Fertile organs and *in situ* spores of a new dipteridaceous fern *Hausmannia sinensis* from the Jurassic of northern China

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As a representative fossil member of the dipteridaceous fern, genus *Hausmannia* was reported worldwide from the Mesozoic strata; however, little is known about the fertile structures, including sporangia and *in situ* spores, of this genus. In this study, a new species *Hausmannia sinensis* was identified from the Middle Jurassic of Nei Mongol (Inner Mongolia), northern China. The specimens are compressions and are well preserved with details of sporangia and *in situ* spores. The leaf laminae are broadly fan-shaped, with an almost entire margin. Primary and lateral veins dichotomously branch to form square or polygonal meshes. Each ultimate mesh bears one to two circular sori of 0.4 mm in diameter. Sori are exindusiate; each sorus contains three to six round to ovoid sporangia. The annulus is developed and oblique, with stomial region present in proximal position. Spores are trilete, circular to oval in shape. Both proximal and distal surfaces are covered with baculate to subverrucate sculptures. Spores range from 20 to 30 µm in diameter (average 28 µm), and are comparable to the dispersed genera *Baculatisporites* Thomas and Pflug and *Apiculatisporis* Potonié and Kremp. *Hausmannia sinensis* represents the first compression species of genus *Hausmannia* from Eurasia, which shows the combination of well-preserved sori, sporangia, annuli and *in situ* spore characters, and is therefore helpful for further understanding the diversity and evolution of the Dipteridaceae fern lineage through time.

Keywords: *Hausmannia*; fertile organs; sporangia; *in situ* spores; Dipteridaceae; Jurassic

1. INTRODUCTION

The Dipteridaceae is a leptosporangiate fern family with a single extant genus, *Dipteris* Reinwardt, which is currently restricted to Indo-Malaysian regions, including northeast India, southern China and from southern Ryukyus to northeast Queensland and Fiji (Kramer 1990a). Recent phylogenetic investigations based on molecular and morphological data suggest that this family should also include the Asiatic genus *Cheiropleuria* C. Presl (approx. three extant species but no fossil record), which is often separated into the closely related family Cheiropleuriaceae (Kato *et al.* 2001; Smith *et al.* 2006; Schuettpelz & Pryer 2007). In addition, the family is considered a monophyletic clade of gleichenioid affinities, including Dipteridaceae, Gleicheniaceae and Matoniaceae (e.g. Pryer *et al.* 2004; Schuettpelz *et al.* 2006; Smith *et al.* 2006; Schuettpelz & Pryer 2007), showing great importance for exploring the phylogeny and evolution of leptosporangiate ferns.

Fossil ferns assigned to the Dipteridaceae appeared first in the Mid-Triassic and their remains are common in the Lower to Middle Jurassic. During the Mesozoic, the family was worldwide in distribution and was more diverse with up to 60 species ascribed to six genera, such as *Dictyophyllum* Lindley & Hutton, *Clathropteris* Brongniart,

Thaumatopteris Goeppert, *Hausmannia* Dunker, *Goeppertella* Oishi & Yamasita and *Camptopteris* Presl em. Nathorst. Among them, *Hausmannia* is one of the most representative fossil genera of the Dipteridaceae with the longest stratigraphic range, from the Triassic to the Cretaceous (Cantrill 1995). Approximately 30–40 species were reported globally from the Mesozoic (Oishi & Yamasita 1936; Cantrill 1995). However, all of the previously described species of *Hausmannia* are based on compression/impression fossils, and little is known about the sporangia and *in situ* spores (Balme 1995). Recently, anatomically preserved fronds of *Hausmannia* with coalified and permineralized sporangia and spores have been reported from the Cretaceous of Vancouver Island (Stockey *et al.* 2006), providing new data for understanding the biological aspects of *Hausmannia*. In this paper, we propose a new species of *Hausmannia* collected from the Jurassic of Nei Mongol (Inner Mongolia), northern China, with exceptionally well-preserved fertile organs. This is the first species of genus *Hausmannia* from Eurasia, showing detailed structures of sori, sporangia, annuli and *in situ* spore characters, and is therefore helpful for further understanding the diversity and evolution of the Dipteridaceae fern lineage through time.

2. MATERIAL AND METHODS

Specimens were collected from the Jurassic deposits in the Changshanzi Coal Mine of the Alxa Right Banner (Alxa Youqi), Nei Mongol (Inner Mongolia), northern China

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Figure 1. Geographical map showing the locality of fossil plants in the Changshanzi Coal Mine, Alxa Right Banner, Nei Mongol, northern China.

(101°52' E, 39°08' N; figure 1). The Jurassic sequences in this region are composed of three units: the Lower Jurassic Jijigou Formation consisting of grey, purple sandstones and mudstones of alluvial–fluvial to lake system up to 60 m in thickness, corresponding to Toarcian in age; the Middle Jurassic Qingtujing Formation, corresponding to Aalenian to Bajocian in age, represented by sandstone, conglomerates, coal-bearing series as well as mudstones and black shales, up to 300–600 m in thickness, indicating an alluvial fan and lake and coal swamp deposition system; and the Upper Jurassic Shazaohe Formation, represented by a series of variegated to purple clastic rocks of arid lake depositional system, corresponding to Bathonian–Callovian age (Zhang *et al.* 1998; figure 2). Fossil materials were collected from the Middle Jurassic Qingtujing Formation, which yields abundant fossil plant foliages, such as *Neocalamites*, *Cladophlebis*, *Hausmannia*, *Coniopteris*, *Nilssonina*, *Ginkgoites*, *Ginkgoidium*, *Baiera*, *Phoenicopsis*, *Podozamites*, *Czekanowskia*, *Pityophyllum* and *Elatocladus* (Zhang *et al.* 1998).

The specimens of *Hausmannia sinensis* include two foliage compressions with distinct venations and well-preserved fertile organs. The soral or sporangial materials were removed mechanically from the specimen and first treated with hydrochloric acid (HCl) and hydrofluoric acid (HF), followed by a maceration in Schulze's solution for several hours. After washing with water, they were then treated with 5 per cent ammonia, followed by several changes in distilled water. Sporangia and spores were picked using anatomical needles under the stereomicroscope. Part of the material was used for slide preparation and observation under light microscopy. The other part was placed on the sample stubs with double-sided sticky tape (although sometimes no adhesive was necessary for the isolated and single grain preparations). Sporangia and spores were then sputter-coated

with gold and viewed on a JSM 6300 microscope for scanning electron microscope (SEM) at an acceleration voltage of 15–20 kV in the State Key Laboratory of Palaeontology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing, China. The specimens figured in this paper are housed in the Palaeobotanical Collection of NIGPAS, Nanjing, China under catalogue numbers PB21157–PB21158.

3. RESULTS

Description of the material

Order Filicales

Family Dipteridaceae Diels

Genus *Hausmannia* Dunker

Hausmannia sinensis Wang and Zhang, sp. nov.

(Figure 3a–d; figure 4a–f; figure 5a–h; figure 6a–h).

Diagnosis. Frond at least 8–10 cm long and 4–5 cm wide, comprising a narrow petiole of 1 mm wide. Lamina dichotomizes once into two approximately equal halves. Lamina broadly fan-shaped, at least 8 cm long and 5 cm wide, margin almost entire or slightly undulate. Primary and lateral veins branching to form square or polygonal meshes. Each ultimate mesh bears one to two circular sori of 0.4 mm in diameter. Sori exindusiate; each sorus contains three to six round to ovoid sporangia. Annulus developed and oblique, with stomial region present in proximal position. Spores trilete, circular to oval in shape, both proximal and distal surfaces covered with baculate to subverrucate sculptures. Spore size ranges from 20 to 30 µm in diameter (average 28 µm).

—*Age and horizon:* Middle Jurassic, the Qingtujing Formation.

—*Type locality:* Changshanzi Coal Mine, Alxa Right Banner, Nei Mongol, China.

Figure 2. Stratigraphic column of the Lower and Middle Jurassic sequences in the Alxa Right Banner area, Nei Mongol, China. The fossil plants are preserved in the upper part of the Middle Jurassic Qingtujiu Formation, corresponding to Aalenian to Bajocian in age. 1, mudstones; 2, shales; 3, coal; 4, siltstones; 5, fine sandstones; 6, medium-grained sandstones; 7, conglomerates; 8, fossil plant horizons; 9, lake system; 10, alluvial–fluvial system.

- *Material studied*: Two fertile specimens numbered PB21157 and PB21158 with well-preserved sori and sporangia.
- *Repository*: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.
- *Holotype*: PB21157 (figure 3a).
- *Paratype*: PB21158 (figure 3d).
- *Etymology*: The specific name *sinensis* refers to the locality of China.

Description. *Megafossil description*: *H. sinensis* is represented by two fronds preserved as compressions (figure 3a,d). The frond is at least 8–10 cm long and 4–5 cm wide, comprising a very narrow and slender petiole at the base, up to 1 mm wide and 1 cm long, perpendicularly attached to the plane of lamina (figure 3a; figure 6a). Although both specimens are incompletely preserved, their frond morphology shows that they are generally symmetrical (figure 6b). Lamina dichotomizes once into two approximately equal halves. Each half is twisted through 90° so as to be oriented horizontally. Lamina is fan-shaped, at least 8 cm long and 5 cm wide in size, and the margin is almost entire or slightly undulate (figure 3a,b; figure 6a,b). Petiole dichotomizes to its apex, and both halves typically dichotomize again. Lamina

begins to develop at about the same level. Through the lamina from the bottom of the sinus or the top of the petiole 6–11 primary veins radiate, branching, dichotomizing to four times, and reach to the margin of the lamina (figure 3a,b; figure 6a–c). Such veins are quite thick at the base, decreasing in size towards the frond margin. From primary veins, the secondary (lateral) veins are given off at an angle of 70°–90°. They branch almost at a right angle to form numerous small square to rectangular or polygonal meshes arranged more or less regularly (figure 3b–d; figure 6c,d). The square meshes are again subdivided by smaller veins into ultimate meshes approximately 0.5–1.0 mm wide. The blind endings are observed in ultimate meshes (figure 3c; figure 6c).

Sori and sporangia: Each ultimate mesh bears one to two sori. The sori are circular, 0.25–0.5 mm in diameter (usually 0.4 mm) and densely distributed in the lower surface of the lamina (figure 3c; figure 4a–b; figure 6d). Sori are exindusiate. Each sorus consists of 3–6 sporangia (usually 4). The fact that the sporangia are generally arranged in a circular pattern in each sorus implies that they possess short sporangial stalks (figure 4e–f; figure 6e). Sporangia walls are coarse on their surfaces (figure 5b). Sporangia are round to ovoid in outline and measure 80–120 µm in size (average 100 µm). Annulus is complete, oblique and interrupted by the stalk, consisting of approximately 15–25 elongated cells (figure 4c–f; figure 5a; figure 6e–f). The stomial region (with lip cells) is present on the annular ring in proximal position (figure 4f; figure 6e). The height of the radial wall of annular cells ranges from 20 to 32 µm, and the radial wall width ranges from 1.0 to 1.5 µm (average 1.4 µm).

In situ spores: Spores are trilete, circular to oval in equatorial outline. Radii of laesura are raised, straight, extending to 0.6–1.0 of the spore radius (figure 5c–h; figure 6g–h). Both proximal and distal surfaces of the spores are densely to sparsely covered with baculate to subverrucate sculptures up to 0.5–1 µm in diameter. Exine is thin, approximately 0.5 µm. No perispore is observed. Folds are generally present, weakly to strongly developed (figure 5c,d,f). Spore size ranges from 20 to 30 µm in diameter (average 28 µm). Each sporangium produces approximately 64–128 spores.

4. DISCUSSION AND COMPARISON

(a) *Comparison with other related Hausmannia species*

The genus *Hausmannia* was created by Dunker (1846) for fossil materials with fan-shaped or reniform frond and dichotoma veins. Since its initial description, many revisions have been made, some species are synonymized, with small reniform fronds formerly described as species of *Protorhops* Andrae (Richter 1906). Oishi & Yamasita (1936) pointed out that there is extreme variability in the degree of laminae dissection, even within a single species. According to the review of *Hausmannia* by Cantrill (1995), three groups were divided for the previously described species based on frond shape: deeply dissected fronds; small reniform fronds; and shallowly dissected fronds.

The specimens described here from China may compare with some species from the ‘shallowly dissected fronds’ group of *Hausmannia* species (Cantrill 1995). This group consists of several Triassic, Jurassic and Cretaceous

Figure 3. Compression leaves of *H. sinensis* sp. nov. (a) One half of leaf showing petiole (arrows), dichotomous major veins and entire lamina margin. PB21157; scale bar, 1 cm. (b) Enlargement of (a), showing the venation and square to polygonal meshes. Scale bar, 0.5 cm. (c) Detail of (b), showing thick major veins, thin lateral veins, third veins polygonal meshes as well as the distribution of sori. Note there are one to two sori in each of the ultimate mesh. Scale bar, 1.25 mm. (d) Enlargement of leaf showing the lamina and venation pattern. See figure 6b for entire leaf shape. PB21158; scale bar, 0.5 cm.

species from Europe, Japan, China, South America, India, Antarctica and Canada (Richter 1906; Oishi 1932; Sze 1933; Oishi & Yamasita 1936; Feruglio 1937; Gupta 1955; Shah & Singh 1964; Cantrill 1995; Stockey *et al.* 2006). Two of the species from India (*Hausmannia indica* Gupta and *Hausmannia crookshankii* Shah and Singh) are fragmentary and poorly preserved, and are difficult to compare with *H. sinensis* and other species of *Hausmannia*. Morphologically, *H. sinensis* resembles several species described from East Asia (table 1). *Hausmannia sinensis* is most closely comparable to *Hausmannia ussuriensis*, which was first described from the Lower Jurassic of Mongugay, East Siberia (Kryshtofovich 1923) based only on line drawings of two impression specimens. The Siberian species is smaller, with distinct undulate lamina margins. The original specimens of *H. ussuriensis* were poorly preserved in the figure and did not provide detailed information on the distribution of sori and sporangia, making further comparison with *H. sinensis* difficult. Specimens that are similar to *H. ussuriensis* in gross morphology were identified as *H. nariwaensis* from the Upper Triassic flora

in Nariwa, Japan (Oishi 1930, 1932). However, the relationship between *H. ussuriensis* and *H. nariwaensis* has long been debated. The Japanese authors regarded these as distinct species (Oishi 1930, 1932, 1940; Oishi & Yamasita 1936). Other authors considered that both of them are closely allied and agree with each other in morphology and venation pattern, and that these two species are conspecific, and used *H. ussuriensis* in preference (Sze 1933; Sze *et al.* 1963; Shen *et al.* 1976; Sun 1981, 1993).

It is noted that specimens described as *H. ussuriensis* or *H. nariwaensis* were often found from the Upper Triassic to Middle Jurassic in Siberia, Japan and China. In some localities, the impression materials are reported as abundant and bearing fertile leaves (Oishi 1932; Sun 1993). However, the detailed structures of fertile organs and *in situ* spores of these two species are still unknown. *Hausmannia dentata* was established based on both sterile and fertile specimens from the Rhaetic of Nariwa in Japan (Oishi 1930). It differs from *H. sinensis* in having a distinct, strongly sinuate-dentate frond margin. The circular sori were described as densely distributed on

Figure 4. Fertile organs of *H. sinensis* sp. nov., showing the sori and sporangia ((a,b) light microscopy photos; (c–f) SEM photos). (a,b) Details of [figure 3c](#), showing the shape of sori in each ultimate mesh. Each sorus consists of three to six sporangia. Scale bar, 0.6 mm. (c–e) Sporangia showing oblique annulus. Note that a part of sporangia wall is present in (e) attached to the sporangia. Scale bars: (c) 30 μ m, (d) 40 μ m and (e) 50 μ m. (f) A well-preserved sporangium showing the annuli of approximately 23 elongated cells, the stomial regions (in between two arrows) and the basal sporangia stalk. Scale bar, 52 μ m.

the lower surface of the lamina, but are larger in size (1 mm) and have more sporangia (6–12?) than the present *H. sinensis*. No other data have been provided on the sporangia of *H. dentata*.

Hausmannia sinensis described in this study is also comparable with *Hausmannia leeiana* from the Jurassic of China ([Sze 1933](#)) in the shape and margin of leaves. But the latter is larger in size, and has very pronounced veins and regular rectangular meshes; however, the secondary venation appears less regular, and the fertile specimen of *H. leeiana* is unknown ([table 1](#)). *Hausmannia emeiensis* Wu from the Upper Triassic in Sichuan, China is also similar to *H. sinensis*, but differs in having the same thick lateral veins and main veins ([Li et al. 1974](#)). The sori were reported to be on the lamina, but the detailed structure is not available.

Hausmannia sinensis also shows some similarities of frond morphology to two species of *Hausmannia* from northeastern China: *Hausmannia wanlongensis* from the Early Cretaceous of Heilongjiang ([Zheng & Zhang 1983](#)), and *Hausmannia shebudaiensis* from the Middle Jurassic in

Western Liaoning ([Zhang & Zheng 1987](#)). They resemble each other by having round or oval fronds with entire or undulate margins. However, fertile structures of *H. wanlongensis* and *H. shebudaiensis* are not preserved, with only limited information of the number of sori/sporangia in ultimate mesh ([table 1](#)). These fertile features are different from the sori/sporangia arrangement and distribution pattern of *H. sinensis* ([table 1](#)).

Well-preserved specimens of *Hausmannia morinii* were recently described from the Lower Cretaceous of Vancouver Island, Canada, based on coalified and permineralized fertile structures ([Stockey et al. 2006](#)). Like *H. sinensis*, *Hausmannia morinii* has fan-shaped lamina and very pronounced veins, but specimens are also wedge-shaped and with crenate margins and distinct paired teeth on the lamina. The sporangia of *H. morinii* are scattered between the veins, 8–12 (or possibly 13) per ultimate mesh (=areola) and do not form distinct sori, which differs from the Chinese specimens of *H. sinensis*. Furthermore, the spore morphology between these two species is quite distinct ([table 1](#)).

Figure 5. Annuli, sporangia walls and *in situ* spores of *H. sinensis* sp. nov. ((a,c,d), light microscopy photos; (b,e–h), SEM photos). (a) Light microscopy view of a part of the annulus. Scale bar, 20 μ m. (b) Sporangium wall showing the course surface. Scale bar, 20 μ m. (c–e) Spore mass containing several spores with baculate or subverrucate sculptures of exine. Scale bars: (c,d) 12.5 μ m, (e) 20 μ m. (f) Detailed view of a spore showing the sculpture of spore exine and a fold. Scale bar, 5 μ m. (g–h) Proximal view of spores with trilete marks and baculate sculptures. Scale bar, 5 μ m.

In addition, *H. sinensis* shows some similarities to *H. buchii* (Andrae) Richter from the Jurassic to Cretaceous of Europe (Andrae 1853; Richter 1906; Seward 1911) in leaf morphology, but the latter has a dentate leaf margin with single and large tooth, and teeth are not paired. Further comparison of fertile structures between these two species is difficult because no details of sporangia and *in situ* spores are known for *H. buchii*.

(b) Comparison with *in situ* spores

Although many species of *Hausmannia* and other genera of fossil Dipteridaceae are described as being fertile with some details of sporangia per sorus, very few *in situ* spores have been described and illustrated (Balme 1995). To date, *in situ* spores of *Hausmannia* have been reported in only three species, excluding *H. sinensis* (table 1).

Spores of *Hausmannia forchammeri* Bartholin (1892) from the Jurassic of Bornholm of Denmark are triangular with convex sides and trilete mark, exine is smooth, diameter is approximately 30 μ m (Potonié 1967), generally comparable to the dispersed type *Cyathidites/Deltoidospora*. Balme (1995) states that the smaller spores are generally assigned to the broad category of dispersed spore *Cyathidites minor* Couper. Krassilov (1969) described spores of *H. leeiana* Sze from the Jurassic of Asiatic Russia as round-triangular with a smooth, thin, frequently folded sporoderm and a diameter range of 60–90 μ m, but these have not been illustrated. The spores of *H. sinensis* differ from those of these two species in spore size and ornamentation. Spores of *H. morinii* from the Early Cretaceous of Vancouver Island are trilete, tetrahedral-deltoid in shape with concave sides, 18–25 μ m in diameter

Figure 6. Reconstruction of the main morphological features and fertile organs of *H. sinensis* sp. nov. (a,b) Line drawing of two specimens showing the leaf, lamina form, petiole and venations. (a) PB21157, (b) PB21158. (c) Details of a lamina showing the dichotomous major vein and lateral veins, as well as tertiary and blind ending veins. (d) Details of a lamina showing the venation and the distribution of sori in each ultimate mesh. (e) A sporangium with annulus and sporangium stalk. (f) Part of a sporangium showing the annulus. (g,h) *In situ* spores with trilete marks and baculate to subverrucate sculptures.

with a relatively smooth exine, corresponding to the sporae dispersae species *Cibotiumspora jurienensis* (Balme) Filatoff. It is noted that *Cibotiumspora* are found from the Triassic to Jurassic in New Zealand and China (Zhang & Grant-Mackie 2001; Raine *et al.* 2005), and belong to the Dicksoniaceae (Zhang & Grant-Mackie 2001), but their occurrence in sporangia of *H. morinii* documents that spores of this type are also produced by dipterid ferns (Stockey *et al.* 2006).

Spores of *H. sinensis* are characterized by peculiar baculati to subverrucate sculptures. If found dispersed, they are comparable with two genera: *Apiculatisporites* Potonié and Kremp and *Baculatisporites* Thomas and Pflug. They are especially similar to *Apiculatisporites variabilis* Pocock and *Apiculatisporites lanjouwi* Jansonius; both are often found in the Triassic to Jurassic sediments. It is noted that *in situ* spores of *Baculatisporites* were once reported in fossil osmundaceous ferns, and *Apiculatisporites* type were recorded from filicopsida of *incertae sedis* affinity (Balme 1995). Our study indicates that such spores also occur in the Dipteridaceae.

Compared with other species of *Hausmannia*, the Chinese material *H. sinensis* shows a special, characteristic spore morphology, and differs from other species in having pronounced spore ornamentations. In addition, spores

of *H. sinensis* show differences from spores of other dipteridaceous taxa, such as *Dictyophyllum*, which has trilete spores with smooth exine and inter-radial thickenings (e.g. Guignard *et al.* in press); however, they show some similarities to spores of *Clathropteris*, another widely distributed dipteridaceous fern from the Mesozoic (for example, *Clathropteris meniscoides* Brongniart and *Clathropteris walkeri* Daugherty, which have trilete spores with baculate spore ornamentations similar to those of the dispersed type *Converrucosisporites*; Couper 1958; Ash 1969; Cornet & Traverse 1975; Litwin 1985).

(c) Comparison with living dipteridaceous spores

Traditionally, Dipteridaceae includes one genus, *Dipteris*, and is restricted to the Indo-Malayan region. The genus *Dipteris* was previously merged into the genus *Polypodium* on account of its sorus being naked and superficial (Bower 1926). However, Seward & Dale (1901) proposed that the genus *Dipteris* should be representative of the family Dipteridaceae. Morphologically, the leaf architecture of *Dipteris* is quite characteristic, arising at distant intervals along a creeping hairy rhizome. The fronds branch dichotomously with veins that branch at right angles to form a reticulate mesh. Sori are exindusiate and arranged

Table 1. The major differences of frond, sporangia and *in situ* spores of related *Hausmannia* species.

species	leaves and lamina	sori and sporangia	annulus	spore shape	spore size	dispersed spore type	horizons and locality	references
<i>H. sinensis</i> sp. nov.	lamina fan-shaped with almost entire margin	each ultimate mesh bears one to two circular exin-cusate sori, each sorus with three to six round to oval sporangia 3–4 to 14–16 (average 10) sporangia per sorus	developed and oblique, with stomial region present in proximal position	trilete, circular to oval, proximal and distal surfaces covered with baculate to subverrucate sculptures	20–30 µm (average 28 µm)	<i>Baculatisporis/ Apiculatisporites</i>	Middle Jurassic, Nei Mongol, China	this paper
<i>H. forchhammeri</i> Bartholin	lamina deeply dissected with teeth irregular in shape	3–4 to 14–16 (average 10) sporangia per sorus	—	triangular with convex sides and trilete mark, exine smooth	30 µm	<i>Cyathidites/ Deltoidospora</i>	Jurassic of Bornholm of Denmark	Bartholin (1892) and Potonié (1967)
<i>H. morinii</i> Stockey, Rothwell and Little	fan- and wedge-shaped with crenulate margin and distinct paired teeth of lamina	sorus indistinct; 8–12 per mesh, scattered, with short stalk	vertical, 8–10 cells	trilete, tetrahedral-deltoid, with concave sides and smooth exine	32 µm	<i>Cibotiumspora</i>	Lower Cretaceous, Vancouver, Canada	Stockey <i>et al.</i> (2006)
<i>H. buchii</i> (Andrae) Richter	leaf margin dentate, teeth single and large, tooth margin with concave, acute tips	—	—	—	—	—	Jurassic–Cretaceous, Europe	Andrae (1853), Richter (1906) and Seward (1911)
<i>H. ussuriensis</i> Kryshstofovich	fan shaped or circular, reniform, lamina, margin crenulate with round teeth	—	—	—	—	—	Jurassic of Siberia, Russia	Kryshstofovich (1923)
<i>H. narivaensis</i> Oishi	lamina reniform, margin mostly entire or undulate	—	—	—	—	—	Upper Triassic, Nariwa, Japan	Oishi (1930, 1932)
<i>H. dentata</i> Oishi	frond margin strongly sinuate to dentate	sori circular, 1 mm in diameter, 6–12 sporangia per sorus	—	—	—	—	Upper Triassic, Nariwa, Japan	Oishi (1932)

(Continued.)

Table 1. (Continued.)

species	leaves and lamina	sori and sporangia	annulus	spore shape	spore size	dispersed spore type	horizons and locality	references
<i>H. leeiana</i> Sze	frond large in size with very pronounced veins and regular rectangular meshes	—	—	—	—	—	Jurassic, China	Sze (1933)
<i>H. eneiensis</i> Wu	fan-shaped lamina	present but no details	—	—	—	—	Upper Triassic, Sichuan, China	Li <i>et al.</i> (1974)
<i>H. wanlongensis</i> Zheng and Zhang	frond with two equal leaves, round or oval with entire or undulate margin	one to four circular or oval sori per ultimate mesh	—	—	—	—	Early Cretaceous, Heilongjiang, China	Zheng & Zhang (1983)
<i>H. shebudaiensis</i> Zhang and Zhang	frond round or oval with undulate margin	approximately 10 sporangia per ultimate mesh	—	—	—	—	Middle Jurassic, Liaoning, China	Zhang & Zheng (1987)

on both sides of the midrib. The annulus of the sporangia is oblique.

Recent molecular and morphological investigations have suggested that, besides the genus *Dipteris*, the family Dipteridaceae may also include a sister taxon *Cheiropleuria* C. Presl, ascribed to the family Cheiropleuriaceae (Kramer 1990b; Kato *et al.* 2001; Smith *et al.* 2006; Schuettpelz & Pryer 2007). The spores of extant *Dipteris* are monolete, rather than trilete as in the fossil members. However, spores of *Cheiropleuria* are tetrahedral and trilete, ranging from 22 to 30 µm in diameter and may be even larger in some species (Tryon & Lugardon 1991; Kato *et al.* 2001). Spores of *H. sinensis* show differences from spores of both extant *Dipteris* and *Cheiropleuria* in having rather complicated spore ornamentation, as well as circular to oval spore morphology. In order to explore the systematic affinities between these spores, the ultrastructural investigation on the spore wall will be necessary, and may provide further evidence for understanding the spore diversity of the genus *Hausmannia* and other genera of the family Dipteridaceae.

Undoubtedly, our study on fertile organs and *in situ* spores of *H. sinensis* provides further evidence that *Hausmannia* has diverse *in situ* spore types and a variety of spore morphologies. It therefore offers an opportunity to make comparisons with the fossil and living records of the Dipteridaceae, and is thus helpful for exploring the diversity and evolution of this important leptosporangiate fern lineage through time.

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