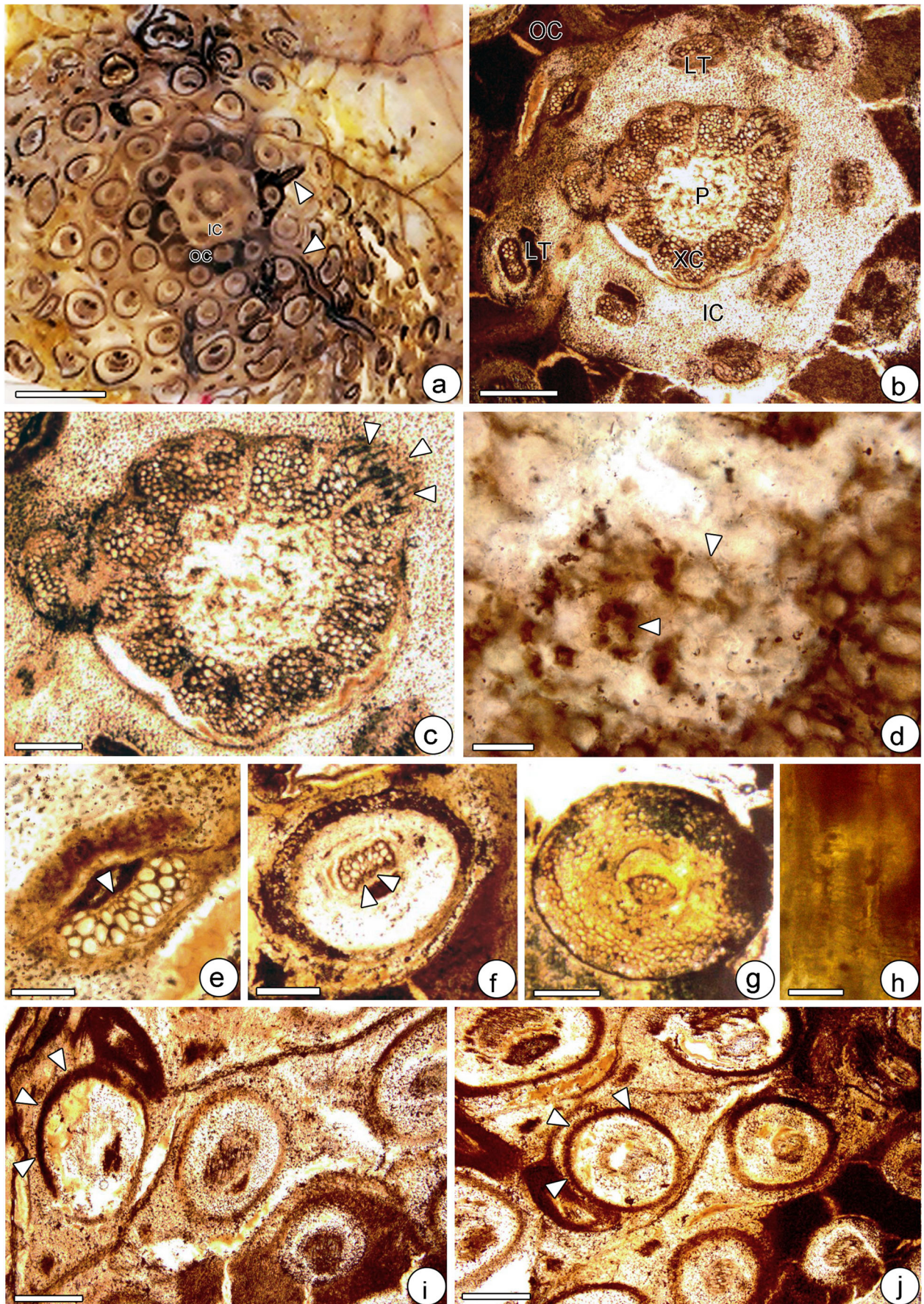


Fig. 2 Stratigraphic column of the Upper Jurassic Manketouebo Formation in Baiyinbaoligao Village of the Horqin Right Wing Middle Banner in Inner Mongolia, Northeast China (draw based on lithologic descriptions of Fu et al. 2012)

referred to *Ashicaulis* have been documented worldwide (Tidwell and Ash 1994; Tian et al. 2008; Cheng 2011; Tian et al. 2014a, b). The petiolar sclerenchyma arrangement is considered a key feature for classifying osmundaceous species (Hewitson 1962; Miller 1971). So far, only six species of *Ashicaulis* incorporate a heterogeneous petiolar sclerotic ring that resembles our present fossil material. These species are *A. johnstonii* (Tidwell, Munzing et Banks) Tidwell, *A. kidstonii* (Stopes) Tidwell, *A. liaoningensis* (Zhang et Zheng) Tidwell, *A. claytoniites* Cheng, *A. wangii* Tian et Wang, and *A. plumites* Tian et Wang (Cheng 2011; Stopes 1921; Tidwell 1994; Tidwell et al. 1991; Tian et al. 2014a, b). It is noted, based on a detailed phylogenetic network analysis of Osmundales, these species were recently recombined to extant genera as *Claytosmunda johnstonii* (Tidwell, Munzing et Banks) Bomfleur, Grimm et McLoughlin, *Osmunda kidstonii* (Stopes) Bomfleur, Grimm et McLoughlin, *Claytosmunda chengii* Bomfleur, Grimm et McLoughlin, *C. liaoningensis* (Zhang et Zheng) Bomfleur, Grimm et McLoughlin, *C. wangii* (Tian et Wang) Bomfleur, Grimm et McLoughlin, and *C. plumites* (Tian et Wang) Bomfleur, Grimm et McLoughlin, respectively (Bomfleur et al. 2017). In this study, we retain the use of the taxonomic name referring to the fossil genus *Ashicaulis* Tidwell.

Compared to *A. kidstonii*, the present specimen has only one sclerenchyma mass in the petiolar vascular bundle concavity, whereas the former bears two sclerenchyma masses (Stopes 1921; Miller 1971). In *A. claytoniites*, the whole periphery of the sclerotic ring is encircled by thick-walled fibers (Cheng 2011). Differing from *A. wangii* and *A. plumites*, the abaxial thick-walled fiber arch on the sclerotic ring never bifurcates into two lateral parts in the new specimen (Tian et al. 2014a, b). Additionally, numerous sclerenchymatous clusters occur in the petiolar inner cortex of *A. wangii* (Tian et al. 2014a). Generally, the present specimen from Inner Mongolia bears great similarities to *A. liaoningensis* and

Fig. 3 *Ashicaulis liaoningensis* (Zheng et Zhang) Tidwell (BY-01-A) from the Upper Jurassic Manketouebo Formation in Horqin Right Wing Middle Banner, Inner Mongolia, NE China. **a** Cross-section of the rhizome with a single stem surrounded by petiole bases and roots, showing the pith, inner cortex (IC), outer cortex (OC), and root trace (arrows), *scale bar* 5.0 mm. **b** Cross-section of the stem, showing the pith (P), xylem cylinder (XC), leaf trace (LT), inner cortex (IC), and outer cortex (OC), *scale bar* 1.0 mm. **c** Enlargement of xylem cylinder, showing an ectophloic dictyoxylic siphonostele and leaf traces; the arrows indicate a departing leaf trace, *scale bar* 0.5 mm. **d** Cross-section of pith, the arrows indicate sclerenchymatous cells, *scale bar* 0.1 mm. **e** Cross-section, showing a leaf trace with one protoxylem cluster (arrow) in inner cortex, *scale bar* 0.2 mm. **f** Cross-section, showing a leaf trace with two protoxylem clusters (arrows) in outer cortex, *scale bar* 0.5 mm. **g** Cross-section of an adventitious root with diarch xylem, *scale bar* 0.5 mm. **h** longitudinal section, showing scalariform pitting in the tracheids of the root trace, *scale bar* 0.05 mm. **i, j** Cross-section of petiole bases, showing heterogeneous sclerotic ring and sclerenchymatous masses in the vascular bundle concavity and stipular wings; the arrows indicate sclerotic fiber arc in the abaxial side of the sclerotic ring, *scale bar* 1.0 mm



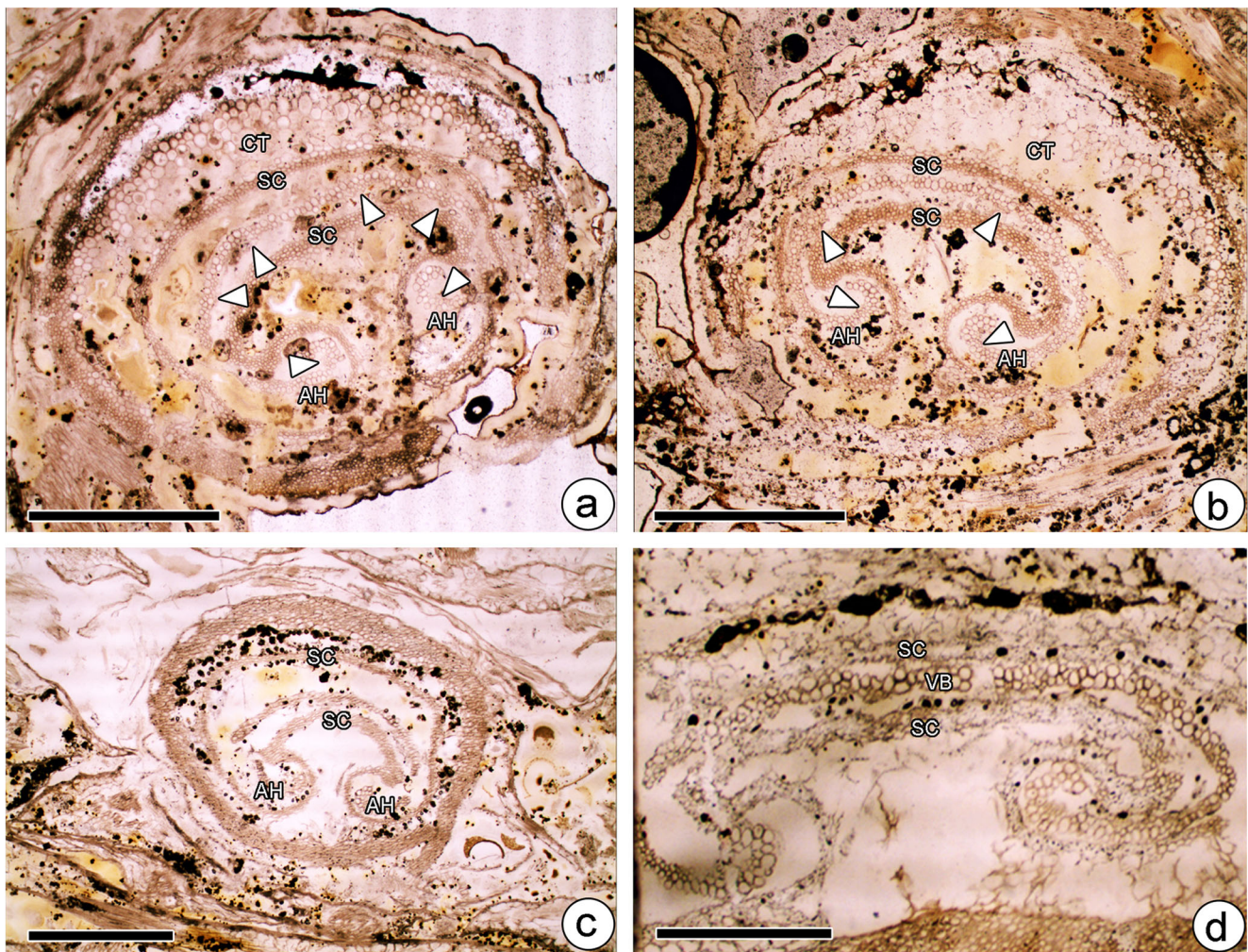


Fig. 4 *Gleicheniorachis sinensis* Tian, Wang, Zhang et Liu sp. nov. (BY-031-A, C) from the Upper Jurassic Manketouebo Formation in Horqin Right Wing Middle Banner, Inner Mongolia, NE China. **a–c** Cross-section of the gleicheniaceous racheids, showing the C-shaped vascular bundle (VB) with two incurved adaxial hooks (AH), the sclerenchyma

sheath (SC), and the cortex (CT); the arrows indicate that protoxylem clusters, *scale bar* 1.0 mm. **d** Cross-section of a rachis, showing details of the C-shaped vascular bundle (VB) with two adaxial hooks and the sclerenchyma sheath (SC), *scale bar* 0.5 mm

A. johnstonii in petiolar structures (Tidwell et al. 1991; Zhang and Zheng 1991). However, the pith of *A. johnstonii* is homogeneous (Tidwell et al. 1991). Therefore, the present specimen from Inner Mongolia is assigned to *A. liaoningensis*.

Ashicaulis liaoningensis was first described by Zhang and Zheng (1991) as *Millerocaulis liaoningensis* Zhang et Zheng based on fossil rhizomes from the Middle to Upper Jurassic Tiaojishan Formation in Fuxin City of western Liaoning Province, NE China. Thereafter, it was reassigned to *Ashicaulis* by Tidwell (1994) based on possession of complete leaf gaps. Just as mentioned, this species was recently recombined as *Claytosmunda liaoningensis* (Zhang et Zheng) Bomfleur, Grimm et McLoughlin, as part of a detailed re-evaluation of phylogenetically significant anatomical characters within Osmundales (Bomfleur et al. 2017). Fossils of this species have also been reported from the Middle to Upper Jurassic Tiaojishan Formation in the Beipiao City of western

Liaoning Province (Tian 2011).

Family Gleicheniaceae (Brown) Presl, 1825

Genus *Gleicheniorachis* Sharma, 1973

Species *Gleicheniorachis sinensis* Tian, Wang, Zhang et Liu sp. nov.

(Figs. 4–5)

Specific diagnosis: Permineralized fern rachides consisting of a C-shaped vascular bundle, a distinct sclerenchyma sheath, an endodermis and a cortex, and 1.5–3.0 mm in diameter. The C-shaped vascular bundle, about 1.6 mm in width, with the lateral margins forming two incurved adaxial hooks. The xylem strands consisting of one to three layers of tracheids with over six protoxylem strands, endarch maturation. Sclerenchyma sheath with a thickness of three to five cells

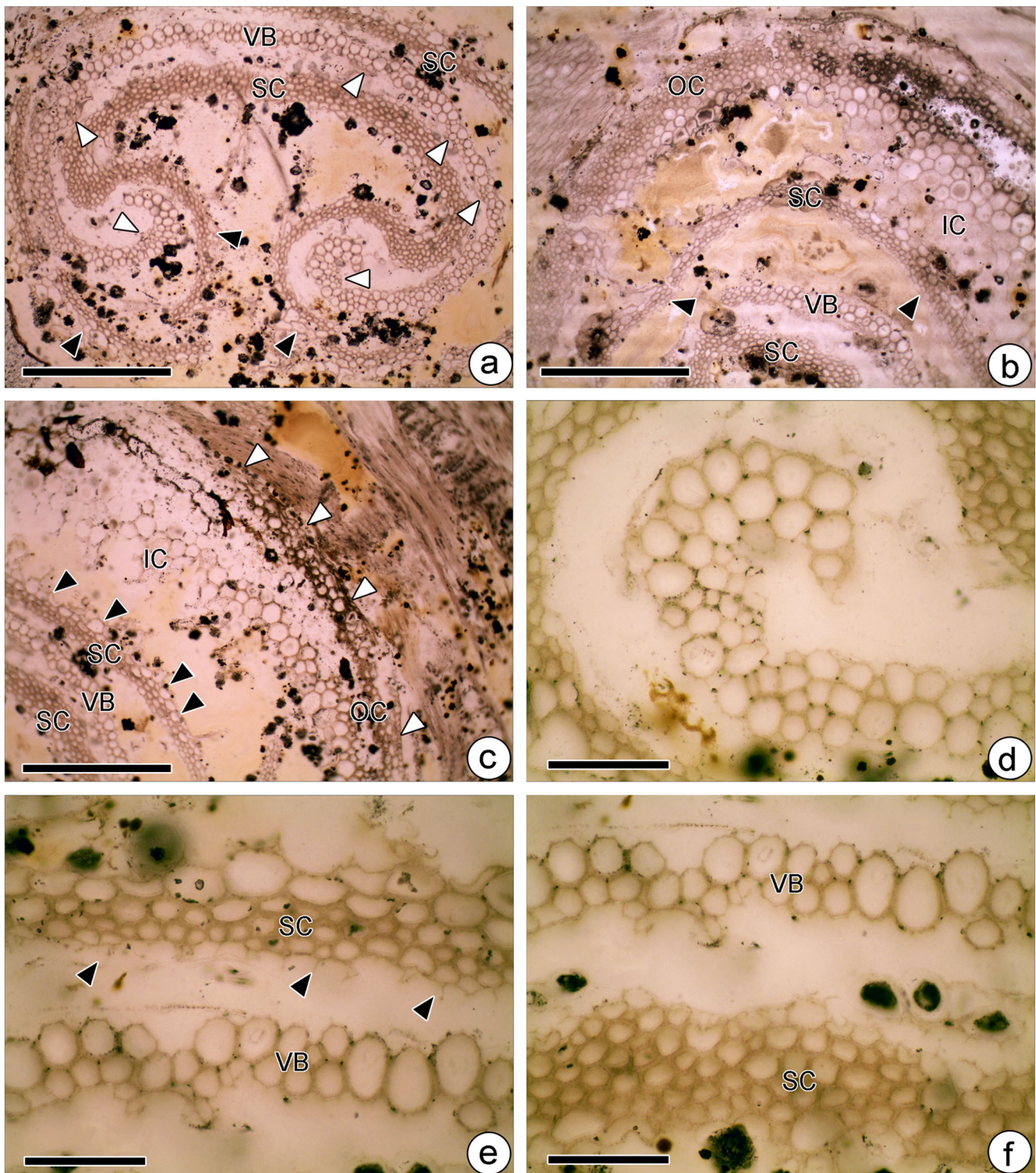


Fig. 5 *Gleicheniorachis sinensis* Tian, Wang, Zhang et Liu sp. nov. (BY-031-C) from the Upper Jurassic Manketouebo Formation in Horqin Right Wing Middle Banner, Inner Mongolia, NE China. **a–f** Cross-section of the gleicheniaceous rachides. **a** Detail of the C-shaped vascular bundle (VB) with two adaxial incurved hooks and the sclerenchyma sheath (SC); the white arrows indicate the protoxylem groups, and the black arrows show the endodermis, *scale bar* 0.5 mm. **b** Abaxial part of the rachis, showing details of the vascular bundle (VB), sclerenchyma sheath (SC), inner zone (IC) and outer zone (OC) of the cortex, the black arrows show

the endodermis, *scale bar* 0.5 mm. **c** Part of the rachis, showing details of the vascular bundle (VB), sclerenchyma sheath (SC), inner zone (IC) and outer zone (OC) of the cortex; the black arrows indicate the endodermis, and the white arrows show the epidermis cells, *scale bar* 0.5 mm. **d** Enlargement of the adaxial incurved hooks of the vascular bundle, *scale bar* 0.1 mm. **e, f** Details of vascular bundle (VB), and sclerenchyma sheath (SC); the black arrows indicate the endodermis cells, *scale bar* 0.1 mm

Table 1 Comparisons on anatomical characters of fossil gleicheniaceae rachides

Species	Rachis diameter	Cortex	Rachis	Protoxylem clusters	Sclerenchyma sheath	Sclerenchyma column	Age	Locality	References
<i>Gleicheniorachis sinensis</i> sp. nov.	1.5–3 mm	Two-zoned, inner parenchymatous, outer sclerenchymatous	Two-zoned, inner parenchymatous, outer sclerenchymatous	Endarch, over 6	present	absent	Late Jurassic	Inner Mongolia, NE China	This paper
<i>Gleicheniorachis jurassica</i> Sharma	4.5–6.0 mm	One layer, sclerenchymatous	One layer, sclerenchymatous	Endarch, 6–8	present	present	Early Cretaceous	Rajmahal Hills, India	Sharma, 1973
<i>Gleicheniorachis mitrii</i> Bohra et Sharma	1.5–7.5 mm	One layer, thin-walled	One layer, thin-walled	Endarch, 3–5	present	present	Early Cretaceous	Rajmahal Hills, India	Bohra & Sharma, 1979
<i>Boodlepteris turoniana</i> Gandolfo	0.8–1.4 mm	One layer, thick-walled fibers	One layer, thick-walled fibers	Endarch, over 2	present	absent	Late Cretaceous	New Jersey, USA	Gandolfo et al., 1997
<i>Gleichenia chaloneri</i> Herendeen et Skog	2–4 mm	One layer	One layer	Endarch, 7–8	present	present	Early Cretaceous	Bedfordshire, England	Herendeen & Skog, 1998
<i>Gleichenia appianensis</i> Mindell, Stockey, Rothwell et Beard	2.5–8.0 mm	Two-zoned, inner parenchymatous, outer sclerenchymatous	Two-zoned, inner parenchymatous, outer sclerenchymatous	Endarch, over 5	present	absent	Middle Eocene	Vancouver Island, Canada	Mindell et al., 2006

Characters that differ from those of the new *Gleicheniorachis sinensis* sp. nov. are in bold

surrounding the vascular zone. No sclerenchymatous central column occurring in the vascular bundle concavity. In fully developed rachides, the cortex well developed and differentiated into a parenchymatous inner zone and a sclerenchymatous outer zone. Endodermis, composed of only one single layer of cells, sandwiched between the pericycle and the inner zone of the cortex.

Holotype: BY-031 with three slides BY-031-(A-C)

Repository: The specimen and slides are deposited in the Shenyang Institute of Geology and Mineral Resources, Shenyang, China

Type locality: Baiyinbaoligao Village of Daiqintala Town, Horqin Right Wing Middle Banner, Inner Mongolia, NE China

Formation and age: Manketouebo Formation, Late Jurassic
Etymology: The specific epithet *sinensis* is proposed for Sino (China), where the fossil locality Horqin Right Wing Middle Banner, Inner Mongolia administratively belongs.

Description: Numerous isolated fossil rachides were found within the tuffaceous matrix. The rachides are elliptical to circular in cross-section, with diameters of 1.5–3.0 mm (Fig. 4a–c). Each rachis consists of a C-shaped vascular bundle, a distinct sclerenchyma sheath, an endodermis, and a cortex (Fig. 4a–c). The surface of the rachides is smooth with no scales (Fig. 4a–c). The C-shaped vascular bundle is about 1.6 mm in width, with the lateral margins forming two adaxial incurved hooks (Figs. 4a–d, 5a, 5d). The xylem strands consist of one to three layers of tracheids (Fig. 4d, 5a). The protoxylem strands vary (over six) and show typical endarch maturation (Figs. 4a–b, 5a). A distinct sclerenchyma sheath is present surrounding the vascular zone, with a thickness of three to five cells (Figs. 4a–c, 5a–c). Cells of the sclerenchyma sheath are circular or angular, closely placed without intercellular spaces (Fig. 5a, b, e, f). No sclerenchymatous central column occurs in the vascular bundle concavity. In fully developed rachides, the cortex is well developed and differentiated into two zones. The inner zone is parenchymatous with a thickness of four to six cells, whereas the outer zone is sclerenchymatous with a thickness of seven to nine cells (Fig. 5b, c). Generally, the cell size of the inner cortex is remarkably larger than that of the outer cortex. A typical endodermis, composed of only one single layer of cell, is sandwiched between the sclerenchyma sheath and the inner zone of the cortex (Fig. 5e). It completely encloses both the external and internal periphery of the vascular bundle arc (Fig. 5b, e, f). The endodermis cells are parenchymatous and larger than adjacent cells of the sclerenchyma sheath.

Comparison: In gross anatomy, the present fossil rachides from Inner Mongolia show typical petiolar characters of the fern family Gleicheniaceae (Boodle 1901; Bower 1926; Chrysler 1943, 1944). *Gleicheniorachis* was established by Sharma (1973) based on fossils from India to include isolated gleicheniaceae petioles and rachides. So far, only two species

have been referred to this genus, i.e., *Gleicheniorachis jurassica* Sharma and *G. mittrii* Bohra et Sharma, which were both reported from the Lower Cretaceous of the Rajmahal Hills, India (Sharma 1973; Bohra and Sharma 1979; Tripathi 2008; Tripathi et al. 2013). Generally, the present fossil material from China resembles *Gleicheniorachis* in the C-shaped petiolar trace with two incurved adaxial hooks and endarch protoxylem points. It is thus reasonable to assign them to *Gleicheniorachis*. The present material from Inner Mongolia resembles the two reported species of *Gleicheniorachis* in gross anatomy but differs in detail, and thus, has been described as a new species *Gleicheniorachis sinensis* sp. nov. Tian, Wang, Zhang et Liu. Compared to the present new species, a distinct sclerenchymatous column occurs in the vascular bundle concavity of both *G. jurassica* and *G. mittrii* (Table 1). However, such a column is absent in the fossil rachides from China. Additionally, only three to five protoxylem points were observed in the xylem of *G. mittrii*, whereas the number is over six in the new species from China.

Besides *Gleicheniorachis*, there are also a series of fossil records referred to gleicheniaceus fern, represented by permineralized rhizomes and their attached rachides. A detailed comparison based on anatomical characters of fossil gleicheniaceus rachides is given in Table 1. Among them, *Boodlepteris turoniana* Gandolfo, represented by well-preserved fusinized rhizomes, petioles, pinnules, sori, and spores, was described from the Upper Cretaceous of New Jersey, USA (Gandolfo et al. 1997). The petiolar cortex of *B. turoniana* is composed of very thick-walled fibers (Gandolfo et al. 1997); whereas, the cortex of *Gleicheniorachis sinensis* sp. nov. is two-zoned. *Gleichenia chaloneri* Herendeen et Skog, described based on fusinized material from the Lower Cretaceous of England, was another anatomically preserved species referred to Gleicheniaceae (Herendeen and Skog 1998). It is noted that the rachis of *Gleichenia chaloneri* is surrounded by scales; however, no scales were found attached with the fossil rachides from China. Additionally, the petiolar xylem of *Gleichenia chaloneri* generally consists of a single row of tracheids and thus, differs from that of *G. sinensis* sp. nov. Karafit (2008) described some permineralized gleicheniaceus rachis segments from the Upper Cretaceous in British Columbia, Canada. They also resemble the present fossil material in gross anatomy. However, their petiolar xylem seems to be also composed of only one single layer of tracheids with a larger size (see in Karafit 2008, Fig. 3). In contrast, the xylem of *G. sinensis* sp. nov. consists of two to three layers of tracheids. Generally, *Gleicheniorachis sinensis* sp. nov. from China has more anatomical similarities to the rachis of *Gleichenia appianensis* Mindell, Stockey, Rothwell et Beard from the Eocene of Vancouver Island, British Columbia, Canada (Mindell et al. 2006), especially in having a two-layered cortex, a sclerenchyma sheath

surrounding the vascular bundle, and the number of protoxylem groups (Table 1). However, further comparisons between the two taxa are not possible, since anatomical details of the rhizome are not known for *Gleicheniorachis sinensis*. Hence, the authors prefer to treat it as a new species of the form genus *Gleicheniorachis*.

Discussion

The discovery of the osmundaceous fern rhizome *Ashicaulis liaoningensis* in the Jurassic of Inner Mongolia provides additional information for understanding the palaeogeographical distribution of the fern taxon. This species has been described from the Middle to Upper Jurassic Tiaojishan Formation in the Fuxin and Beipiao regions of western Liaoning Province, NE China (Zhang and Zheng 1991; Tian 2011). The current new finding expands its geographic distribution and indicates that *A. liaoningensis* was a common component of the Jurassic flora in Northeast China. It is noted, the occurrence of *A. liaoningensis* is also of stratigraphical significance. The present fossil-bearing strata in Inner Mongolia are preliminarily considered as the Upper Jurassic Manketouebo Formation (Fu et al. 2012). It is noted that the fossil wood assemblages of the Manketouebo Formation, represented by *Protaxodioxylon romanense* Philippe, *Xenoxylon hopeiense* Chang and *Araucarioxylon batuense* Duan (Fu et al. 2012), have also been found from the Middle to Upper Jurassic Tiaojishan Formation in western Liaoning and northern Hebei Provinces (Zhang et al. 2006). This implies that the fossil-bearing strata in Inner Mongolia may be stratigraphically correlated in age with the Tiaojishan Formation in western Liaoning Province.

The family Gleicheniaceae is a primitive leptosporangiate fern lineage represented by about 130 living species referred to six genera (Ogura 1972). The family is considered to have a Palaeozoic origin. Mesozoic Gleicheniaceae ranges from the Early Triassic to the Cretaceous (Tidwell and Ash 1994). In China, Gleicheniaceae have diverse fossil records ranging from the late Palaeozoic to the Cenozoic (Wang et al. 2009). A systematic review of the fossil gleicheniaceus megaplants recorded in China suggests that gleicheniaceus ferns are remarkably diverse in the Early Cretaceous with 12 species (Wang et al. 2009). However, they are very scarce and limited in the Jurassic with only three species of one genus, i.e., *Gleichenites nitida* Harris from the Lower Jurassic in Hunan Province, southern China; and *G. nordenskioldi* (Heer) Seward and *G. porsildi* (Heer) Seward from the Middle to Upper Jurassic Chaoyangtun Formation in Heilongjiang Province, northeastern China (Zheng and Zhang 1982; Zhou 1984). It is noted, the age of the Chaoyangtun Formation is now considered to be Early Cretaceous (Zheng et al. 2005). In other words, no Jurassic gleicheniaceus fossils have been recorded in northern China. Hence, the new discovery represents the first

unequivocal record of Jurassic gleicheniaceous ferns in northern China. It is also the first record of the Jurassic permineralized gleicheniaceous fern in the Northern Hemisphere. Undoubtedly, the new findings not only provide information on petiolar anatomy of Gleicheniaceae in the Jurassic, but also contribute to better understanding of the evolution of gleicheniaceous plants in China.

In conclusion, the current discovery of the permineralized fern remains from Inner Mongolia provides new data and evidence for exploring the anatomical diversity of Mesozoic ferns in China, and contributes to further understanding the floral composition of Late Jurassic flora in Northeast China.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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