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A new *Ginkgo* from the Lower Cretaceous of Liaoning, Northeast China and its evolutionary implications

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ABSTRACT

A new species of *Ginkgo* L., *G. pediculata* sp. nov., is described from the Lower Cretaceous of Liaoning Province, Northeast China, on the basis of a well-preserved ovule-bearing organ. The cuticles of the integument and peduncle are generally similar to those of the lamina and petiole of the associated *Ginkgoites manchurica* (Yabe et Ôishi) Cao, which is among the most widely distributed *Ginkgo*-like leaves in the Lower Cretaceous of Northeast China. The new species is close to the Jurassic *Ginkgo yimaensis* Zhou et Zhang and clearly distinguished from the Paleogene species *Ginkgo cranei* Zhou et al. and the extant *Ginkgo biloba*. Although the coeval *Ginkgo apodes* Zheng et Zhou and *G. neimengensis* Xu et al. from Northeast China bear more ovules, they both have no pedicel when matured as the living species. The associated *Ginkgoites*-type leaves morphologically also resemble those of the Jurassic species. Therefore, *Ginkgo pediculata* sp. nov. appears to be closely related to the Jurassic species and is the latest representative of the group with primitive type ovulate organs and vegetative leaves so far known of *Ginkgo*. Since there co-exist two different types of ginkgoes, one with primitive characters (*Ginkgo pediculata*) and the other such as *Ginkgo apodes* and *G. neimengensis* which resemble the extent species *G. biloba*, the Lower Cretaceous is a critical time in the morphological evolution of the genus *Ginkgo*, roughly corresponding to the major global floristic transformation marked by the rapid decline of gymnosperms and drastic rise of flowering plants.

1. Introduction

Although *Ginkgo*-like leaves are prominent elements in many Mesozoic floras, associated reproductive organs are extremely rare (Harris et al., 1974). Well-preserved ovule-bearing organs had not been recorded until the discovery of *Ginkgo yimaensis* Zhou et Zhang from the Middle Jurassic of Central China late in the last century (Zhou and Zhang, 1989). In recent years, well-preserved ovule-bearing organs of *Ginkgo* associated with *Ginkgo*-like leaves have been reported from the Middle Jurassic of Sweden (Yang et al., 2008) and Uzbekistan (Nosova, 2012, 2017), the Lower Cretaceous Yixian Formation and Xiaoming'anbei Formation of western Liaoning (Zhou and Zheng, 2003; Zheng and Zhou, 2004; Deng et al., 2004) and the Huolinhe Formation of Inner Mongolia (Xu et al., 2017), Northeast China. All these discoveries considerably advance our knowledge of the morphological diversity and evolutionary trends of the genus *Ginkgo* in the Mesozoic.

So far, there are two morphological groups within the genus *Ginkgo*, despite of their general resemblance to *G. biloba* L. One is represented by the Jurassic species *G. yimaensis*, characterized by the "primitive" type of ovulate organs and deeply divided vegetative leaves; the other is typified by *G. biloba*, with "modern" type ovulate organs and nearly entire leaves (Zhou, 2009; Zhou et al., 2020). The former group prevails in the Middle Jurassic of Eurasia with a number of species, while the latter group is recorded since the Paleogene (Crane et al., 1990; Zhou et al., 2012).

In the Cretaceous, there are few *Ginkgo* ovulate organs (Zhou and Zheng, 2003; Zheng and Zhou, 2004; Xu et al., 2017) and we know still little about the morphological transformation process of the genus from the Jurassic to the Paleogene. *Ginkgo apodes* Zheng et Zhou and *G. neimengensis* Xu et al. from Northeast China have no pedicel when matured as the living species, but bear more ovules and associated vegetative leaves are more or less divided. In order to further explore the morphological diversity and possible evolutionary pattern among

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ginkgos in the Mesozoic we here present a detailed study of the Lower Cretaceous *Ginkgo* ovulate organs and associated *Ginkgo*-like leaves *Ginkgoites* fossils from the Tiefa Basin, northern Liaoning, which had only been briefly reported before (Deng et al., 2004).

2. Stratigraphy, material and method

The studied specimens were collected from the Xiaoming'anbei Formation of the Tiefa Basin located at the northern part of Liaoning Province, Northeast China (Fig. 1). The Cretaceous strata in the Tiefa Basin are composed of the volcanic rock unit, i.e. the Datai Formation at the base and the successively overlying coal-bearing formations, the Beijiagou Formation and the Xiaoming'anbei Formation (Fig. 2). The Xiaoming'anbei Formation was referred to the Neocomian-Aptian based on the fossil plant assemblage, and was correlated with the Fuxin Formation of western Liaoning and roughly with the Chengzihe Formation and the Muling Formation of Jixi Basin, Heilongjiang Province and other Lower Cretaceous coal-bearing formations in northeastern China (Zheng and Zhang, 1982; Zhang and Xiong, 1983; Chen et al., 1988; Deng, 1995; Deng et al., 1997). The lower part of the Chengzihe Formation is about the Valanginian–Hauterivianin age based on marine dinoflagellates (He and Sun, 2000). Recent studies, however, show that the Fuxin Formation, the Chengzihe Formation and the Muling Formation are mainly the Aptian, although the lower parts may include lower Barremian deposits (Sha, 2007; Sha et al., 2003; Yang, 2003; Yang et al., 2007).

The flora from the Xiaoming'anbei Formation is dominated by ferns, conifers and Ginkgoales, and composed of more than 80 species in 40 genera (Chen et al., 1988; Deng, 1992; Deng and Chen, 2001). The ovule-bearing organ studied in the present paper was found associated with leaves of *Ginkgoites manchurica* (Yabe et Ôishi) Cao (1992) formerly referred as *Ginkgo manchurica* (Yabe et Ôishi) Meng et Chen, one of the most common species in the Lower Cretaceous floras of Northeast China (Chen et al., 1988).

The ovule-bearing organ and associated leaves are compressions with well-preserved cuticles. They were first photographed using digital camera, and then small pieces of coaly films were treated with hydrofluoric acid for 24 h. Cuticles of integument, nucellus, megaspore membrane and leaf were obtained by macerating with Schulze's solution, followed by dilute ammonia or sodium potassium hydroxide. The cuticles were examined and photographed under a Nikon light microscope, and a JSM-6300 scanning electronic microscope after being fixed to the stubs and sputter coated with gold.

All specimens, slides, and SEM stubs studied in the present paper are housed in Research Institute of Petroleum Exploration and Development (Beijing).

3. Systematic description

3.1. Ovulate organ

Ginkgoales
Ginkgoaceae
Ginkgo L., 1771
Ginkgo pediculata sp. nov. (Plate I, 1–2; Plate II, 4–8; Plate III; Plate IV, 1–3)
Synonym:
2004. *Ginkgo* sp.: Deng et al., p. 1775; figs. 1a, b.
Holotype: TDQ95-324
Etymology: Specific name "*pediculata*" indicates the ovulate organ having distinct pedicels when mature.
Type locality: Tiefa, Liaoning Province, China
Stratigraphical horizon: Xiaoming'anbei Formation
Age: Early Cretaceous

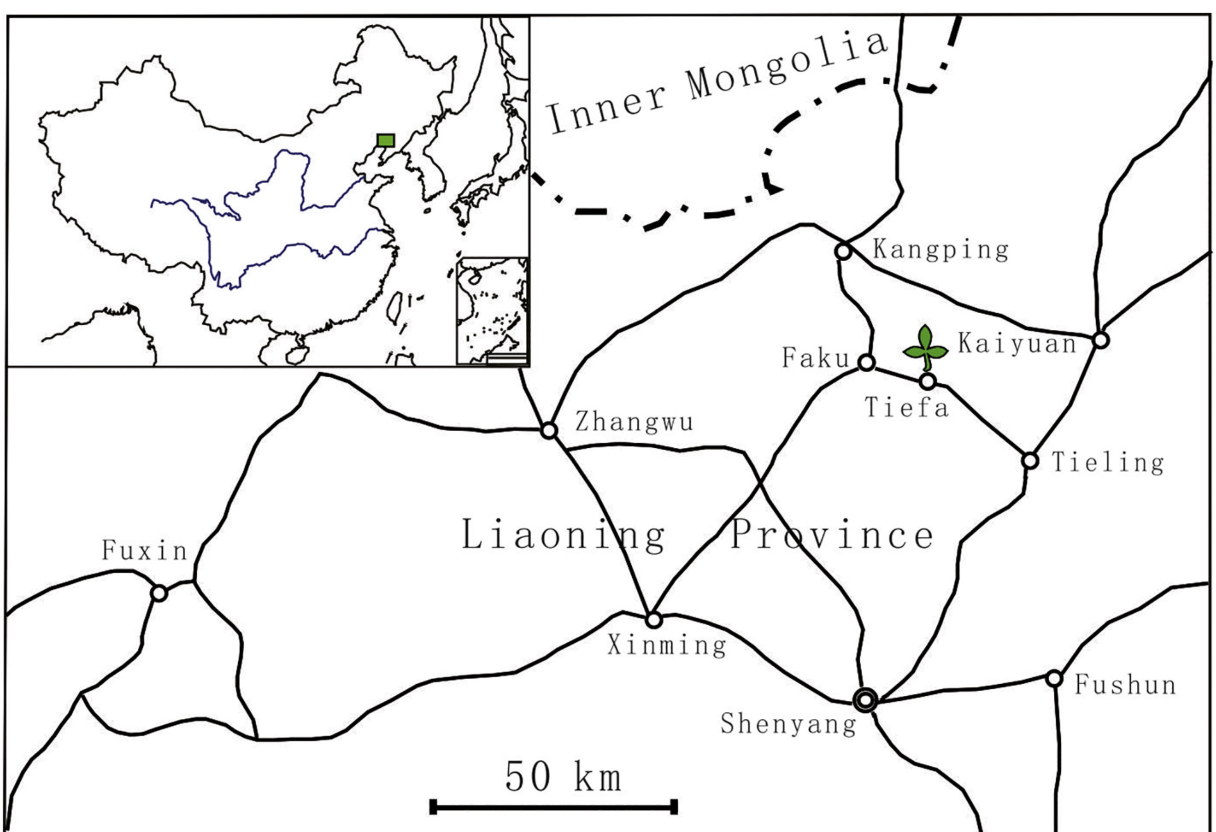

Fig. 1. Sketching map showing fossil locality.

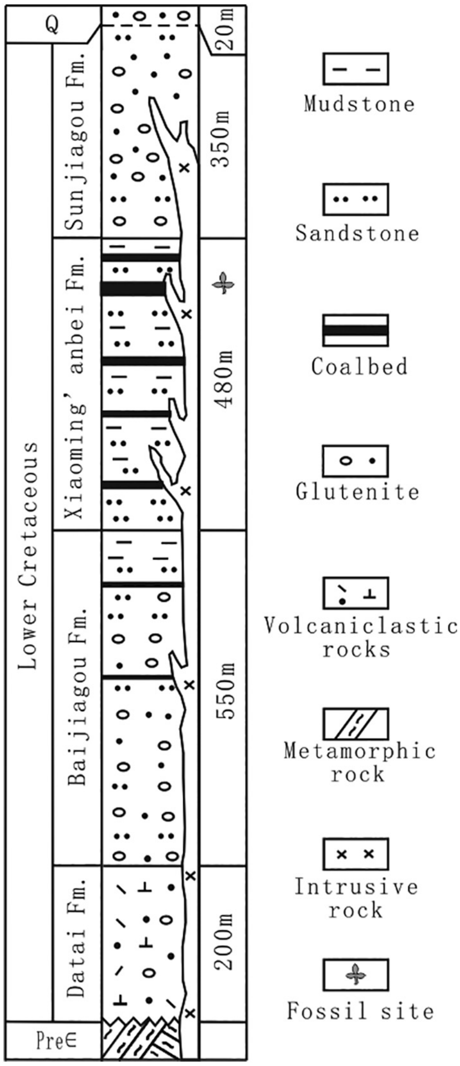

Fig. 2. Lithological column section of the Tiefa Basin.

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Diagnosis: Ovule-bearing organ consisting of a peduncle furcating into 4 pedicels and ovules borne in a shallow cup-shaped collar on the pedicel. Ovules 3–5 in number, ovate, with an obtusely acute or acute to mucronate apex and a broad base. Mature ovules (seeds)oval in shape. Outer cuticle of integument thick with few stomata. Cuticle of megasporangium (nucellus) thin, with elongate or irregular-shaped epidermal cells. Megaspore membrane rather thick, composed of an extremely thin base layer and a relatively thick and network-structured upper layer.

Description

General morphology: The ovulate organ (Plate I, 1) consists of a peduncle, pedicels, collars and ovules. The peduncle is about 43 mm long and 1.5–2.2 mm wide, furcating into 4 pedicels (Plate I, 2). The pedicels are up to 6.5 mm long and 1.8–2.5 mm wide with fine, irregular and longitudinal lines on the surface; the angles between the adjacent pedicels are around 55°. The two middle pedicels are about 2.5 mm wide, each with one ovule (seed), while the two lateral pedicels are about 2.0 mm wide with either a small ovule (aborted or immature seed, middle left of Plate I, 2) or bifurcating again with no ovule preserved (middle right of Plate I, 2) .

Ovules: Ovules are borne singly at the apex of pedicels, in a shallow cup-shaped collar. The two large ovules (seeds) are similar to each other, being broadly ovate or nearly rounded in shape with an obtusely acute distal end and a mucronate apex,14 mm long and 13.5 mm wide. The sarcotesta forms the margin up to about 2–3 mm thick, the sclerotesta is about 10 mm long and 9 mm wide (Plate I, 2). The collar is shallow, about 7 mm wide and 2 mm high. The small immature ovule is elliptical, with a wide rounded basal end and an acute or obtuse apex, about 7 mm long and 6 mm wide.

Cuticle of integument: Only the outer cuticle of the integument is observed with SEM (Plate III, 4–5). It is thick and consists of rectangular or isodiametric epidermal cells, 30-40 μm × 20-30 μm in size (Plate III, 5). The outer surface is rough and characterized by longitudinal furrows and irregularly distributed small holes and pits, occasionally slightly bulging or papillate (Plate III, 4). The anticlinal walls of the epidermal cells are partly thickened, forming flanges on the inner surface. Stomata are few, sparsely and irregularly distributed or arranged in short files (Plate III, 5, upper left and lower middle).

Cuticle of nucellus: Only small pieces being obtained (Plate II, 7; Plate III, 3), the nucellus cuticle is very thin and difficult to separate from the megaspore membrane. The epidermal cells are large and quadrangular, rectangular or elongate in shapes, usually 60–150 μm × 20–50 μm in size. The periclinal cell walls are smooth but sometimes slightly papillate (Plate III, 3), the anticlinal walls are thin but distinct.

Megaspore membrane: The megaspore membrane is thick, consisting of a thin basal layer and a thick patterned layer. It is granular in optical view. Under SEM, the basal layer is very finely granular, while the patterned layer consists of bacula (Plate III, 6–8). These bacula are smaller and thinner (1–1.5 μm long and 0.3–0.5 μm wide) in the lower part and become larger and thicker (2–3 μm long and 1–1.5 μm wide) toward the upper part, sometimes bacula irregularly branched and anastomosed (Plate III, 6).

Cuticle of collar: The cuticle of the collar is thick. The outer surface is coarse(Plate III, 1). The epidermal cells are rectangular or irregularly polygonal in shape, and 30–50 μm × 20–30 μm in size (Plate III, 2). Most epidermal cells are irregularly arranged, but sometimes are in more or less defined rows (Plate III, 2). Stomata are rounded, and about 40 μm in diameter, bearing 6 subsidiary cells with each a papilla (Plate II, 8).

Cuticles of peduncle and pedicel: The cuticles of the peduncle and pedicel are similar in general features. Both are thick (Plate IV, 1–3), consisting of epidermal cells in well-defined longitudinal files. The ordinary epidermal cells are elongate or rectangular in shape, usually 30–50 μm long and 10–20 μm wide in size. The periclinal walls are smooth on the outer surface and less smooth on the inner surface, the anticlinal walls are straight and thick. The cells are usually 40 μm × 10 μm in size. The transverse walls are straight or oblique, while longitudinal walls are more or less parallel to one another. Some of the elongated cells have thickened longitudinal anticlinal walls. Stomata are sunken, sparse and irregularly distributed, elliptical or rounded in shape and about 40–60 μm in size. The guard cells and subsidiary cells are not well preserved. The subsidiary cells are papillate; papillae overhang the stomatal pit (Plate IV, 1).

3.2. Associated leaves

Ginkgoales

Ginkgoites Seward, 1919

Ginkgoites manchurica (Yabe etÔishi) Cao

(Plate I, 1 lower right, 3–4; Plate II, 1–3; Plate IV, 4–6; Plate V)

Synonyms:

Baiera manchurica, Yabe et Ôishi, 1933, p. 218; pl. 32, figs. 12, 13A; pl. 33, fig. 1.

Ginkgo manchurica, Chen et Meng, 1988, p. 65; pl. 35, figs. 1–9; pl. 36, figs. 1–6; pl. 64, figs. 3–4; pl. 65, fig. 5.

Ginkgoites manchuricus (Yabe et Ôishi), Cao, 1992, p. 234; pl. 1, figs. 1–7; pl. 2, fig. 17.

Ginkgo manchurica, Zhao et al., 1993, p.75; figs. 2–6.

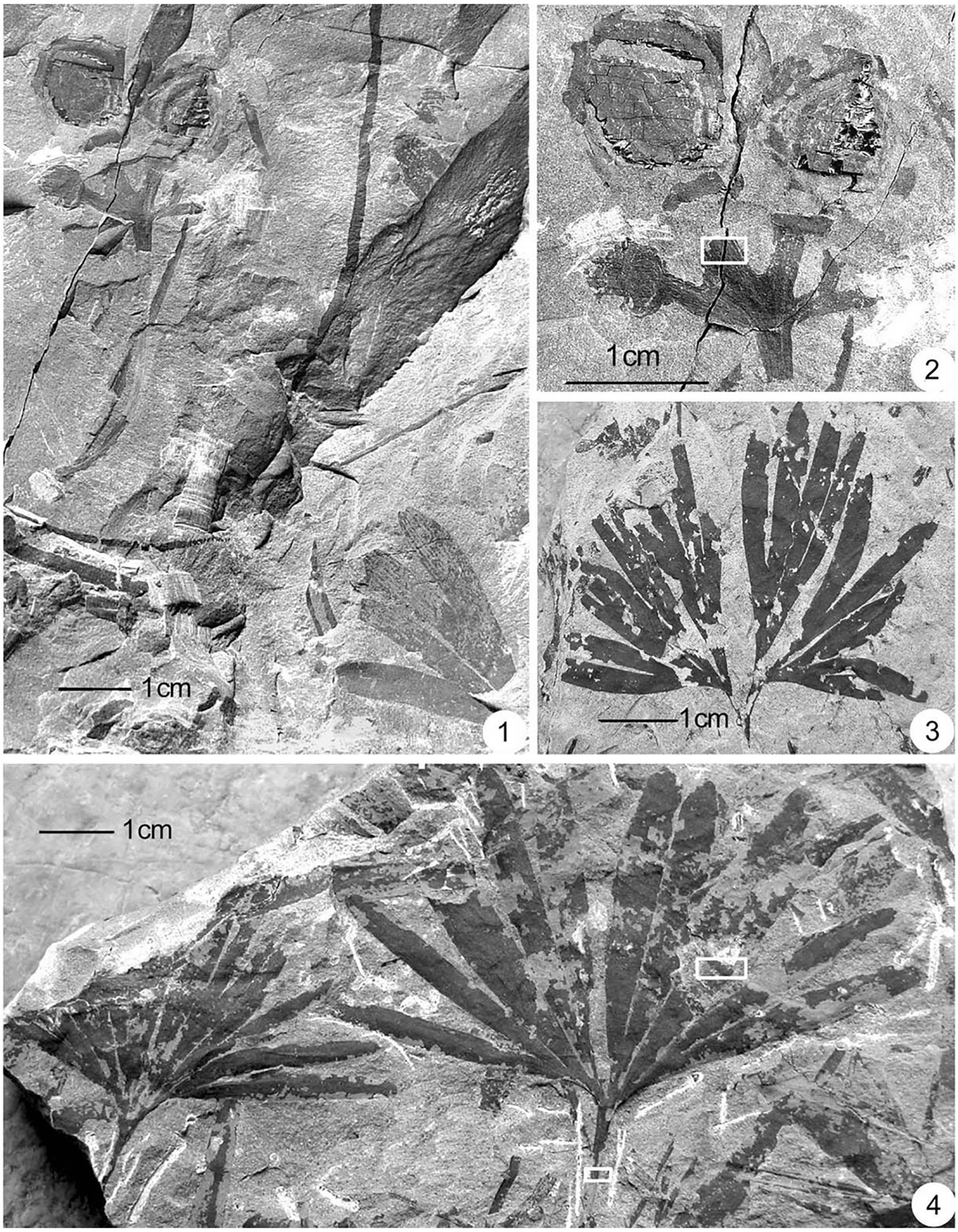

Plate I. 1–2. *Ginkgo pediculata* sp. nov., furcated ovule-bearing organ with three (to five?) pediculate, orthotropous ovules; Holotype (TDQ-95-302), the associated leaf on the lower right was attributed to *Ginkgoites manchurica*. Fig. 2, enlargement of fig. 1, showing branching of peduncle; cuticles studied are from the white rectangular area. 3–4. *Ginkgoites manchurica* (Yabe et Ôishi) Cao, collected from the same bed of ovule-bearing organ (TXM-012, Tf62-1); cuticles studied are from the white rectangular area.

Ginkgo manchurica, Deng, 1995, p. 53; pl. 25, fig. 2; pl. 28, fig. 1; pl. 42, figs. 1–2; pl. 43, figs. 1–6.

General morphology: Leaves are fan-shaped or semicircular (Plate I, 3–4) with a basal angle of 90°–180°, about 20–70 mm wide and usually 40–50 mm high. The petiole is at least 45 mm long and 1–2 mm wide. The lamina is usually divided deeply (almost to the petiole) into two parts and then each part is further dichotomously divided two to four times into segments with narrow and petiole-like bases (Plate I, 3–4). The ultimate segments are 8–24 in number. The segment is fairly slender, usually no more than 7 mm wide, oblanceolate with an acute or obtuse apex. Each segment bears 4–5 veins. Veins are fine and sometimes indistinguishable, 10–15 per centimeter.

Cuticle of leaf: The adaxial cuticle has a smooth to uneven outer surface without distinct outline of epidermal cells (Plate V, 8). Ordinary epidermal cells are distinctly seen in inner surface, generally rectangular or polygonal in shape and about 15–30 μm × 8–12 μm in size. The periclinal cell walls are smooth inside, while the anticlinal walls are irregularly thickened (Plate V, 7). Stomata are sporadic and slightly sunken, usually with five to six elliptical subsidiary cell papillae (about 9–15 μm × 6–9 μm in size) (Plate V, 8–9).

The abaxial cuticle has well-defined stomatal and non-stomatal zones (Plate V, 1–4). Epidermal cells are elongate, regularly arranged in longitudinal files in non-stomatal zones (Plate V, 1, 2), but

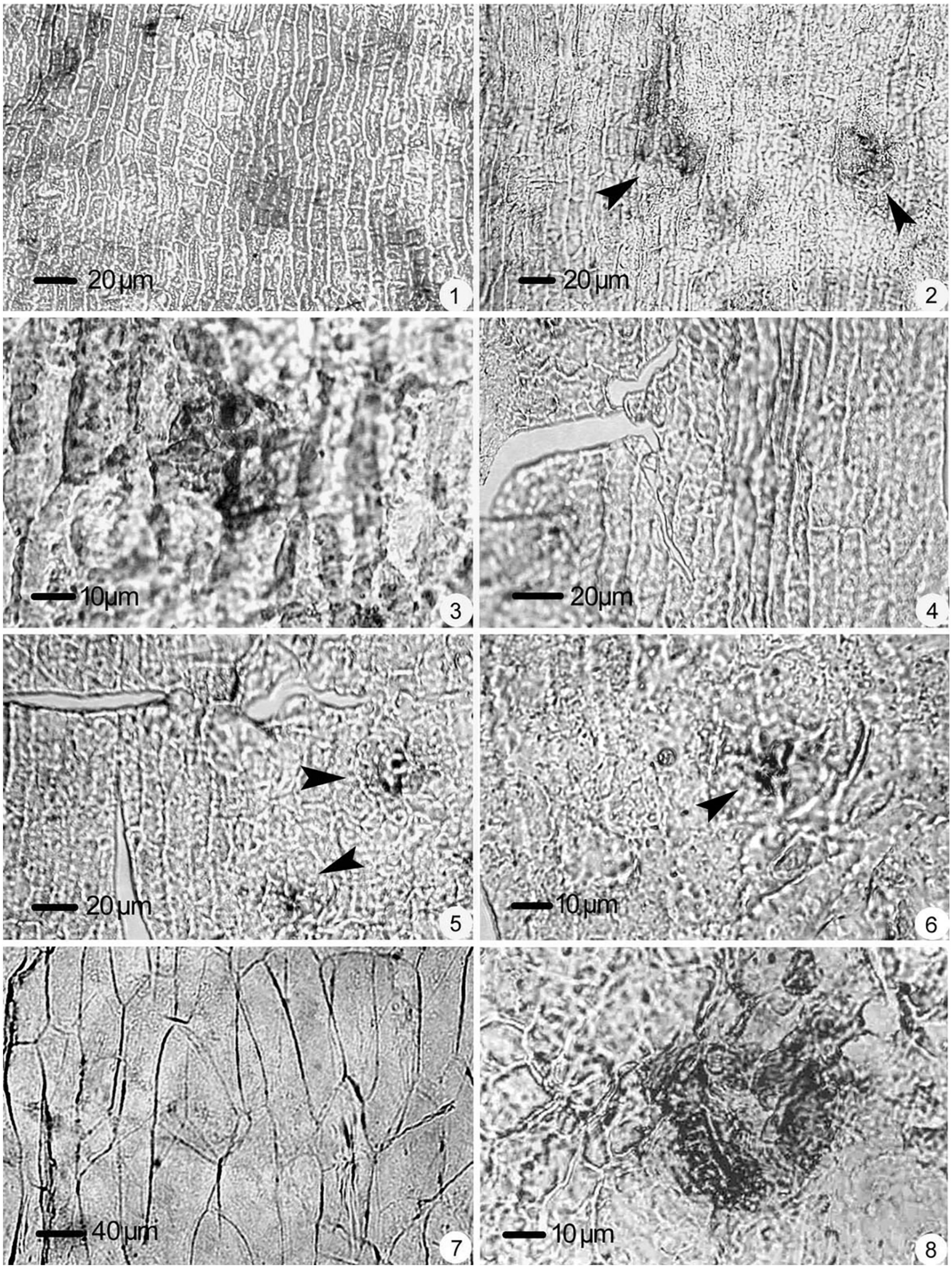

Plate II. 1–3. *Ginkgoites manchurica* (Yabe et Ôishi) Cao (LM) 1. Cuticle of petiole, showing rectangular epidermal cells arranged regularly. 2. Cuticle of petiole, showing ordinary cells and stomata (arrows). 3. Cuticle of petiole, showing a stoma with papillae hanging over the aperture. 4–8.*Ginkgo pediculata* sp. nov. (LM). 4. Cuticle of pedicel, showing rectangular epidermal cells arranged regularly. 5. Cuticle of pedicel, showing ordinary cells and stomata (arrows). 6. Cuticle of pedicel, showing a stoma (arrow). 7. Cuticle of nucellus, characterized by large cells with thin anticlinal walls. 8. A stoma of collar.

isodiametric in stomatal zones (Plate V, 3–4). The non-stomatal zones are 300 μm wide, composed of more than 20 files of elongate cells. The stomatal zones are 330 μm wide with ordinary epidermal cells and irregularly distributed stomata. The density of stoma is about 180–220 per mm^2. Stomata are sunken, usually surrounded by five to six large subsidiary cells with rounded or elliptical papillae (8–12 μm in diameter) overhanging the stomatal pit (Plate V, 5–6).

Cuticle of petiole: The petiole cuticle has an uneven to nearly smooth outer surface (Plate IV, 4). Most epidermal cells are rectangular, about 15–65 μm × 8–20 μm in size, longitudinally arranged regularly with straight and thick anticlinal walls (Plate IV, 5; Plate II, 1–2). Stomata are sporadically scattered (Plate II, 2). The stoma is elliptical with five subsidiary cells; each subsidiary cell bears a papilla hanging over the stomatal pit (Plate II, 3; Plate IV, 6). Guard cells are about 15 μm × 30 μm and sunken, and the stomatal aperture appears obliquely oriented (Plate IV, 6).

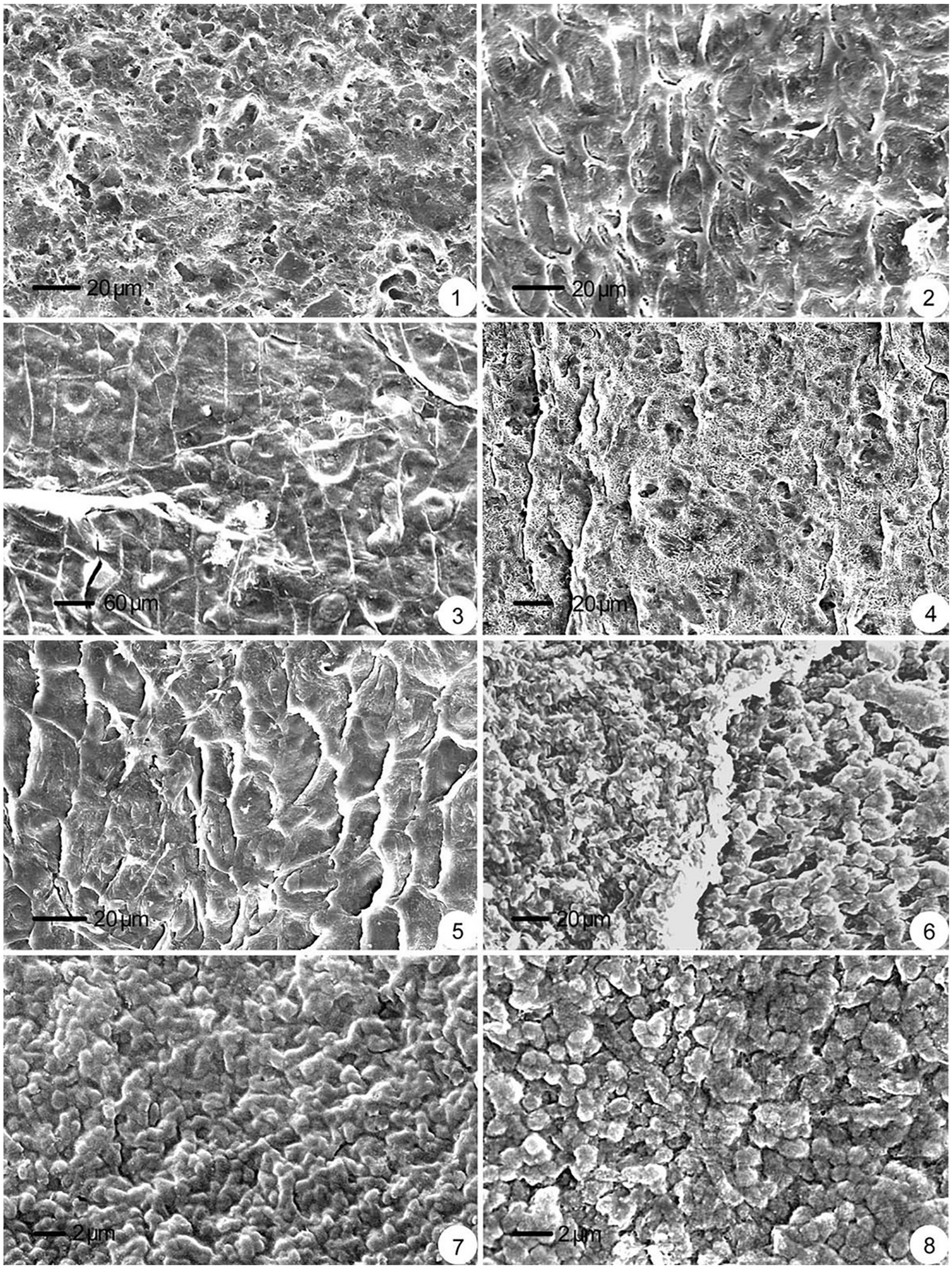

Plate III. *Ginkgo pediculata* sp. nov. (SEM) 1. Outer surface of collar, showing irregularly arranged holes and pits of different size. 2. Inner surface of collar, showing the arrangement of epidermal cells. 3. Inner surface of nucellus, showing large, elongate, but somewhat irregularly arranged cells. 4. Outer surface of integument, showing furrows and irregularly arranged small holes and pits. 5. Inner surface of integument, showing rectangular epidermal cells with thickened flanges of anticlinal walls. 6. Inner (left) and outer (right) surfaces of the megaspore membrane, showing different size and structure of bacula. 7. Inner surface of megaspore membrane, showing small bacula. 8. Outer surface of megaspore membrane, showing the irregularly branched and anastomosing bacula.

4. Discussion

4.1. The possible relation between the ovule-bearing organ and the associated leaves

The present ovule-bearing organ was found in close association with leaf fragments of *Ginkgoites manchurica* on the same slab. *G. manchurica* is the most abundant species of the morphogenus *Ginkgoites* in the same plant-bearing bed and in the coal-bearing Xiaoming'anbei Formation. The two type of organs show considerable similarities in cuticular structure. The lamina and petiole cuticles of *Ginkgoites manchurica* have a non-papillate outer surface (Plate II, 1–2; Plate IV, 4) as the integument and pedicel cuticles of *Ginkgo pediculata* (Plate II, 4–5; Plate III, 4; Plate IV, 1). The inner surface of the petiole cuticle of *Ginkgoites manchurica* is also closely comparable to that of the pedicel cuticle of the ovule organ (Plate IV, 2 and 5). Their stomata show a general similarity in shape (Plate II, 3 and 6; Plate V, 5–6 and 8–9) and the stomatal pit is more or less concealed by papillae of subsidiary cells in both forms.

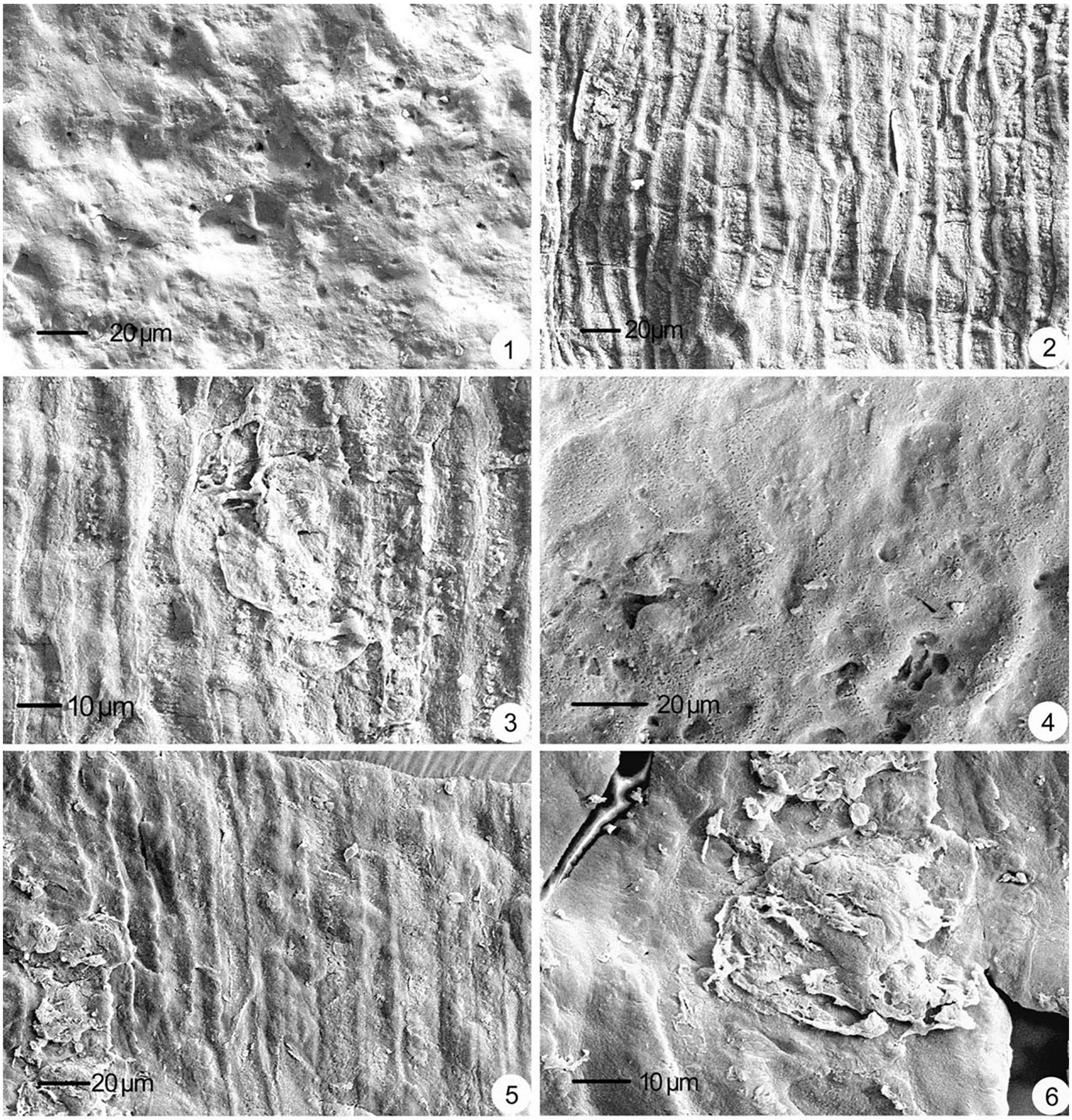

Plate IV. 1–3. *Ginkgo pediculata* sp. nov.(SEM) 1. Outer surface of pedicel, showing the smooth outer surface. 2. Inner surface of pedicel, showing rectangular epidermal cell arranged regularly. 3. Inner view of a stoma of pedicel. 4–6. *Ginkgoites manchurica* (Yabe et Ôishi) Cao, petiole cuticles (SEM). 4. Outer surface of petiole. Note the nearly smooth outer surface, and a possible stoma in the middle. 5. Inner surface of petiole, showing rectangular epidermal cells arranged regularly. 6. Inner surface of petiole and inner view of a stoma.

Although a detailed comparison of their cuticles is impossible due to limited material of the ovule-bearing organ, available evidence suggests that the two organs likely belong to the same plant (Fig. 3). Three other types of *Ginkgo*-like leaves occur in the same formation, assigned to *Ginkgo pluripartita* (Schimper) Heer, *Ginkgo truncata* Li and *Ginkgo paraadiantoides* Samylina (Chen et al., 1988). They all differ from *Ginkgoites manchurica* and *Ginkgo pediculata* in having distinct papillae on the outer surface of cuticles.

4.2. Comparisons among ovule-bearing organs of fossil and living Ginkgo species

There are seven species described based on well-preserved ovulate organs of fossil *Ginkgo* from the Jurassic to the Paleogene. The present ovulate organ is morphologically distinguished from those of all other fossil species and extant *Ginkgo biloba* (Table 1).

So far, two ovulate organs from the Lower Cretaceous have been attributed to *Ginkgo*, namely *Ginkgo apodes* from the Yixian Formation in Liaoning Province (Zhou and Zheng, 2003; Zheng and Zhou, 2004) and *Ginkgo neimengensis* from the Huolinhe Formation of East Inner Mongolia (Xu et al., 2017). Both differ from the present species in having a higher number of ovules and mature seeds (respectively with 1–3 and 5) and the ovules are much smaller in size (usually 7–8 mm) (Table 1). Another important difference is that the pedicels of *G. apodes* and *G. neimengensis* are very short, about 2–3 mm long in young ovulate organs and missing in mature organ.

The ovulate organ of *Ginkgo pediculata* is generally similar to that of other Jurassic *Ginkgo* species in shape and size, but differs in the length

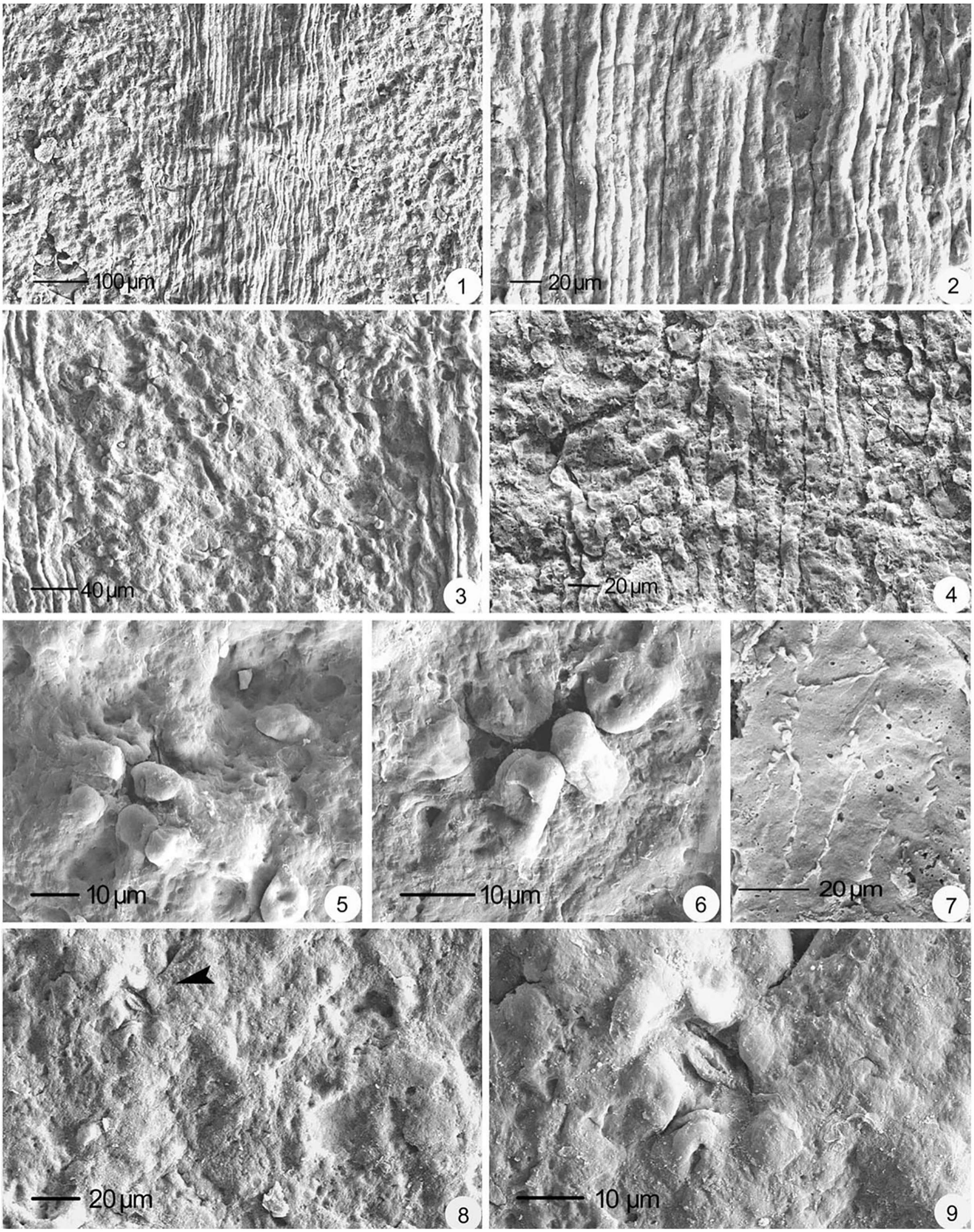

Plate V. *Ginkgoites manchurica* (Yabe et Ôishi) Cao, lamina cuticles (SEM) 1. Outer surface of abaxial cuticle, showing the stomatal and non-stomatal zones. 2. Outer surface of abaxial cuticle, showing the longitudinal cell files of the non-stomatal zone. 3. Outer surface of abaxial cuticle, showing the stomatal zone. 4. Outer surface of abaxial cuticle, showing the elongate cells in the non-stomatal zone (middle) and the epidermal cells and papillate stomata in the lateral stomatal zones. 5–6. Outer view of stomata of abaxial cuticle. Note papillae surrounded and hanging over the pit of stomata. 7. Inner surface of adaxial cuticle, showing smooth periclinal walls and irregularly thickened anticlinal walls. 8. Outer surface of adaxial cuticle, showing a stoma (arrow). 9. Outer view of a stoma of adaxial cuticle, magnified from fig. 8.

of the pedicels and the number of the ovules (Table 1). Both *Ginkgo yimaensis* Zhou et Zhang from the Middle Jurassic of Henan, China (Zhou and Zhang, 1988, 1989) and *Ginkgo ginkgoidea* (Tralau) Yang, Friis et Zhou from the Middle Jurassic of Scania, Sweden (Tralau, 1966; Yang et al., 2008) have long pedicels (up to 16 or 7 mm) about 1/3 to 3/5 of the peduncle in length, but *Ginkgo pediculata* has much shorter pedicels of 6.5 mm long, only about 1/5 of the peduncle in length. The number of mature ovules are 2–3 (or 4) in the Jurassic species

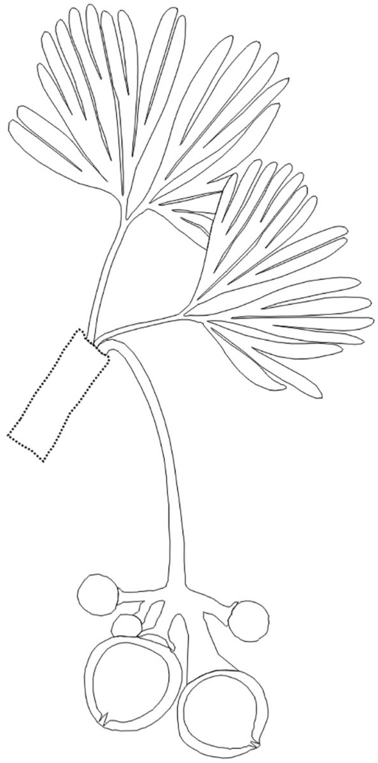

Fig. 3. Reconstruction of *Gingko pediculata* sp. nov.

G. yimaensis (Zhou and Zhang, 1989), *G. ginkgoidea* (Yang et al., 2008) and *Ginkgo gomolitzkyana* Nosova (2012, 2017), but only 2 in the present species (Table 1).

The ovulate organs of the Paleogene *Ginkgo cranei* Zhou, Quan et Liu (Crane et al., 1990; Zhou et al., 2012), and the living *G. biloba* are clearly different in having only one large mature ovule (seed) attached directly on the peduncle, and without a pedicel.

4.3. Evolutionary implication of Ginkgo pediculata

The recent fossil discoveries (Zhou and Zhang, 1989; Crane et al., 1990; Zhou, 1991, 1997; Zhou and Zheng, 2003; Zheng and Zhou, 2004; Yang et al., 2008; Xu et al., 2017) suggest three evolutionary pathways for the ovule-bearing organs of *Ginkgo*: (1) reduction of the number of ovules, both in the juvenile and mature ovulate organs; (2) pedicels becoming shortened and disappeared; (3) increasing of ovule size. The ovulate organ of the Lower Cretaceous *Ginkgo pediculata* resembles generally that of the Jurassic species, but is intermediate in all the three aspects between the Jurassic species (*G. yimaensis* and *G. ginkgoidea*) and the Paleogene species *G. cranei*. The two other Lower Cretaceous species *G. apodes* (Zheng and Zhou, 2004) and *Ginkgo neimengensis* (Xu et al., 2017) are mainly distinguished from *Ginkgo pediculata* by the absence of pedicels in mature specimens as is also the case for the Paleogene *G. cranei* and living *G. biloba*. The present discovery provides further evidence supporting the inference that the ovulate organ of the genus has undergone successive reduction during the geological history. As noted before that such reduction trend of *Ginkgo* ovulate organs and leaves in the geological history roughly corresponds with the developmental sequences seen in the extant species (Zhou, 1991, 1997, 2009; Zhou and Zheng, 2003; Zhou et al., 2020).

So far two types of *Ginkgo* ovulate organs have been documented in the Lower Cretaceous, the *Ginkgo apodes* (Zhou and Zheng, 2003; Zheng and Zhou, 2004) and *Ginkgo neimengensis* (Xu et al., 2017) type, which resemble the extant *Ginkgo biloba* in having no pedicel, but bear more ovules, while the *G. pediculata* type is close to the Jurassic *Ginkgo yimaensis* and *G. ginkgoidea* in having pedicels in mature organs. The presence of pedicels in mature ovule organ is a primitive character state and the absence of pedicels is characteristic of the advanced (or modern) group of the genus *Ginkgo* (Table 1). *G. apodes* and *G. neimengensis*, may also belong to the modern group, but bear some intermediate characters, while *G. pediculata* is the latest member so far known of the primitive group.

Table 1
Ovulate organs and associated leaves of living and fossil species of ***Ginkgo*** (revised based on tables 10 and 14 of Zhou et al., 2020).

	G G.biloba	*G.cranei*	*G.apodes*	*G. neimengensis*	*G.pediculata*	*G.ginkgoidea*	*G.gomolitzkyana*	*G.huttonii*	*G.yimaensis*
Type of ovulate organ	modern	modern	intermediate	Intermediate	primitive	primitive	primitive	primitive	primitive
Number of ovule (mature ovule)	2(1)	2(1)	2–7(1–3)	6(5)	4–5(2)	2–3(2)	?1–4(1–4)	>2(>2)	2–4(2–4)
Size of seed (mm)	30 × 20 × 15	10–19 × 12–17	7.3–8 × 6–8	7–10 × 6–9	7–14 × 6–13.5	9–12 × 8–12	5.3–9.2 × 4–7.5	10.5–12 × 8–10	10–15 × 8–12
Size of stone (mm)	>(21 × 15)	8–15 × 7–12	6.5–7.5 × 5–7	–	10 × 7	–	–	6–7 × 5.5	7.5–12.5 × 5.5–9.5
Pedicel (length in mm)	Missing	Missing	Missing when mature	Missing when mature	Present (>6.5)	Present (5–7)	Present, short	Present?	Present (15–16)
Leaf (attached or associated)	Nearly entire	Nearly entire	Divided	Dividted	Deeply divided	Deeply divided	Deeply divided	Deeply divided	Deeply divided
Age	Recent	Late Paleocene	Early Cretaceous	Early Cretaceous	Early Cretaceous	Middle Jurassic	Middle Jurassic	Middle Jurassic	Middle Jurassic
Locality	Chnia	Dakota, USA	Liaoning, China	Northeast Inner Mongolia, China	Liaoning, China	Scania, Sweden	Uzbekistan	England	Henan, China
References	Zhou et al. (2012)	Crane et al. (1990); Zhou et al. (2012)	Zheng and Zhou (2004)	Xu et al. (2017)	Deng et al. (2004); present paper	Tralau (1966); Yang et al. (2008)	Nosova (2012)	Harris et al. (1974)	Zhou and Zhang (1989)

The associated leaves (*Ginkgoites manchurica*) show also a primitive (plesiomorphic) feature. They are characterized by having deeply divided lamina with numerous narrow ultimate segments (Chen et al., 1988; Zhao et al., 1993). Such type of leaves is prevailing in the Jurassic, and known to be closely associated with *Ginkgo yimaensis*, *G. gomolitzkyana* and *G. ginkgoidea* (i.e. *Ginkgoites regnellii* Tralau) (Table 1; Nosova, 2012, 2017; Tralau, 1966; Zhou and Zhang, 1989; Yang et al., 2008) characterized by having primitive type ovulate organs. It differs markedly from the modern type of leaves which bear nearly entire or shallowly wavy and notched distal margin, typical of *G. cranei* (i.e. *Ginkgoites adiantoides*) and *G. biloba* with modern type ovulate organs.

Conclusion

The new species of *Ginkgo*, *G. pediculata* described in the present paper from the Lower Cretaceous of Liaoning Province, China bears primitive characters and generally resembles the Jurassic species of *Ginkgo* in ovulate organs and vegetative leaves. It represents the latest representative of the primitive group of the genus so far known.

The coeval *G. apodes* and *G. neimengensis* have ovulate organs with sessile ovules when mature as the modern type, but more in number, and the associated vegetative leaves are also more or less divided and morphologically closer to the Jurassic species than the extant species *G. biloba*. It indicates that the morphological transition from the primitive group to the modern group in *Ginkgo* was not abrupt, with both primitive and intermediate type fossil ginkgoes in the Lower Cretaceous of Northeast China.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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