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TERTIARY *GINKGO* OVULATE ORGANS WITH ASSOCIATED LEAVES FROM NORTH DAKOTA, U.S.A., AND THEIR EVOLUTIONARY SIGNIFICANCE

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The evolutionary history of *Ginkgo* is poorly understood for the Cenozoic Era because of the rarity of fossil reproductive organs. We here describe a new species, *Ginkgo cranei* sp. nov., on the basis of well-preserved ovulate organs and associated leaves from the Upper Paleocene Sentinel Butte Formation of North Dakota, USA. The ovulate organ is of the modern type, which lacks a pedicel supporting each of the two ovules. The ovules are seated in separate collars directly attached to the peduncle, but only one of them is mature. Stomatal complexes are mostly amphicyclic, with deeply sunken guard cells and slightly raised subsidiary cells. They are sparsely distributed among epidermal cells characterized by domelike, strongly bulging periclinal walls and developed anticlinal wall flanges in integument and collar cuticles. The associated leaves are generally similar to the ovulate organ in cuticular structure. *Ginkgo cranei* is the only Tertiary species of the genus described in which the ovulate organs are studied in some detail. The study further corroborates the hypothesis that modern *Ginkgo* evolved from its ancestors by reduction and is helpful to classify Cenozoic ginkgos in a natural system.

Keywords: *Ginkgo cranei* sp. nov., North Dakota, ovulate organs, reduction evolutionary trends, Sentinel Butte Formation, Tertiary.

Introduction

The living fossil *Ginkgo* (Ginkgoaceae) is a distinct major group of gymnosperms with an extraordinarily long history, as demonstrated by extensive fossil leaf remains from the Jurassic to Tertiary in both the Northern and the Southern Hemispheres (Harris 1935; Samylina 1967; Tralau 1968; Douglas 1969; Harris et al. 1974; Hill and Carpenter 1999; Zhou 2009). However, our knowledge of the evolutionary history of *Ginkgo* is still rudimentary for several geological stages because of the absence of well-preserved reproductive organs, from which the most evolutionarily informative characters of the ginkgoalean plants are generally obtained (Archangelsky 1965; Krassilov 1972; Stanislavsky 1973; Zhou and Zhang 1989, 1992; Zhou 1991, 1997; Kvaček et al. 2005). Reproductive organs recorded from the Jurassic and Cretaceous of Eurasia have revealed the early evolutionary history of the genus (Harris et al. 1974; Zhou and Zhang 1989; Zhou and Zheng 2003; Deng et al. 2004; Zheng and Zhou 2004; Liu et al. 2006; Yang et al. 2008), but information from the Cenozoic is rather poor. Given that more than a dozen foliar morphospecies of Tertiary ginkgos have been reported worldwide (Samylina 1967; Tralau 1968; Hill and Carpenter 1999; Quan et al. 2010), it is perhaps surprising that the associated reproductive organs have been documented only rarely (Crane et al. 1990) and have not yet been studied in detail. Although both *Ginkgo* leaves and isolated seeds have been reported from some Tertiary localities (e.g., Akhmetiev et al. 2002; Royer et al. 2003; Aulenback 2009), such fragmentary information is not sufficient to provide evidence of the evolutionary state of the genus during this time interval.

We here describe *Ginkgo cranei* sp. nov. on the basis of well-preserved ovulate organs (fig. 1*A*–1*J*) and associated leaves (fig. 1*K*–1*P*) from the Upper Paleocene of North Dakota, USA. This is the first Tertiary *Ginkgo* for which the ovulate organ has been studied in detail, providing important evidence to document the evolutionary history of the genus. In this article, the long-standing taxonomic and nomenclatural problems of Tertiary ginkgos are also briefly reviewed.

Material and Methods

Geological Setting

The *Ginkgo* fossils were collected from the Paleocene Sentinel Butte Formation of the Fort Union Group, near Almont, North Dakota, USA. The deposits of this formation are silica rich, and the fossils are preserved in hard, iron-stained, yellow-brown, fine-grained shale (Crane et al. 1990). Many of the fossil plants of the Almont Flora are three-dimensionally preserved, including both fruits and stems. More than 37 genera of gymnosperms and angiosperms have been identified from the shale of this locality (Manchester and Dilcher 1982;

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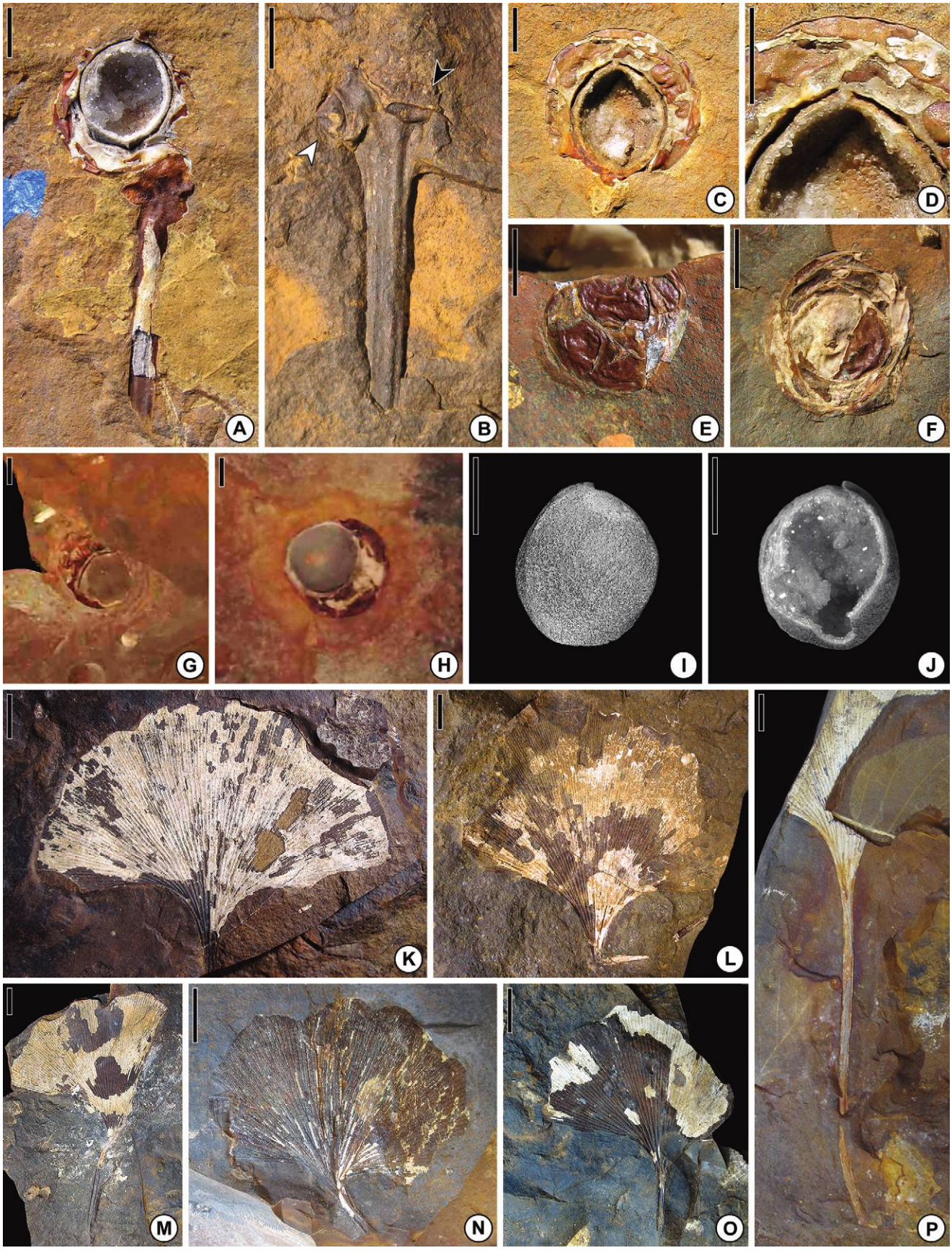
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Crane et al. 1990; Manchester et al. 2004; Pigg et al. 2008; Pigg and DeVore 2010; literature therein). *Ginkgo* ovulate organs are well preserved, and leaves are very common in certain horizons. The associated leaves were previously described as *Ginkgo adiantoides* (Ung.) Heer, on the basis of the general gross morphology (Crane et al. 1990).

The geological age of the formation is regarded as late Paleocene, on the basis of the plant assemblage and palynological data (e.g., Manchester and Dilcher 1982; Crane et al. 1990; Pigg et al. 2008). This conclusion is also supported by the discovery of late Tiffanian mammals from the upper part of the formation (Kihm and Hartman 1991). Recently, Clechenko et al. (2007), on the basis of the bulk organic carbon isotope ($\delta^{13}C_{org}$) data, defined the Paleocene-Eocene boundary in the lowest part the Bear Den Member of the Golden Valley Formation, which rests conformably on the Sentinel Butte Formation, unequivocally indicating a late Paleocene age of the flora.

Material Preparation

Although some seeds in the collection are three-dimensionally preserved, they are stone casts and yield no anatomical structure due to crystallization (fig. 1*A*, 1*C*, 1*D*, 1*J*). Occasionally, however, the outer seed cuticle is preserved. Cuticles of leaves, seed coats (integuments), and occasional woody tissues are also available for study from the compressed specimens. Pieces of cuticles were removed from the ovulate organs and leaves and macerated, using conventional methods LM and SEM. Specimens were treated with HF for ~12 h followed by HNO_3. After becoming translucent and yellow in color, the fossils were rinsed with water and treated with dilute 5% KOH for a few seconds before a thorough rinsing with water. Cuticle preparations were mounted on the stub with tape and coated with gold for SEM observation. For comparison, ovulate organs of *Gingko biloba* L. were collected from the campus of East Tennessee State University (ETSU) and the Nanjing Institute of Geology and Palaeontology (NIGP), respectively, in September and December 2010. They were treated with the same methods as the fossils.

The SEM observations on the ovulate organs were made at the State Key Laboratory of Palaeontology and Stratigraphy, NIGP (Leo 1530 VP and JSM-6300), while those on fossil leaves and some modern samples were made at the College of Medicine of ETSU (Zeiss DSM940). The cuticle terminology mainly follows Zhou and Zhang (1989). The fossil specimens labeled with a PP prefix are in the Geology Department at the Field Museum, Chicago, while specimens prefixed with UWSP are housed in the Biological Department of the University of Wisconsin, Stevens Point.

Systematics and Descriptions

Family—Ginkgoaceae Engler, 1897

Genus—Ginkgo *Linnaeus, 1771*

Species—Ginkgo cranei *Zhou, Quan et Liu, sp. nov. (Figs. 1*A*–1*J*, 2, 3)*

Previous names. *Ginkgo adiantoides* (Unger) Heer, Crane et al. 1990 (p. 6, fig. 2*B*, 2*D*–2*G*); *Ginkgo* sp., Royer et al. 2003 (p. 85, fig. 1*B*).

Diagnosis. *Ginkgo cranei* is distinguished from *Ginkgo biloba* in its smaller seeds (seed 10–19 mm × 12–17 mm vs. 30 mm × 20 mm; stone 8–15 mm × 7–12 mm vs. 21 mm × 15 mm) and in having a characteristic seed integument cuticle consisting of epidermal cells with domelike, thickened periclinal walls and flange-developed anticlinal walls (instead of less bulging periclinal walls and less developed anticlinal wall flanges, as in the extant species). Stomata complexes are fewer and sparser than in *G. biloba*, mostly amphicyclic and with nonpapillate subsidiary cells, differing from those usually monocyclic and sometime with papillate subsidiary cells in the extant species. The leaves associated with *G. cranei* ovules can also be distinguished from *G. biloba* by having fewer stomata and less papillate epidermal and subsidiary cells.

Types. Holotype, UWSP42706 (fig. 1*A*). Paratype, PP34187 (fig. 1*B*).

Number of specimens examined. Seven. In addition to the holotype and paratype, five other specimens were examined: PP34195, UWSP2493, UWSP14906, UWSP2241, and UWSP3363.

Etymology. The specific epithet *cranei* is given in honor of Peter Crane, who with S. R. Manchester and D. L. Dilcher first discovered the ovulate organs and leaves of the Tertiary *Ginkgo* from Almont, North Dakota.

Type locality. Almont, North Dakota.

Stratigraphy. Upper Paleocene; Sentinel Butte Formation.

Description. Gross morphology: The ovulate organs and detached ovules are three-dimensional or compressed (fig. 1*A*–1*J*). Two ovules were directly attached to the peduncle without a pedicel, one being larger and believed to be mature, the other smaller and aborted (fig. 1*A*, 1*B*). Ovules are each borne in a cup-shaped collar. Both collars are situated at the apex of the peduncle; the larger one is 7–9 mm wide and 3–4 mm high, while the smaller one is 2 mm wide and

Fig. 1 Ovulate organs and associated leaves of *Ginkgo cranei* sp. nov. *A*–*J*, Ovulate organs. *A*, Ovulate organ with an in situ seed. Holotype; UWSP42706. *B*, Ovulate organ stalk with an aborted ovule in the collar (white arrowhead) and an empty collar left by detached mature seed (black arrowhead; =fig. 2*G* of Crane et al. 1990; rephotographed). Paratype; PP34187. *C*, Platyspermic ovule with three-dimensional sclerotesta (stone) and impression of surrounding sarcotesta (=fig. 2*D* of Crane et al. 1990; rephotographed). PP34195. *D*, Enlargement of PP34195, showing well-preserved integument outer cuticle, impression with fragmentary cuticle of sarcotesta, and the mucronate apex of sclerotesta. *E*, *F*, Compressed seeds. UWSP3363, 2243. *G*, Mold of a seed. UWSP2493 (courtesy of D. Royer). *H*, Three-dimensional sclerotesta surrounded by impressed sarcotesta. UWSP14906 (courtesy of D. Royer). *I*, *J*, Sclerotesta removed from UWSP42706, showing the exterior and a lateral ridge. *K*–*P*, Gross morphology of associated leaves. PP34024, 54863, 34037, 34027, 34022, 54859-B. Scale bars = 5 mm.

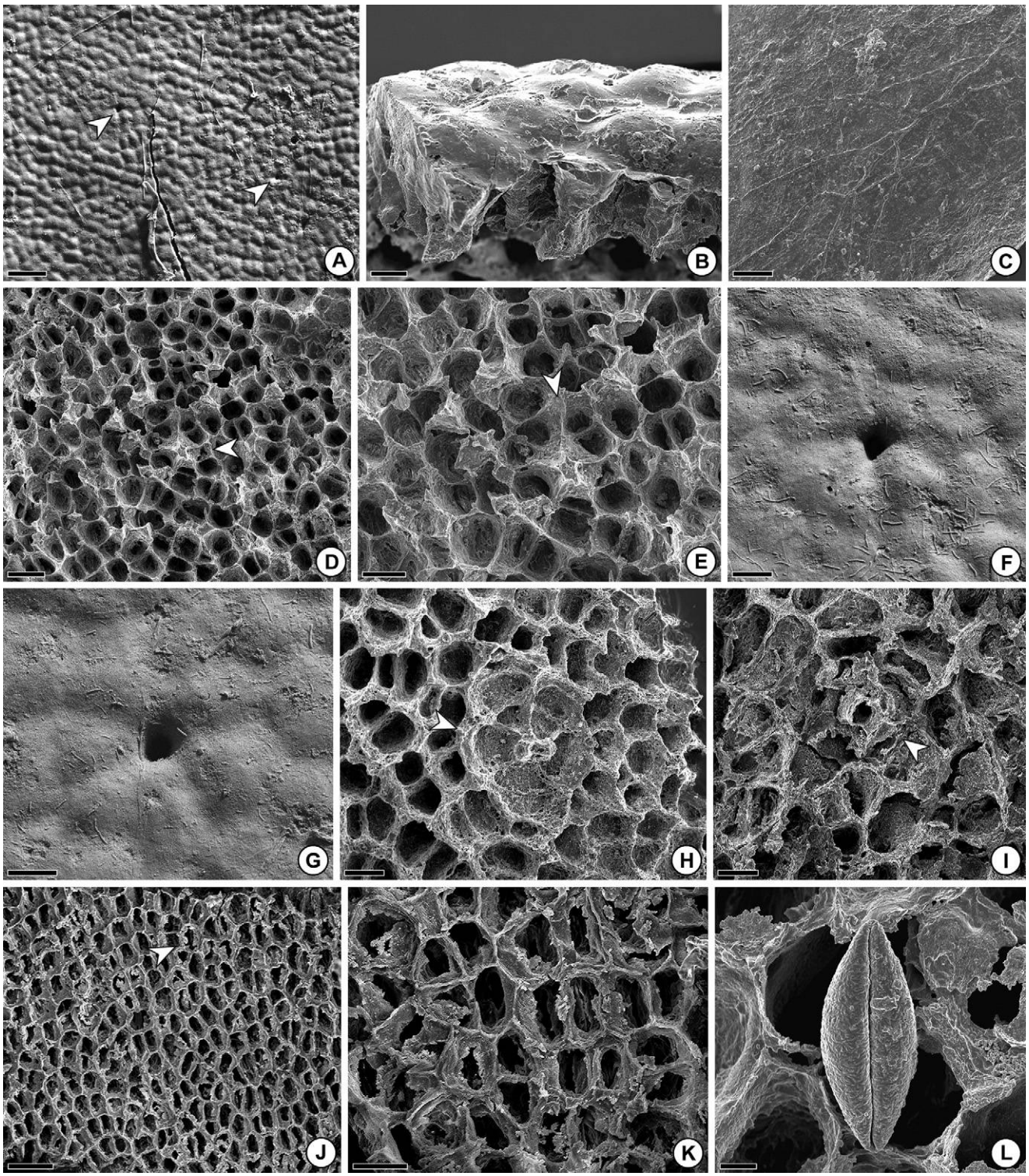

Fig. 2 SEM views of seed integument, collar, and possible pollen grain of *Ginkgo cranei* sp. nov. *A–I*, Integument outer cuticle. *A*, Outer surface view of the integument outer cuticle, showing the domelike periclinal walls of epidermal cells and stomata (arrowheads). UWSP42706. *B*, Section of integument outer cuticle, showing thick periclinal walls and well-developed anticlinal wall flanges of epidermal cells. UWSP42706. *C*, Outer surface, showing hyphae of epiphyllous fungi. UWSP2241. *D*, Inner view, showing isodiametic and polygonal ordinary cells, well-developed flanges, and a stoma (arrowhead). UWSP2241. *E*, Enlarged from *D*, showing the stoma (arrowhead). *F*, *G*, Outer view, showing stomatal complexes characterized by having a deep pit with open rounded mouth surrounded by nearly radially arranged subsidiary cells; note the bulging surfaces of subsidiary and epidermal cells. UWSP42706. *H*, *I*, Inner view of stomatal complexes (arrowheads), showing the well-developed flanges

4 mm high (fig. 1*A*, 1*B*; =fig. 2*B* of Crane et al. 1990 from the same locality). The peduncle is more than 33 mm long and ~4.5–5 mm wide in the upper part, narrowing downward to a width of 2.5 mm at the broken end (fig. 1*A*, 1*B*). The ovules are platyspermic, ovate in outline, with an obtuse distal end and a mucronate apex, 10–19 mm long and 12–17 mm wide in the widest middle part and estimated at ~10–12 mm thick (fig. 1*A*, 1*E*–1*J*). The sarcotesta is wrinkled in compressions, up to ~5 mm thick (fig. 1*A*, 1*C*, 1*D*), and on the surface is irregularly folded (fig. 1*C*, 1*D*). The stone (sclerotesta) is sometimes well preserved in three dimensions with a lateral longitudinal ridge, 11–13 mm high and 9–11 mm wide, and estimated at ~8 mm thick (fig. 1*A*, 1*C*, 1*D*, 1*G*–1*J*).

Integument cuticle (fig. 2*A*–2*I*): Only the outer cuticle of integument is known. It is very thick (up to 12 μm) and consists of nearly isodiametric epidermal cells, 12–15 μm × 20–40 μm (fig. 2*A*–2*E*). The epidermal cells are rather evenly distributed and form only occasional, short, irregular files (fig. 2*A*, 2*E*). The periclinal cell walls are domelike on the outer surface (fig. 2*A*, 2*B*); anticlinal walls strongly cutinized, forming well-developed flanges on the inner surface (fig. 2*B*, 2*D*, 2*E*, 2*H*, 2*I*).

Stomata are sparse, irregularly oriented and distributed (fig. 2*E*–2*I*). The stomatal complexes are somewhat rounded to oblong, 70–110 μm in diameter (fig. 2*H*, 2*I*). Guard cells are deeply sunken below the surface of the subsidiary cells, with only small cutinized patches left (~10 μm wide; fig. 2*H*, 2*I*). Subsidiary cells are 5–7(8) in number, nearly equal in shape and size and more or less radially arranged (fig. 2*E*–2*H*), with usually one being polar and the rest lateral (fig. 2*I*). The subsidiary cells are without papillae, similar to ordinary epidermal cells in shape, but less prominent on the surface and slightly smaller in size, usually 10–26 μm in diameter, forming a small, nearly rounded stomatal pit mouth ~10 μm wide (fig. 2*A*, 2*F*, 2*G*). Encircling cells are usually present, rectangular in shape, but never form a complete ring (fig. 2*I*).

Collar (fig. 2*J*, 2*K*): Only the inner surface of the collar cuticle is observed with SEM. The epidermal cells are generally similar in shape and size, irregularly distributed without distinct cell files (fig. 2*J*, 2*K*). They are 15–25 μm long and 10–20 μm wide, slightly elongate. Stomatal complexes are sparse, randomly distributed, and mostly longitudinally oriented, ~95 μm long and 64 μm wide; guard cells are sunken and represented by small cutinized patches; subsidiary cells are 6–8 in number, similar in shape and size to the ordinary cells. Encircling cells are not observed (fig. 2*J*).

Woody tissues (fig. 3*A*–3*C*): Compressed woody tissues were obtained from the left side of the ovulate organs beside the in situ ovule in UWSP42706 (fig. 1*A*). It is not certain whether it is from the ovule or from the upper part of peduncle. Only the radial section is known. Tracheids show discrete bordered pits in a single row, 20–23 μm wide (fig. 3*A*). Bordered pits are rounded, 10–14 μm in diameter, with a margin of 3–5 μm wide; pores are rounded, 3–6 μm wide (fig. 3*B*). Rays are composed of 4–14 rows of cells 20–30 μm high, with smooth horizontal and tangential walls (fig. 3*A*, 3*C*). Cross field pits are of the cupressoid type, rectangular, with 2–3 pits of ~10 μm in diameter; some well-preserved pits have a central pore of 3–4 μm and a distinct border of 2–3 μm wide (fig. 3*C*).

Peduncle cuticle (fig. 3*D*–3*M*): Cuticles of both upper and lower sides are similar in general features, consisting of epidermal cells in more or less regular longitudinal files (fig. 3*D*–3*F*). Only very occasionally, two or three stomata form a short file (fig. 3*F*, 3*H*). Ordinary cells are mostly rectangular, with some of polygonal or isodiametric shape, 25–50 μm long and 13–35 μm wide (fig. 3*I*). The periclinal wall slightly bulges on the outer surface (fig. 3*D*–3*F*). Anticlinal walls are straight, thick, and well cutinized and form developed flanges; longitudinal walls are more or less parallel to one another; transverse walls are mostly horizontal and some oblique (fig. 3*E*–3*G*).

Stomatal complexes are irregular in orientation, mostly longitudinal or slightly oblique (fig. 3*D*–3*M*). They are oblong or polygonal, 80–111 μm long and 60–65 μm wide. The stomatal pit mouth is small, 10–35 μm in diameter, rounded or elongate, sometimes surrounded by an indistinct Florin ring (fig. 3*J*, 3*K*). Guard cells are deeply sunken, partly cutinized (fig. 3*G*–3*I*, 3*L*, 3*M*). Subsidiary cells are 6, occasionally 7 in number, generally 1(–2) of them being polar, without papillae and similar to the ordinary cell in shape (fig. 3*G*–3*I*) but usually smaller, with less projected periclinal walls on the upper surface (fig. 3*D*–3*F*, 3*J*, 3*K*). Cuticular flanges between guard and subsidiary cells are usually well developed (fig. 3*L*, 3*M*). Polar encircling cells are common, but lateral ones are also present (fig. 3*M*).

Associated leaves (figs. 1*K*–1*P*, 4): The leaf lamina is largely fan shaped to semicircular, 28–83 mm long and 32–113 mm wide. The leaf margin is entire, irregularly erose or shallowly notched (fig. 1*K*–1*O*). The basal angle ranges from 60° to 190° (fig. 1*K*–1*P*). The veins arise from the basal part of the leaf lamina, dichotomously branched and mainly subparallel to one another toward the distal margin. There are 11–14 veins per 10 mm in the widest part of the leaf.

The leaf is hypostomatic (fig. 4). In both cuticles, the costal zone is well defined by elongate epidermal cells (fig. 4*A*–4*C*). In the upper cuticle (78–135 μm wide, containing 5–11 files of cells), it is slightly narrower than in the lower cuticle (83–225 μm wide, containing 9–17 files of cells; fig. 4*A*, 4*B*). The cells in costal zones of both cuticles are similar in size, ~28–54 μm long and 14–29 μm wide; the anticlinal walls are well cutinized and pitted, forming pronounced flanges inside; the periclinal walls are without or with indistinct papillae (fig. 4*A*–4*C*). Papillae are seen in the intercostal zones of the lower cuticle (fig. 4*B*, 4*C*) but are absent in the upper cuticle (fig. 4*A*).

between guard and subsidiary cells, more or less radially arranged subsidiary cells, and the incomplete rings formed by encircling cells. UWSP2241, 42706. *J*, *K*, Collar. *J*, Inner view, showing isodiametric cells and a stoma (arrowhead). *K*, Inner view, showing an enlarged stoma (lower left) and developed cuticle flanges of epidermal cells. *L*, Possible pollen grain adhering to inner side of integument cuticle, being fusiform with a narrow medium colpus and finely granulate exine. Scale bars = 100 μm (*A*), 10 μm (*B*), 30 μm (*C*), 20 μm (*D*–*I*, *K*), 50 μm (*J*), 5 μm (*L*).

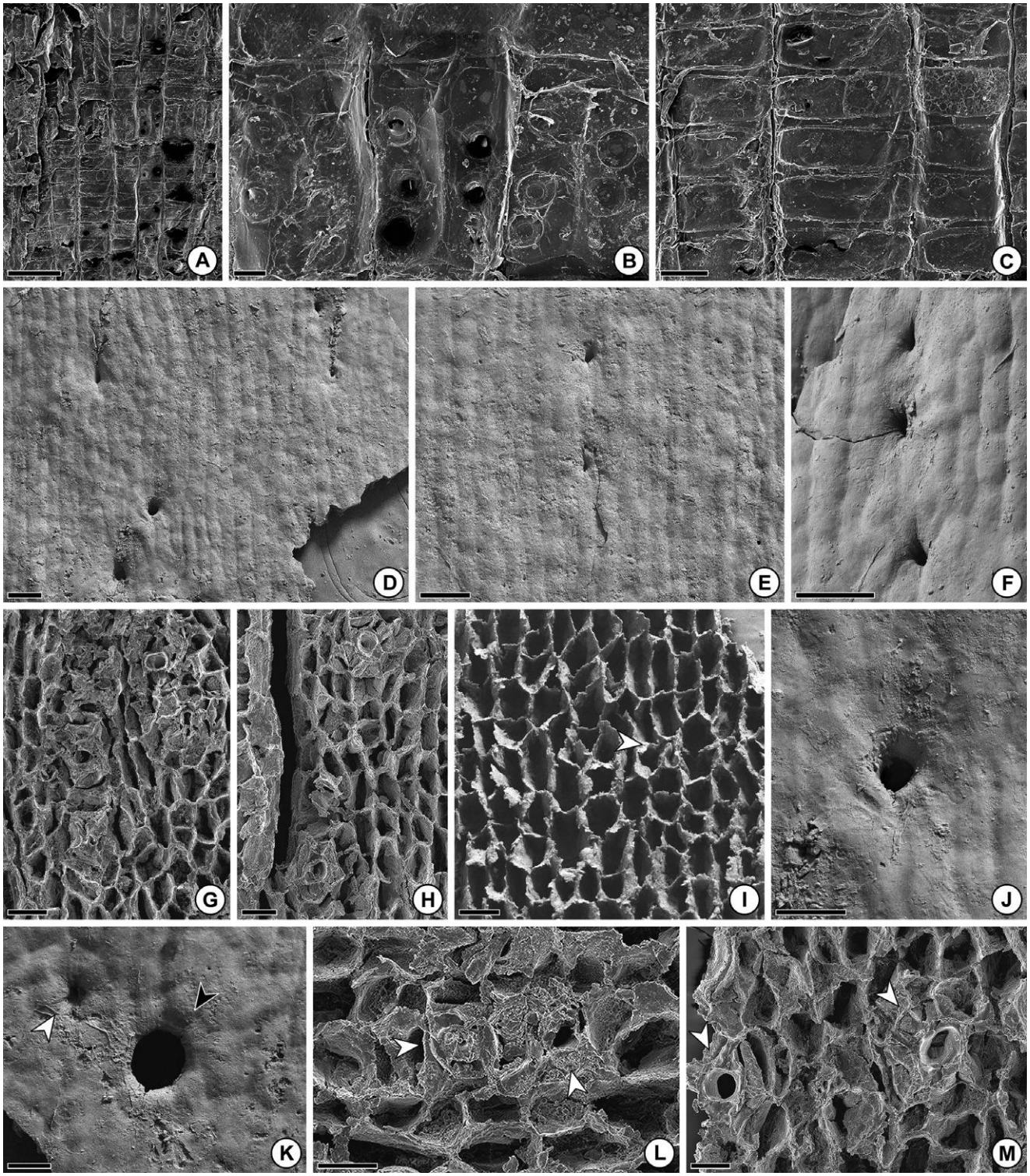

Fig. 3 SEM views of woody tissues and peduncle cuticles of *Ginkgo cranei* sp. nov. UWSP42706. *A–C*, Woody tissues. *A*, Radial section, showing cross fields and ray cells of 4–10 cells high. *B*, Radial section, showing tracheids with bordered pits separated from each other in a single longitudinal row. *C*, Cross fields, showing 2–4 bordered pits per field, transverse and tangential walls of ray cells smooth. *D–M*, Peduncle cuticle. *D–F*, Outer surface view, showing regularly longitudinally arranged epidermal cells with bulging periclinal walls, a few scattered stomata, and short longitudinal stomatal files. *G–I*, Inner surface view. *G*, Short longitudinal file of 3–4 stomata. *H*, Three differently oriented stomata. *I*, Ordinary cells with developed anticlinal wall flanges and a stoma (arrowhead). *J*, Outer view of a stoma. *K*, Outer view, showing a stoma (white arrowhead) and a circular larger pit possibly caused by insect damage (black arrowhead). *L*, *M*, Inner view of stomatal complexes. *L*, Clustered stomatal complexes (arrowheads). *M*, Two stomata (arrowheads) longitudinally or slightly obliquely oriented. Scale bars = 100 μm (*A*), 10 μm (*B*), 20 μm (*C*, *L*, *M*), 50 μm (*D–F*), 30 μm (*G–K*).

In the lower cuticle, stomata are irregularly distributed in the intercostal stomatal zone and are randomly oriented (fig. 4*B*, 4*E*–4*G*). The stomatal complexes are incompletely bicyclic, ~78–109 μm long and 81–105 μm wide (fig. 4*E*–4*G*). The guard cells are deeply sunken below the surface of the subsidiary cells (fig. 4*F*, 4*G*). The subsidiary cells are 4–7 in number, with usually 1(–2) polar and the rest lateral, quadrangular to pentagonal in shape, ~36–62 μm long and 18–27 μm wide, sometimes thickened or papillate, surrounding the deep, elliptic or rounded stomatal pit (fig. 4*E*–4*G*). The epidermal cells in the stomatal zone are nearly isodiametric, ~18–36 μm long and 13–29 μm wide, polygonal in shape and irregular in arrangement (fig. 4*B*, 4*D*). Anticlinal wall flanges of epidermal cells and those between guard and subsidiary cells are usually developed, irregularly thickened, and pitted (fig. 4*C*, 4*F*).

In the petiole (fig. 4*H*–4*L*), the stomatal zone comprising 1 or 2 files of stomata alternates with the nonstomatal zone composed of 6–11 regular longitudinal files of elongated ordinary cells. The epidermal cells, ~44–96 μm long and 11–16 μm wide, are mostly rectangular, with parallel lateral walls and horizontal or oblique end walls (fig. 4*H*, 4*J*). Periclinal walls of the ordinary cells are smooth but thickened and bulged or occasionally papillate (fig. 4*H*–4*K*), while the anticlinal walls are straight, pitted, and well cutinized, forming distinct flanges inside (fig. 4*J*, 4*K*). Stomata are usually longitudinally distributed and oriented. Stomatal complexes are incompletely amphicyclic, similar in size and shape to those of the leaf lower surface (fig. 4*B*, 4*F*–4*H*, 4*K*, 4*L*), 71–104 μm wide and 80–110 μm long, with 2 sunken guard cells and 5–7 thickened subsidiary cells (fig. 4*K*, 4*L*), forming an indistinct Florin ring and with occasional proximal papillae (fig. 4*K*).

Discussion

Attribution of Ovulate Organs and Leaves to the Same Plant

Although these two organs are not organically connected with each other, they are found in close association exclusive of any other ginkgoalean plants in the same formation. This condition differs from that in the Mesozoic, where *Ginkgoites*-type leaves sometimes coexist with different reproductive organs, such as *Karkenia* or *Yimaia* (Archangelsky 1965; Zhou and Zhang 1989, 1992; Rothwell and Holt 1997; Zhou 1997; Zheng and Zhou 2004; Zhou et al. 2007; Yang et al. 2008).

Of most importance in attributing both organs to the same plant species is their close similarity in cuticular structures. Both ovulate organs and leaves are free of trichomes, and the epidermal cells lack or bear only indistinct papillae (figs. 2*A*, 3*D*, 4*A*, 4*D*, 4*H*). Their epidermal cells are usually strongly cutinized and characterized by more or less outward-bulging, domelike periclinal walls and well-developed anticlinal wall flanges. These features are less pronounced in leaf cuticle, which is much thinner than the outer cuticle of the ovule integument (figs. 2*A*, 4*A*, 4*B*). However, the cuticle flanges between the guard and subsidiary cells are similarly developed (figs. 3*G*, 3*H*, 3*L*, 3*M*, 4*F*, 4*G*, 4*K*) in leaves and the integument. The leaf petiole and peduncle of ovulate organs are more closely comparable in all these respects (figs. 3*D*–3*M*, 4*I*–4*L*). The other important feature that links the separated leafy and ovulate organs is the similarities in stomatal structure. Stomatal complexes of both organs are characterized by deeply sunken guard cells in a stomatal pit with an open, usually rounded mouth (figs. 2*F*, 2*G*, 3*D*–3*F*, 3*J*, 3*K*, 4*B*, 4*E*, 4*H*, 4*K*), typically with 5–7 subsidiary cells, and encircling cells usually present (figs. 2*H*, 2*I*, 3*G*, 3*H*, 3*L*, 3*M*, 4*F*, 4*G*, 4*L*). All these strongly suggest that the two organs belong to the same species.

Comparison between Ginkgo cranei *sp. nov. and Other Ginkgo Species with Known Ovulate Organs*

Unequivocal and complete ovulate organs of *Ginkgo* are very rare in the fossil record. To date, only six species have been reported from the Mesozoic of the Northern Hemisphere, in which the ovulate organs are more or less well preserved (table 1).

Morphologically, ovulate organs of the present species obviously differ from those of the Jurassic taxa referred to as the ancestral type (*yimaensis* type; Zhou 1994; Zhou and Zheng 2003; Zheng and Zhou 2004). The ovules of *Ginkgo yimaensis* Zhou et Zhang from the Middle Jurassic Yima Formation of Henan, China, are each borne on a long pedicel (Zhou and Zhang 1989). The case is similar for *Ginkgo ginkgoidea* (Tralau) Yang, Friis et Zhou, another well-documented species from the Middle Jurassic of Scania, Sweden (Yang et al. 2008). Both Jurassic *Ginkgo* ovulate organs are found in association with deeply divided leaves and can be readily distinguished from those associated with *Ginkgo cranei* sp. nov. by cuticular details (table 1).

In the Early Cretaceous, species with ovulate organs of both *G. yimaensis* (ancestral) and *Ginkgo biloba* (modern) types coexisted (table 1). The oldest modern-type ovulate organs without pedicels when mature are described as *Ginkgo apodes* Zheng et Zhou from the Early Cretaceous Jehol Biota of western Liaoning, China. In the fossils, the pedicels are present only in the juvenile stage (Zhou and Zheng 2003; Zheng and Zhou 2004). Leaves ascribed to *G. apodes* are more or less deeply lobed (table 1). Another early Cretaceous species—*Ginkgo manchurica* (Yabe et Oishi) Meng et Chen from the Xiaoming'anbei Formation, northern Liaoning, China, erected for abundant deeply divided leaves—has been found to be associated with an ovulate organ bearing pedicellate ovules (*Ginkgo* sp. 1 in table 1; Deng et al. 2004). The cuticular structure of both Early Cretaceous ovulate organs mentioned above remains unknown.

In addition to the well-preserved ovulate organs, there are also several isolated seeds and imperfectly preserved ovulate organs that are believed to belong to the genus *Ginkgo*, including *Ginkgo huttonii* (Sternberg) Heer (characterized by deeply divided leaves with very different cuticles from the Middle Jurassic of Yorkshire, England; Harris et al. 1974), *Ginkgo* seeds from the Upper Cretaceous of Alberta, Canada (*Ginkgo* sp. 2 in table 1; Rothwell and Holt 1997), and *Ginkgo* seeds from the Paleocene of Amur Region, Far East Asia of Russia (Akhmetiev et al. 2002). No cuticular structures of the Late Cretaceous and Paleocene seeds have been described (table 1), and we have no knowledge of their ovulate organs.

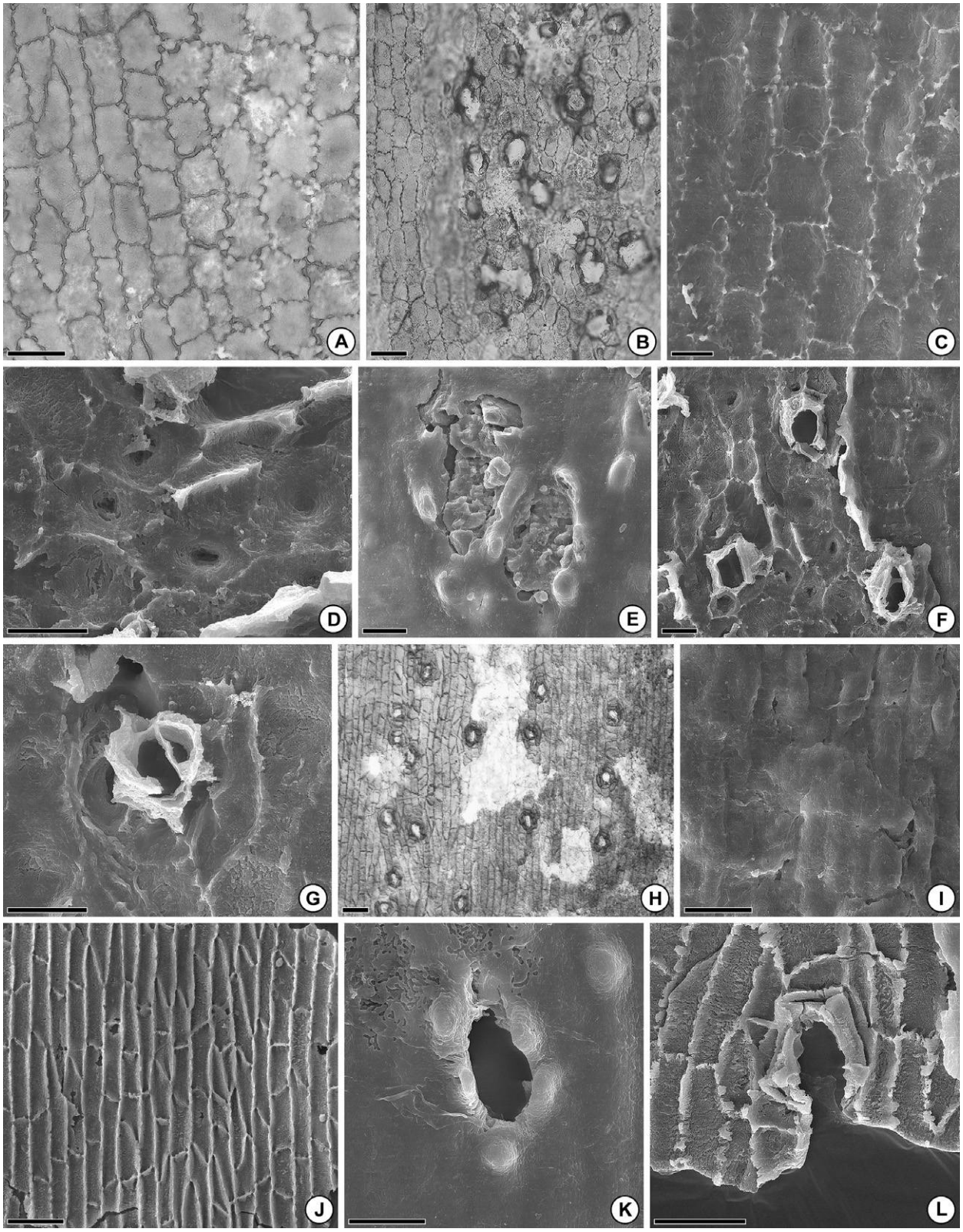

Fig. 4 Cuticular features of leaves associated with *Ginkgo cranei* sp. nov. *A*, Upper cuticle (LM), showing undulate flanges of anticlinal walls and indistinct papillae on periclinal walls of epidermal cells; cells elongated in costal zone and polygonal in intercostal zone (right). PP34022. *B–G*, Lower leaf cuticle. PP34022. *B*, LM, showing well-defined stomatal and nonstomatal zone. *C*, SEM inner view, elongated cells with undulate and pitted anticlinal wall flanges and smooth inner surface of periclinal walls in the nonstomatal zone. *D*, SEM inner view, showing isodiametric

There is no doubt that ovulate organs of *G. cranei* closely resemble those of *G. biloba*, and therefore it is of the modern type (fig. 1*A*, 1*B*; fig. 2*B* of Crane et al. 1990). By having smaller seeds, *G. cranei* can be distinguished from *G. biloba* (table 1). Furthermore, the characteristic cuticular structures of the fossil preclude them from being included in the modern species. As shown in figure 5*A*–5*C*, the seed integument of *G. biloba* bears numerous stomatal complexes, which are mostly monocyclic and sometimes with papillate subsidiary cells. The epidermal cells are also different in having less bulging periclinal walls (fig. 5*A*) and less thickened anticlinal wall flanges (fig. 5*B*, 5*C*), as compared with those of the fossil species. The leaves of *G. biloba* are also readily distinguished from the associated fossil leaves by having a higher density of stomata and more strongly papillate epidermal and subsidiary cells (figs. 4*B*, 4*E*–4*G*, 5*D*–5*G*). Moreover, the subsidiary cell papillae of *G. biloba* are sometimes finger-like and overhanging the stomatal pit (fig. 5*D*, 5*F*), and its epidermal cell anticlinal walls are not pitted and form less developed or indistinct flanges (fig. 5*E*, 5*G*).

Comparison between the Associated Leaves and Other Ginkgo Leaf Species

Only entire and notched leaves associated with *G. cranei* sp. nov. have so far been found. It is easy to separate them from many Jurassic and Early Cretaceous species characterized by deep-divided leaves (table 1).

In the Tertiary, more than 19 species of *Ginkgo* leaves have been reported, on the basis of leaf gross morphology and/or epidermal features (e.g., Florin 1936; Manum 1966; Samylina 1967; Uemura 1997; Hill and Carpenter 1999; Mustoe 2002; Golovneva 2010; for a brief summary, see table 1 of Quan et al. 2010). Recent studies reveal that most Tertiary ginkgo leaves with entire or notched margins should be ascribed to *Ginkgo adiantoides* (Ung.) Heer (e.g., Tralau 1968; Denk and Velitzelos 2002), because the subtle distinctions in leaf cuticle structure might be caused by ecological and intraspecific variation. According to such a concept, there were only three species of *Ginkgo* in the Northern Hemisphere during the Tertiary, that is, *G. adiantoides* (Ung.) Heer, *Ginkgo gardneri* Florin, and *Ginkgo jiayinensis* Quan, Sun et Zhou (Florin 1936; Tralau 1968; Quan et al. 2010). *Ginkgo jiayinensis* from the Paleocene of Heilongjiang Province, China, is clearly different from the present leaves in having amphistomatic leaves (Quan et al. 2010). *Ginkgo gardneri* from the Paleocene of Mull, United Kingdom, differs from the present leaves in having prominent papillae on periclinal walls of the upper cuticle (Florin 1936; Boulter and Kvaček 1989). The leaves from Almont are generally similar in gross morphology and cuticular structure to the widely reported species *G. adiantoides*, as defined by Tralau (1968) and Denk and Velitzelos (2002; see table 1 of Quan et al. 2010).

Given the consistency in occurrence and cuticular structure between the ovulate organs and associated leaves of the North Dakota specimens, it might be argued that both organs should be referred to *Ginkgo adiantoides* (Ung.) Heer, as originally treated by Crane et al. (1990). Here we briefly review the long-standing taxonomic problem of Tertiary ginkgos to explain the reason why the North Dakota Paleocene ginkgo ovulate organs deserve a new name.

The leaf polymorphism (heterophylly) in ginkgoalean plants of both living and fossil species is a commonly encountered phenomenon (Seward 1919; Zhou 1997, 2003; Czier 1998), and therefore cuticular features are important in the classification of ginkgo leaf fossils (e.g., Krassilov 1970; Watson et al. 1999). Unfortunately, the first described Tertiary *Ginkgo* species, *G. adiantoides* (Ung.) Heer (=*Salisburia adiantoides* Unger 1850), was established on the basis of some poorly preserved leaf imprints without preservation of any cuticle from the upper Miocene of Senigallia, northeastern Italy (Unger 1850; Heer 1878). This has led to taxonomic confusion of Tertiary ginkgo leaf fossils ever since. Florin (1936) reported the cuticular features of fossil leaves assigned to *G. adiantoides* for the first time, but his specimens were collected from the Pliocene of Frankfurt, Germany. Because the type specimens of *G. adiantoides* from Italy lack any cuticular features, Samylina (1967) therefore suggested establishing a new species for the German specimens with known cuticular features, *Ginkgo florinii* Samylina. In the following decades, more than a dozen Tertiary ginkgo leaf species have been erected chiefly on the basis of the cuticular characters (see above and table 1 of Quan et al. 2010). As mentioned above, some authors (e.g., Tralau 1968; Denk and Velitzelos 2002) insist that most Tertiary ginkgo morphotypes are conspecific and belong to *G. adiantoides* (Ung.) Heer, including the Pliocene leaves from Germany, despite the poor preservation and absence of cuticular details in the type. The name has been used in an even broader sense to include not only Neogene and Paleogene but also Cretaceous ginkgo leaves with entire margins (Baikovskaya 1956; Samylina 1963). Whether these leaves from different areas of the world and from strata ranging more than ~100 million years in age all belong to a single natural species is questionable.

Although the cuticular features of the ginkgo leaves from Almont generally resemble some of the leaf specimens re-

ordinary cells in stomatal zone with a central papilla. *E*, SEM outer view, showing stomatal complexes and indistinct papillae of subsidiary and ordinary cells. *F, G*, SEM inner view of stomatal complexes. Note the well-developed cuticle flanges between guard and subsidiary cells. *H*, *L*, Petiole cuticle. PP54859-B. *H*, LM, showing longitudinally oriented but mostly irregularly arranged stomata, and elongated ordinary cells with irregularly thickened periclinal walls and straight anticlinal walls. *I*, SEM view, showing bulging cell surfaces. *J*, SEM inner view, showing elongated ordinary cells with straight anticlinal wall flanges. *K*, SEM outer view, showing a stoma and indistinct subsidiary and ordinary cell papillae. *L*, SEM inner view of an incompletely dicyclic stoma, showing the encircling cells and developed cuticle flanges between guard and subsidiary cells and irregularly thickened and pitted anticlinal walls of epidermal cells. Scale bars = 40 μm (*A*, *B*), 20 μm (*C–G*, *K*, *L*), 40 μm (*H*, *I*), 50 μm (*J*).

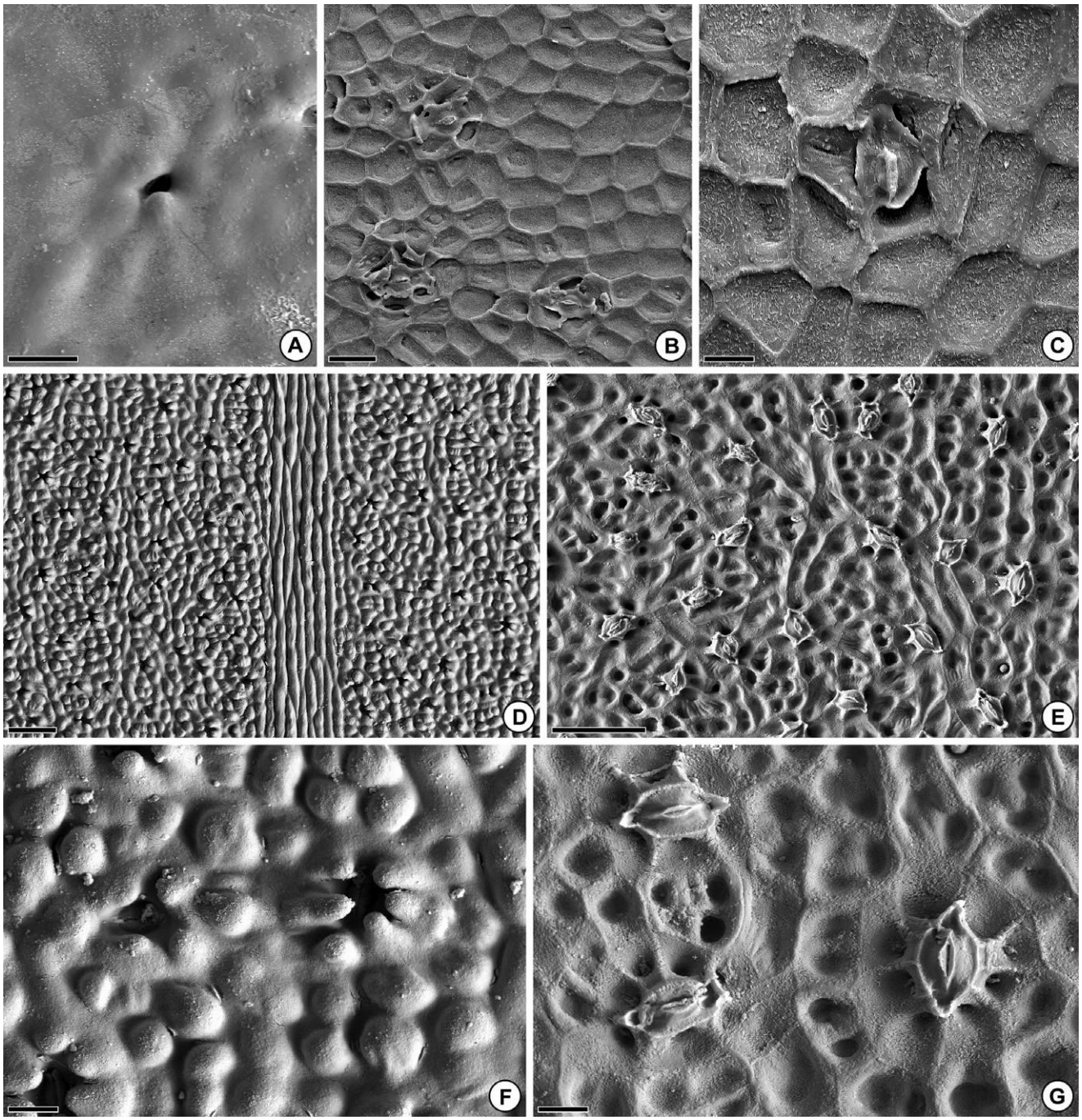

Fig. 5 Cuticular features of modern *Ginkgo*. *A–C*, Seed integument cuticles. *A*, Outer surface view, showing the stomatal pit, the periclinal walls of subsidiary and epidermal cells only slightly bulged. *B*, Inner surface view, showing stomata and slightly thickened flanges of epidermal cell anticlinal walls. *C*, Inner view of a stomatal complex, consisting of monocyclic subsidiary cells and well-cutinized guard cells with polar extensions. *D–G*, Leaf cuticle. *D*, Outer surface view, showing numerous stomata and developed epidermal cell papillae. *E*, Stomatal complexes in outer surface view, showing the developed subsidiary cell papillae, sometime figure-like and overhanging the pit. *F*, Inner surface view, showing numerous stomata and cavities of cells corresponding to the papillae on the outer surface. *G*, Three stomatal complexes in inner surface view, showing subsidiary and epidermal cells with developed cavities. Scale bars = 50 μm (*A*, *B*), 20 μm (*C*, *F*, *G*), 100 μm (*D*, *E*).

ferred to *G. adiantoides*, such as those described from the Tertiary of Europe by Tralau (1968) and Denk and Velitzelos (2002), no reproductive organs have been found with such leaf fossils. It is unreasonable, therefore, at least in the present state, to ascribe the North Dakota ovulate organs to an inadequately circumscribed species on the basis of foliage imprints. We proposed to name the ovulate organs as a new species, *G. cranei* (fig. 6).

Table 1

Comparisons between Ovulate Organs of Selected Fossil and Living *Ginkgo* Species

	G. yimaensis	*G. huttonii*	*G. ginkgoidea*	*Ginkgo* sp. 1	*G. apodes*	*Ginkgo* sp. 2	*G. cranei*	*G. biloba*
Organ type	Ancestral	Ancestral	Ancestral	Ancestral	Modern	?	Modern	Modern
No. ovules (seeds)	2–4 (2–4)	>2 (>2)	2–3 (2)	4 (2)	2–6 (1–3)	...	2 (1)	2 (1)
Seed size (mm)	10–15 × 8–12	10.5–12 × 8–10	9–12 × 8–12	7–14 × 6–13.5	7.3–8 × 6–8	Length >10	10–19 × 12–17	30 × 20
Stone size (mm)	7.5–12.5 × 5.5–9.5	6–7 × 5.5–6	...	10 × 7	6.5–7.5 × 5–7	10	8–15 × 7–12	>21 × 15
Pedicel	Present	Present?	Present	Present	Absent after mature	?	Absent	Absent
Integument outer cuticle:								
Thickness (μm)	5(–7.5)	...	5–9	...	...	...	Up to 12	>17
Cell size (μm)	12.5–22.5 × 35–85	...	15–45 × 25–90	...	...	...	12–15 × 20–40	8–13 × 17–36
Periclinal walls	Mottled	...	Smooth	...	...	...	Domelike on the outer surface	Slightly bulging on the outer surface
Anticlinal walls	Straight or slightly sinuous	...	Straight or slightly sinuous	...	...	...	With well-developed flanges	Straight, flanges less developed
Stomata in integument outer cuticle:								
Stomata size (μm)	150–175 × 100–125	...	50–90 × 60–120	...	...	...	Sparse, 70–110	Numerous, 74–124
Guard cells	Sunken	...	Sunken	...	...	...	Deeply sunken	Deeply sunken
Subsidiary cells	6–8	...	4–6(7)	...	...	...	5–6(9), not papillate	5–7, papillate
Encircling cells	Present occasionally	...	Present occasionally	...	...	...	Usually present, forming amphicyclic stomata	Usually absent and stomata monocyclic
Associated leaves:								
Leaf shape	More or less deeply divided	More or less deeply divided	Deeply divided	Deeply divided	More or less deeply divided	Shallowly divided	Upper margin wavy or notched; cuticles differing from *G. biloba*	Wavy or notched
Leaf cuticle	Rarely amphistomatic	Rarely amphistomatic	Hypostomatic	Rarely amphistomatic	...	...	Hypostomatic	Hypostomatic
Occurrence:								
Age	Middle Jurassic	Middle Jurassic	Middle Jurassic	Early Cretaceous	Early Cretaceous	Late Cretaceous	Late Paleocene	Present
Locality	Henan, China	Yorkshire, England	Scania, Sweden	Northern Liaoning, China	Eastern Liaoning, China	Alberta, Canada	North Dakota, USA	Tennessee, USA
Reference	Zhou and Zhang 1989	Harris et al. 1974	Tralau 1966; Yang et al. 2008	Deng et al. 2004	Zheng and Zhou 2004	Rothwell and Holt 1997	Crane et al. 1990; this study	Quan et al. 2010; Z. Zhou, C. Quan, and Y.-S. Liu, personal observations

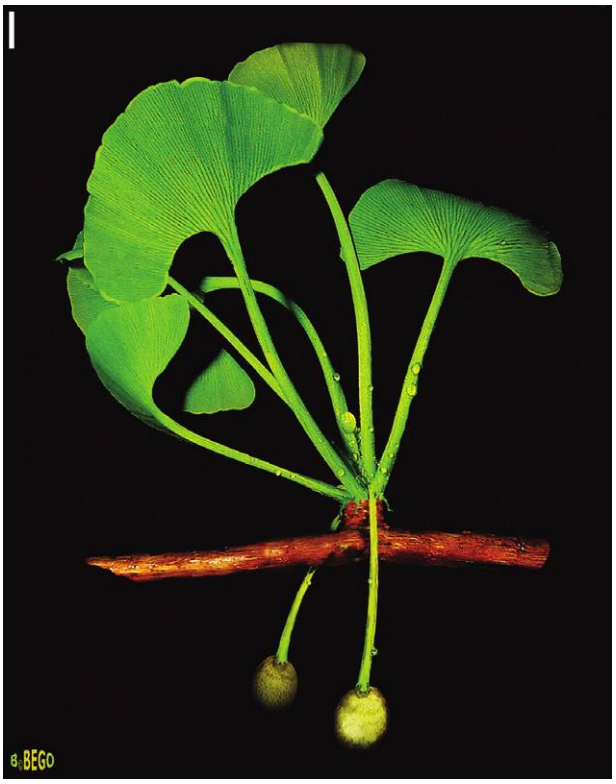

Fig. 6 Reconstruction of *Ginkgo cranei* Zhou, Quan et Liu, sp. nov., courtesy of B. M. Begović Bego, slightly modified. Scale bar = 1 cm.

Evolution of Genus Ginkgo

Extant *G. biloba* has been long hypothesized to have evolved from its ancestors by reduction (Coulter and Chamberlain 1917; Seward 1919; Florin 1949), but it is not until recent decades that the evolutionary history of the genus *Ginkgo* became clearer, because well-preserved fossil reproductive organs are rare. Recent discoveries provide conclusive evidence for the reduction of pollen organs, ovulate organs, and leaves in the geological ages through heterochrony (peramorphosis) from the Jurassic to the Paleogene (Zhou 1994, 1997, 2003, 2009; Rothwell and Holt 1997; Liu et al. 2006).

Although informative ovulate organ fossils have not been found so far from the Upper Cretaceous, *Ginkgo* ovulate organs recorded from the Middle Jurassic and Lower Cretaceous (Zhou and Zhang 1989; Deng et al. 2004; Zheng and Zhou 2004; Yang et al. 2008) and especially those from the Paleocene described in this study well corroborate this hypothesis.

The evolution trends of ovulate organs include the reduction in number and increase in size of ovules and the shortening and then disappearance of pedicels. The Jurassic species *G. yimaensis* and *G. ginkgoidea* bear ancestral (*yimaensis*-) type ovulate organs with 2–3 or 4 pedicellate ovules and 2–4 mature. Ovulate organs of the Paleocene *G. cranei* and the extant *G. biloba* are of the modern type, normally with only 2 sessile ovules and one maturing (table 1; fig. 6). The Early Cretaceous species *G. apodes* bears up to 6 ovules, with only 1–3 of them matured, and they are without pedicels (table 1). The ovules of ginkgos increase in size from 10–15 mm × 8–12 mm and 9–12 mm × 8–12 mm in the Jurassic species to 10–19 mm × 12–17 mm in the Paleocene species and then to ~30 mm × 20 mm in the extant species (table 1). In the Early Cretaceous, both types of *Ginkgo* ovulate organs coexisted (table 1).

It is of interest that some changes in microscopic features have also occurred in ovulate organs of different geological ages. From the Middle Jurassic to the Cenozoic, the outer cuticles of the integument appear thickened from 5–9 μm to more than 12 μm; meanwhile, epidermal cells decreased in size (table 1). We currently do not know whether these microscopic changes are consistent with macromorphological evolutionary trends, but an integument with a thicker outer cuticle and smaller cells may be beneficial to the survival of *Ginkgo* in unfavorable environments, when the ovules decrease in number but increase in size through geological time.

The leaves, despite being less informative, also exhibit changes in gross morphology. The deeply divided leaf is the dominant type in the Jurassic groups (e.g., Harris et al. 1974; Zhou and Zhang 1989; Yang et al. 2008), but in the Lower Cretaceous both deep- and shallow-divided ones existed (e.g., Deng et al. 2004; Zheng and Zhou 2004). However, leaf remains with nearly entire margins and a median notch are fairly common in the Upper Cretaceous, accompanied by shallow-divided type leaves (e.g., Rothwell and Holt 1997). In the Tertiary, the notched and entire-margin leaves are the predominant type (e.g., Manum 1966; Tralau 1968; Horiuchi and Kimura 1986; Uemura 1997; Mustoe 2002; Greenwood et al. 2005). Such evolutionary trends among leaves roughly correspond to the developmental sequences in *G. biloba*, since similar deeply divided leaves are borne on saplings, long shoots, or young trees.

Conclusions

Although the Jurassic and Cretaceous ginkgo fossils are highly informative for studying the evolutionary history of the genus *Ginkgo*, *Ginkgo cranei* sp. nov. is the only Tertiary species known so far with both well-preserved ovulate organs and associated leaves. Study of the North Dakota Paleocene ovulate organs of the modern type and associated leaves with entire margins sheds new light on the evolution of *Ginkgo* in the Tertiary by linking the Jurassic and Cretaceous species with the extant *Ginkgo biloba*. It also provides further corroborating evidence for the reduction hypothesis of ginkgo ovulate structures and is helpful to classify and understand Tertiary ginkgo species toward a natural classification.

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Literature Cited

Akhmetiev MA, TV Kezina, TM Kodroul, SR Manchester 2002 Stratigraphy and flora of the Cretaceous-Paleogene boundary layers in the southeast part of the Zeya-Bureya sedimentary basin. Pages 275–315 *in* MA Akhmetiev, AB Herman, MP Doludenko, IA Ignatiev, eds. Special volume, dedicated to the memory of the corresponding member of the USSR Academy of Sciences, Professor Vsevolod Andreevich Vakhrameev (the 90th anniversary of his birth). GEOS, Moscow. (In Russian with English abstract.)

Archangelsky SA 1965 Fossil Ginkgoales from the Ticò flora, Santa Cruz Province, Argentina. Bull Br Mus (Nat Hist) Geol 10:121–137.

Aulenback KR 2009 Identification guide to the fossil plants of the Horseshoe Canyon Formation of Drumheller, Alberta. University of Calgary Press, Calgary.

Baikovskaya TN 1956 Upper Cretaceous floras of northern Asia. Palaeobotanica 2:47–184. (In Russian.)

Boulter MC, Z Kvaček 1989 The Palaeocene flora of the Isle of Mull. Special Papers in Palaeontology. Vol 42. Palaeontological Association, London.

Clechenko ER, DC Kelly, GJ Harrington, CA Stiles 2007 Terrestrial records of a regional weathering profile at the Paleocene-Eocene boundary in the Williston Basin of North Dakota. Geol Soc Am Bull 119:428–442.

Coulter JM, CJ Chamberlain 1917 Morphology of gymnosperms. University of Chicago Press, Chicago.

Crane PR, SR Manchester, DL Dilcher 1990 A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. Fieldiana Geol 20:1–63.

Czier Z 1998 *Ginkgo* foliage from the Jurassic of the Carpathian Basin. Palaeontology 41:349–381.

Deng S, X Yang, Z Zhou 2004 An early Cretaceous *Ginkgo* ovule-bearing organ fossil from Liaoning, Northeast China and its evolutionary implications. Chin Sci Bull 49:1774–1776.

Denk T, D Velitzelos 2002 First evidence of epidermal structures of *Ginkgo* from the Mediterranean Tertiary. Rev Palaeobot Palynol 120:1–15.

Douglas JG 1969 The Mesozoic floras of Victoria. Pt 1, 2. Geol Surv Vic Mem 28:1–310.

Florin R 1936 Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesoischen Alters. I. Spezieller Teil. Palaeontogr Abt B 82:71–173.

——— 1949 The morphology of *Trichopitys heteromorpha* Saporta, a seed-plant of Palaeozoic age, and the evolution of the female flowers in the Ginkgoinae. Acta Horti Bergiani 15:79–109.

Golovneva LB 2010 Variability in epidermal characters of *Ginkgo tzagajanica* Samylina (Ginkgoales) from the Paleocene of the Tsagayan Formation (Amur region) and the taxonomy of Tertiary species of *Ginkgo*. Paleontol J 44:584–594.

Greenwood DR, SB Archibald, RW Mathewes, PT Moss 2005 Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape. Can J Earth Sci 42:167–185.

Harris TM 1935 The fossil flora of Scoresby Sound, East Greenland. 4. Ginkgoales, Coniferales, Lycopodiales and isolated fructifications. Meddelelser om Grønland, Kobenhavn.

Harris TM, W Millington, J Miller 1974 The Yorkshire Jurassic flora. IV. Ginkgoales and Czekanowskiales. British Museum (Natural History), London.

Heer O 1878 Miocene flora der insel Sachalin. Mem Acad Imp Sci St Petersb Ser 7 25:1–61.

Hill RS, RJ Carpenter 1999 *Ginkgo* leaves from Paleogene sediments in Tasmania. Aust J Bot 47:717–724.

Horiuchi J, T Kimura 1986 *Ginkgo tzagajanica* Samylina from the Palaeogene Noda Group, Northeast Japan, with special reference to its external morphology and cuticular features. Trans Proc Palaeontol Soc Jpn, NS, 142:341–353.

Kihm AJ, JH Hartman 1991 The age of the Sentinel Butte Formation, North Dakota. J Vertebr Paleontol 11:40A.

Krassilov VA 1970 An approach to the classification of Mesozoic ginkgoalean plants from Siberia. Palaeobotanica 18:12–19.

——— 1972 Meszoic flora from the Bureja River (Ginkgoales and Czekanowskiales). Nauka, Moscow. (In Russian.)

Kvaček J, HJ Falcon-Lang, J Daskova 2005 A new Late Cretaceous ginkgoalean reproductive structure *Nehvizdyella* gen. nov from the Czech Republic and its whole-plant reconstruction. Am J Bot 92: 1958–1969.

Liu XQ, CS Li, YF Wang 2006 The pollen cones of *Ginkgo* from the Early Cretaceous of China, and their bearing on the evolutionary significance. Bot J Linn Soc 152:133–144.

Manchester SR, DL Dilcher 1982 Pterocaryoid fruits (Juglandaceae) in the Paleogene of North America and their evolutionary and biogeographic significance. Am J Bot 69:275–286.

Manchester SR, KB Pigg, PR Crane 2004 *Palaeocarpinus dakotensis* sp.n. (Betulaceae: Coryloideae) and associated staminate catkins, pollen, and leaves from the Paleocene of North Dakota. Int J Plant Sci 165:1135–1148.

Manum S 1966 *Ginkgo spitsbergensis* n. sp. from the Paleocene of Spitsbergen and a discussion of certain Tertiary species of *Ginkgo* from Europe and North America. Nor Polarinst Arbok 1965:49–58.

Mustoe GE 2002 Eocene *Ginkgo* leaf fossils from the Pacific Northwest. Can J Bot 80:1078–1087.

Pigg KB, ML DeVore 2010 Floristic composition and variation in late Paleocene to early Eocene floras in North America. Bull Geosci 135–154.

Pigg KB, SR Manchester, ML DeVore 2008 Fruits of Icacinaceae (tribe Iodeae) from the Late Paleocene of western North America. Am J Bot 95:824–832.

Quan C, G Sun, Z Zhou 2010 A new Tertiary *Ginkgo* (Ginkgoaceae) from the Wuyun Formation of Jiayin, Heilongjiang, northeastern China and its paleoenvironmental implications. Am J Bot 97:446–457.

Rothwell GW, B Holt 1997 Fossils and phenology in the evolution of *Ginkgo biloba*. Pages 223–230 *in* T Hori, RW Ridge, W Tulecke, P Del Tredici, J Trémouillaux-Guiller, H Tobe, eds. *Ginkgo biloba*, a global treasure: from biology to medicine. Springer, Tokyo.

Royer DL, LJ Hickey, SL Wing 2003 Ecological conservatism in the "living fossil" *Ginkgo*. Paleobiology 29:84–104.

Samylina VA 1963 The Mesozoic flora of the lower course of the Aldan River. Palaeobotanica 4:57–139. (In Russian.)

——— 1967 The final stages of the history of the genus *Ginkgo* L. in Eurasia. Bot J 52:303–316. (In Russian with English abstract.)

Seward AC 1919 Fossil plants. IV. Cambridge University Press, Cambridge.

Stanislavsky FA 1973 The new genus *Toretzia* from the Upper

Triassic of the Donetz Basin, and its relation to the genera of the order Ginkgoales. Paleontol J 1:88–96. (In Russian.)

Tralau H 1966 Botanical investigations in the fossil flora of Eriksdal in Fyledalen, Scania. Sver Geol Unders Arsb Ser C 611:1–63.

——— 1968 Evolutionary trends in the genus *Ginkgo*. Lethaia 1:63–101.

Uemura K 1997 Cenozoic history of *Ginkgo* in East Asia. Pages 207–221 *in* T Hori, RW Ridge, W Tulecke, P Del Tredici, J Trémouillaux-Guiller, H Tobe, eds. *Ginkgo biloba*, a global treasure: from biology to medicine. Springer, Tokyo.

Unger F 1850 Genera et species plantarum fossilium. Wilhelm Braumüller, Vienna.

Watson J, SJ Lydon, NA Harrison 1999 Consideration of the genus *Ginkgoites* Seward and a redescription of two species from the Lower Cretaceous of Germany. *Cretaceous Res* 20:719–734.

Yang XJ, EM Friis, ZY Zhou 2008 Ovule-bearing organs of *Ginkgo ginkgoidea* (Tralau) comb. nov., and associated leaves from the Middle Jurassic of Scania, South Sweden. Rev Palaeobot Palynol 149:1–17.

Zheng SL, ZY Zhou 2004 A new Mesozoic *Ginkgo* from western Liaoning, China and its evolutionary significance. Rev Palaeobot Palynol 131:91–103.

Zhou ZY 1991 Phylogeny and evolutionary trends of Mesozoic ginkgoaleans: a preliminary assessment. Rev Palaeobot Palynol 68: 203–216.

——— 1994 Heterochronic origin of *Ginkgo biloba*–type ovule organs. Acta Palaeontol Sin 33:131–139. (In Chinese with English summary.)

——— 1997 Mesozoic ginkgoalean megafossils: a systematic review. Pages 183–206 *in* T Hori, RW Ridge, W Tulecke, P Del Tredici, J Trémouillaux-Guiller, H Tobe, eds. *Ginkgo biloba*, a global treasure: from biology to medicine. Springer, Tokyo.

——— 2003 Mesozoic ginkgoaleans: phylogeny, classification and evolutionary trends. Acta Bot Yunnanica 25:377–396. (In Chinese with English abstract.)

——— 2009 An overview of fossil Ginkgoales. Palaeoworld 18:1–22.

Zhou ZY, BL Zhang 1989 A Middle Jurassic *Ginkgo* with ovule-bearing organs from Henan, China. Palaeontogr Abt B 211:113–133.

——— 1992 *Baiera hallei* Sze and associated ovule-bearing organs from the Middle Jurassic of Henan, China. Palaeontogr Abt B 224: 151–169.

Zhou ZY, SL Zheng 2003 The missing link in *Ginkgo* evolution. Nature 423:821–822.

Zhou ZY, SL Zheng, LJ Zhang 2007 Morphology and age of *Yimaia* (Ginkgoales) from Daohugou Village, Ningcheng, Inner Mongolia, China. Cretac Res 28:348–362.