

Re-investigations of the fossil fern *Xiajiajienia mirabila* (Dicksoniaceae) based on new material from the Lower Cretaceous of western Liaoning, China

Li Zhang ^{a, b, c}, Yongdong Wang ^{a, b, *}, Micha Ruhl ^c, Yanbin Zhu ^{b, d}, Haijun Li ^e

^a Center for Research and Education on Biological Evolution and Environments, School of Earth Sciences and Engineering, Nanjing University, Nanjing 210023, China

^b State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences (CAS), Nanjing 210008, China

^c Department of Geology, Trinity College Dublin, The University of Dublin, College Green, Dublin 2 D02PN40, Ireland

^d University of Chinese Academy of Sciences, Beijing 100049, China

^e Sanya Feitian Dinosaur Fossil Museum, Sanya, Hainan, 572000, China

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ABSTRACT

As one of the essential Mesozoic floristic elements, the family Dicksoniaceae experienced two flourishing periods, one in the Middle Jurassic and the other in the Early Cretaceous. Several fossil genera that yield cup-shaped or bivalvate indusia in sori have been considered members of this family. Among them, the genus *Xiajiajienia* Sun, Zheng et Mei 2001 presents unique characteristics with unlobed drepaniform sterile pinnules, marginal sori and bivalvate indusia. However, its systematical investigation was poorly documented due to the limit preservation of fossil specimens, which would compromise its taxonomic significance. Here, we report new fertile pinnae of *Xiajiajienia mirabila* from the Jianshangou Bed, Yixian Formation in western Liaoning, China. Based on the distinguishable characters of the newly-found specimen, a minor emendation of species diagnosis is proposed. A phylogenetic analysis was performed with a molecular scaffold, suggesting *Xiajiajienia* had a closer relationship with both modern and fossil *Dicksonia*. Previous research on the Yixian Formation's palaeoenvironment (Jehol biota) suggests that *X. mirabila* lived in a cool, temperate mid-latitude climate with seasonal variations, especially in a humid area near water. The genus was suggested to be endemic to the Jianshangou flora of the Jehol biota, along with other genera in Dicksoniaceae, which witnessed the second flourishing period of the family around the world back to the Early Cretaceous.

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1. Introduction

The tree fern family Dicksoniaceae belongs to the order Cyatheaales A.B. Franklin Leunis, containing three genera, of which *Calochlaena* (Maxon) M.D. Turner & R.A. White, has been recovered as a sister to a clade including *Dicksonia* L'Héritier, and *Lophosoria* C. Presl (Hasebe et al., 1995; Noben et al., 2018; PPG I, 2016; Smith et al., 2006). The family was considered to have a long fossil record extending into the Triassic and experienced two flourishing

periods, one in the Middle Jurassic and the other in the Early Cretaceous (Harris, 1961; Van Konijnenburg-Van Cittert, 1989; Tidwell and Ash, 1994; Collinson, 2002; Deng, 2002; Van Konijnenburg-Van Cittert, 2002; Noben et al., 2017; Noben et al., 2018; Li et al., 2020). In addition to fossil occurrences of the extant genus *Lophosoria* (Cantrill, 1998; Noben et al., 2017), several extinct genera have been ascribed to Dicksoniaceae including some with bivalvate indusia: *Dicksonia*, *Acanthopteris* Sze, *Onychiopsis* Yokoyama and *Xiajiajienia* Sun, Zheng et Mei, and some with cup-shape indusia: *Coniopteris* Brongniart, *Eboracia* Thomas, *Kylikopteris* Harris and *Gonatosorus* Raciborski (Harris, 1961; Van Konijnenburg-Van Cittert, 1989; Friis and Pedersen, 1990; Sun et al., 2001; Deng, 2002; Li et al., 2020; Li et al., 2022).

The genus *Xiajiajienia* Sun, Zheng et Mei was first reported from the Lower Cretaceous in western Liaoning, China (Sun et al., 2001),

* Corresponding author. State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences (CAS), Nanjing 210008, China.
E-mail address: ydwang@nigpas.ac.cn (Y. Wang).

originally described as a unique dicksoniaceous fern with 'Arctopteris'-like sterile pinnules and *Dicksonia*-like fertile sori (Sun et al., 2001). It has marginal-borne sori with bivalvate indusia in the fertile pinnule, consistent with the Dicksoniaceae diagnosis. Besides, it bears unlobed drepaniform sterile pinnules, which are readily distinguishable from other genera in Dicksoniaceae (Sun et al., 2001). However, there are very few reports of *Xiajiajienia* in the subsequent studies, and some specimens were reconsidered and assigned to a 'cycadophyte' genus, *Rehezamites* Pott, McLoughlin, Lindstrom, Wu et Friis (Pott et al., 2012). The sole report of *Xiajiajienia* from the Jianshangou flora in northeastern China lacked detailed descriptions of fertile pinnae, which might impede further understanding of its taxonomic significance. *Xiajiajienia* possesses unique characteristics among Dicksoniaceae; thus, further systematic investigations are needed with necessarily comprehensive discussions.

In this study, we report a newly collected specimen of *Xiajiajienia mirabila* Sun, Zheng et Mei (the impression and counterpart) from Jianshangou Bed, Lower Yixian Formation in western Liaoning, China. Based on the well-preserved fertile specimen, we provide a minor emendation of the specific diagnosis. A detailed comparison of *Xiajiajienia* with other potential genera in Dicksoniaceae was also reached. A phylogenetic analysis, constrained by a molecular scaffold, was performed, aiming further to discuss its classification and relationships with other dicksoniaceous ferns. Helped by the previous studies on paleoenvironment reconstructions of the Jianshangou Bed/the Yixian Formation, the living habit of *Xiajiajienia* was inferred.

2. Materials and methods

2.1. Geological setting

The Jianshangou Bed is a set of fossil-bearing sedimentary interlayers of the basal volcano-sedimentary deposits of the Yixian Formation in western Liaoning. It is rich in volcanic composition and consists of upper and lower grey-black shale, basal sandy conglomerate, top tuffaceous sandstone, middle massive silty mudstone and siltstone, as well as andesite, with a thickness of 28–95 m (Sun et al., 2001; Chen et al., 2005). The Yixian Formation is famous for bearing early birds, angiosperms, and feathered dinosaurs (Friis et al., 2004; Sun et al., 1998; Sun et al., 2001; Xu et al., 2003; Zhou, 2006a,b; Zhou and Wang, 2000). It also yields bivalves, gastropods, conchostracans, ostracods, shrimps, insects, fish, amphibians, primitive mammals, and other reptiles (Zhou et al., 2003; Chen et al., 2005; Zhou, 2006b, 2014; Pan et al., 2013). The weighted-mean age of the Jianshangou bed was suggested as $125.457 \pm 0.051/0.064/0.27$ Ma by the latest $^{206}\text{Pb}/^{238}\text{U}$ dating data (Chang et al., 2017; Zhong et al., 2021), indicating Barremian to Aptian age of the Early Cretaceous.

The fossil pinna specimens were collected from Member No.3 (the sandstone and shale Member) of the Jianshangou Bed in the Huangbanjigou-Jianshangou area, particularly in Beds No. 8 and No. 6 of the Huangbanjigou-West Hill of Jianshangou section (Sun et al., 2001).

2.2. Fossil and living materials

The fossil specimen was preserved as the impression with counterpart, and was collected from siltstone, Huangbanjigou-West Hill of Jianshangou Bed, with fine preservation of delicate structures of sterile and fertile pinnules, sori, and annuli. The previously reported *Xiajiajienia* fossil specimens deposited in the Palaeobotanical collection, Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGPAS), were also examined to

compare with the newly found fossils, including the sterile pinna specimen of *X. mirabila*, No. PB19025; the fertile pinna (fully), No. PB19032; and the additional specimens No. PB1026A, PB1028, PB1028A, and PB19030 (Sun et al., 2001). The newly collected specimens used in this study are housed in the palaeontology collection, at Sanya Feitian Dinosaur Fossil Museum, Hainan, China, with catalog numbers, SFDFM02001A and SFDFM02001B. Observation and photography were done with a Nikon HM stereomicroscope for details of morphological and fertile structures.

In order to obtain fossil *in situ* spores, we tried the lab process with the conventional methods for sporangium material, as reported by Wang et al. (1998) and Wang et al. (2015). However, due to the fossil preservation status, we did not acquire the *in situ* spores from these fertile sporangia. Fossil specimens did not show more characters under fluorescent light. Therefore, no further observations under LM and SEM were conducted.

The images of the fertile pinnules of modern *Dicksonia* material (*D. lanata*) were used to compare the morphological characters of fossil specimens and the living material. *D. lanata* is an endemic species found at higher elevations on the North Island, favouring damp areas near the tree lines and down to sea level on the South Island. The images were supported by Dr Lawrence Jensen, University of Auckland, New Zealand.

2.3. Phylogenetic analysis

Plant fossils often preserve limited morphological characters and can hardly offer molecular data, which makes it difficult for them to be involved in the phylogenetic analysis of extant species. To properly discuss the family-level classification of the genus *Xiajiajienia*, we performed phylogenetic analyses using a molecular scaffold (Springer et al., 2001), which was believed to be an efficient approach to deal with fossil taxa in phylogenetic reconstructions (Manos et al., 2007; Hermsen and Hendricks, 2008; Shi et al., 2014; Kay, 2015; Cui et al., 2019; Li et al., 2020).

The molecular scaffold, or the constraint backbone, established on molecular data of modern taxa, followed after PPG I (2016), in which the *Lygodium microphyllum* (Cavanilles) R. Brown (Lygodiaceae) was set as an outgroup and the species spanning from the families of Thyrsopteridaceae C. Presl, Dicksoniaceae M.R. Schomb, Dennstaedtiaceae Lotsy, and Lindsaeaceae C. Presl ex M.R. Schomb, were involved. The morphological character states for the Cyatheales and Polypodiales were adopted from Tryon and Tryon (1982), Tryon and Lugardon (1991), Lehtonen et al. (2010), Li et al. (2020), and Harris (1961) (Table S1–S2). Three fossil genera, including *Dicksonia* L'Héritier (2 spp.), *Xiajiajienia* (1 sp.), and *Coniopteris* Brongniart (3 spp.) were involved in the phylogenetic analysis (Harris, 1961; Sun et al., 2001). All the genera have characteristics of marginal borne sori with a cup-like or bivalvate indusium, and these features were deemed significant in the classifications of leptosporangiate ferns (Stewart and Rothwell, 1993; Deng and Chen, 2001; Taylor and Wilson, 2009). It is noted that the characteristics of vegetative organs were not included in the morphological matrix here because few fossil specimens were reported with preservation of leaf cuticles, stems, or appendages (hairs and scales).

The phylogenetic analysis here was performed on 22 species (16 extant species and 6 fossil species). Characters for cladistic analyses were based mainly on the matrix of Li et al. (2020), in which 14 characters of reproductive organs were coded (Table S1–S2) (Lehtonen et al., 2010; Li et al., 2020; PPG I, 2016; Smith et al., 2006). We used parsimony to build trees. Tree space was searched using the following options implemented in PAUP* (Swofford, 2002): Branch and Bound or heuristic searches with 1000 random addition replicates, tree bisection-reconnection (TBR)

branch swapping, MulTrees, and the steepest descent options. Starting trees were obtained via stepwise addition, addition sequence: random, and the number of replicates was set as 10. The molecular scaffold was set using the constraint backbone option of PAUP*.

3. Results

3.1. Systematics

Order: Cyatheaales A.B. Franklin Leunig, 1877

Family: Dicksoniaceae M.R. Schomb, 1849

Genus *Xiajiajienia* Sun, Zheng et Mei, 2001

Species: *Xiajiajienia mirabila* Sun, Zheng et Mei, 2001 emend. Zhang, Wang et Ruhl

Figs. 2–6

Selected references:

1992 *Coniopteris* sp. Sun et Zhao, p. 527, pl. 28. fig. 8;

1999 *Coniopteris burejensis*, Wu, p.12, pl. 3. fig. 5.

Studied material:

Sterile pinna, PB19025 (Fig. 2C, G) (Sun et al., 2001);

Fertile pinna (fully), PB19032 (Fig. 2D; Fig. 3D) (Sun et al., 2001);

Fertile pinna (partly), SFDFM02001A (Fig. 2A, E; Fig. 3A, C, F-H; Fig. 4A-F), SFDFM 02001B (Fig. 2B, F; Fig. 3B, E; Fig. 4G-I);

Additional material: PB1026A, PB1028, PB1028A, and PB19030 (Sun et al., 2001), pl. 39, fig. 3-4, 6-10).

Repository for the new specimen. Palaeontological collection, Sanya Feitian Dinosaur Fossil Museum (SFDFM), Hainan, China.

Type locality. Huangbanjigou, Beipiao City, Liaoning Province, China (Fig. 1).

Horizon. Jianshangou Beds, Lower Yixian Formation, the Lower Cretaceous (~125.5 Ma) (Chang et al., 2017; Zhong et al., 2021).

Emended species diagnosis (modified from Sun et al. (2001), emended parts are marked in *Italics*). Lamina large, pinnate, broadly linear to lanceolate. Sterile pinnules *unlobed*, drepaniform to long tongue-shaped, strongly decurrent. Venation of *sphenopterid type*, veins distinct, free, *bi- or three-furcate*, the third fork of the veins occurring in the lower branch of each vein cluster, and *stably anadromous* in both sterile and fertile pinnules. Frond partly or fully fertile; fertile pinnules only found in the upper part of the partly fertile pinna. Pinnules on the two sides of equal size. Fertile segments slightly contracted and reduced. Sori with bivalvate indusium, mixed development. Mature sori singly at the apex of the fertile pinnule occupying one vein; immature sori on an unlobed fertile pinnule occupying 2–3 veins. Placenta elevated. Annulus developed, likely oblique. Spores trilete.

Description. Lamina is large, pinnate, broadly linear to lanceolate, about 12 cm long by 4–5 cm wide in a typical leaf (Sun et al., 2001). In the sterile pinnae (9 cm × 3 cm), pinnules are drepaniform to long tongue-shaped, unlobed, usually 14.1 ± 1.3 mm long and 3.5 ± 0.5 mm wide (measurement times $N_m = 10$) (Fig. 2C, G); margins are slightly wavy in the upper part of the pinnules and recurved to a bow shape in the lower part (Fig. 2C, G); apex is blunt or obtusely acute, base is contracted and decurrent bearing on the pinna rachis. Venation is sphenopterid type (free, without distinct mid-vein) and stably anadromous in both sterile and fertile pinnules. Fertile pinnules can be subdivided into



Fig. 1. Fossil locality of *Xiajiajienia* in western Liaoning of China.

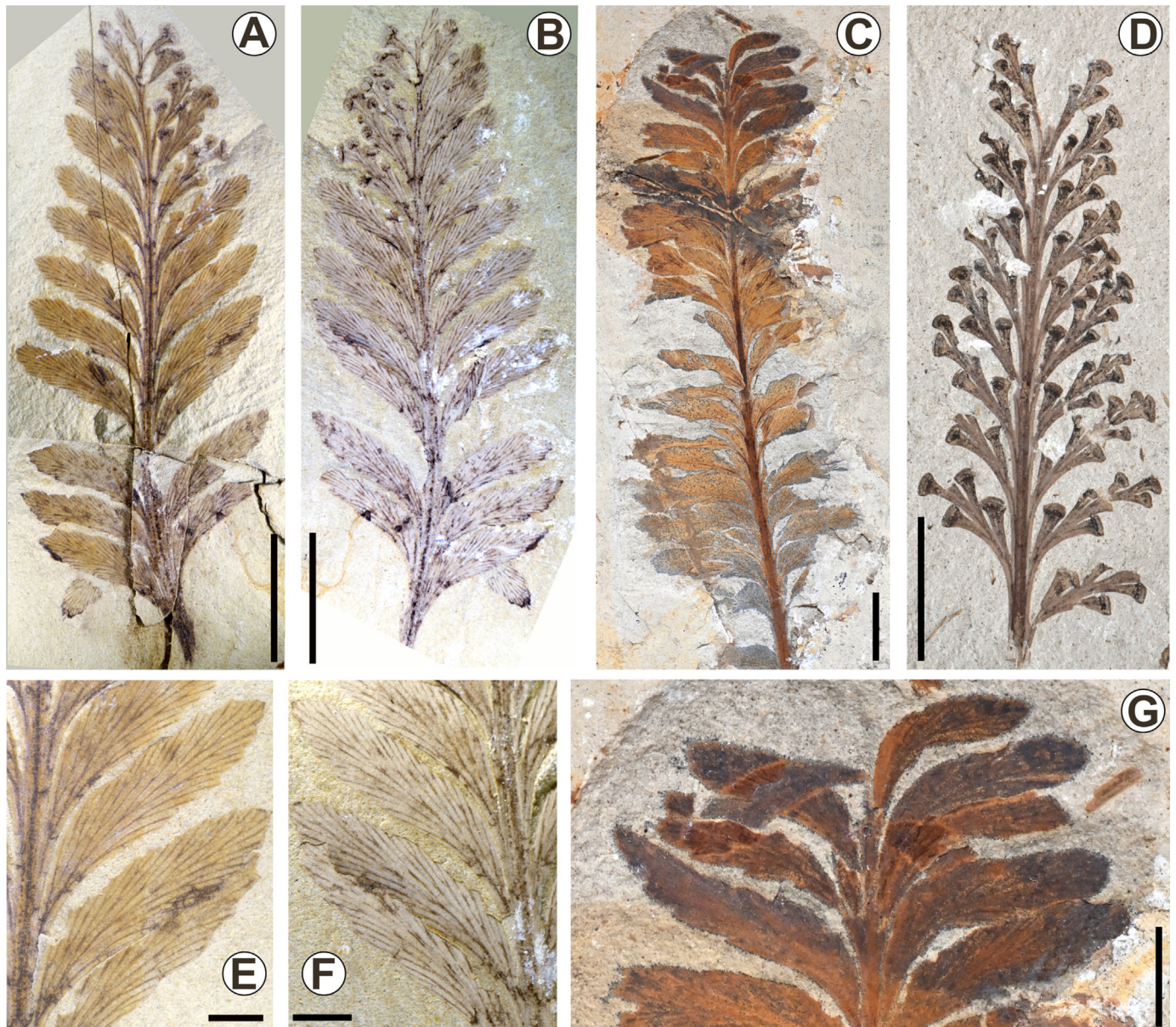


Fig. 2. Morphology of *Xiajiajiania mirabila* Sun, Zheng et Mei. A (No. SFDFM02001A) and B (No. SFDFM 02001B), the new fossil material of *X. mirabila* reported in this paper, showing a (partly) fertile pinna comprised of sterile pinnules and fertile pinnules, the fertile part only found in the top of the pinna, scale bars = 1 cm; C, the previously reported sterile pinna of *X. mirabila*, No. PB19025 (Sun et al., 2001), scale bar = 1 cm; D, the previously reported fertile pinna (fully) of *X. mirabila*, No. PB19032 (Sun et al., 2001), scale bar = 1 cm; E (No. SFDFM02001A) and F (No. SFDFM 02001B), the close-up of pinnules of *X. mirabila* from A and B, showing the long tongue-shaped pinnules with sphenopterid type venation, scale bars = 2 mm; G, the close-up of pinnules from C, the specimen No. PB19025 (Sun et al., 2001), scale bar = 5 mm.

partly fertile form (5 cm × 2 cm) (Fig. 2A-B) or fully fertile form (4 cm × 1.5 cm) (Fig. 2D). In the partly fertile pinnae, fertile pinnules are found in the upper part of the lamina (Fig. 2A-B). Fertile pinnules from both types of fertile pinna are the same size, usually 8.4 ± 1.1 mm long and 2.4 ± 0.6 mm wide ($N_m = 18$) (Fig. 2A-B, D). Sterile pinnules from partly fertile pinna were smaller than those from sterile pinna, about 10.7 ± 0.7 mm long and 2.7 ± 0.2 mm wide ($N_m = 15$) (Fig. 2A-B, E-F). Fertile segments are contracted and reduced to a petiole-like form (Fig. 2A-B, D; Fig. 3A-H; Fig. 4; Fig. 5; Fig. 6B, D-E). Sori are marginally borne, with distinct bivalvate indusia (Fig. 3C-H; Fig. 4A-B, D-E; Fig. 5; Fig. 6B). Sori are shown mixed development, including immature ones (usually found in the upper part of the pinnae) (Fig. 3C-H) and mature ones (Fig. 3E-F). Immature sori bore on the margin of the unlobed

fertile pinnule (Fig. 3C) occupying 2–3 veins (Fig. 3C-D). With the development of pinna, an odd number (usually 3, 5, 7) of mature sorus can be found singly at one fertile pinnule (Fig. 2A-B, D; Fig. 3A-B, Fig. 6D-E). The single vein joined the slightly elevated receptacle (Fig. 3E-F; Fig. 4G-H; Fig. 5B-D). Sporangia are unknown, while the annulus is developed, likely oblique (Fig. 4C, F, I, Fig. 6C). Spores are trilete, amb triangular, about $35 \mu\text{m} \times 30 \mu\text{m}$ (Fig. 6C) (Sun et al., 2001).

3.2. Topology

The cladistic analysis here was performed on 22 species (16 extant species and 6 fossil species), which was constrained by a

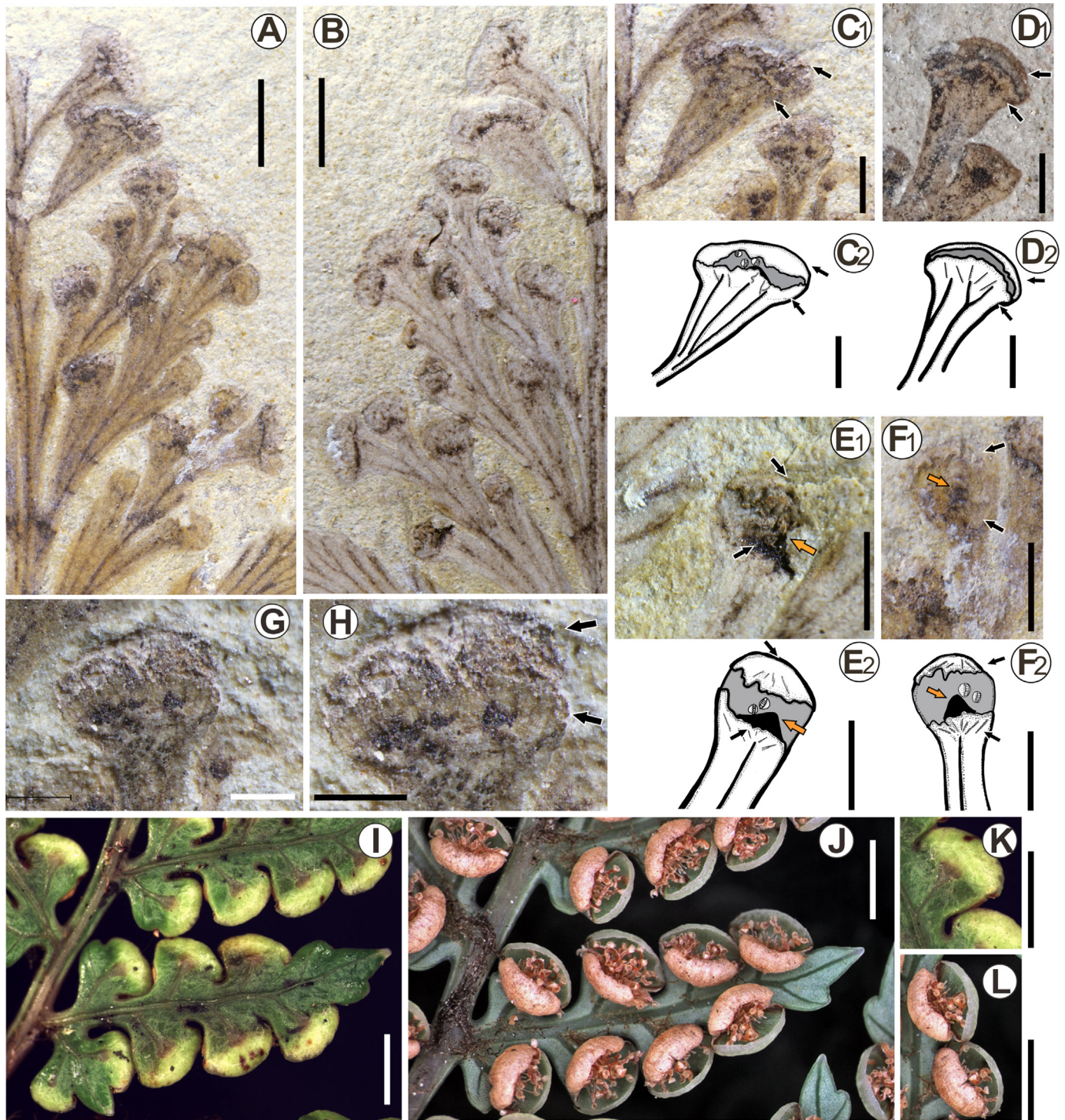


Fig. 3. Fertile pinnules and sori comparisons between *X. mirabila* and modern *Dicksonia*. A (No. SFDFM02001A) and B (No. SFDFM02001B), the fertile pinnules of fossil materials of *X. mirabila* reported in this paper, scale bars = 2 mm; C (No. SFDFM02001A), D (No. PB19032 (Sun et al., 2001)), E (No. SFDFM02001B) and F (No. SFDFM02001A), the morphology sori (C₁–F₁) and their sketches (C₂–F₂), the black arrows indicating the bivalvate indusium, the orange arrows marking the elevated receptacle in the sori, scale bars = 1 mm; G–H (No. SFDFM02001A), the close-up of a single sorus, the bivalvate indusia indicated by the black arrows, scale bars = 500 µm; I–L, the fertile pinnules of modern *Dicksonia* material (*D. lanata*), as a comparison to show the similarly contracted and reduced fertile segments and bivalvate indusia in the sori, scale bars = 2 mm. Dr Lawrence Jensen, University of Auckland, provided the modern *Dicksonia* images.

molecular phylogenetic backbone from the extant taxa (PPG I, 2016) (Fig. 7A). Overall, 14 morphological characters of reproductive organs were coded (Table S1–S2) (Lehtonen et al., 2010; Li et al., 2020; PPG I, 2016; Smith et al., 2006).

The majority-rule consensus (tree length = 46, consistency index [CI] = 0.48, retention index [RI] = 0.70, Fig. 7B) was rooted by

the outgroup *Lygodium microphyllum* (Cavanilles) R. Brown. Two main clades were observed in the results. One is the clade comprising Thyrsopteridaceae and Dicksoniaceae with acceptable-level support (bootstrap value = 71) (Soltis and Soltis, 2003), and the fossil *Dicksonia* and *Xiajiajienia* were found within the clade. The other main clade contained the families of Dennstaedtiaceae

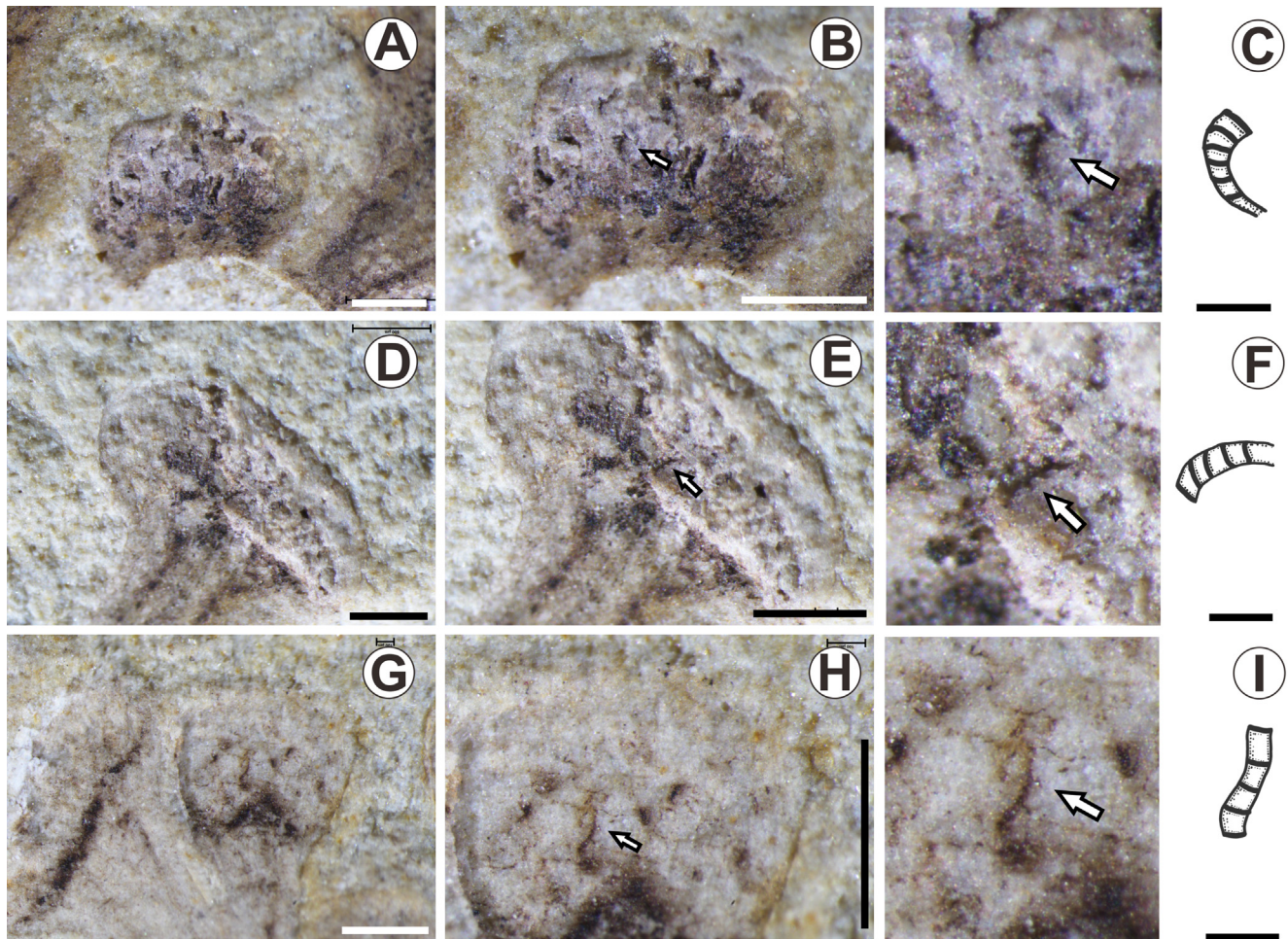


Fig. 4. Sori of *X. mirabila*. The close-up of the fertile sori of *X. mirabila*, each row as a group in different magnifications, A-F (No. SFDFM02001A); G-I (No. SFDFM02001B); the white arrows and sketches in C, F and I indicating the visibly developed annulus of the sorus, likely oblique. Scale bars in A-B, D-E, G-H are 500 μ m, and in C, F and I are 100 μ m.

Marginal Sori

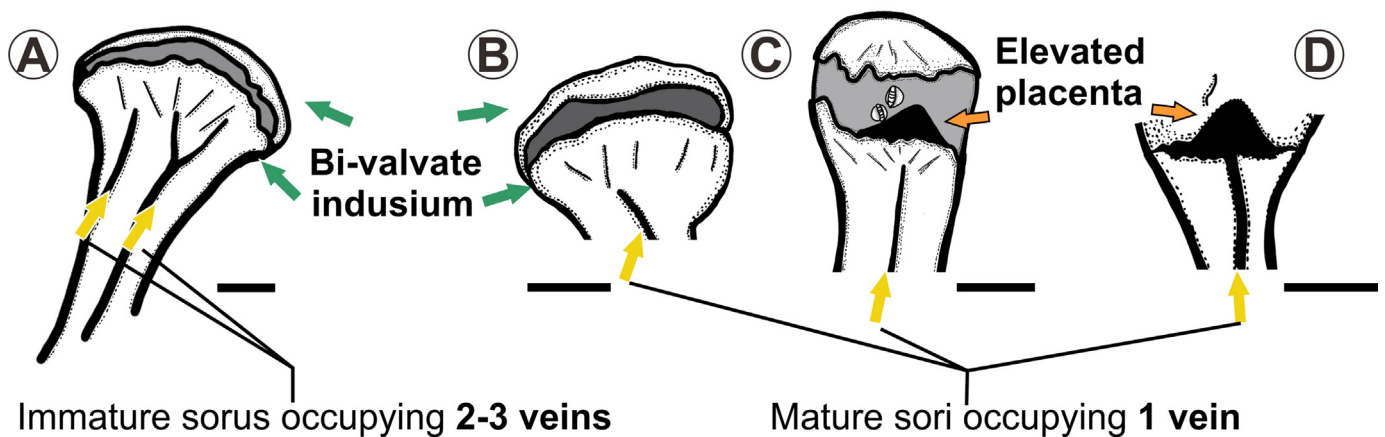


Fig. 5. Sori sketches of *X. mirabila*, showing characters of marginal borne sori; bivalvate indusium (green arrows), elevated placenta (orange arrows), and the variant number of veins occupied by the sori (yellow arrows). A. was based on specimen No. PB19032 (Fig. 3D₁); B. on specimen No. SFDFM02001A (Fig. 3G and H); C. on specimen No. SFDFM02001B (Fig. 3E₁); D. on specimen No. SFDFM02001B (Fig. 4G, H, and I). All scale bars = 500 μ m.

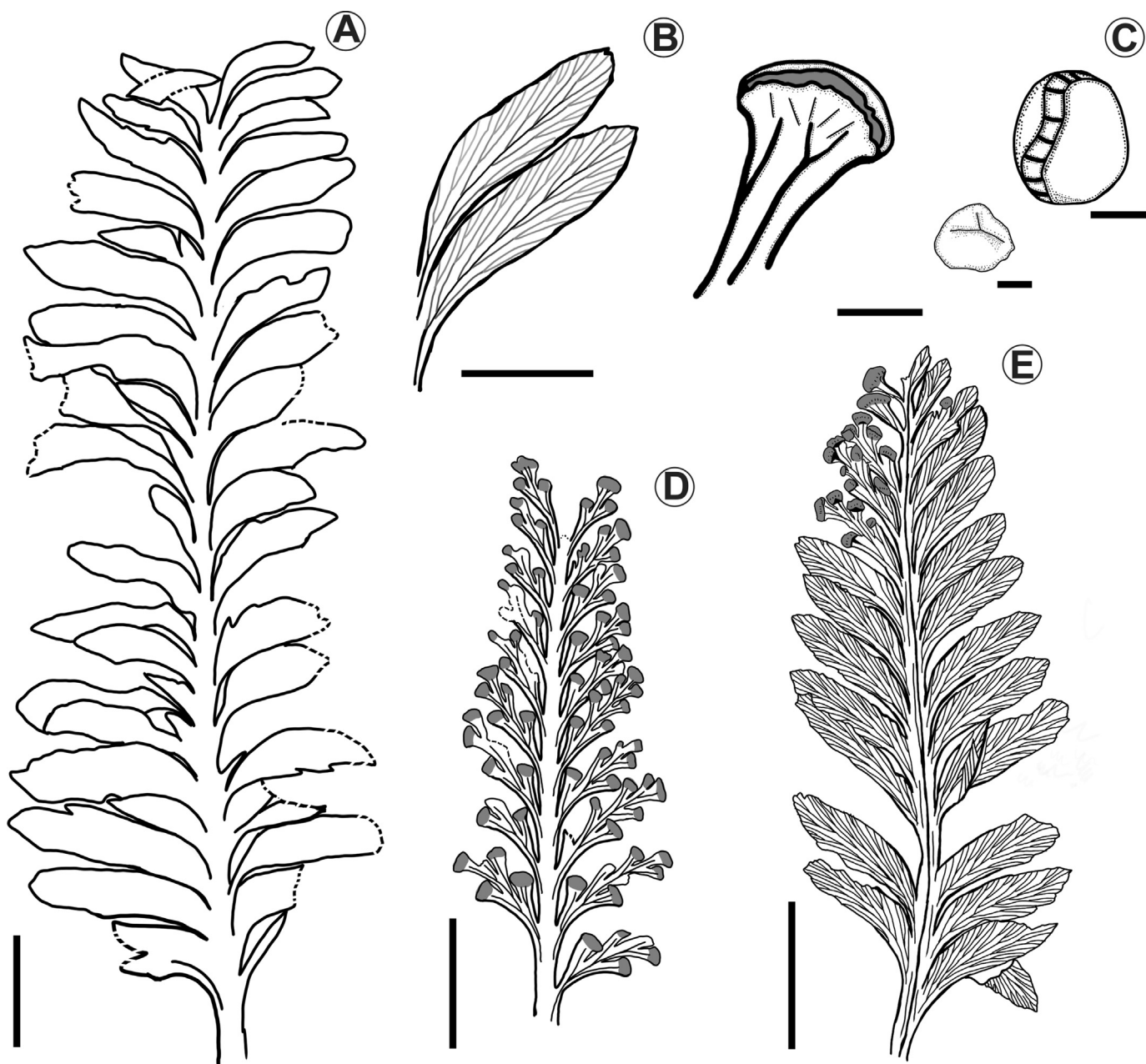


Fig. 6. Sketch reconstructions of *X. mirabila*. A, the sterile pinna, No. PB19025 (Sun et al., 2001), scale bar = 1 cm; B, the sterile pinnules (present article) scale bar = 5 mm; C, sorus, scale bar = 1 mm, spore (Sun et al., 2001), scale bar = 20 μ m, and possible sporangium (inferred from Fig. 4), scale bar = 100 μ m; D, fertile pinna (fully), No. PB19032 (Sun et al., 2001), scale bar = 1 cm; E, fertile pinna (partly) (this study, No. SDFM02001A-B).

and Lindsaeaceae with a lower support level (Bootstrap value = 57) (Fig. 7B).

4. Discussions

4.1. Comparisons of *Xiajiajienia* with potential fossil genera

Marginal-borne sori is an important identifying characteristic of the family Dicksoniaceae Bower (Harris, 1961). However, due to the convergence (Pigg et al., 2021), the characteristic of marginal sori is not only confined to the Dicksoniaceae but common in the families of Hymenophyllaceae Link and Dennstaedtiaceae Lotsy (Korall et al., 2007; Korall et al., 2006; Schölch, 2000; Smith et al., 2006). Hymenophyllaceae are characterised by their membranaceous laminae (Herrera et al., 2017). It can be easily differentiated from

Dicksoniaceae because none of the laminae in species of Dicksoniaceae (including *Xiajiajienia*) is membranaceous (Harris, 1961; Wolf et al., 1999; Herrera et al., 2017). In Dennstaedtiaceae, only the genus *Dennstaedtia* possesses cup-like indusium (Pigg et al., 2021), which was considered similar to the fossil genus *Coniopteris* in terms of the reproductive structures (Li et al., 2020). However, in contrast to Dennstaedtiaceae (the first appearance ~ 100 Ma) (Serbet and Rothwell, 2003), Dicksoniaceae had a long fossil record extending into the Triassic (Van Konijnenburg-Van Cittert, 1989; Friis and Pedersen, 1990; Deng, 2002; Van Konijnenburg-Van Cittert, 2002). *Xiajiajienia* is collected from Jianshangou Beds, Lower Yixian Formation, the Lower Cretaceous (~125.5 Ma) (Chang et al., 2017; Zhong et al., 2021), which is earlier than the first known appearance of *Dennstaedtia* records in the Paleogene (~60 Ma) (Pigg et al., 2021; Serbet and Rothwell, 2003). Besides, *Xiajiajienia* can be

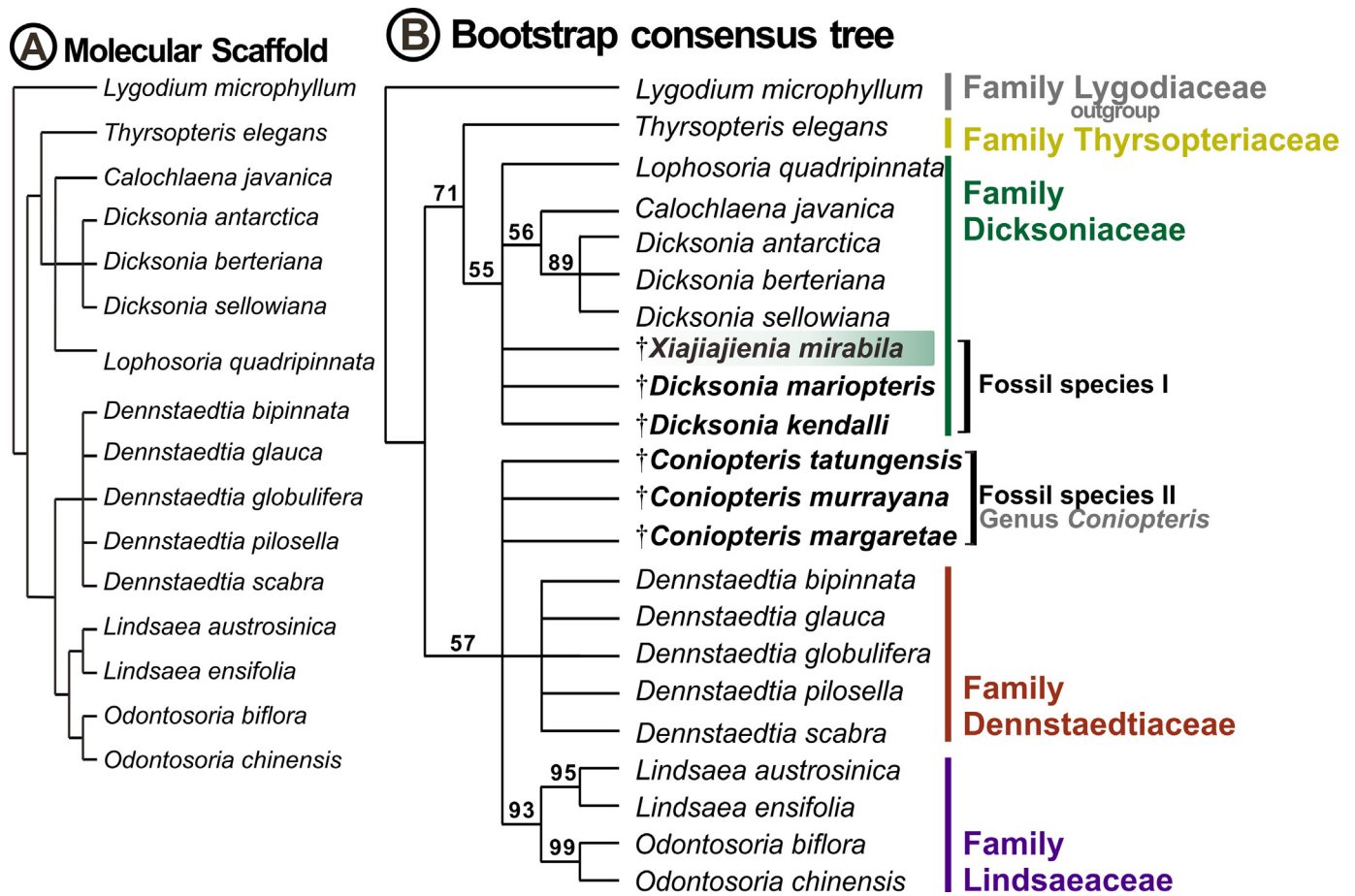


Fig. 7. Majority-rule consensus tree of *Xiaiajienia* and its related groups by a cladistic analysis of reproductive structure characters. A, the molecular backbone, adopted from PPG I (2016); B, the Majority-rule consensus tree, numbers on branches of the consensus tree represent bootstrap values based on 1000 replications (only >50 are given). Fossil genera were marked with '†'.

distinguished from the genus *Dennstaedtia* by their unlobed drepaniform sterile pinnules and dimorphic fertile segments with reduced laminae (Pigg et al., 2021; Taylor and Wilson, 2009). Considering these differences, families of Hymenophyllaceae and Dennstaedtiaceae can be excluded.

Xiaiajienia can be placed in Dicksoniaceae with confidence on the basis of the reproductive structures. According to the original diagnosis, except for some fossil genera with cup-shape indusia, such as *Coniopteris*, *Eboracia*, *Kylikopteris* and *Gonatosorus* (Table 1) (Harris, 1961; Sun et al., 2001; Deng, 2002; Li et al., 2020; Yuan et al., 2020), the fossil specimens that had been assigned to Dicksoniaceae have the typical characteristics of marginal position of the sori with bivalvate indusia (Harris, 1961; Deng and Chen, 2001; Li et al., 2020), such as fossil records of *Dicksonia* (Harris, 1961; Krassilov, 1978; Sun et al., 2001), *Acanthopteris* Sze (Yang et al., 1994; Deng, 2002), *Onychiopsis* Yokoyama (Friis and Pedersen, 1990; Blanco-Moreno and Prestianni, 2021), and *Xiaiajienia* Sun, Zheng et Mei (Sun et al., 2001). The fossil specimens reported here, accordingly, can be placed in the family Dicksoniaceae with confidence as they possess: 1) marginal sori (Fig. 2A–B, D; Fig. 3); 2) bivalvate indusia (Figs. 3–5); 3) elevated receptacle (Fig. 3E–F; Fig. 4G–H; Fig. 5C–D); and 4) developed, likely oblique annulus (Fig. 4).

In terms of generic assignment of the fossil specimens, there are a few Mesozoic dicksoniaceous candidates: *Acanthopteris*, *Dicksonia*, *Lophosoria*, *Onychiopsis* and *Xiaiajienia* (Table 1) (Harris, 1961; Friis and Pedersen, 1990; Yang et al., 1994; Cantrill, 1998; Sun et al., 2001). *Lophosoria* and *Onychiopsis* can be easily ruled out by their unique

characteristics in the fertile organs. The former genus is distinguished by its 'naked' (indusia-lacking) sori (Cantrill, 1998) and the latter by its linear and 'fully covered' (indusia-overlapping) sori (Friis and Pedersen, 1990), which are observably different from the fossil specimens here. The genus *Acanthopteris*, although it has marginal sori and bivalvate (or transition type) indusia (Deng and Chen, 2001), still can be differentiated from the fossil specimens by its toothed indusia and the presence of the intercalated pinnules in fronds (Deng and Chen, 2001; Sun et al., 2001).

Only two genera, *Dicksonia* and *Xiaiajienia*, cover almost all the fertile characteristics of the fossil specimens reported here. Both genera have marginal borne sori with bivalvate indusia and produce rounded triangular spores in the fertile pinnule (Harris, 1961; Deng and Chen, 2001; Sun et al., 2001). Only one vein was shown through every sorus in *Dicksonia*. However, we found up to 2–3 veins occupied by some single immature sori (Fig. 3C–D; Fig. 4D; Fig. 5A), and the character was only presented in *Xiaiajienia*. Besides, the two genera have disparate forms of sterile pinnules. Pinnules are usually sphenopterid in *Dicksonia* (Harris, 1961; Deng and Chen, 2001; Sun et al., 2001). Specifically, they are round, ovate, lobed or digitate. By contrast, pinnules of *Xiaiajienia* are drepaniform and unlobed, with slightly wavy margins and sphenopteris-type venation. This form can be found in both fertile (Fig. 2A–B, E–F) and sterile pinnae (Fig. 2C–G). Therefore, instead of *Dicksonia*, we assigned the newly found fossil specimens to *Xiaiajienia mirabila*, based on their having 1) mature sorus occupied one vein, and immature sorus occupied 2–3 veins; and 2) distinctively unlobed drepaniform sterile

Table 1
Comparisons of *Xiajiajienia* with typical fossil species in Dicksoniaceae on sterile and fertile character; grey cells showing the specific discrepancies of fossil species from the *Xiajiajienia*; the unknown characters of the genera were marked with ‘—’.

Fossil species in Dicksoniaceae	Sterile pinnules form	Sori location	Placenta shape	Indusium shape	Annulus	Spores type	Vein number of sori occupied	Reference	Epoach	Location
<i>Xiajiajienia mirabila</i> Sun, Zheng et Mei emended	unlobed, drepaniform, with sphenopterid venation	marginal	protuberant	bi-valvate	oblique (?)	trilete	1 or >1	This study & Sun et al., 2001	Early Cretaceous	China, Asia
<i>Dicksonia mariopteris</i> Wilson et Bates	sphenopterid, ovate, with rounded lobes	marginal	protuberant	bi-valvate	oblique (?)	trilete	1	Harris, 1963	Middle Jurassic	UK, Europe
<i>Onychiopsis psilotoides</i> (Stockes et Webb) Ward	narrow, varied by positions	marginal	—	bi-valvate & fully covered	oblique	trilete	—	Friis and Pedersen, 1990	Early Cretaceous	Denmark, Europe
<i>Eboracia lobifolia</i> (Phillips) Thomas	pecopterid	marginal	elongated	transition type (cup-like to bi-valvate)	—	trilete	1	Harris, 1961	Early–Middle Jurassic	UK, Europe
<i>Kylikipteris arguta</i> (Lindley & Hutton) Harris	pecopterid	marginal	elongated	transition type (cup-like to bi-valvate)	—	trilete	1	Harris, 1961	Early–Middle Jurassic	UK, Europe
<i>Lophosoria cupulatus</i> Cantrill	unlobed, circular to elliptical	abaxial leaf surface	—	without indusium	oblique	trilete, cingulate with a raised foveolate pad in proximal contact faces	—	Cantrill, 1998	Early Cretaceous	Antarctica
<i>Coniopteris murrayana</i> (Brongniart) Brongniart	sphenopterid, lobed	marginal	flat or nearly so	cup-shaped	vertical	trilete	1	Harris, 1961	Early–Middle Jurassic	Europe & Asian
<i>Coniopteris tatungensis</i> Sze	sphenopterid, lobed, linear to linear-lanceolate	marginal	flat or nearly so	cup-shaped	vertical	trilete	1	(Ma et al., 1998)	Late–Middle Jurassic	China, Asia
<i>Acanthopteris gothani</i> Sze	pecopterid	marginal	flat or nearly so	bi-valvate & toothed	vertical	trilete	1	Deng and Chen, 2001	Late Jurassic–Early Cretaceous	China, Asia

pinnules. The newly found specimens can be regarded as new material and representative of the partly fertile pinna, together with previously found fully fertile pinna and sterile pinna, presenting the three types of laminae of *Xiaijiajienia mirabila* (Fig. 6).

4.2. Phylogenetic-analysis implications

Dicksoniaceae flourished in the Mesozoic, as shown by various fossil records (Harris, 1961; Sze et al., 1963). The genus *Xiaijiajienia* has been assigned to Dicksoniaceae, but its relationships with other genera in the family have never been discussed since its establishment. A phylogenetic analysis with a molecular scaffold of extant taxa thus has been performed here (Fig. 7A) (Springer et al., 2001) to better understand the systematic positions of *Xiaijiajienia* in Dicksoniaceae.

From the parsimonious tree, three *Coniopteris* species were clustered with Dennstaedtiaceae + Lindsaeaceae (Fig. 7B). It generally agreed with the previous study (Li et al., 2020), in which the genus was re-considered closer to Polypodiales because they have vertical and incomplete annulus of the sporangia. However, the results were shown here with a minor-moderate support rate (Bootstrap value = 57), which may be caused by the missing data in the fossil samples, indicating the need for further classification research of this genus on more fossil records, as subsequent studies suggested (Pigg et al., 2021; Zhang et al., 2019).

In contrast, the genus *Xiaijiajienia* had been successfully recovered within the Thyrsopteriaceae + Dicksoniaceae clade, clustered with two fossil records of *Dicksonia* with an effective support rate (Bootstrap value = 71) (Fig. 7B). The cladistic results indicated that, in terms of fertile organs' characteristics, *Xiaijiajienia* had a closer relationship with Dicksoniaceae. Besides the dicksonid sori, the genus also possesses unlobed & drepaniform pinnules and sphenopterid-type venation, which supported the establishment of *Xiaijiajienia*.

Further discussions on where the genus *Xiaijiajienia* should be placed in the evolutionary path of Dicksoniaceae along the Mesozoic to the present day may not be easily concluded. Dicksoniaceae has a long fossil record. The earliest report can be traced back to the Late Triassic (Van Konijnenburg-Van Cittert, 2002). The family also presented twice flourishing periods in the Middle Jurassic and the Early Cretaceous (Harris, 1961; Van Konijnenburg-Van Cittert, 1989; Deng, 2002; Noben et al., 2017; Noben et al., 2018). The evidence indicates that fossil elements of Dicksoniaceae were widely distributed, and the genus-level diversity had probably arisen simultaneously with the breakups of the supercontinents during the Mesozoic (Noben et al., 2017). If so, its evolutionary path seems more complicated. The genus *Xiaijiajienia* (China, Asia), given its sole fossil locality so far, was probably the endemic species to Jianshangou flora, along with *Acanthopteris* (China, Asia), *Lophosoria* (Antarctica), and *Onychiopsis* (Europe) witnessed the second flourishing period of the Dicksoniaceae in the Early Cretaceous world.

4.3. The living habits of *Xiaijiajienia*

The Early Cretaceous Jehol Biota, renowned for its exceptionally well-preserved volcanic-influenced ecosystem, was buried in lacustrine and occasionally fluvial sediments (Zhou et al., 2003). Most important scientific issues that have been attracting the attention of scientists from all over the world, including the origin of birds, the evolution of feathers and flight, the early diversification of angiosperms, and the timing of the placental mammal radiation, have been studied and answered based on fossil collections there (Amiot et al., 2011; Chang et al., 2017; Chen et al., 2005; Pan et al., 2013; Zhou, 2006b, 2014; Zhou et al., 2003). As

an important aspect of understanding the palaeo-world of the Jehol Biota, the paleoclimates have been studied with more evidence. It, of course, can help us understand the living habits of *Xiaijiajienia mirabila*.

Our fossil specimen was collected from the Jianshangou Bed, the lower part of the Yixian Formation, in northeastern Liaoning Province, China (Chang et al., 2017; Zhong et al., 2021). The Jianshangou flora yields various types of fossil plants: besides xerophilous plants such as Ephedraceae, Cherolepidiaceae and Bennettitales, the Bed also yields Ginkgoales, which indicate a generally temperate climate condition, and hydrophilic plants such as Bryophytes, Lycopods and Sphenopsids (Sun et al., 2001; Liu et al., 2008). From the oxygen isotope data, the Yixian Formation was reconstructed under a cool temperate mid-latitude climate with an average air temperature of $10 \pm 4^\circ\text{C}$ (Amiot et al., 2011). These studies suggest that *X. mirabila* was living in a cool, temperate mid-latitude climate with seasonal variations and regionally in a water-near humid area. The humidity probably played an important role in its lifetime under a temperate climate. It's worth mentioning that this estimated habit is similar to that of some species of modern *Dicksonia*, which not only have pantropical distributions but also can adapt to the temperate climate in maritime places such as Ireland, Britain and some temperate forests around the globe (Large and Braggins, 2004; Noben et al., 2018).

5. Conclusions

Two pieces of well-preserved fertile pinnae fossils (the impression and counterpart) were found in the Lower Cretaceous of the Jianshangou Bed, Yixian Formation, western Liaoning, China. They presented a partly fertile pinna showing combined characters of unlobed drepaniform sterile pinnules and marginal borne sori with bivalvate indusia and had been assigned to *Xiaijiajienia mirabila* (Dicksoniaceae). The new fossil material can be regarded as representative of the partly fertile pinna, along with previously reported records presenting three forms of fronds of the species. The phylogenetic results suggested that *Xiaijiajienia* is closer to Dicksoniaceae, where the genus was clustered with the fossil records of *Dicksonia* rather than the other dicksonid-related ferns. The habit of *X. mirabila* can be inferred as preferring a temperate mid-latitude climate with seasonal variations, emphasising the importance of humidity to the species under a temperate climate. As one of the unique endemic species to Jianshangou flora, the genus *Xiaijiajienia*, along with *Acanthopteris* (China, Asia), *Lophosoria* (Antarctica), and *Onychiopsis* (Europe), witnessed the second flourishing of the Dicksoniaceae in the Early Cretaceous world.

Data availability

All data are available in the Supplementary materials

Acknowledgements

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References

- Amiot, R., Wang, X., Zhou, Z., Wang, X., Buffetaut, E., Lécuyer, C., Ding, Z., Fluteau, F., Hibino, T., Kusuhashi, N., Mo, J., Suteethorn, V., Wang, Y., Xu, X., Zhang, F., 2011. Oxygen isotopes of East Asian dinosaurs reveal exceptionally cold Early Cretaceous climates. *Proceedings of the National Academy of Sciences of the United States of America* 108, 5179–5183.
- Blanco-Moreno, C., Prestianni, C., 2021. Taxonomic revision and palaeoecological interpretation of the plant assemblage of Bernissart (Barremian, Belgium). *Cretaceous Research* 124, 104814.
- Cantrill, D.J., 1998. Early Cretaceous fern foliage from President Head, Snow Island, Antarctica. *Alcheringa: An Australasian Journal of Palaeontology* 22, 241–258.
- Chang, S., Gao, K., Zhou, C., Jourdan, F., 2017. New chronostratigraphic constraints on the Yixian Formation with implications for the Jehol Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology* 487, 399–406.
- Chen, P., Wang, Q., Zhang, H., Cao, M., Li, W., Wu, S., Shen, Y., 2005. Jianshangou Bed of the Yixian Formation in West Liaoning, China. *Science in China, Series D: Earth Sciences* 48, 298–312.
- Collinson, M.E., 2002. The ecology of Cainozoic ferns. *Review of Palaeobotany and Palynology* 119, 51–68.
- Cui, Y.-M., Wang, W., Ferguson, D.K., Yang, J., Wang, Y.-F., 2019. Fossil evidence reveals how plants responded to cooling during the Cretaceous–Paleogene transition. *BMC Plant Biology* 19, 402.
- Deng, S., 2002. Ecology of the Early Cretaceous ferns of Northeast China. *Review of Palaeobotany and Palynology* 119, 93–112.
- Deng, S., Chen, F., 2001. The Early Cretaceous Filicopsida from Northeast China. Geological Publishing House, Beijing.
- Friis, E.M., Pedersen, K.R., 1990. Structure of the Lower Cretaceous fern *Onychiopsis psilotoides* from Bornholm, Denmark. *Review of Palaeobotany and Palynology* 66, 47–63.
- Friis, E.M., Pedersen, K.R., Crane, P.R., 2004. Araceae from the Early Cretaceous of Portugal: evidence on the emergence of monocotyledons. *Proceedings of the National Academy of Sciences* 101, 16565–16570.
- Harris, T.M., 1961. The Yorkshire Jurassic Flora. Thallophyta–Pteridophyta. British Museum, London.
- Hasebe, M., Wolf, P.G., Pryer, K.M., Ueda, K., Ito, M., Sano, R., Gastony, G.J., Yokoyama, J., Manhart, J.R., Murakami, N., Crane, E.H., Haufler, C.H., Hauk, W.D., 1995. Fern phylogeny based on rbcL nucleotide sequences. *American Fern Journal* 85, 134–181.
- Hermesen, E.J., Hendricks, J.R., 2008. W(h)ither fossils? Studying morphological character evolution in the age of molecular sequences. *Annals of the Missouri Botanical Garden* 95, 72–100, 129.
- Herrera, F., Moran, R.C., Shi, G., Ichinnorov, N., Takahashi, M., Crane, P.R., Herendeen, P.S., 2017. An exquisitely preserved filmy fern (Hymenophyllaceae) from the Early Cretaceous of Mongolia. *American Journal of Botany* 104, 1370–1381.
- Kay, R.F., 2015. Biogeography in deep time – what do phylogenetics, geology, and paleoclimate tell us about early platyrrhine evolution? *Molecular Phylogenetics and Evolution* 82, 358–374.
- Korall, P., Pryer, K.M., Metzgar, J.S., Schneider, H., Conant, D.S., 2006. Tree ferns: monophyletic groups and their relationships as revealed by four protein-coding plastid loci. *Molecular Phylogenetics and Evolution* 39, 830–845.
- Korall, P., Conant, D.S., Metzgar, J.S., Schneider, H., Pryer, K.M., 2007. A molecular phylogeny of scaly tree ferns (Cyatheaaceae). *American Journal of Botany* 94, 873–886.
- Krassilov, V.A., 1978. Mesozoic lycopods and ferns from the Bureja Basin. *Palaeontographica Abteilung B Palaeophytologie* 166 (1), 16–29.
- Large, M.F., Braggins, J.E., 2004. Tree Ferns. CSIRO Publishing, Clayton, Victoria.
- Lehtonen, S., Tuomisto, H., Rouhan, G., Christenhusz, M.J., 2010. Phylogenetics and classification of the pantropical fern family Lindsaeaceae. *Botanical Journal of the Linnean Society* 163, 305–359.
- Li, C., Miao, X., Zhang, L., Ma, J., Hao, J., 2020. Re-evaluation of the systematic position of the Jurassic–Early Cretaceous fern genus *Coniopteris*. *Cretaceous Research* 105, 104136.
- Li, F., Tian, N., Wu, Z., Jiang, Z., Tan, X., 2022. New Middle Jurassic record of fern genus *Eboracia* (Dicksoniaceae, Filicales) and its spatio-temporal distribution in China. *Palaeoworld* 32, 104–115.
- Liu, H., Ferguson, D.K., Hueber, F.M., Li, C., Wang, Y., 2008. Taxonomy and systematics of *Ephedrites chenierae* and *Allophedra xingxuei* (Ephedraceae). *Taxon* 57, 577–582.
- Ma, Q., Wang, Y., Chen, Y., Li, C., 1998. Studies on *Coniopteris tatungensis* of Jurassic from western Hills of Beijing. *Journal of Systematics and Evolution* 36, 173.
- Manos, P.S., Soltis, P.S., Soltis, D.E., Manchester, S.R., Oh, S.-H., Bell, C.D., Dilcher, D.L., Stone, D.E., 2007. Phylogeny of extant and fossil Juglandaceae inferred from the integration of molecular and morphological data sets. *Systematic Biology* 56, 412–430.
- Noben, S., Kessler, M., Quandt, D., Weigand, A., Wicke, S., Krug, M., Lehnert, M., 2017. Biogeography of the Gondwanan tree fern family Dicksoniaceae—a tale of vicariance, dispersal and extinction. *Journal of Biogeography* 44, 2648–2659.
- Noben, S., Kessler, M., Weigand, A., Tejedor, A., Duque, W.D.R., Gallego, L.F.G., Lehnert, M., 2018. A Taxonomic and biogeographic reappraisal of the genus *Dicksonia* (Dicksoniaceae) in the Neotropics. *Systematic Botany* 43, 839–857, 819.
- Pan, Y., Sha, J., Zhou, Z., Fürsich, F.T., 2013. The Jehol Biota: definition and distribution of exceptionally preserved relicts of a continental Early Cretaceous ecosystem. *Cretaceous Research* 44, 30–38.
- Pigg, K.B., DeVore, M.L., Greenwood, D.R., Sundue, M.A., Schwartzburd, P., Basinger, J.F., 2021. Fossil Dennstaedtiaceae and Hymenophyllaceae from the Early Eocene of the Pacific Northwest. *International Journal of Plant Sciences* 182, 793–807.
- Pott, C., McLoughlin, S., Lindström, A., Shunqing, W., Friis, E.M., 2012. *Baikalophyllum lobatum* and *Rehezamites anisobolus*: two seed plants with “Cycadophyte” foliage from the Early Cretaceous of Eastern Asia. *International Journal of Plant Sciences* 173, 192–208.
- PPG I, 2016. A community-derived classification for extant lycophytes and ferns. *Journal of Systematics and Evolution* 54, 563–603.
- Schölch, A., 2000. Relations between submarginal and marginal sori in ferns I. The sori of selected Hypolepidaceae and Dennstaedtiaceae. *Plant Systematics and Evolution* 220, 161–183.
- Serbet, R., Rothwell, G.W., 2003. Anatomically preserved ferns from the Late Cretaceous of Western North America: Dennstaedtiaceae. *International Journal of Plant Sciences* 164, 1041–1051.
- Shi, G., Leslie, A.B., Herendeen, P.S., Ichinnorov, N., Takahashi, M., Knopf, P., Crane, P.R., 2014. Whole-plant reconstruction and phylogenetic relationships of *Elatides zhoui* sp. nov. (Cupressaceae) from the Early Cretaceous of Mongolia. In: Michael, T.D. (Ed.), *International Journal of Plant Sciences* 175, 911–930.
- Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G., 2006. A classification for extant ferns. *Taxon* 55, 705–731.
- Soltis, P.S., Soltis, D.E., 2003. Applying the bootstrap in phylogeny reconstruction. *Statistical Science* 256–267.
- Springer, M.S., Teeling, E.C., Madsen, O., Stanhope, M.J., de Jong, W.W., 2001. Integrated fossil and molecular data reconstruct bat echolocation. *Proceedings of the National Academy of Sciences* 98, 6241–6246.
- Stewart, W.N., Rothwell, G.W., 1993. *Paleobotany and the Evolution of Plants*, second ed. Cambridge University Press, Cambridge.
- Sun, G., Dilcher David, L., Zheng, S., Zhou, Z., 1998. In search of the first flower: A Jurassic Angiosperm, *Archaeofructus*, from Northeast China. *Science* 282, 1692–1695.
- Sun, G., Zheng, S., Dilcher, D., Wang, Y., Mei, S., 2001. Early Angiosperms and Their Associated Plants from Western Liaoning, China. Shanghai Scientific and Technological Education Publishing House, Shanghai, China.
- Swofford, D.L., 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b10. Sinauer Associates, Massachusetts.
- Sze, H.C., Li, X.X., Li, P.J., 1963. Chinese Fossil Plants: Mesozoic Plant in China. Science Press, Beijing.
- Taylor, P.D., Wilson, M.A., 2009. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews* 62, 1–103.
- Tidwell, W.D., Ash, S.R., 1994. A review of selected Triassic to Early Cretaceous ferns. *Journal of Plant Research* 107, 417–442.
- Tryon, A.F., Lugardon, B., 1991. Spores of the Pteridophyta: Surface, Wall Structure, and Diversity based on Electron Microscope Studies. Springer-Verlag, New York.
- Tryon, R.M., Tryon, A.F., 1982. Ferns and Allied Plants: with Special Reference to Tropical America. Springer Science & Business Media, New York.
- Van Konijnenburg-Van Cittert, J.H.A., 1989. Dicksoniaceae spores in situ from the Jurassic of Yorkshire, England. *Review of Palaeobotany and Palynology* 61, 273–301.
- Van Konijnenburg-Van Cittert, J.H.A., 2002. Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. *Review of Palaeobotany and Palynology* 119, 113–124.
- Wang, Y., Jiang, D., Yang, H., Feng, S., 1998. Middle Jurassic Spore-pollen Assemblages from Turpan-Shanshan Area, Xinjiang. *Journal of Integrative Plant Biology* 40, 969.
- Wang, Y., Li, L., Guignard, G., Dilcher, D.L., Xie, X., Tian, N., Zhou, N., Wang, Y., 2015. Fertile structures with in situ spores of a dipterid fern from the Triassic in southern China. *Journal of Plant Research* 128, 445–457.
- Wolf, P.G., Sipes, S.D., White, M.R., Martinez, M.L., Pryer, K.M., Smith, A.R., Ueda, K., 1999. Phylogenetic relationships of the enigmatic fern families Hymenophyllopsidaceae and Lophosoriaceae: evidence from rbcL nucleotide sequences. *Plant Systematics and Evolution* 219, 263–270.
- Xu, X., Zhou, Z., Wang, X., Kuang, X., Zhang, F., Du, X., 2003. Four-winged dinosaurs from China. *Nature* 421, 335–340.
- Yang, G., Chen, F., Huang, Q., 1994. Palaeobotany. Geology Press, Beijing.
- Yuan, X.-C., Xiong, C.-H., Sun, F.-K., Wang, Z.-X., Mao, T., Li, Y.-J., Liu, C.-H., Sun, M.-X., Dong, J.-L., Sun, B.-N., 2020. The geological significance of a new species of *Coniopteris* from the Middle Jurassic of northwestern China. *Historical Biology* 32, 267–280.
- Zhang, Y., Liu, B., Liang, F., 2019. A new species of *Coniopteris moguqiensis* sp. nov. from the Middle Jurassic Wanbao Formation in Eastern Inner Mongolia, China. *Acta Geologica Sinica - English Edition* 93, 1317–1324.

- Zhong, Y., Huyskens, M.H., Yin, Q., Wang, Y., Ma, Q., Xu, Y., 2021. High-precision geochronological constraints on the duration of 'Dinosaur Pompeii' and the Yixian Formation. *National Science Review* 8, nwab063.
- Zhou, Z., 2006a. Adaptive radiation of the Jehol Biota and its evolutionary ecological background. In: Rong, J., Fang, Z., Zhou, Z., Zhan, R., Wang, X., Yuan, X. (Eds.), *Originations, Radiations and Biodiversity Changes—Evidence from the Chinese Fossil Record*. Science Press, Beijing, pp. 705–732, 943–945.
- Zhou, Z., 2006b. Evolutionary radiation of the Jehol Biota: chronological and ecological perspectives. *Geological Journal* 41, 377–393.
- Zhou, Z., 2014. The Jehol Biota, an Early Cretaceous terrestrial Lagerstätte: new discoveries and implications. *National Science Review* 1, 543–559.

- Zhou, Z., Wang, X., 2000. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, Northeast China. *Vertebrata Palasiatica* 38, 111–127.
- Zhou, Z., Barrett, P.M., Hilton, J., 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421, 807–814.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2023.105543>.