

The presumed ginkgophyte *Umaltolepis* has seed-bearing structures resembling those of Peltaspermales and Umkomasiales

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The origins of the five groups of living seed plants, including the single relictual species *Ginkgo biloba*, are poorly understood, in large part because of very imperfect knowledge of extinct seed plant diversity. Here we describe well-preserved material from the Early Cretaceous of Mongolia of the previously enigmatic Mesozoic seed plant reproductive structure *Umaltolepis*, which has been presumed to be a ginkgophyte. Abundant new material shows that *Umaltolepis* is a seed-bearing cupule that was borne on a stalk at the tip of a short shoot. Each cupule is umbrella-like with a central column that bears a thick, resinous, four-lobed outer covering, which opens from below. Four, pendulous, winged seeds are attached to the upper part of the column and are enclosed by the cupule. Evidence from morphology, anatomy, and field association suggests that the short shoots bore simple, elongate *Pseudotorellia* leaves that have similar venation and resin ducts to leaves of living *Ginkgo*. *Umaltolepis* seed-bearing structures are very different from those of *Ginkgo* but very similar to fossils described previously as *Vladimaria*. *Umaltolepis* and *Vladimaria* do not closely resemble the seed-bearing structures of any living or extinct plant, but are comparable in some respects to those of certain Peltaspermales and Umkomasiales (corystosperms). Vegetative similarities of the *Umaltolepis* plant to *Ginkgo*, and reproductive similarities to extinct peltasperms and corystosperms, support previous ideas that *Ginkgo* may be the last survivor of a once highly diverse group of extinct plants, several of which exhibited various degrees of ovule enclosure.

Umaltolepis | Cretaceous | Mongolia | *Ginkgo*

The living species *Ginkgo biloba*, which today is native only to China (1), is the single remaining species of a group of plants that was once more widespread and more diverse. Fossil plants with characteristic *Ginkgo*-like leaves, or similar, more deeply divided forms (e.g., *Ginkgoites* leaves associated with *Karkenian*; *Baiera* leaves associated with *Yimaia*), are recorded from the Early Permian (Cisuralian) onward, and the morphology of their seed-bearing structures, where known, has been compared with that of extant *Ginkgo* (2). Two other extinct genera, *Umaltolepis* and *Toretzia*, have also been interpreted as part of the *Ginkgo* lineage (2–5), but in both cases the morphology of their seed-bearing structures is poorly understood, and the attribution to Ginkgoales is based mainly on the venation, resin bodies, and stomata of associated simple, strap-shaped, parallel-veined leaves assigned to *Pseudotorellia* (e.g., 2, 6).

In this paper we provide information on *Umaltolepis*, based on abundant and exceptionally well-preserved lignified material from the Early Cretaceous (Aptian–Albian; ~100–125 Ma) of central Mongolia. The *Umaltolepis* seed-bearing structure is umbrella-like, quite different from how it was originally described and also very distinct from the seed-bearing structures of fossil and living *Ginkgo*. The seed-bearing structures of *Umaltolepis* are more

similar to those of certain Peltaspermales and Umkomasiales (corystosperms), although they are unique in many respects. The combination of *Ginkgo*-like leaves with peltasperm-like and corystosperm-like seed-bearing structures exhibited by the reconstructed *Umaltolepis* plant is consistent with previous ideas that interpret extant *G. biloba* as the last survivor of a once highly diverse lineage that included not only extinct close relatives of living *G. biloba*, such as *G. yimaensis* and *Yimaia*, but also plants assigned to Peltaspermales, Umkomasiales, and perhaps other groups within a broadly defined Ginkgoopsida (7, 8).

Results

The Early Cretaceous fossils described here consist of shoots with attached seed-bearing structures. They also include leaves (*Pseudotorellia resinosa*) (9) that are linked to the shoots by association evidence as well as by features of morphology and anatomy. A detailed description of the fossils, illustrated by additional light and scanning electron micrographs, is provided in *SI Appendix*.

Order—Vladimariales Gordenko.

Family—Umaltolepidaceae Zhou.

Genus—*Umaltolepis* Krassilov, here emended.

Emended generic diagnosis—Woody plant with long and short shoots (Figs. 1C and 2E and G). Short shoots with alternating

Significance

Understanding the origins of the five groups of living seed plants requires well-supported hypotheses of their relationships to extinct groups, many of which are poorly understood. New information from the Early Cretaceous of Mongolia on the enigmatic extinct plant *Umaltolepis* shows that its leaves are similar to those of *Ginkgo*, but its seed-bearing structures are unique, and more comparable to those of certain extinct Peltaspermales and Umkomasiales. *Umaltolepis* provides new data for understanding relationships among living and fossil seed plants and supports previous ideas that *Ginkgo biloba* may be the sole surviving relict of a once very diverse group of Mesozoic seed plants.

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pseudowhorls of persistent bud scales and persistent leaf bases (Fig. 2 *G* and *H*). Short shoots generally branched, commonly with a seed-bearing structure near the tip (Fig. 1 *C*). Seed-bearing structure a radially symmetrical cupule borne on a short stalk that expands into a prominent flange just below the cupule base (Fig. 1 *B* and *H*). Cupule consisting of a slender central column bearing an umbrella-like, four-lobed covering at the apex (Fig. 1 *B–F*). Each cupule lobe thick, resinous, and with a thick outer cuticle (Fig. 1 *B–F*). Cupule lobes extending downward to clasp the central column just above the level of the flange (Fig. 1 *F* and *H*). Near its tip, just below where the cupule covering is attached, the column is four-angled and bears four winged seeds, one along each angle (Fig. 2 *A–D*). Each seed is pendulous and entirely covered by one of the cupule lobes. The micropyle of each seed (Fig. 2 *A–D*) is inside the cupule just above the level of the flange (*SI Appendix*).

Species—*Umaltolepis mongoliensis* Herrera, Shi, Ichinnorov, Takahashi, Bugdaeva, Herendeen, et Crane sp. nov.

Species diagnosis—Each pseudowhorl of persistent bud scales on the short shoots consisting of about 8 to 10 scales. Each

foliar pseudowhorl on the short shoots composed of five persistent leaf bases. Leaf bases with two lateral flaps flanking a broad cup-shaped leaf abscission scar (Fig. 2 *G* and *H*). Cuticle of leaf bases bearing deciduous to persistent, unicellular trichomes (Fig. 3 *E*). Isolated four-lobed cupules ovate to elliptical in outline (Fig. 1 *B* and *D–F*). Each lobe with a semicircular distal notch, which clasps the four-angled central column (Fig. 1 *E*, *G*, and *H*). Outer cuticle of cupule lobes thick, with scattered, more or less longitudinally oriented stomata (Fig. 3 *A* and *C*). Six to eight resin ducts in each cupule lobe. Seeds winged, each pendulous from near the apex of the column. Each seed elliptical to ovate in outline, composed mainly of wing tissue with abundant resin bodies (Fig. 2 *A–D*). Seed body very small, wider than long, obovate to more or less triangular in outline, with a small apical micropyle.

Detailed description—See *SI Appendix*.

Holotype—PP56446 (Figs. 1 *B* and 2 *A–C*).

Other material—PP56332–PP56445, PP56447, PP56450–PP56464, PP56470–PP56479.

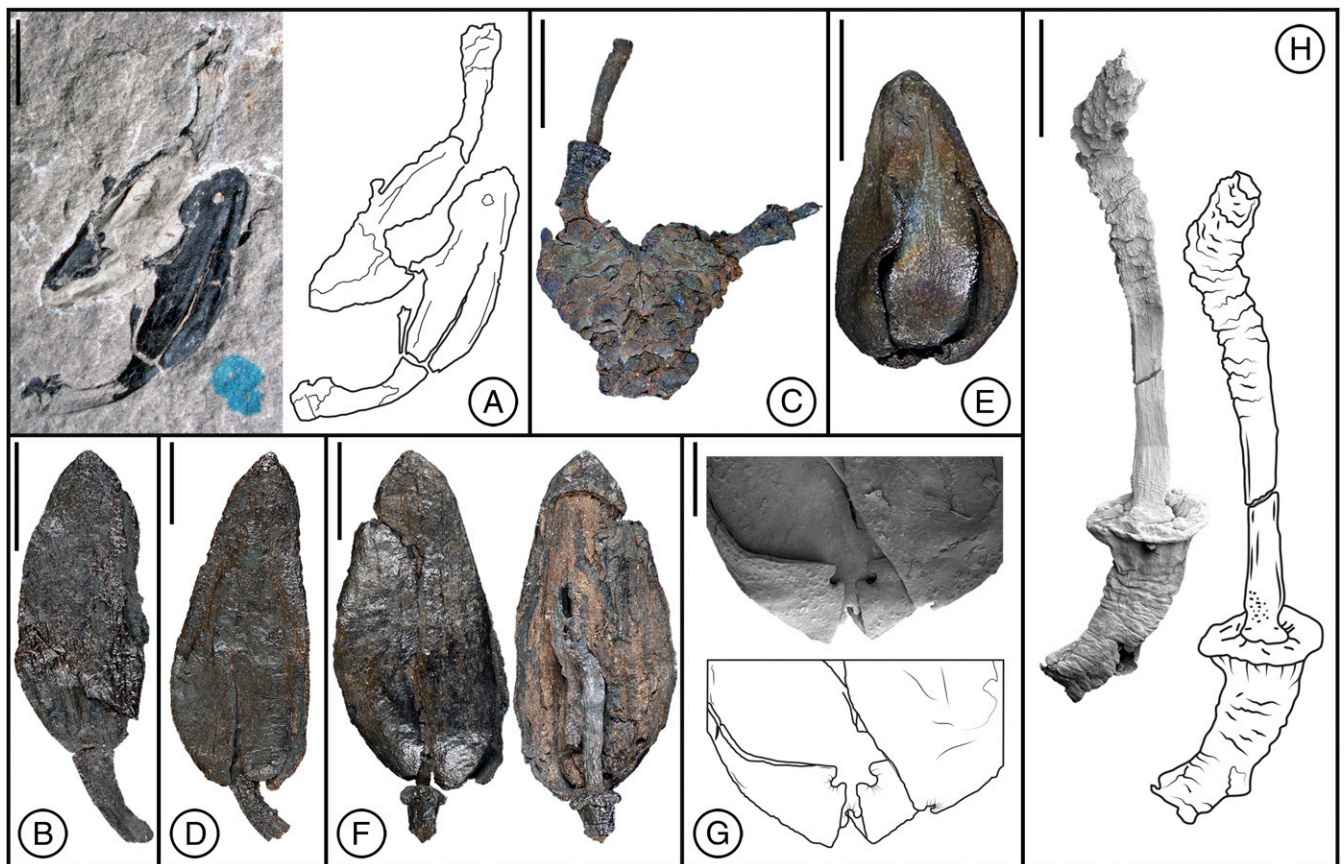


Fig. 1. Light and scanning electron micrographs (SEM) of seed-bearing structures of *Umaltolepis vachrameevii* (*A*) from the Late Jurassic of the Bureya River Basin, Siberia, Russia, and *U. mongoliensis* sp. nov. from the Early Cretaceous of Mongolia (*B–H*). (*A*) *U. vachrameevii* [holotype: Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences (FSCEATB FEBRAS), Russia, specimen no. 515–271a] with line drawing showing two isolated seed-bearing structures. Specimen on the *Left* shows the impression of the stalk and cupule in the sediment. Specimen on *Right* shows the stalk and three of the four cupule lobes. (*B*) *U. mongoliensis* seed-bearing structure (holotype: PP56446) showing stalk and closed cupule. Dissection of this specimen revealed three seeds in situ (Fig. 2 *A–C*). (*C*) Branched short shoot with two incomplete seed-bearing structures each consisting of a stalk, flange, and a broken central column (PP56348). (*D*) Seed-bearing structure showing the stalk and three partially open lobes of the cupule (PP56425). (*E*) Three-dimensionally preserved open four-lobed cupule (lacking the stalk and column) from which the seeds have been shed: note the stippled appearance of the outer surface indicating the presence of abundant sunken stomata (PP56429). (*F*) A partially open four-lobed cupule attached to the stalk and column. (*Right*) The same cupule with two lobes removed to better expose the central column and the umbrella-like form of the cupule (PP56347). (*G*) SEM with line drawing showing the notch in the tip of each cupule lobe. Each notch clasps the four-angled central column (PP56375). (*H*) SEM with line drawing of an isolated stalk of a seed-bearing organ showing the flange and central column: note the corrugated surface of the column in its distal part (PP56334). [Scale bars, 5 mm (*A–F*); 2 mm (*G* and *H*).]

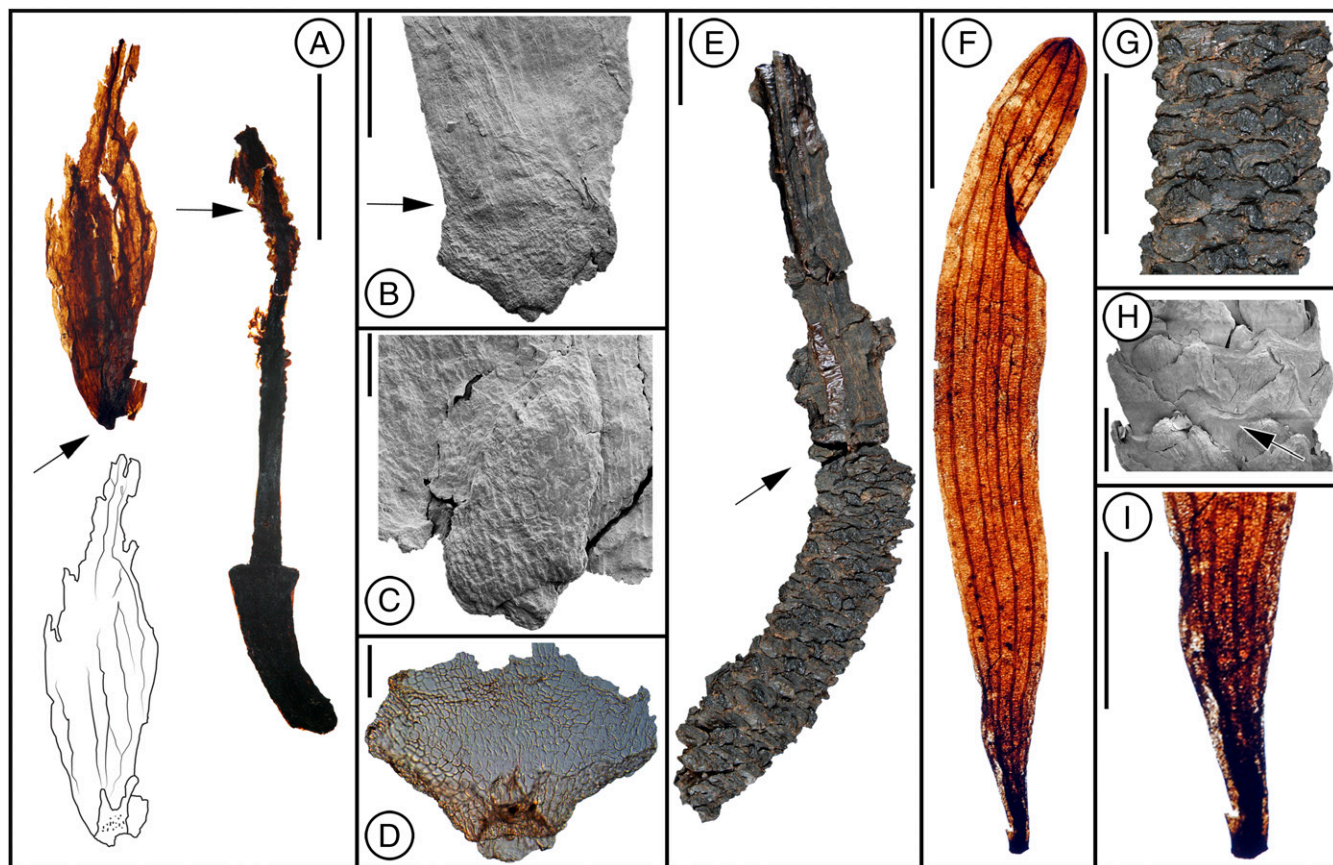


Fig. 2. Light and SEM of seed-bearing structure and shoots of *Umaltolepis mongoliensis* sp. nov. and associated leaves of *Pseudotorellia resinosa* from the Early Cretaceous of Mongolia. (A) Stalk showing flange and central column (Right) from the seed-bearing organ in Fig. 1B (holotype) showing one of three winged seeds (Top Left; line drawing below) dissected from the cupule: note seed body (Lower arrow). Each winged seed was attached to the upper part of the column and completely enclosed by the cupule: note remains of wing tissue (orange) attached to the edges of the column (Upper arrow). (B) SEM of micropylar region of second winged seed dissected from holotype (Fig. 1B) showing the transition (arrow) between the wing and the seed body that has an apical micropyle. (C) SEM of micropylar region of third winged seed dissected from holotype (Fig. 1B) showing the transition between the wing and seed body: note apical micropyle. (D) Isolated and macerated seed body from specimen in *SI Appendix*, Fig. S16F, showing isodiametric outlines of epidermal cells and micropyle (PP56428). (E) Fragment of branch showing transition (arrow) between a short shoot (below) and a long shoot (above): note numerous persistent bud scales and leaf bases on the short shoot (PP56338). (F) Leaf of *P. resinosa* associated with the seed-bearing structures of *U. mongoliensis*: note four longitudinal veins within the leaf that converge at the leaf apex and resin ducts between the veins (PP56268). (G) Detail of short shoot from E showing at least six growth increments, each consisting of a pseudowhorl of persistent bud scales below, with a pseudowhorl of persistent leaf bases above. (H) SEM of short shoot showing three pseudowhorls of persistent triangular bud scales alternating with two pseudowhorls of leaf bases (arrow) (PP56409). (I) Detail from F showing leaf base: note that two veins enter the lamina and that each dichotomizes, resulting in four longitudinal veins within the leaf. [Scale bars, 5 mm (A, E, F, and G); 2.5 mm (H); 500 μ m (B); 200 μ m (D); 100 μ m (C).]

Repository—Paleobotanical Collections, Department of Geology, The Field Museum, Chicago.

Etymology—Specific epithet refers to Mongolia, where the fossils were found.

Age, stratigraphic unit, and locality—Aptian–Albian stage, ~100–125 Ma, Early Cretaceous. Tevshiin Govi Formation. Tevshiin Govi coal mine, central Mongolia (45°58'54" N, 106°07'12" E).

Assignment to *Umaltolepis* and Comparison with Previously Described Species. The type species of *Umaltolepis*, *U. vachrameevii* (Fig. 1A), described from the Late Jurassic of the Bureya River Basin, Siberia (4), was reconstructed originally as an unlobed or bilobed bract with a single inverted seed in its axil, which Krassilov interpreted as a highly reduced fertile axis. However, examination of the type material (Fig. 1A) shows that *U. vachrameevii* is structurally very different from what Krassilov envisaged and is very similar to *U. mongoliensis*.

There are small differences in the *Pseudotorellia* leaves that are associated with *U. mongoliensis* (Fig. 1B–H) and *U. vachrameevii* (see below; Fig. 1A), but otherwise *U. mongoliensis* differs from

U. vachrameevii in only two relatively minor features: the absence of papillae on the lateral subsidiary cells of stomata on the outer cuticle of the cupule and the slightly larger cupule size (*U. mongoliensis*: ~9–19 mm long, 5.6–9 mm wide vs. *U. vachrameevii*: ~8–14 mm long, 4–6 mm wide) (*SI Appendix*).

Three other species of *Umaltolepis* have been reported from Lower Jurassic to Lower Cretaceous deposits based on compression and impression fossils (*SI Appendix*, Table S2). Both *U. coleoptera* from the Early Jurassic of Iran (10) and *U. hebeiensis* from the Early Cretaceous of China (11, 12) are known from only a few isolated cupules that are not well preserved. Both are probably valid records of the genus, but are difficult to compare with the better-preserved material from Mongolia. *Umaltolepis rarinervis* is better known based on material from the Bureya River Basin in Siberia (4), and is probably slightly younger (Early Cretaceous: Valanginian) than the material of *U. vachrameevii*. *Umaltolepis rarinervis* differs from *U. mongoliensis* in that the outer cuticle of the cupule has papillate epidermal cells and stomata that are arranged in more regular longitudinal rows than in *U. mongoliensis*. The impressions of elongate resin ducts in

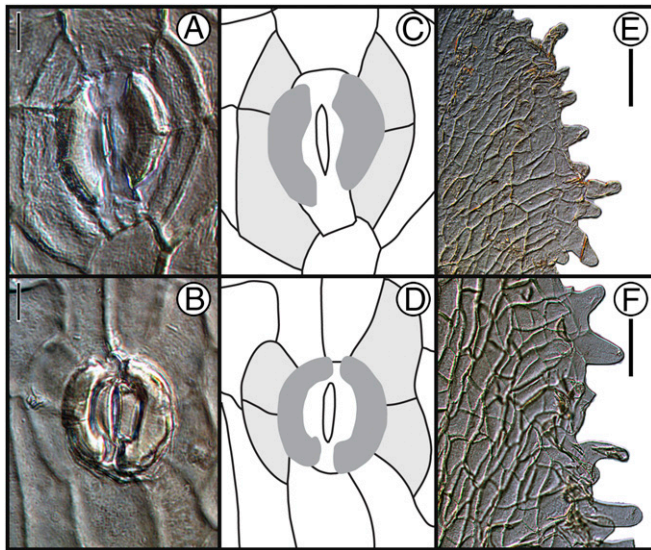


Fig. 3. Light micrographs showing similarities between cuticles of the stomata on the cupule lobes of *Umaltolepis mongoliensis* (A and C) and *Pseudotorellia resinosa* (B and D), and similarities between the persistent leaf bases of *U. mongoliensis* and leaves of *P. resinosa* (E and F). (A) Stomatal complex from cupule lobe of *U. mongoliensis* showing a stoma with four lateral subsidiary cells and bow-shaped ridges flanking the stomatal pit (PP56447). (B) Stomatal complex from leaf lamina of *P. resinosa* showing a stoma with four lateral subsidiary cells and bow-shaped ridges flanking the stomatal pit (PP56448). (C) Line drawing of A; note four lateral subsidiary cells (light gray) and bow-shaped ridges (dark gray). (D) Line drawing from B; note four lateral subsidiary cells (light gray) and bow-shaped ridges (dark gray). (E) Well-developed unicellular trichomes on a persistent leaf base isolated from short shoot of *U. mongoliensis* (PP56430). (F) Well-developed unicellular trichomes on the lamina margin near the leaf base of *P. resinosa* (PP56449). [Scale bars, 20 μ m (A and B); 100 μ m (E and F).]

cupules of *U. rarinervis* also appear branched, rather than unbranched, as is the case in *U. mongoliensis* (SI Appendix).

Among other fossils, *U. mongoliensis* is remarkably similar to the isolated, well-preserved seed-bearing structures described as *Vladimaria octopartita* from the Middle Jurassic of European Russia (13). The shoots and leaves of *Vladimaria* are unknown, but based on the seed-bearing structures there is no doubt that the two genera are closely related. *Vladimaria* was interpreted as a “composite seed-bearing capsule” in which each locule contained a pendulous winged seed (13). Like *U. mongoliensis*, *Vladimaria* is thick, resinous, and has a thick outer cuticle with sunken guard cells that have distinct butterfly-like flanges at their junction with the subsidiary cells (SI Appendix, Table S2). The most significant differences between the two taxa are that the cupule of *U. mongoliensis* splits into four lobes at maturity, whereas that of *V. octopartita* splits into eight, and that *U. mongoliensis* is borne on a more slender stalk. Stomata on the cupule lobes are also less regularly oriented in *Vladimaria* than in *U. mongoliensis*. However, in all other respects *Vladimaria* and *U. mongoliensis* are very similar. As in *U. mongoliensis*, the cupule of *V. octopartita* was attached to the apex of a central column and a few specimens show that, before dehiscence, the cupule lobes clasped the central column just above a prominent flange on the stalk as in *U. mongoliensis* (SI Appendix).

Leaves of *Umaltolepis mongoliensis*. Krassilov (4) noted the pattern of co-occurrence between seed-bearing structures of *U. vachrameevii* and leaves of *Pseudotorellia angustifolia*, which in a few cases were attached to short shoots like those bearing *U. vachrameevii*. A similar pattern linking *U. coleoptera* and leaves of *Pseudotorellia roobana* was reported (10). In addition to this evidence based on field association, there are also similarities be-

tween the resin bodies and epidermal features of the seed-bearing organs and those of the shoots and leaves. The consistent association of these kinds of leaves and reproductive structures is also seen at Tevshii Govi. Together with morphological and anatomical similarities, this suggests strongly that the short shoots of *Umaltolepis* bore simple, elongate, and deciduous *Pseudotorellia* leaves (Fig. 4).

Two species of *Pseudotorellia*, *P. resinosa* (Fig. 2 F and I) and *P. palustris*, are consistently associated with the seed-bearing structures and shoots of *U. mongoliensis* at Tevshii Govi (9) (SI Appendix, Table S1). Both species have thick cuticles with scattered, more or less longitudinally oriented stomata, in which the two guard cells are sunken and have butterfly-like flanges of cuticle at their junction with the subsidiary cells (Fig. 3). These features are similar to those on the cupule cuticle of *U. mongoliensis* (Fig. 3 A and C).

Of the two species of *Pseudotorellia* at Tevshii Govi (9), *P. resinosa* is linked more strongly to *U. mongoliensis* than to *P. palustris*, by its abundant resin, which is consistent with the abundant resin found in the cupule lobes, seeds, and shoots of *U. mongoliensis* and also by the form of the stomata, which have two lateral bow-shaped cuticular ridges flanking the stomatal pit (Fig. 3 B and D). Still more decisive in linking *U. mongoliensis* and *P. resinosa* is that the margin of the leaf base in isolated *P. resinosa* leaves has unicellular trichomes (Fig. 3F) that are identical to those on the persistent leaf bases attached to the short shoots of *U. mongoliensis* (Fig. 3E). These trichomes are not present in the leaves of *P. palustris*. Leaves of *P. resinosa* that are associated with *U. mongoliensis*, and leaves of *P. angustifolia* associated with *U. vachrameevii*, are also very similar. As with the cupules, the only differences are that *P. resinosa* lacks the papillae seen on the lateral subsidiary cells of the stomata in *P. angustifolia* (4) and that



Fig. 4. Reconstruction of *Umaltolepis mongoliensis* sp. nov. showing four seed-bearing structures and attached *Pseudotorellia resinosa* leaves. Note that three seed-bearing organs have split at the level of the flange into four lobes releasing the seeds. The seeds (Right) were probably membranous and wind-dispersed. The cupule has been shed from one of the seed-bearing structures leaving the stalk, flange and column attached to the short shoot. Most, probably all, of the small dark spots on leaves are the remains of fungal stomata.

P. angustifolia has well-defined stomatal bands, whereas in *P. resinosa* the stomata are scattered and less regularly arranged (9).

Discussion

Ecology and Biology of the *Umaltolepis*–*Pseudotorellia* plant. Records of the *Umaltolepis*–*Pseudotorellia* plant across Asia, from both Jurassic and Lower Cretaceous sediments (4, 10–12), indicate that it was once widespread, and its abundance in many samples at Tevshiiin Govi indicates that it was an important element in the swamp vegetation that created the lignite. Also present were Umkomasiales (*Umkomasia mongolica*) (14), extinct conifer-like plants (*Krassilovia*) (15), archaic probable Pinaceae (*Schizolepidopsis*) (16), early Pinaceae (*Pityostrobus*, *Picea*) (17), and Cupressaceae [*Elatides* (18); *Pentakonos*, *Stutzeliastrobus* (19)]. Diversity in the swamp flora was low, perhaps including only about 10 woody species, all of which have leaves with thick cuticles (except *Podozamites*) (9). Other than the tiny leaves of a probable epiphytic or climbing fern, the flora is devoid of pinnately compound leaves. In all cases the leaves in the fossil assemblage are needle-like (*Schizolepidopsis*, *Picea*) (16, 17), scale-like (*Stutzeliastrobus*) (19), or simple and parallel-veined (*Podozamites*, both species of *Pseudotorellia*) (9).

Based on what is known so far, all of the woody plants in the Tevshiiin Govi swamp vegetation seem likely to have been wind-pollinated. The pendulous seeds, with the micropyle positioned just above the level of the flange where the cupule lobes separate from the stalk, suggest that this was probably also the case in *Umaltolepis*. Pollination probably involved a hanging pollination drop and buoyant pollen as in many extant conifers (20). Krassilov (4) associated bisaccate pollen (*Entylissa umaltensis*) with *U. vachrameevii* based on their occurrence on the surface of *P. angustifolia* leaves, but we regard this hypothesized link as unconfirmed.

We have been unable to establish conclusively if pollen had direct access to the micropyles of the seeds in *U. mongoliensis*; however, we think that this was likely the case, as has been shown in other Mesozoic seed plants (e.g., *Caytonia*, *Umkomasia*) in which the ovules are partially or completely enclosed (21–23). *Umaltolepis* provides another example of ovule enclosure among Mesozoic seed plants, the main presumed advantage of which would have been protection of the ovules. This appears especially to have been the case in *Umaltolepis* in which the cupule is thick and resinous, whereas the seeds are thin-walled. Partial separation of the cupule lobes at maturity and shedding of the cupule from the stalk would have provided the means by which the seeds were released (Fig. 4). We have not identified dispersed seeds in the Tevshiiin Govi samples, suggesting that the seeds, like those of some other Mesozoic plants (e.g., Bennettitales), were delicate and not easily preserved.

Phylogenetic Relationships of the *Umaltolepis*–*Pseudotorellia* Plant.

The order Vladimariales was erected to accommodate the seed-bearing organs of *Vladimaria* (13), and given the similarities to *Umaltolepis*, we place both genera within this order. Krassilov (4) proposed the family name Pseudotorelliaceae to accommodate the leaves of *P. angustifolia* and seed-bearing organs of *U. vachrameevii* (Fig. 1A). However, *Umaltolepis* is best placed in the family Umaltolepidaceae (2, 5), considering that *Pseudotorellia* is reserved for a specific kind of strap-shaped, parallel-veined leaf. We include *U. mongoliensis* in Umaltolepidaceae, along with *U. vachrameevii* (4), *U. rarinervis* (4), and also, less securely, *U. coleoptera* (10) and *U. hebeiensis* (11, 12). We regard *Vladimaria* as closely related to Umaltolepidaceae, but we exclude it from the family until it is better understood as a “whole plant.”

Previous authors have considered the *Umaltolepis*–*Pseudotorellia* plant as closely related to Ginkgoales (2, 4, 6, 9, 24), based on similarities between the cuticles of *Pseudotorellia* leaves and those of living *Ginkgo*, including stomata that are sparse and scattered in ill-defined bands on the presumed abaxial surface, together with

the similarities between the elongated resin bodies that occur between adjacent veins in both the fossil and the modern leaves. There are also similarities in leaf venation. In both *Pseudotorellia* and extant *Ginkgo*, two veins enter the leaf lamina from the petiole, and each then dichotomizes one, two, or more times (9).

It is more difficult to reconcile the structure of the seed-bearing organs of *Umaltolepis* with those of *Ginkgo*. In *Ginkgo*, *Yimaia* (Middle Jurassic) (25, 26), and probably related fossil forms with simple leaves such as *Nagrenia samylinae* (Middle Jurassic) (27) and *Nehvizdyella bipartita* (Late Cretaceous) (28), there is no evidence of the umbrella-like structure seen in *Umaltolepis*. In all these taxa the single, terminal, erect seed on each branch of the seed-bearing structure is very different from the several pendulous seeds present in *Umaltolepis* and *Vladimaria*. More productive comparisons are with the seed-bearing organs of Peltaspermales and Umkomasiales (SI Appendix, Table S2).

Recent reviews of the Peltaspermales include Peltaspermaceae (e.g., *Autunia*, *Peltaspermum*), Angaropeltaceae (e.g., *Angaropeltis*), Vetlugospermaceae (e.g., *Vetlugospermum*), and Matatiellaceae (e.g., *Matatiella*) (29–32). In most cases, such as *Autunia*, *Peltaspermum*, *Vetlugospermum*, *Matatiella*, and other genera, there is no indication that the seeds are attached to a stalk. Instead, they appear to be naked on the lower surface of an open peltate, lobed, fan-shaped to disc-shaped structure (SI Appendix, Table S2). This is different from the situation in *Umaltolepis* and *Vladimaria* where the seeds are attached to the central column and almost completely enclosed.

Potentially more similar are the seed-bearing organs of Permian Angaropeltaceae, including *Angaropeltis* (formerly *Cardiolepis*), *Permoxylocarpus*, and *Sylvocarpus*, in which the seeds are more completely enclosed (32–35). In *Angaropeltis* the enclosing structure also appears resinous, and the associated leaves are simple, strap-shaped, and parallel-veined (29, 36) (SI Appendix, Table S2). Unfortunately, the preservation of *Angaropeltis* and similar genera means that the details of seed attachment are not well understood.

A further interesting comparison for the seed-bearing structures of *Umaltolepis* and *Vladimaria* is provided by the cupules of Umkomasiales (13, 14). In Umkomasiales, as in *Umaltolepis*, the seeds are also partially to completely enclosed within a “cupule,” which is formed by the stalk on which the seed is borne, together with a bilobed or multilobed flap of tissue (14, 30). In most Umkomasiales there is one seed in each cupule, but *Umkomasia resinosa* from the early Middle Triassic of Antarctica has resinous cupules like *Umaltolepis*, and when each cupule has two seeds, one flap of tissue corresponds to each seed (37). *Umaltolepis* and *Vladimaria* may reflect a situation in which four or eight corystosperm cupules are fused around a central column. *Umkomasia uniramia* from the Triassic of Antarctica, in which four to eight cupules are borne in a whorl on a single stalk, potentially approaches this condition (38). Each multicupule unit of *U. uniramia* is also borne at the tip of short shoots similar to those of *Umaltolepis*.

Both Peltaspermales and Umkomasiales commonly have pinnately compound leaves, which are often referred to the genera *Lepidopteris* or *Dicroidium*, respectively (7, 30). However, the leaves of *Angaropeltis* and *Permoxylocarpus* are simple, and referred to the genus *Phylladoderma* (32). Similarly, the fan-shaped basal elements seen in some pinnate *Dicroidium* leaves resemble *Ginkgo* foliage (39), and the leaves of some *Umkomasia*-like plants (e.g., *Kannaskoppia*) are very *Ginkgo*-like (30). The resin cells that occur in the mesophyll of *Dicroidium* leaves (40) also recall those of *Ginkgo*. Given the similarities between leaves of *P. resinosa* and *P. palustris*, it may be significant that preliminary data on patterns of cooccurrence suggest that *P. palustris* may be the leaf of the corystosperm reproductive structure *Umkomasia mongolica* (9).

Current phylogenetic analyses of seed plant relationships based on morphological data include only a small proportion of the potentially relevant extinct diversity and contain significant missing data as well as many uncertain homologies.

However, inclusion of *Umaltolepis* in a previous published matrix (ref. 41, based mainly on ref. 42) places it in a polytomy with several other groups (SI Appendix). Depending on exactly how key characters of *Umaltolepis* and other extinct taxa are scored, the taxa in the polytomy include *Glossopteris*+*Pentoxylon*, *Ginkgo*+cordaites+conifers, corystosperms, peltasperms, the BEG group (Bennettitales+Erdmanthicales+Gnetales), and *Caytonia*+angiosperms. This relatively unresolved phylogenetic result is consistent with the observation that the *Umaltolepis*–*Pseudotorellia* plant is morphologically distinct from all previously recognized groups of seed plants.

Implications for Seed Plant Evolution. Reconstruction of the *U. mongoliensis*–*Pseudotorellia resinosa* plant (Fig. 4) together with improved information on the seed-bearing structures adds significantly to knowledge about extinct seed plants from the Mesozoic. This is important for understanding large-scale patterns of seed plant evolution, including the origin of angiosperms, and for attempts to harmonize information on the molecular phylogenetics of living seed plants with paleobotanical data. It is especially interesting that the leaves and short shoots of the *Umaltolepis*–*Pseudotorellia* plant are similar to those of living *Ginkgo*, whereas the seed-bearing structures are more similar to those of certain extinct Peltaspermales and Umkomasiales. The diversity of Peltaspermales includes several forms in which the seeds are almost fully enclosed by the umbrella-like peltate heads of the seed-bearing structures. Similarly, the possibility of a closer relationship between Umkomasiales and *Ginkgo* has been emphasized recently based on information on the corystosperm ovulate reproductive structures [e.g., *Doylea* (43) and *Umkomasia* (14)].

The emerging picture suggests that *Ginkgo*, and very closely related extinct genera, such as *Yimaia* (25) and *Karkeniania* (44, 45), are part of a larger group of *Ginkgo*-like plants that also included simple-leaved forms, such as *Nagrenia* (27) and *Nehvizdyella* (28). Corystosperms (Umkomasiales) and peltasperms may be closely related to this group. These ideas need to be tested in a new generation of seed plant phylogenetic analyses that include critical assessments of putative homologies among diverse reproductive structures and new information on other potentially relevant, but currently poorly understood, extinct forms (e.g., Angaropeltaceae, *Toretzia*). Nevertheless, indications so far recall the concept of the Ginkgoopsida, a large and very inclusive clade defined by Meyen (7, 8) based on similarities in short shoots, leaves, cuticles, seeds, and pollen morphology. Meyen's concept of Ginkgoopsida included not only Ginkgoales, but also Peltaspermales, Umkomasiales, and other extinct plants. This idea, supported by the potential links highlighted here between *Ginkgo*, Peltaspermales, and Umkomasiales, suggests that *G. biloba* may be the sole surviving relict of a group of seed plants that was once even more diverse than has been commonly recognized.

Materials and Methods

Plant Locality. Fossil plants described in this study were collected in central Mongolia from the Tevshiiin Govi Formation, which comprises sandstones and siltstones with thick coal and lignite seams, at the Tevshiiin Govi locality, a small open-cast lignite mine, ~220 km southwest of Ulaanbaatar (45°58'5" N, 106°07'12" E; paleolatitude: ~44° N; 55° E). The age of the Tevshiiin Govi Formation is Aptian–Albian (ca. 125–100 Mya) based on analyses of palynomorphs (46, 47) and stratigraphic correlations with the

Khukhteeg Formation (48). Thirty-five samples of siltstone and lignite were collected from the Tevshiiin Govi mine, of which 27 are rich in mesofossils that are exquisitely preserved. The Tevshiiin Govi lignites are composed of diverse macerals and a minimal amount of detrital sediment. We presume that these lignites are largely autochthonous in origin. The fossil taxon described in this paper is common to very abundant in the 27 lignite samples. Most of the specimens are isolated four-lobed cupules (~500 specimens) (SI Appendix). However, many four-lobed cupules attached to short shoots have also been recovered (SI Appendix).

Fossil Preparation. Lignite samples were prepared as previously described (16, 18). Fossil specimens were cleaned with dilute hydrochloric acid for half an hour, followed by concentrated hydrofluoric acid (50%) for 1 d. Specimens were then thoroughly washed and soaked in distilled water for 1 wk with changes of water every day. Fossils were picked from the disaggregated lignite under Leica stereomicroscopes using a small brush and insect forceps. Specimens were selected for further study using a Carl Zeiss EVO 60 scanning electron microscope at The Field Museum of Natural History in Chicago. Large specimens were photographed at the Chicago Botanic Garden using a Canon Rebel camera with 100-mm macrolens attached to a Stackshot system, and the digital photos were merged using Helicon Focus software. Several specimens were examined using a General Electric dual-tube X-ray computed tomography scanner in the Department of Organismal Biology and Anatomy at the University of Chicago. Tomographic sections were analyzed using Avizo 8.1. Cuticles were obtained by macerating shoots, leaves, cupules, and seeds in dilute household bleach (~1% sodium hypochlorite solution) after removal of residual sediment. Maceration times varied from several seconds to several minutes, depending on the degree of lignification. Large pieces of cuticle were mounted on slides with glycerin jelly and sealed with nail polish. Fossils selected for anatomical study were soaked in 10% (wt/vol) hydrochloric acid followed by Aerosol OT [10% (wt/vol) solution of sodium dioctyl sulfosuccinate in alcohol]. Specimens were then taken through a series of ethanol concentrations (70% to absolute ethanol) and embedded in Technovit 7100 following the prescribed mounting protocol. Transverse and longitudinal sections ~4–7 μm thick were made of the embedded material using a Leica 2030 microtome. Slides were mounted in Hydromount no. 17966.

Phylogenetic Analyses. We analyzed the relationships of *U. mongoliensis*–*P. resinosa* with respect to other seed plants by adding it to a published morphological matrix (41, 42). Character scoring for *Umaltolepis*–*Pseudotorellia* is available in SI Appendix. The matrix used includes 51 taxa and 102 morphological characters. *Tetraxylopteris* was used as the outgroup. Parsimony analyses were conducted using Winclada (49). All characters were treated as equally weighted and unordered. A combination of ratchet searches (to detect islands of trees) followed by a heuristic search was used. An initial set of most parsimonious trees was generated using the "Ratchet" option (200 iterations/replicate; hold 1 tree/iteration; random constraint level = 10; three sequential ratchet runs). Trees obtained from the ratchet analysis were submitted to the tree bisection-reconnection branch swapping with the maximum number of trees saved set to 5,000 (hold = 5,000). The analysis yielded 2,573 most parsimonious trees [length = 318, consistency index (CI) = 44, retention index (RI) = 79].

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