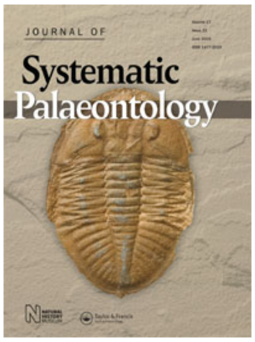

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Diversity and homologies of corystosperm seed-bearing structures from the Early Cretaceous of Mongolia

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New discoveries of corystosperm seed-bearing structures from the Tevshiin Govi locality, Mongolia, which is of Early Cretaceous (Aptian–Albian) age, show that the individual seed-bearing units of *Umkomasia mongolica* were borne in a cone, as also documented for the very similar reproductive units of *Doylea tetrahedrasperma*. New material from the Tevshiin Govi locality also documents two additional species of *Umkomasia* – *U. corniculata* sp. nov. and *U. trilobata* sp. nov. – that most likely grew in a different environment to *U. mongolica*. The occurrence of three different *Umkomasia* species in the Early Cretaceous of Mongolia, together with other records from the Early Cretaceous of the Northern Hemisphere, indicate that previous concepts of corystosperms, based mainly on material from the Southern Hemisphere, need to be revised. The consistent reproductive architecture of the seed-bearing structures in all three corystosperm species, with a bract subtending a variously modified axis bearing ovules, is similar to the situation in *Ginkgo* and conifers. These underappreciated architectural commonalities among the reproductive structures of major groups of seed plants are likely significant for a deeper understanding of seed plant evolution and require further exploration.

Keywords: corystosperms; *Umkomasia*; Early Cretaceous; Mongolia; seed; seed ferns

Introduction

Umkomasiaceae, commonly known as corystosperms, are a key group of extinct Mesozoic plants that have long been central in discussions of the phylogeny and evolution of living seed plants (Thomas 1933; Crane 1985; Doyle 2006; Hilton & Bateman 2006; Taylor *et al.* 2006; Taylor & Taylor 2009; Rothwell & Stockey 2016). The family was proposed by Thomas (1933) for the seed-bearing organs *Umkomasia* H. H. Thomas, *Pilophorosperma* H. H. Thomas and *Spermatocodon* H. H. Thomas, the pollen organs of *Pteruchus* H. H. Thomas and the bifurcate leaves of *Dicroidium* Gothan, based on compressed material from the Late Triassic Molteno flora in Natal, South Africa. Although the different organs were not attached, their consistent association in the same bed, the similarities in the structure of their cuticles, and the presence of the same kind of pollen in the pollen sacs of *Pteruchus* and in the micropyle of *Umkomasia* seeds, suggest strongly that they were produced by the same group of plants, a hypothesis that has been widely accepted (Crane 1985; Rothwell & Serbet 1994; Doyle 2006; Hilton & Bateman 2006; Taylor *et al.* 2006; Taylor & Taylor 2009).

The close association of *Umkomasia*, *Pteruchus* and *Dicroidium* has been confirmed by studies of corystosperm fossils from other parts of the Southern Hemisphere (e.g. Townrow 1965; Holmes & Ash 1979; Holmes 1982; Retallack 1983; Cantrill *et al.* 1995; Yao *et al.* 1995; Axsmith *et al.* 2000; Holmes & Anderson 2005; Pattemore 2016b) and these plants have been reconstructed as small to large woody shrubs and trees based on anatomy of the stems associated with *Dicroidium* leaves (Archangelsky 1968; Meyer-Berthaud *et al.* 1992, 1993; Decombeix *et al.* 2014). Corystosperms are thought to have evolved in the palaeotropics during the Late Permian (Kerp *et al.* 2006; Abu Hamad *et al.* 2008, 2017), later becoming a very prominent element in Gondwanan terrestrial ecosystems during the Triassic (Anderson & Anderson 1983, 2003).

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Corystosperms appear to have declined significantly in the Southern Hemisphere prior to the biotic crisis around the Triassic–Jurassic boundary (Retallack 1977; Ash 1986; Bomfleur & Kerp 2010; Pattemore 2016a), although a few relicts may have persisted until as late as the Eocene (McLoughlin *et al.* 2008).

While corystosperms have been considered typical Triassic Gondwanan plants, occurrences of probable corystosperms from the Triassic (Zan *et al.* 2008) and Jurassic (Harris 1964; Kirchner & Müller 1992) of the Northern Hemisphere suggest that the group was much more widespread during the Mesozoic, and this is confirmed by recent descriptions of unequivocal corystosperms from the Early Cretaceous of Western North America (Stockey & Rothwell 2009; Rothwell & Stockey 2016) and North-eastern Asia (Shi *et al.* 2016). This Early Cretaceous material has added new morphological and anatomical information on the structure of corystosperm cupules, which is important because of their potential relevance for understanding the homologies of other seed plant reproductive organs, including perhaps the anatropous ovules of angiosperms (Crane 1985; Frohlich 2003; Doyle 2006; Hilton & Bateman 2006; Frohlich & Chase 2007; Taylor & Taylor 2009).

In this paper, we provide new information on the seed-bearing structures described previously from Early Cretaceous lignites in central Mongolia as *Umkomasia mongolica* G. Shi, A. B. Leslie, Herend., F. Herrera, Ichinnorov, Takahashi, Knopf & P. R. Crane (Shi *et al.* 2016). We emend the diagnosis of *U. mongolica* to include features of the seed cones and we suggest that the leaf of *U. mongolica* is *Pseudotorellia palustris* G. Shi, F. Herrera, Herend., A. B. Leslie, Ichinnorov, Takahashi, & P. R. Crane (Shi *et al.* 2018). We reject the reassignment of *U. mongolica* to the genus *Doylea* Stockey & G. W. Rothwell, as well as the assessment that *Doylea* and *U. mongolica* are only distantly related to corystosperms (Rothwell & Stockey 2016). We also describe two new species of corystosperm cupule from different sedimentary facies at the same locality as *U. mongolica*. These three *Umkomasia* species document unexpected diversity among Early Cretaceous corystosperms, and together with *Doylea tetrahedrasperma* Stockey & G. W. Rothwell imply that our previous understanding of corystosperms based mainly on material from the Southern Hemisphere requires significant revision.

Material and methods

The mesofossils described in this paper were collected from the Tevshiin Govi Formation at Tevshiin Govi, a small open-cast lignite mine (45°58′54″ N, 106°07′12″ E) in central Mongolia, *c.* 220 km southwest of Ulaanbaatar (Leslie *et al.* 2013), during field seasons in 2011, 2012, 2013 and 2015. The Tevshiin Govi Formation is one of several Lower Cretaceous terrestrial coal/lignite bearing units in eastern and central Mongolia (Erdenetsogt *et al.* 2009). It comprises a sequence of terrestrial and fluvio-lacustrine deposits including conglomerates, sandstones and siltstones, as well as thick coal and lignite seams (Ichinnorov 2003; Ichinnorov *et al.* 2012). The formation is considered to be of Aptian–Albian age (125–100.5 Ma) based on stratigraphical correlations (Erdenetsogt *et al.* 2009) and palynomorphs from the Tevshiin Govi locality (Ichinnorov 2003; Ichinnorov *et al.* 2012).

Extensive collections have been made from the Tevshiin Govi locality, with about 100 samples from 49 individual sample collection sites processed and analysed; each sample is designated using a three-digit number with the prefix ‘PSH’ (e.g. PSH261). Most of these collections have come from the lignites, which have yielded abundant and well-preserved material, including the specimens of *Umkomasia mongolica* described previously (Shi *et al.* 2016) and the new specimens of this species described here. Much less extensively collected have been the clastic sediments associated with the lignites. The two new species of *Umkomasia* come from six Tevshiin Govi samples (PSH177, 281, 286, 287, 288, 295), four of which (PSH177, 286, 287, 288) are from the carbonaceous sandy siltstones above the lignites.

The lignites at Tevshiin Govi locality contain diverse, abundant and exquisitely preserved plant fossils, including fertile and sterile fronds of the filmy fern *Hymenophyllum iwatsukii* F. Herrera *et al.* (Hymenophyllaceae) (Herrera *et al.* 2017a), leaves of *Podozamites* (Presl) Braun, *Pseudotorellia* Florin (Shi *et al.* 2018) and seed-bearing structures of *Umkomasia* (Shi *et al.* 2016) and *Umaltolepis* Krassilov (Herrera *et al.* 2017b). Also important in the Tevshiin Govi assemblages are abundant conifer leaves as well as seed cones and seeds of Cupressaceae (Shi *et al.* 2014; Herrera *et al.* 2016b), probable stem group and crown group Pinaceae (Leslie *et al.* 2013; Herrera *et al.* 2016a), and the putative voltzian conifer *Krassilovia* F. Herrera, G. Shi, A. B. Leslie, Knopf, Ichinnorov, Takahashi, P. R. Crane & Herend (Herrera *et al.* 2015).

Mesofossils are abundant in the poorly consolidated lignites and carbonaceous sandy siltstones of the Tevshiin Govi Formation and were extracted from bulk samples by disaggregation and sieving in soap and water. Specimens were then cleaned in HCl and HF, thoroughly rinsed in water, dried in air and sorted under a stereomicroscope. Cuticles of leaf fossils from Tevshiin Govi (Shi *et al.* 2014, 2018; Herrera *et al.* 2016b), including cuticles of *Pseudotorellia palustris*, were obtained by gentle maceration in dilute household bleach (*c.* 1% sodium hypochlorite solution), but the same technique applied to *Umkomasia* seed-bearing structures yielded only small cuticular fragments.

Mesofossils prepared for anatomy were first soaked in 10% HCl, followed by Aerosol OT (10% solution of sodium dioctyl sulfosuccinate in alcohol). Specimens were taken through a series of ethanol concentrations (70% to absolute ethanol) and embedded in Technovit 7100 following the manufacturer's protocol. Embedded mesofossils were sectioned into transverse and longitudinal sections *c.* 4–7 μm thick using a Leica 2030 microtome at the Chicago Botanic Garden.

The mesofossils were examined, photographed and measured using a Leica M165 C stereomicroscope with a Leica DMC4500 digital camera system at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Selected specimens and small pieces of cuticles were mounted on stubs, coated with gold, and examined and photographed using a Leo1530 VP field-emission scanning electron microscope at the Nanjing Institute of Geology and Palaeontology and a Carl Zeiss EVO 60 scanning electron microscope at The Field Museum, Chicago, Illinois, USA. All type and figured specimens are deposited in the Palaeobotanical Collections of The Field Museum. Additional specimens are deposited at the Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia. As far as possible, authority abbreviations follow the International Plant Names Index (IPNI).

Systematic palaeontology

Order **Umkomasiales** Doweld, 2001
Family **Umkomasiaceae** Petriella, 1981
Genus ***Umkomasia*** H. H. Thomas, 1933

Type species. *Umkomasia macleanii* H. H. Thomas, 1933.

Umkomasia mongolica G. Shi, A. B. Leslie, Herend., F. Herrera, Ichinnorov, Takahashi, Knopf & P. R. Crane, here emended.
(Figs 1A–D, 2)

2016 *Umkomasia mongolica* G. Shi, A. B. Leslie, Herend., F. Herrera, Ichinnorov, Takahashi, Knopf & P. R. Crane: 1419.

2016 *Doylea mongolica* (G. Shi, A. B. Leslie, Herend., F. Herrera, Ichinnorov, Takahashi, Knopf & P. R. Crane); Rothwell & Stockey: 929.

Material. Holotype: PP55648 deposited in the Paleobotanical Collections, The Field Museum, Chicago, USA, first illustrated by Shi *et al.* (2016, fig. 1) and re-illustrated here in Fig. 1A–D. Other illustrated material: PP56614 (Fig. 2A, B), PP56615 (Fig. 2C, D), PP56616 (Fig. 2E, F), PP56617 (Fig. 2G, H).

Emended diagnosis. Seed cone consists of a central axis bearing deciduous, helically and loosely arranged lateral seed-bearing units. Individual seed-bearing units consist of a narrow elongate bract, subtending and partially fused to an axis that bifurcates into two narrow, broadly diverging, cupule stalks, the distal parts of which are strongly inflexed (curved adaxially) relative to the cone axis, but reflexed (curved abaxially) relative to the cupule bearing axis. Each cupule stalk bears a single cupule that contains a single erect seed. The inflexed cupule stalks result in the micropyle of the seed being oriented back towards the cone axis and the base of the seed-bearing unit. Each cupule consists of the inflexed cupule stalk with the seed borne at or near its tip, and two lateral flaps that are partially fused to form a bilobed structure. Apex of the cupule often with a short, generally inconspicuous, protrusion. Apex of the cupule and the lateral flaps smooth, lacking teeth. Seeds ovate in lateral outline, three-angled with a flat basal triangular attachment scar.

Remarks. *Umkomasia mongolica* is similar to *U. corniculata*, a new species described in this paper, in the organization of seed-bearing units. Both species have a bifurcate axis bearing two cupules, and individual cupules are formed by the cupule stalk and two lateral flaps. Each cupule partially encloses a single seed. However, *U. mongolica* differs from *U. corniculata* in having cupules that lack a prominent, robust protrusion at the apex, and that lack teeth on the surface. In addition, compared with *U. corniculata*, the cupule stalks of each seed-bearing unit in *U. mongolia* are longer, more slender and more broadly diverging.

Description and comments. The material of *Umkomasia mongolica* described previously, including the type specimen (Shi *et al.* 2016; Fig. 1A–D), consists of seed-bearing units composed of a bract that subtends and is partially fused to a bifurcate axis that bears a cupule at the tip of each stalk. These structures were interpreted as deciduous, lateral units shed from a cone-like structure (Shi *et al.* 2016). Subsequent discoveries of similar material from North America (Rothwell & Stockey 2016) confirmed that seed-bearing structures very like those of *U. mongolica* were borne in a cone. New collections from Mongolia now document this for *U. mongolica* and enable us to emend our original diagnosis to include features of the seed cones. Comparisons with the two new species described here, *U. corniculata* and *U. trilobata*, also permit

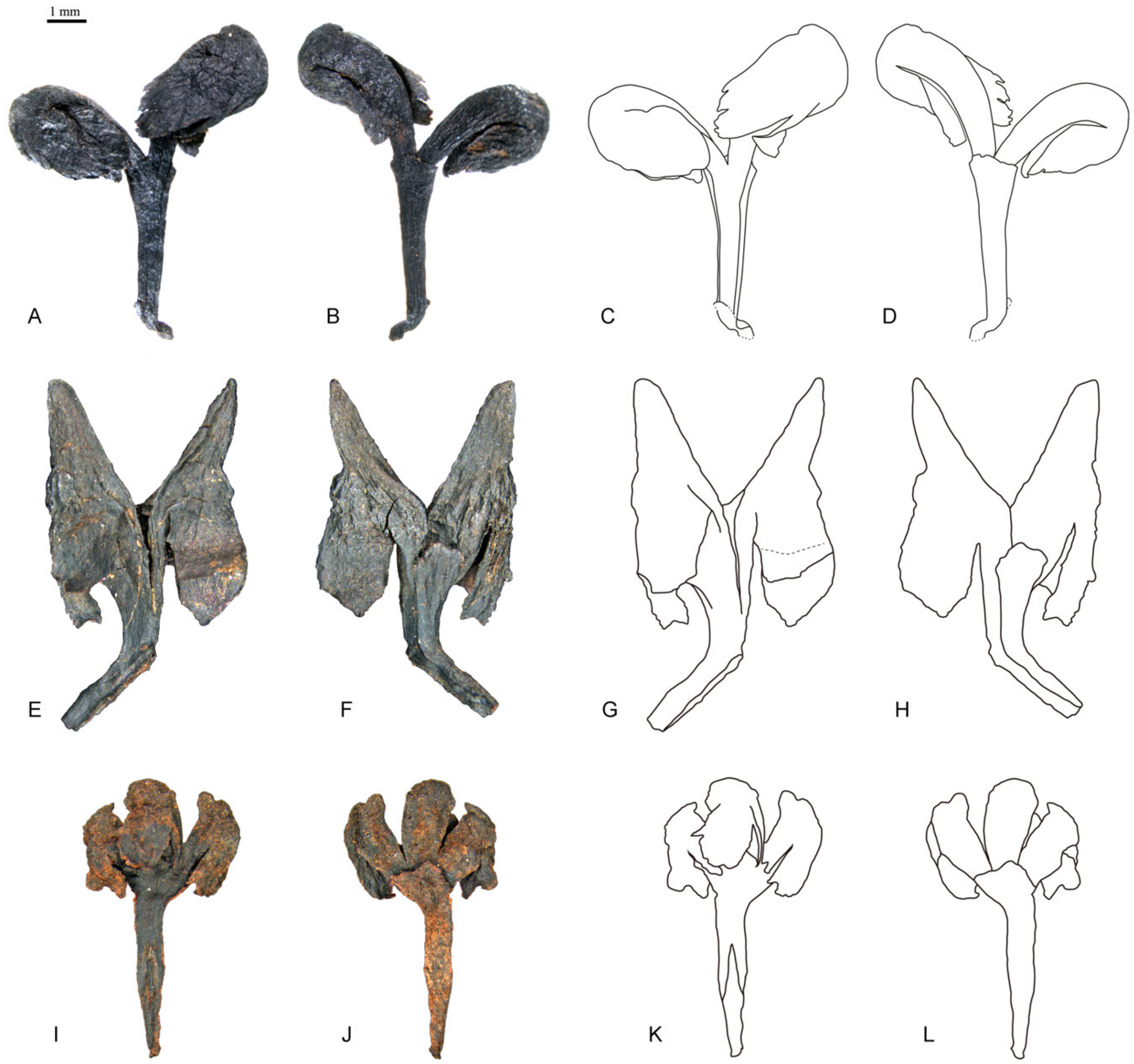


Figure 1. Light micrographs and drawings of *Umkomasia* seed-bearing units from the Lower Cretaceous of Tevshiin Govi, central Mongolia. **A–D,** *Umkomasia mongolica*, holotype, PP55648, sample PSH261; **A,** adaxial view; **B,** reverse of specimen in A; **C,** line drawing of A; **D,** line drawing of B. **E–H,** *Umkomasia corniculata* sp. nov., PP56628, sample PSH286; **E,** adaxial view; **F,** reverse of E; **G,** line drawing of E; **H,** line drawing of F. **I–L,** *Umkomasia trilobata* sp. nov., PP56683, sample PSH286; **I,** adaxial view; **J,** reverse of specimen in I; **K,** line drawing of I; **L,** line drawing of J.

a comparative assessment that was not possible previously, which also allows our original diagnosis to be refined.

Four incomplete seed cones, all compressed laterally and lacking both base and apex, have been recovered (Fig. 2A–H). The two most complete specimens are 8 mm (Fig. 2A) and 10.8 mm wide (Fig. 2G), and up to 17 mm long (Fig. 2G). The cone consists of a flexible axis *c*. 0.8 mm in diameter bearing helically and loosely arranged lateral seed-bearing units at acute angles of *c*. 35–45° (Fig. 2A–D). Each seed-bearing unit consists of a bifurcate axis in the axil of a narrow elongate bract to which it is partially fused. Each fork of the bifurcating axis (cupule stalk) bears a cupule that is strongly reflexed (curved abaxially) relative to the bifurcate axis of the lateral unit, but inflexed (curved adaxially) relative to the main axis of the cone. Each cupule contains a single three-angled seed for which details of the micropyle are unknown (see Shi *et al.* 2016 for detailed description of lateral seed-bearing units and cupules).

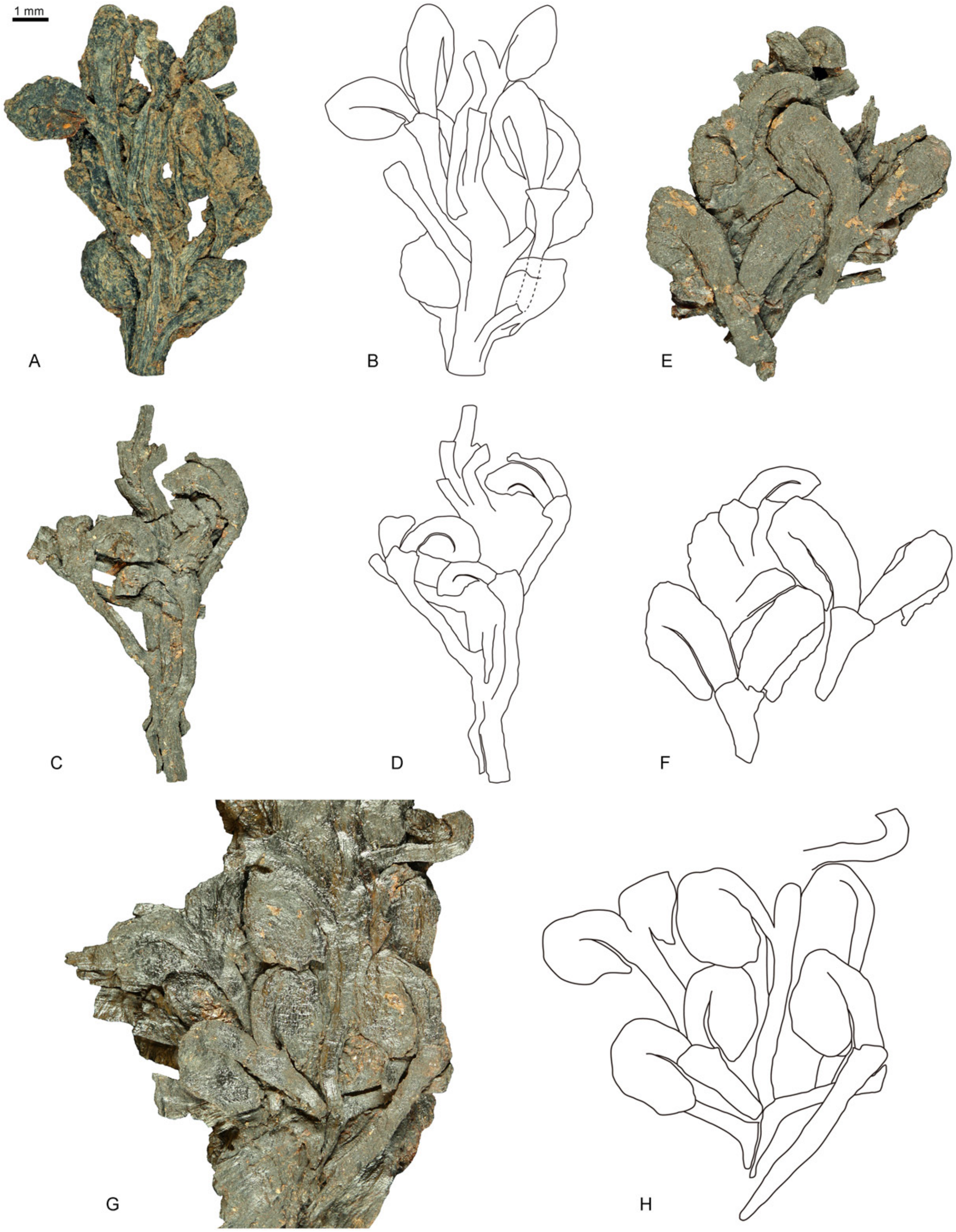


Figure 2. *Umkomasia mongolica*, light micrographs and drawings of seed cones showing arrangement of lateral seed-bearing units, all from sample PSH289. **A,** seed cone with lateral seed-bearing units loosely and helically arranged; each seed-bearing unit consists of a bract subtending a bifurcating axis; PP56614; **B,** line drawing of A. **C,** seed cone with lateral seed-bearing units; PP56615; **D,** line drawing of C. **E,** incomplete seed cone without cone axis preserved but showing lateral orientation of seed-bearing units each with two cupules; PP56616; **F,** line drawing of E. **G,** cluster of seed-bearing units each with two cupules; PP56617; **H,** line drawing of G.

Umkomasia corniculata G. Shi, P. R. Crane, Herend., Ichinnorov, Takahashi & F. Herrera sp. nov. (Figs 1E–H, 3–6)

Diagnosis. Individual seed-bearing units consist of a broad linear elongate bract, subtending and partially fused to an axis that bifurcates into two stout, weakly diverging, cupule stalks, the distal parts of which are strongly inflexed (curved adaxially) relative to the presumed cone axis, but reflexed (curved abaxially) relative to the cupule-bearing axis. Each cupule stalk bears a single cupule that contains a single erect seed. The inflexed cupule stalk results in the micropyle of the seed being oriented back towards the base of the seed-bearing unit. Each cupule consists of the inflexed cupule stalk and two lateral flaps that are partially fused to form a bilobed structure. Apex of the cupule with an enlarged and very prominent, corniculate, apical protrusion. Cupule with very small teeth on the outer surface and along the margins. Seeds ovate in lateral outline, three-angled with a flat basal triangular attachment scar and apex with a bifid micropyle.

Remarks. *Umkomasia corniculata* is distinguished from *U. mongolica* by the stouter axis of the seed-bearing unit, the stouter cupule stalks that are only weakly diverging, and the prominent, corniculate protrusion at the apex of the cupule. The cupules of *U. corniculata* also have minute teeth and the seed has a distinctive bifid micropyle, neither of which are seen in *U. mongolica*. *Umkomasia corniculata* closely resembles *Doylea tetrahedrasperma* from the Early Cretaceous of Canada but differs in having minute teeth on the cupule and a cupule that only partially and loosely encloses the seed. In the larger cupules of *D. tetrahedrasperma*, the lateral flaps are completely fused to one another and also to the cupule stalk to form a cupule that completely encloses the seed.

Derivation of name. The specific epithet refers to the prominent, corniculate protrusion at the cupule apex.

Material. Holotype: PP56618 (Figs 4A, 5A). Other illustrated material: PP56628 (Fig. 1E–H), PP56629 (Fig. 3A–D), PP56630 (Fig. 3E–H), PP56631 (Fig. 3I–L), PP56619 (Fig. 4B), PP56620 (Fig. 4C), PP56621 (Figs 4D, 5E), PP56622 (Figs 4E, 5F), PP56623 (Fig. 4F), PP56624 (Figs 4G, 5H, I), PP56625 (Fig. 4H), PP56626 (Figs 4I, 5B–D), PP56627 (Fig. 5G), PP56632 (Fig. 6A–E). Additional unfigured material: PP56633–PP56669. All specimens are deposited in the Paleobotanical Collections of The Field Museum, Chicago, USA.

Type locality. Sample PSH287, Tevshiin Govi coal mine (45°58′54″ N, 106°07′12″ E), Central Mongolia.

Stratigraphy and age. Tevshiin Govi Formation, Aptian–Albian (125–100.5 Ma), Early Cretaceous.

Description and comments. *Umkomasia corniculata* is known from *c*. 450 seed-bearing units (Figs 1E–H, 3–6) and some isolated individual cupules. There are also some isolated seeds (Fig. 7A–F) similar to those borne in the cupules, some of which were almost certainly produced by this species (e.g. from samples PSH177 and 295). Each seed-bearing unit has the same basic construction as in *U. mongolica*, with a bract that subtends and is partially fused with a stout axis that bifurcates into two short cupule stalks (Figs 1E, F, 3A–L, 4A–C). Each cupule stalk bears one cupule, which is strongly reflexed (curved abaxially) relative to the bifurcate axis, but inflexed (curved adaxially) relative to the cone axis. Each cupule has a very prominent, corniculate extension at its tip, which is the most distinctive feature of the species (Figs 1E, F, 3A–L, 4A–D). Each cupule is formed by the cupule stalk and the two lateral flaps, which partially enclose the single three-angled seed (Figs 4A–C, 6A, B).

The bract extends upwards from the base of the seed-bearing unit. It is fused with the axis of the seed-bearing unit below but is free at the apex and along the lateral margins (Figs 1F, H, 3B, D, 4C, D). The bract is laminar, broadly linear, and *c*. 1.1–1.6 mm wide. For most of its length it is slightly wider than the axis and gradually broadens distally towards the rounded apex. The bract separates from the axis close to the point where it bifurcates (Fig. 4A, C). In some small, presumed immature, seed-bearing units the free apex of the bract is prominent and extends distally beyond the level at which the cupules are borne (Fig. 4E, F). Compared to *Umkomasia mongolica* the bract of *U. corniculata* is typically broader, and both the axis and the two cupule stalks are more robust.

The lower part of the axis of each seed-bearing unit is 2.5–4.4 mm long with an elongate abscission zone on the opposite side to the bract (Figs 1E, 3A, I, 4A, B), indicating that the lower part of each seed-bearing unit was decurrent down the axis to which it was attached. It is likely that the seed-bearing units of *Umkomasia corniculata* were borne in a cone similar to that of *U. mongolica*. Relative to the lower part of the seed-bearing unit, which mainly comprises the abscission zone, the upper part of each axis forms an angle of *c*. 30–90° with the two cupules inflexed (curved adaxially) relative to the main axis of the cone and reflexed (curved abaxially) relative to the bifurcating axis.

The lower part of the axis of the seed-bearing unit, adjacent to the abscission zone, grades distally into a short, straight, stout upper part, 0.7–1.4 mm long and 0.6–1.2 mm wide. The axis bifurcates into two stout

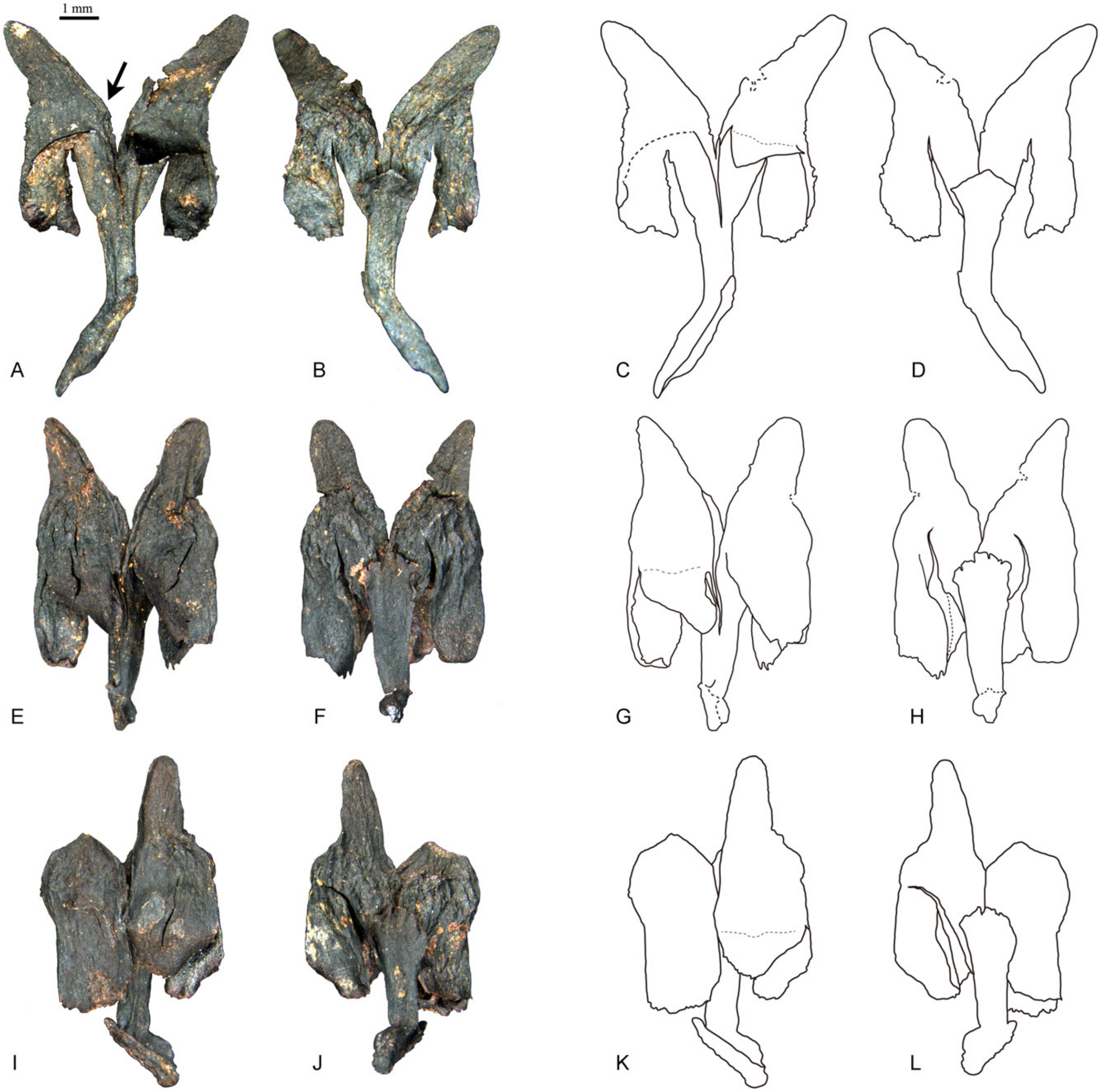
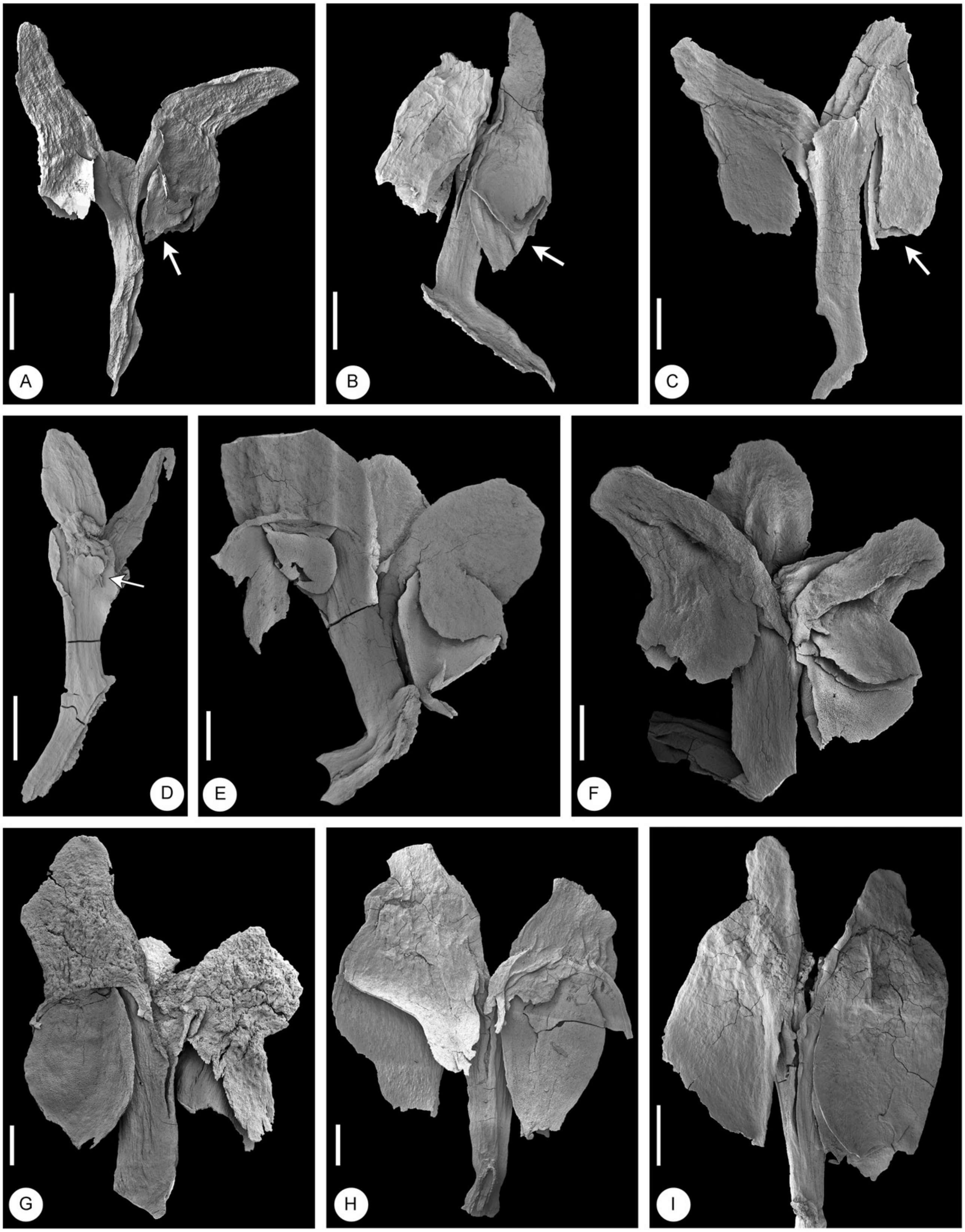


Figure 3. *Umkomasia corniculata* sp. nov., light micrographs and drawings of seed-bearing units showing their organization. **A,** seed-bearing unit with two empty cupules showing the prominent protrusion at the tip of each cupule, the well-developed lateral flaps with minute teeth along their margins, and the long attachment scar to the central axis; note the cupule (arrow) with one lateral flap removed to show the position of attachment of the seed; PP56629, sample PSH286; **B,** reverse of A showing the broad subtending bract; **C,** line drawing of A; **D,** Line drawing of B. **E,** seed-bearing unit showing the short, stout forked axis, the broad subtending bract and the prominent protrusion at the tip of each cupule; PP56630, sample PSH286; **F,** reverse of E, showing the free apex of the broad subtending bract and its thin, partly abraded, apex; note the cleft between the body of the cupule and its apical protrusion; **G,** line drawing of E; **H,** line drawing of F. **I,** seed-bearing unit showing two cupules, one with the apical protrusion complete, and the other with the apical protrusion broken; PP56631, sample PSH286; **J,** reverse of I; **K,** line drawing of I; **L,** line drawing of J.

cupule stalks that diverge at a very narrow angle of *c.* 5°, resulting in the two forks of the axis being very close to one another with very little space between them (Fig. 4A, B, H, I). In most cases, the two cupule stalks are similar in length and both cupules are equally well developed, but in a few specimens, one cupule is significantly smaller than the other and probably failed to mature. Isolated cupules are not common in our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collection indicating that they were probably persistent on the robust cupule stalks.

The cupules vary considerably in size. Larger, presumed mature, cupules are ovate in outline (Figs 1E, 3E, I, 4B, C, I), 2.1–2.6 mm wide and 3.0–4.2 mm long (excluding the prominent, stout corniculate apical protrusion above the point of seed attachment). The apical protrusion is robust, flattened, *c*. 1.8–2.5 mm long, with a rounded (Fig. 4E, G) to acute apex (Fig. 4A, B, I). In some specimens the protrusion has been lost from the cupule apex indicating that it could be easily detached (Figs 3I, J, 4B).

The two lateral flaps are partially fused along their outer margins into a symmetrical or asymmetrical bilobed structure (Figs 1E, G, 3E, G, 4H) that is borne on the cupule stalk close to the point of seed attachment. The bilobed structure is free from the cupule stalk except at the base. The outer surface of the lateral flaps is wrinkled (Fig. 4A–C, H, I), suggesting that they were probably originally fleshy. Some especially well-preserved specimens show that the cupules have very small teeth on their outer surface, including along the margins of the protrusion and the lateral flaps (Fig. 5A). These teeth are *c*. 30 µm long and irregularly distributed. The cupule stalk (Fig. 6C) and lateral flaps (Fig. 6D) show distinct inner and outer cortical zones in transverse section. Cells of the inner cortical zone are more consistently thick-walled compared to the cells in the outer cortical zone.

Larger cupules are often empty, indicating that in most cases the seeds, as well as the seed-bearing units, were shed at maturity. Where the seed is attached, it is loosely and partially enclosed by the cupule (Fig. 4A–C). The three lateral faces of the three-angled seed correspond to, and are covered by, the two lateral flaps and the cupule stalk (Fig. 6A, B).

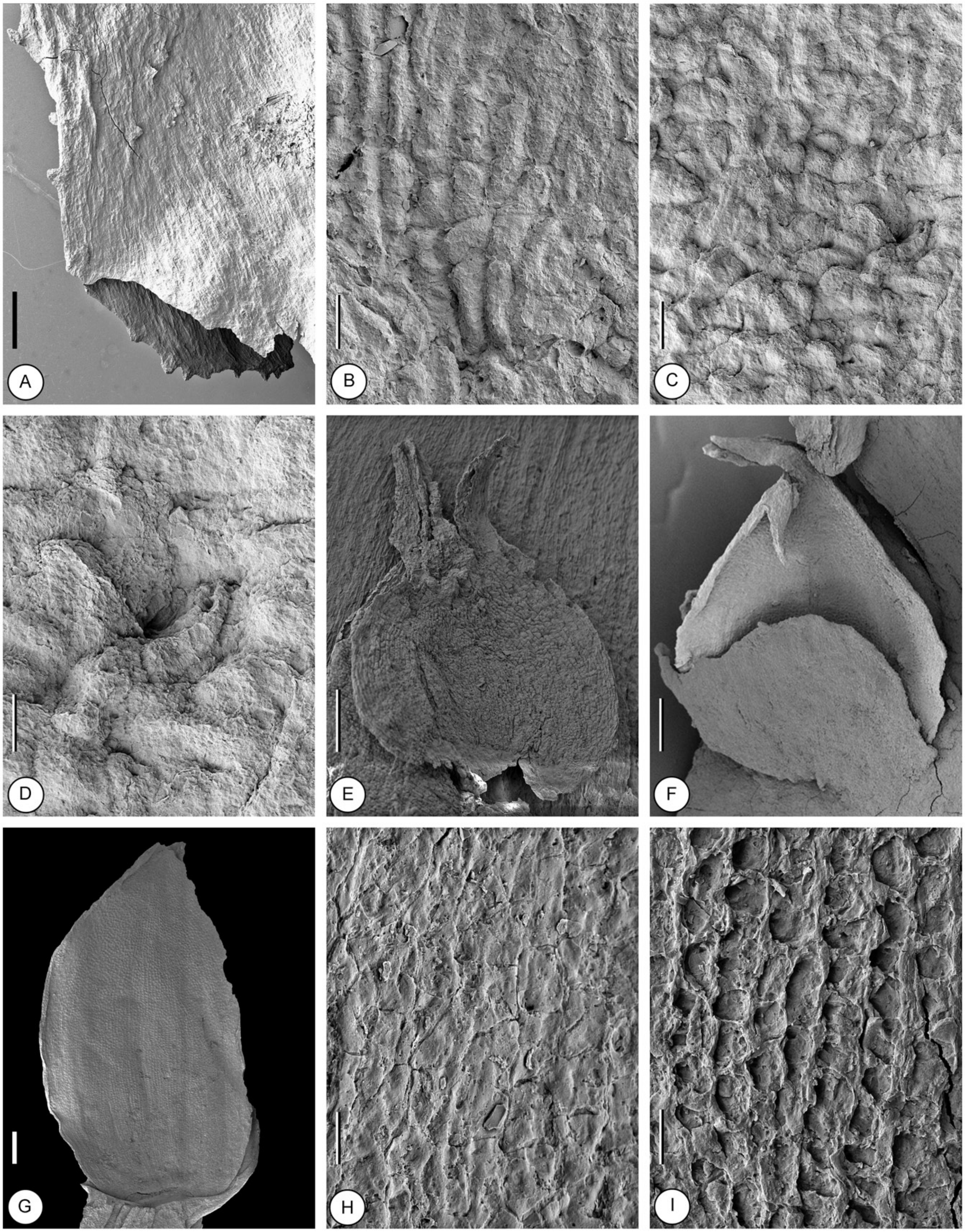
In seed-bearing units with smaller cupules, which were perhaps aborted or preserved at an early stage of development, the bract is well developed and its apex is often free and prominent (Fig. 4E, F). The protrusion at the tip of the cupule is also well developed (Fig. 4D–G), even though the lateral flaps only cover the base of the seed (Fig. 4E, F). This suggests that the lateral flaps came to enclose the seed during the development of the cupule, as has also been inferred for *Doylea tetrahedrasperma*. In some specimens the lateral flaps are broken or abraded (Fig. 4D), which may have happened during transport and burial, or during the preparation of the material, with the result that the seed is entirely exposed.

Cuticles of the seed-bearing units are thin and delicate. In most cases the outlines of epidermal cells are only faintly visible when the inner surfaces of cuticles isolated by maceration are examined with SEM. Epidermal cell outlines are more clearly visible by SEM on the outer surfaces of unmacerated seed-bearing units. Epidermal cells on the abaxial surface of the bract are rectangular with straight to slightly curved anticlinal walls and are arranged in more or less regular longitudinal files. Stoma-like pits are visible on the outer surface of the bract. Epidermal cells of the bifurcating axis are similar to those of the bract in form, size and arrangement.

The outer cuticle of the lateral flaps has a few scattered stomata that are irregular in orientation and distribution (Fig. 5B, C). In non-stomatal regions epidermal cells are 14–45 µm long and 10–18 µm wide, and normally elongated, with a length/width ratio of 1–2.8. They are rectangular to irregularly polygonal in outline with straight to slightly curved anticlinal walls (Fig. 5B). They are typically arranged in more or less regular longitudinal files (Fig. 5B). Epidermal cells near the stomata are irregular in shape and orientation. Trichomes are absent in the cuticle of the unit. Some well-preserved specimens show that the outer surface of the cuticle of lateral flaps is probably papillate (Fig. 5C).

Stomatal complexes are monocyclic (Fig. 5D), with an elliptical stomatal pit that is *c*. 15 µm long and 8 µm

Figure 4. *Umkomasia corniculata* sp. nov., scanning electron micrographs of seed-bearing units. **A,** seed-bearing unit with a seed attached in one of the cupules (arrow), showing the prominent, corniculate, extensions of the cupule stalk and the orientation of the micropyle towards the base of the seed-bearing unit; note the long attachment scar to the presumed cone axis; holotype, PP56618, sample PSH287. **B,** seed-bearing unit showing an attached, partially and loosely enclosed seed protruding from one of the cupules (arrow), the pronounced divergence of the upper part of the seed-bearing axis from the lower part that mainly comprises the attachment scar, and the prominent extension of one cupule stalk (the other broken); PP56619, sample PSH286. **C,** seed-bearing unit showing the subtending bract and the forked seed-bearing axis with prominent extensions of the cupule stalk; PP56620, sample PSH286. **D,** seed-bearing unit with one cupule poorly developed, and the other with a more pronounced extension of the cupule stalk and the lateral flaps of the cupule abraded exposing a small seed with bifid micropyle; PP56621, sample PSH286. **E,** seed-bearing unit with two small seeds attached; note the three-angled seed with bifid micropyle and the flattened extension of the cupule stalk; PP56622, sample PSH286. **F,** seed-bearing unit with two small cupules, one attached seed, and a very prominent subtending bract; note that the lateral flaps only cover the base of the seed; PP56623, sample PSH286. **G, H,** seed-bearing units with the lateral flaps of cupules removed to show the seed attachment; note that the seed is erect but reflexed with the micropyle oriented toward the base of the seed-bearing structure; **G,** PP56624, sample PSH286; **H,** PP56625, sample PSH287. **I,** seed-bearing unit showing two completely preserved mature cupules with prominent extensions of the cupule stalk; PP56626, sample PSH286. Scale bars: A–D, I = 1 mm; E–H = 500 µm.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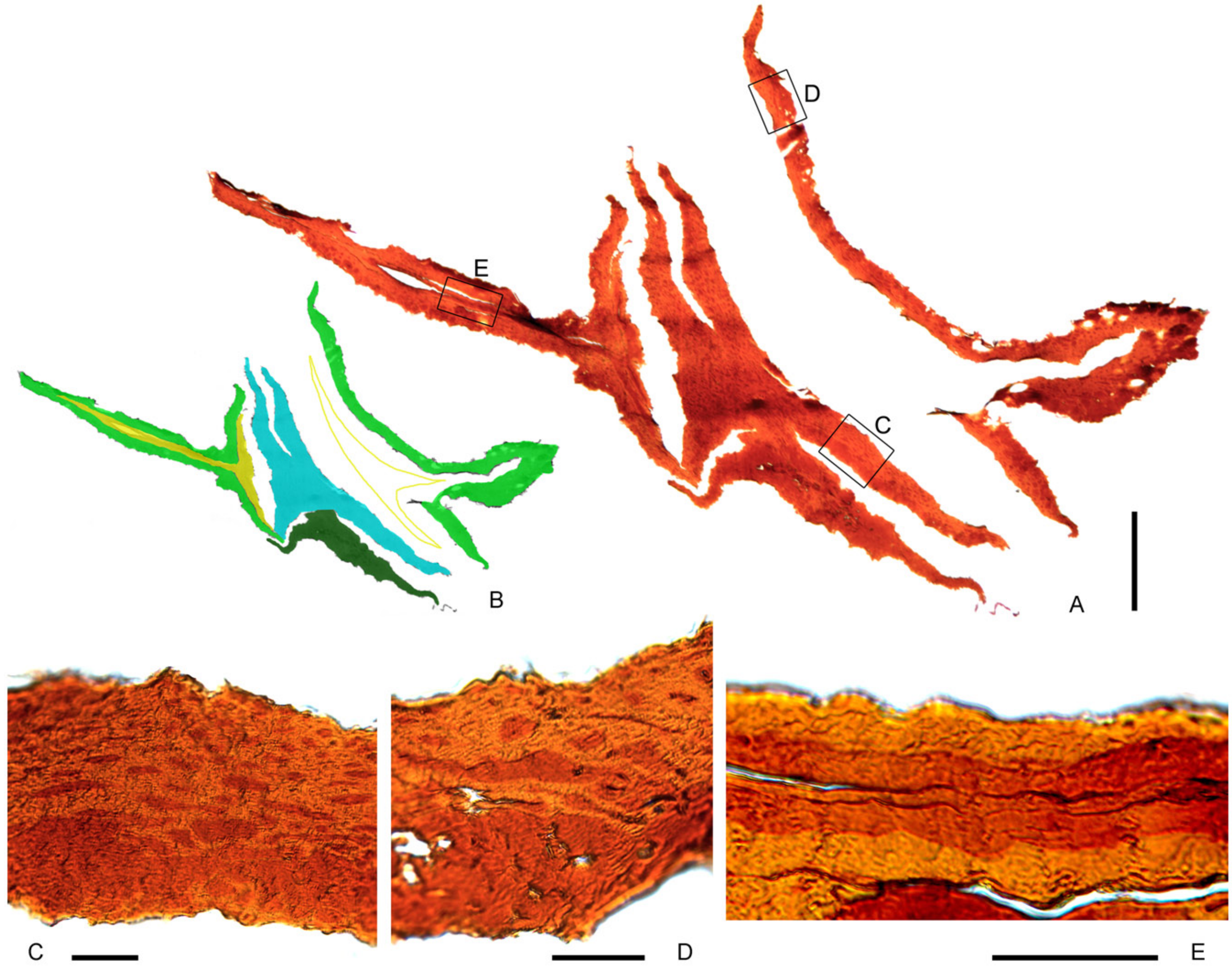


Figure 6. *Umkomasia corniculata* sp. nov., light micrographs showing anatomy; PP56632, sample PSH286. **A,** transverse section of seed-bearing unit: squares indicate areas in the cupule stalk (C), lateral flap (D) and seed (E) that are enlarged in **C, D** and **E,** respectively. **B,** interpretation of **A** showing the bract (dark green), cupule stalk (blue), lateral flap (light green) and seed (yellow); the seed is present in the cupule on the left but missing (presumed shed) in the cupule on the right (indicated by a hollow triangle). **C,** detail of cupule stalk, enlarged from **A**, showing the inner and outer cortical zones (light and dark respectively). **D,** detail of lateral flap of cupule, showing distinct inner and outer cortical zones (light and dark respectively). **E,** detail of seed, showing the light sclerenchymatous zone and darker endotesta. Scale bars: A = 500 μm; C–E = 50 μm.

Figure 5. *Umkomasia corniculata* sp. nov., scanning electron micrographs of seed-bearing units. **A,** portion of cupule showing the minute teeth along margin of lateral flap of a cupule (enlarged from Fig. 4A); PP56618, sample PSH287. **B,** outer surface of cuticle of lateral flap of a cupule showing epidermal cells arranged in longitudinal files (enlarged from Fig. 4I); PP56626, sample PSH286. **C,** outer surface of cuticle of lateral flap of a cupule showing the bulging epidermal cells forming poorly developed papillae (enlarged from Fig. 4I); PP56626, sample PSH286. **D,** detail of stoma in outer cuticle of lateral flap of a cupule showing sunken guard cells surrounded by five subsidiary cells (enlarged from C). **E,** small seed attached to the seed-bearing unit in Fig. 4D (rotated vertically) showing the prominent, bifid micropyle; PP56621, sample PSH286. **F,** small seed attached to the cupule (rotated vertically) with bifid micropyle, enlarged from Fig. 4E; note that only the base of the seed is loosely enclosed in the cupule; PP56622, sample PSH286. **G,** cupule with lateral flap removed showing the seed attached to the seed-bearing unit attachment (rotated vertically); note that the seed is sessile and erect; PP56627, sample PSH287. **H,** outer cuticle of seed showing epidermal cells arranged in longitudinal files (enlarged from the attached seed in Fig. 4G); PP56624, sample PSH286. **I,** detail of outer surface of sclerenchymatous zone showing cells with impressions of crystals (enlarged from the seed in Fig. 4G); PP56624, sample PSH286. Scale bars: A, E, G = 200 μm; B, C, H, I= 20 μm; D = 10 μm; F = 100 μm.

wide. Guard cells are sunken and surrounded by 5–7 subsidiary cells that are irregular in shape and size and are generally smaller than ordinary epidermal cells (Fig. 5D).

The seed is borne near the apex of the cupule stalk. It is erect, sessile and three-angled with three major faces and a flattened basal attachment area (Figs 4G, H, 5G). Because the distal portion of the cupule stalk is strongly reflexed relative to the axis on which it is borne, the micropyle of the seed is oriented back towards the base of the seed-bearing unit (Fig. 4A–H). In many specimens the micropyle is broken or abraded (Fig. 5G) but in the best-preserved specimens it is prominent and bifid (Fig. 5E, F). Seeds attached to the cupule stalks are ovate in lateral view, up to 2.3 mm long and 1.4 mm wide, with three large lateral faces separated by weakly developed, narrow, lateral wings.

The outer cuticle of the seed is delicate and lacks stomata (Fig. 5H). It consists of rectangular cells that are arranged in more or less regular longitudinal files (Fig. 5H). The cells have straight anticlinal walls and smooth periclinal walls. Beneath the seed cuticle, the seed coat is formed by an outer zone of sclerenchyma and an endotesta, which appear light and dark in our sections respectively (Fig. 6E). The outer cuticle, and the epidermal cells to which it was attached, are often missing, exposing the outer surface of the sclerenchymatous zone that is immediately beneath (Fig. 5I). Cells on the surface of the sclerenchymatous zone are more or less isodiametric, with straight anticlinal walls, arranged in longitudinal files (Fig. 5I). In the centre of each cell is an angular pit, *c.* 10–15 μm in diameter (Fig. 5I), which probably reflects the former presence of a cuboidal crystal.

Isolated, three-angled seeds similar in form and anatomy to those *in situ* within *Umkomasia corniculata* cupules occur dispersed in the samples that yield the seed-bearing units (Fig. 7A–F). However, in three samples from the sandy siltstones (PSH286, 287, 288) it is impossible to ascertain if these isolated seeds were produced by *U. corniculata* or by *U. trilobata.* Both species occur in the same samples (see below). When attached seeds of the two species are compared they are indistinguishable.

Isolated seeds are ovate in lateral view (Fig. 7A–C), 2.0–3.0 mm long and 1.5–2.0 mm wide, with a prominent, flat, triangular attachment scar at the base that is *c.* 0.7–1.0 mm across (Fig. 7D). In none of the isolated seeds is the micropyle intact. The bifid micropyle is preserved in only a few attached seeds.

Umkomasia trilobata G. Shi, P. R. Crane, Herend., Ichinnorov, Takahashi & F. Herrera sp. nov.

(Figs 1I–L, 8–11)

Diagnosis. Individual seed-bearing units consist of a narrowly obovate bract subtending and partially fused to a flattened axis that is divided distally into three modified branches that together form a three-lobed scale. Each lobe of the scale bears a single cupule and the cupules on each lobe of the scale are commonly similar in size. Each cupule consists of one of the lobes of the scale, lateral flaps and contains a single seed that is borne erect on a short stalk. Each lobe, and the stalk on which the seed is borne, is inflexed (curved adaxially) relative to the presumed cone axis, but reflexed (curved abaxially) relative to the three-lobed scale; this results in the micropyle of the seed being oriented back towards the base of the seed-bearing unit. The cupule on the central lobe is formed by the lamina of the lobe and three flaps, one median and two laterals. Cupules on the lateral lobes are formed by the lamina of the lobe and two lateral flaps. The flaps of the central and lateral lobes may be free from each other or partially fused. The apex of the cupule is formed by the apical portion of one of the three lobes, which extends beyond the point at which the seed is attached. Apex of the cupule and the lateral flaps smooth, lacking teeth. Seeds ovate in lateral outline, three-angled, with a flat basal triangular attachment scar.

Remarks. *Umkomasia trilobata* differs from *U. mongolica* and *U. corniculata* in having a flattened three-lobed scale bearing three cupules, a short, persistent seed stalk on each lobe of the scale, and the central cupule formed by the lamina of the lobe and three lateral flaps. In these respects, it is also distinct from all other species of *Umkomasia*.

Derivation of name. The specific epithet refers to the flattened, three-lobed scale (modified cupulate axis) of the seed-bearing units.

Material. Holotype: PP56946 (Fig. 9A). Other illustrated material from samples PSH286, 287, 288: PP56683 (Fig. 1I–L), PP56684 (Fig. 8A–D), PP56685 (Fig. 8E–H), PP56686 (Fig. 8I–L), PP56947 (Figs 9B, 10F), PP56672 (Figs 9C, 10H), PP56673 (Fig. 9D), PP56674 (Fig. 9E), PP56675 (Fig. 9F), PP56676 (Fig. 9G), PP56677 (Fig. 9H), PP56678 (Fig. 9I), PP56679 (Fig. 10A, I), PP56680 (Fig. 10B, G), PP56681 (Fig. 10C, D), PP56682 (Fig. 10E), PP56687 (Fig. 11A, B, G), PP56688 (Fig. 11C–F). Additional unfigured material: PP56689–PP56699, PP56948–PP56976. All specimens are deposited in the Paleobotanical Collections of The Field Museum, Chicago, USA.

Type locality. Sample PSH287, Tevshiin Govi coal mine (45°58′54″″ N, 106°07′12″ E), Central Mongolia.

Stratigraphy and age. Tevshiin Govi Formation, Aptian–Albian (125–100.5 Ma), Early Cretaceous.

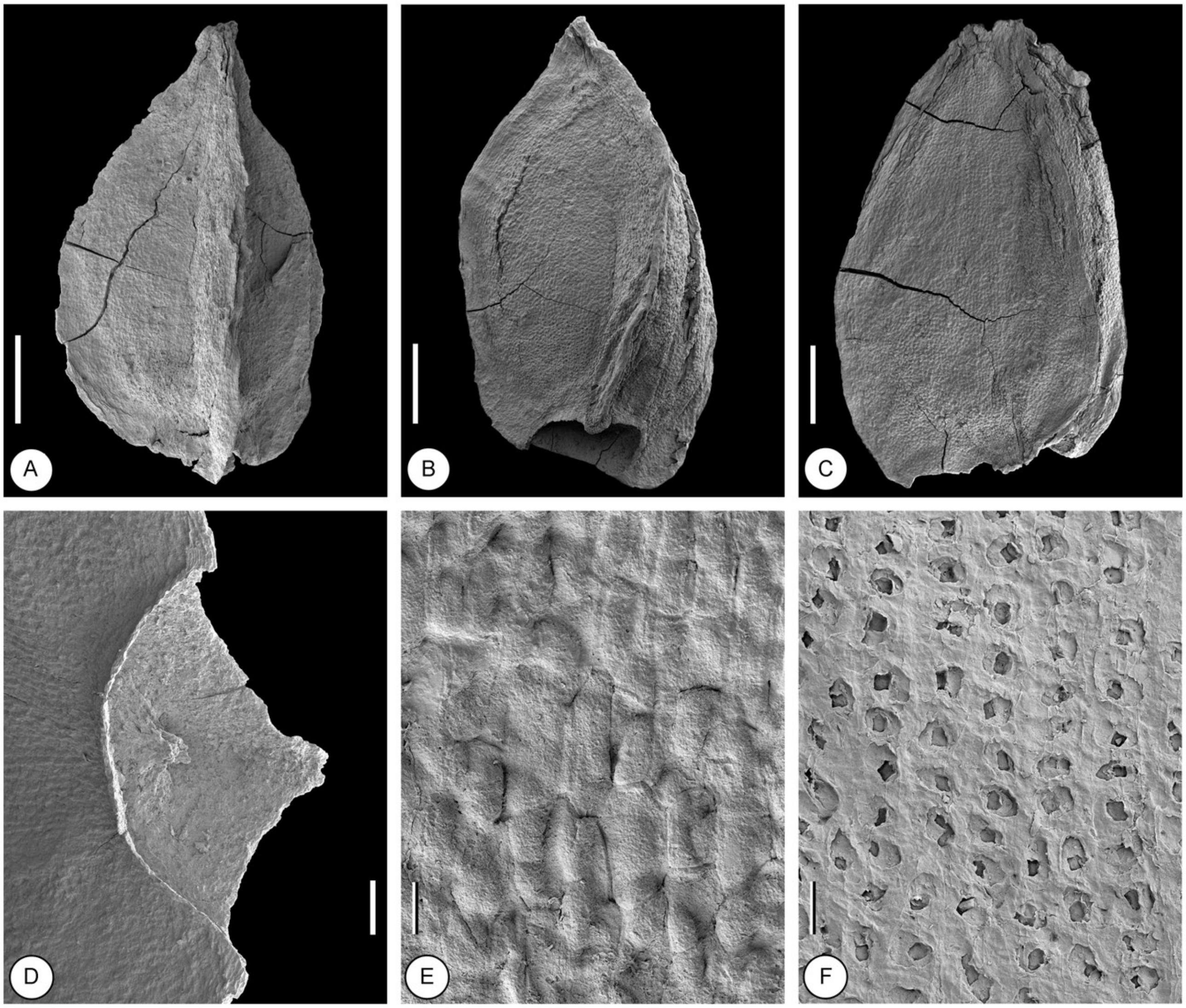


Figure 7. Scanning electron micrographs of isolated, three-angled seeds closely resembling those attached to the cupules of *Umkomasia corniculata* sp. nov. and *Umkomasia trilobata* sp. nov. **A,** lateral view of seed showing ovate outline, the rib separating two of the faces, and the elongated micropyle; PP56977, sample PSH286. **B,** lateral view of seed showing triangular attachment scar, ovate outline, the rib separating two of the faces (left) and acute apex; PP56978, sample PSH286. **C,** lateral view of seed showing acute apex and weakly developed marginal flanges between the faces; PP56979, sample PSH286. **D,** basal view of seed (rotated left) showing detail of triangular attachment scar of seed; PP56980, sample PSH287. **E,** outer cuticle of seed showing outlines of epidermal cells, enlarged from C. **F,** detail of outer surface of sclerenchymatous zone showing cells with outlines of angular crystals; PP56981. Sample PSH286. Scale bars: A–C = 500 μm; D = 100 μm; E, F = 20 μm.

Description and comments. *Umkomasia trilobata* is known from *c*. 250 highly distinctive seed-bearing units, each of which bears three cupules (Figs 1I–L, 8–11). All specimens are from just three of 49 samples analysed from Tevshiin Govi (PSH 286, 287, 288), all of which have also yielded *U. corniculata.*

All the seed-bearing units of *Umkomasia trilobata* are consistent in their organization, although they may be slightly compressed in different orientations, ranging from dorsiventral (Figs 1I, J, 8A, B, I, J, 9C–I) to lateral (Figs 8E, F, 9B, 10A). Each seed-bearing unit consists of a bract subtending and partially fused to a highly modified, flattened, three-lobed axis (Figs 8A–L, 9C–G). By comparison with *U. mongolica* and *U. corniculata*, if each of the lobes is regarded as a cupule stalk then *U. trilobata* has three cupule stalks that are expanded and fused together in their lower parts to form a single coherent three-lobed laminar scale. Each lobe of this three-lobed scale bears a cupule on its upper (adaxial) surface on the opposite side to which the bract is attached (Fig. 8A–L).

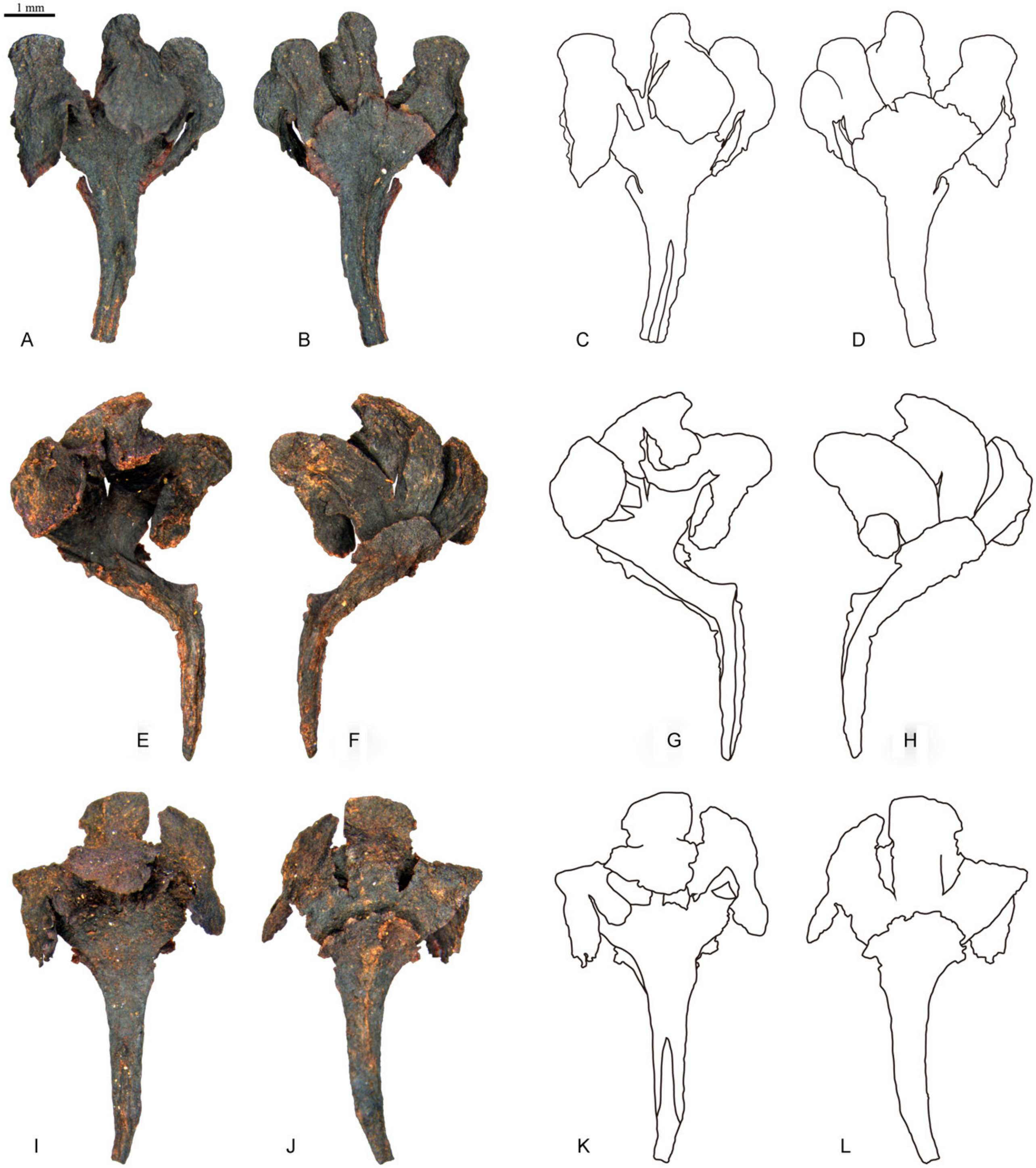
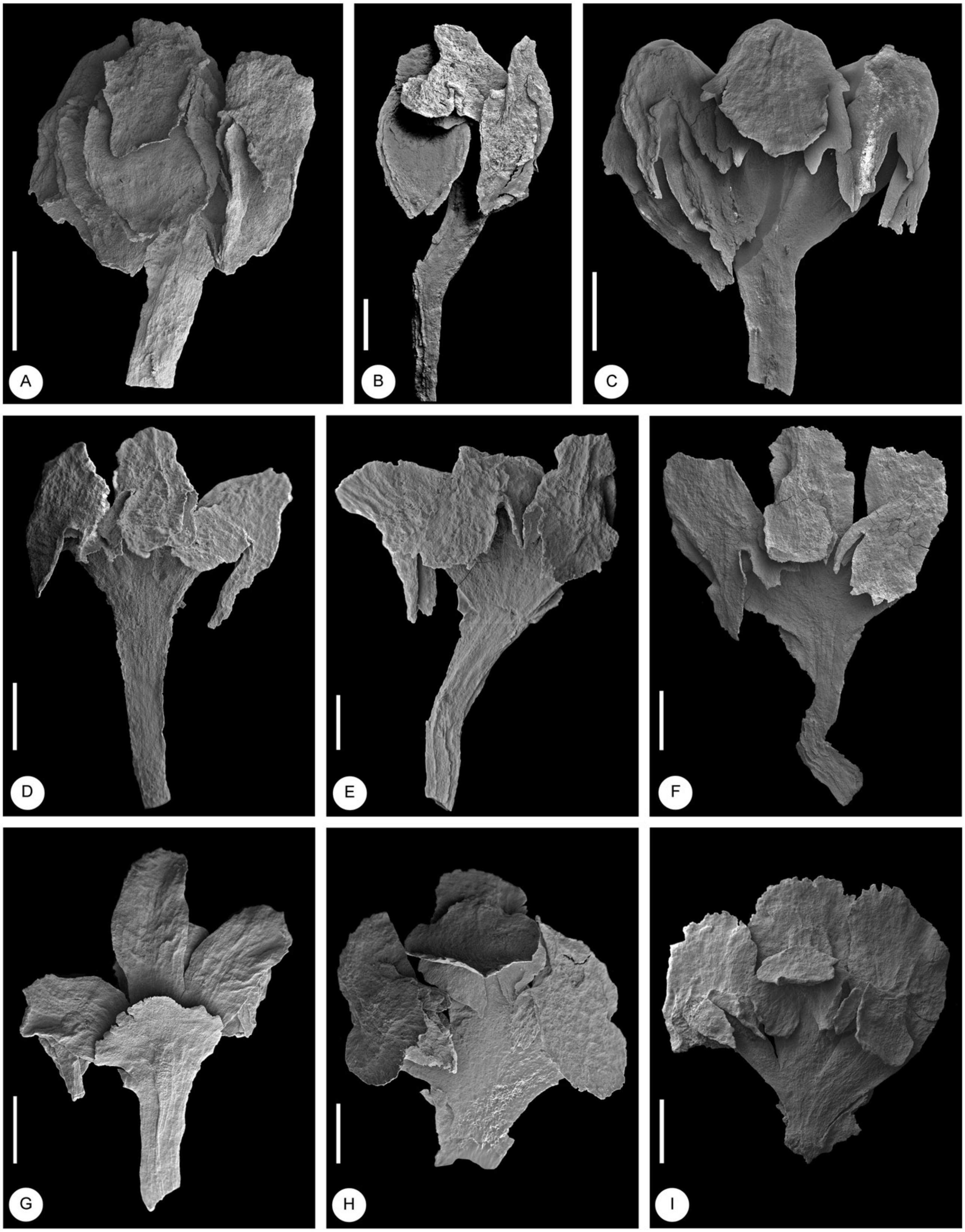


Figure 8. *Umkomasia trilobata* sp. nov., light micrographs and drawings of seed-bearing units showing their organization. **A,** seed-bearing unit showing three cupules of similar size and the weakly developed extensions of the cupule stalk; PP56684, sample PSH286; **B,** reverse of A showing the subtending bract with a prominent, broad fan-shaped apex; **C,** line drawing of A; **D,** line drawing of B. **E,** seed-bearing unit showing three cupules of similar size, the weakly developed extensions of the cupule stalk and the lower part of the axis with an elongated abscission scar; PP56685, sample PSH286; **F,** reverse of E, showing cupule stalks that are reflexed (curved abaxially) relative to the axis of the seed bearing structure on which they are borne but inflexed (curved adaxially) in relation to the presumed cone axis; **G,** line drawing of E; **H,** line drawing of F. **I,** seed-bearing unit showing flattened and expanded three-lobed scale bearing three cupules; PP56686, sample PSH288; **J,** reverse of I, showing the keeled bract with a broad apex; **K,** line drawing of I showing elongated attachment scar; **L,** line drawing of J.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The bract extends from the base of the seed-bearing unit on the opposite side to the abscission scar (see below). It is fused with the axis along its midline, but free along the lateral margins and at the apex (Figs 8B, D, F, H, J, L, 9G). The bract is narrowly obovate, narrow and more or less keeled below (Fig. 8B, J) where it is fused to the axis, but it gradually broadens distally into a free, broad, fan-shaped apex (Figs 8B, J, 9G) that is up to *c.* 2 mm wide. The margin of the bract is entire and distally the margin is often thin and partly abraded (Fig. 8B, J). The bract separates from the seed-bearing scale near the point at which it trifurcates, but its apex does not extend beyond the point at which the seeds are attached.

In its lower part, the seed-bearing scale consists of an axis with an elongate abscission zone, 2.8–3.8 mm long and 0.5–0.8 mm wide, on the opposite side of the bract (Fig. 8A–L). This prominent abscission zone suggests that as in *Umkomasia mongolica* the seed-bearing units were most likely shed from a cone-like structure. The abscission zone was attached to, and decurrent down, the axis to which it was attached. Relative to the lower part of the seed-bearing unit, which mainly comprises the abscission zone, the upper part of each axis forms an acute angle of 40–65° with the cupules inflexed (curved adaxially) relative to the presumed cone axis and reflexed (curved abaxially) relative to the three-lobed scale.

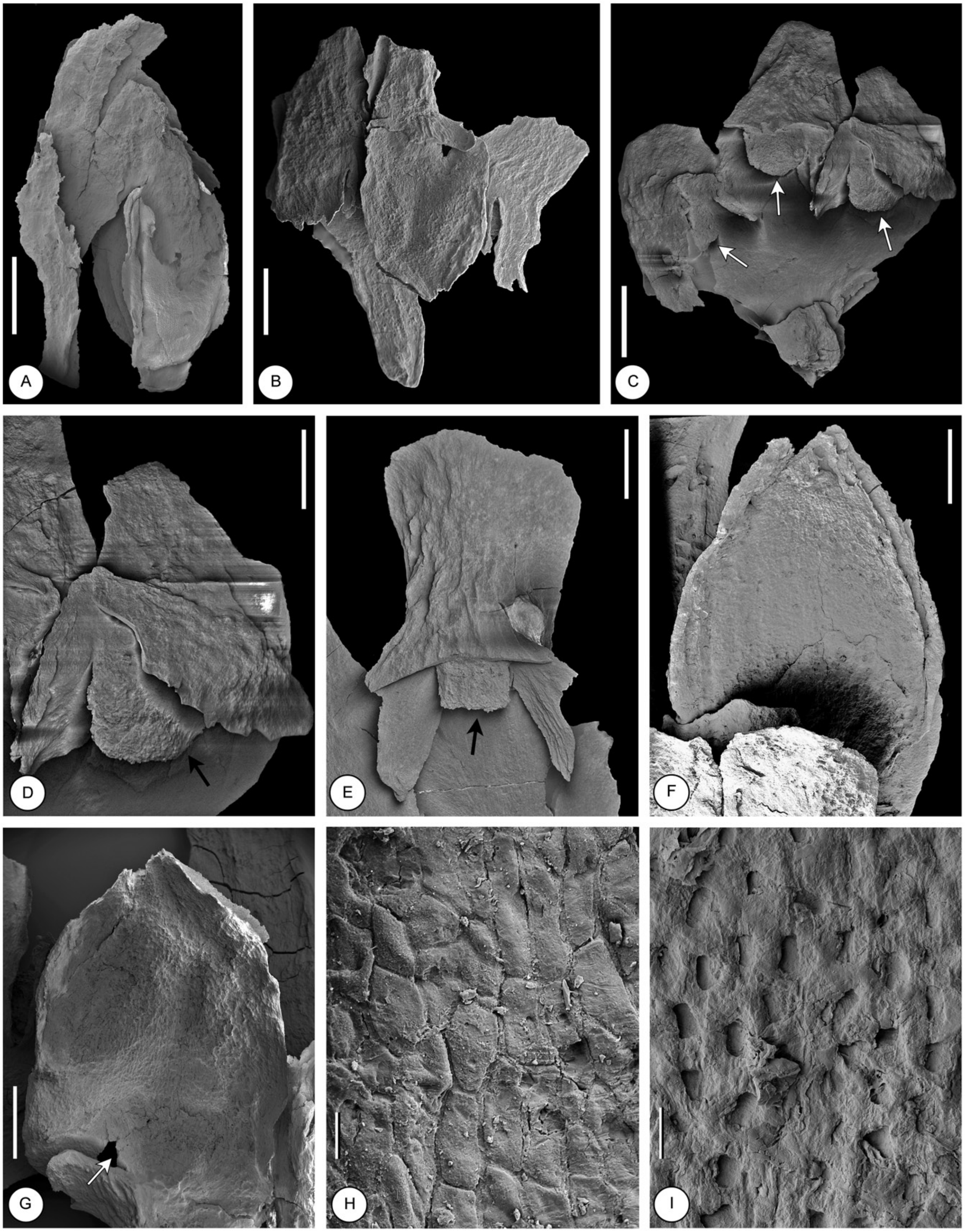
The upper part of the seed-bearing axis broadens gradually distally into a flattened three-lobed scale. At the level at which the lobes diverge, the flattened seed-bearing scale is 2.0–3.2 mm wide. In most cases, the three lobes are similar in length and width (Fig. 8A–L). Each is strongly flattened (Fig. 9E, F, H, I), 1.8–3.0 mm long and 0.8–1.8 mm wide, with its broadest part near the middle or near the rounded apex. Each lobe is slightly reflexed toward the base of the seed-bearing unit (Figs 8F, 9B, E, G), with a cupule borne in the middle (Fig. 9D, F, H, I) or near the apex (Fig. 9A, B, C, E) of the lobe. Distal to the cupule there is a prominent, laminar extension with a rounded tip and entire lateral margins (Figs 9H, I, 10B, E). In a few specimens the apical margin is toothed (Fig. 9I), but in most specimens the apical margin is abraded.

In those specimens in which seeds are still present, each cupule contains a single, three-angled seed (Figs 9A–C, 10A, B). The three cupules of a single seed-bearing unit are similar in size (Fig. 9D–F, H, I) and when empty they are obovate in outline, 1.8–3.0 mm long and 1.3–2.0 mm wide. The lateral flaps that form part of the cupule are attached close to the point of attachment of the seed. They are free from the lobe on which the cupule is borne except at the base. In some cases, the outer surface of the flaps is slightly wrinkled, suggesting that they were originally somewhat fleshy (Fig. 9B–H).

The cupule of the central lobe is formed by the middle portion of the lobe on which it is borne and three flaps, one median and two lateral (Figs 9A–C, H, I, 11C, D), which are mostly separate from each other or very slightly fused near the base (Fig. 9B, C, H, I). The two lateral flaps are similar in size and are borne opposite each other in the space between the seed and the central seed lobe (Figs 9H, I, 11C, D). The outer, median flap is adaxial relative to the axis on which the seed-bearing unit was borne. The three flaps cover the three lateral faces of the three-angled seed in the cupule (Fig. 9A, B), but the central seed lobe also contributes to seed enclosure since the two inner flaps are small (Figs 10C, E, 11C, D). The cupule stalk (Fig. 11E) and lateral flaps (Fig. 11F) show distinct inner and outer cortical zones. Cells of the inner cortical zone are more consistently thick walled compared with cells in the outer cortical zone.

The cupules on the two lateral lobes are similar in organization to those of *Umkomasia mongolica* and *U. corniculata.* Each is formed by the middle portion of a

Figure 9. *Umkomasia trilobata* sp. nov., scanning electron micrographs of seed-bearing units. **A,** seed-bearing unit with three seeds, one in each of the three cupules; note that the micropyle of the three seeds is oriented towards the base of the unit; PP56946, holotype, sample PSH287. **B,** seed-bearing unit with two seeds attached to the two lateral cupules; note that only the base of the seed is enclosed in the central cupule; PP56947, sample PSH287. **C,** seed-bearing unit with three cupules of similar size, and with a seed attached to the lateral cupule on the left showing that two of the lateral faces of the seed correspond to the two lateral flaps of the cupule; note the median and two lateral flaps of the central cupule; PP56672, sample PSH288. **D–F,** seed-bearing units with three empty cupules, showing their overall organization and the prominently flattened, laminar, broadly expanded cupule axes; **D,** PP56673, sample PSH286; **E,** PP56674, sample PSH286; **F,** PP56675, sample PSH287. **G,** seed-bearing unit showing the subtending bract with a broad, prominent, fan-shaped apex; note that the lobes of the three-lobed scale are more or less similar in thickness and not as prominently extended as in *Umkomasia corniculata*; PP56676, sample PSH286. **H,** seed-bearing unit showing that the central cupule is formed by three flaps (one median and two lateral) and the cupule stalk, while the two lateral cupules are formed by two lateral flaps and the cupule stalk itself; PP56677, sample PSH286. **I,** seed-bearing unit showing that the lateral flaps of the central cupule are almost free from one another and the flattened expansions of the three-lobed scale at the tip of the cupules; PP56678, sample PSH286. Scale bars =1 mm.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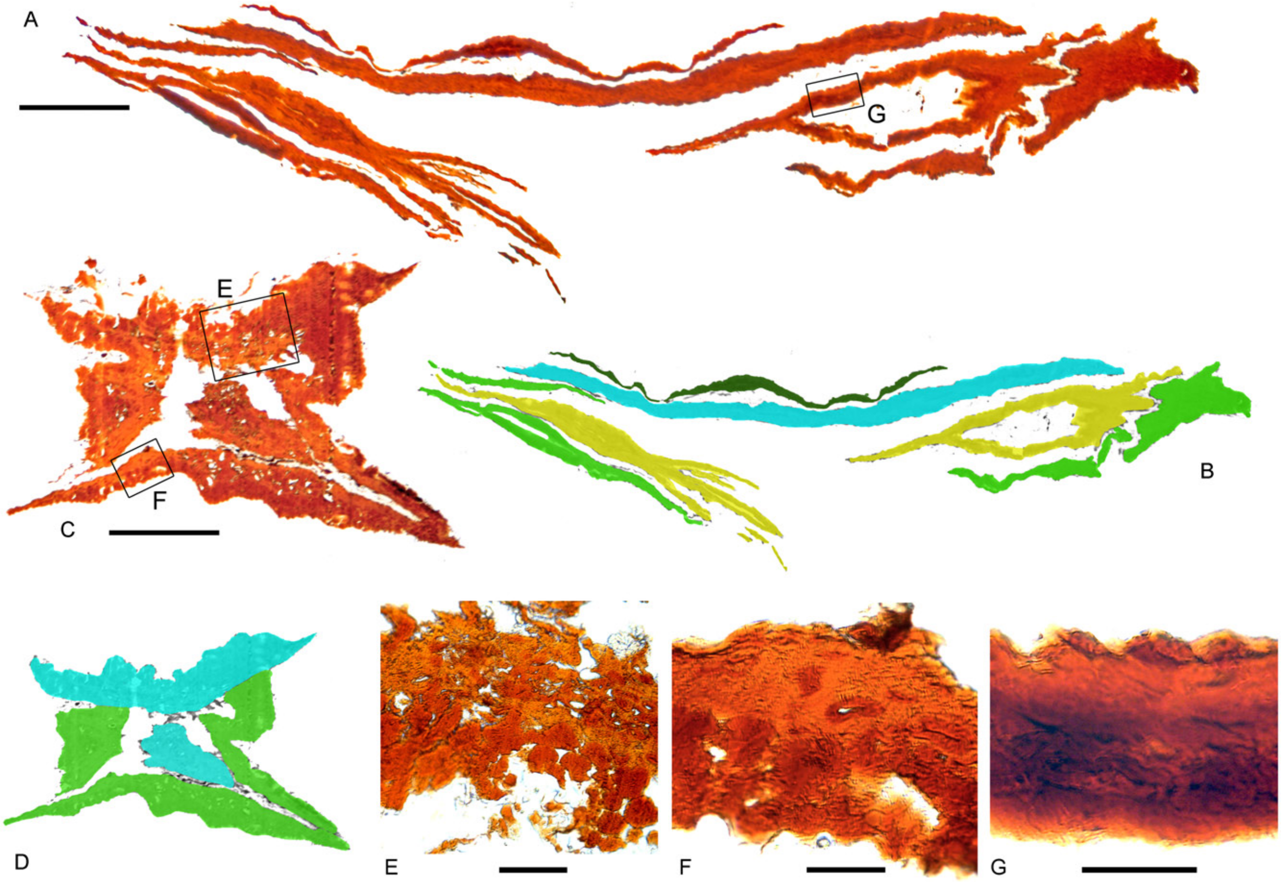

Figure 11. *Umkomasia trilobata* sp. nov., light micrographs showing anatomy. **A,** transverse section of seed-bearing unit showing the flattened, laminar axis with only two lateral cupules at this level of section and square area in seed coat that is enlarged in G; PP56687, sample PSH286; **B,** interpretation of **A** showing the bract (dark green), laminar seed-bearing scale (blue), lateral flap of cupule (light green) of cupules and seeds (yellow). **C,** transverse section of central cupule showing that it is formed by the cupule stalk and three lateral flaps: square areas in cupule stalk and lateral flap are enlarged in E and F, respectively; PP56688, sample PSH287; **D,** interpretation of C showing the flattened cupule stalk (blue), three flaps of the cupule (light green one median and two lateral) and the reflexed persistent seed stalk (blue); **E,** detail of cupule stalk, enlarged from **C,** showing the inner (light-coloured upper layer) and outer (dark-coloured lower layer) cortical zones; **F,** detail of lateral flap of cupule, enlarged from C, showing distinct inner (light-coloured upper layer) and outer (dark-coloured lower layer) cortical zones; **G,** detail of seed, showing the light sclerenchymatous zone and darker endotesta. Scale bars: A, C = 500 µm; E = 100 µm; F, G = 50 µm.

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Figure 10. *Umkomasia trilobata* sp. nov., scanning electron micrographs of seed-bearing units and seeds. **A,** seed-bearing unit showing a seed attached to one of the two lateral cupules in which the lateral flaps are partly abraded; note that the micropyle is oriented towards the base of the seed-bearing unit and that the seed is only partly enclosed by the cupule; PP56679, sample PSH286. **B,** seed-bearing unit with the median flap removed to show the attached seed in the central cupule; note that the seed is erect and attached terminally to the reflexed cupule stalk; PP56680, sample PSH286. **C,** seed-bearing unit with three empty cupules showing the short stalks (arrows) on which the seeds were borne terminally; PP56681, sample PSH288; **D,** detail from the lateral cupule in C showing the triangular scar at the tip of the short stalk (arrow) where the seed was attached. **E,** central cupule from which the seed has been shed with the median flap removed to show the short stalk (arrow) on which the seed was borne terminally; PP56682, sample PSH286. **F,** three-angled seed attached to the central cupule of the seed-bearing unit in Fig. 9B (rotated vertically). **G,** detail of the three-angled seed attached to the central cupule of the seed-bearing unit in B; note the ovate lateral outline and the short stalk (arrow) on which the seed is borne (rotated vertically). **H,** outer cuticle of seed showing epidermal cells arranged in longitudinal files (enlarged from the attached seed in Fig. 9C); PP56672, sample PSH288. **I,** detail of outer surface of sclerenchymatous zone showing cells with impressions of crystals (enlarged from the attached seed in A). Scale bars: A–D = 1 mm; E–G = 500 µm; H, I = 20 µm.

lateral lobe (modified cupule stalk) and two lateral flaps (Figs 9C–F, H, I, 11A, B). The two flaps are commonly partially fused along their outer margin to form a symmetrical or asymmetrical bilobed structure (Fig. 9C, F, H, I). Two of the three lateral faces of the seed are covered by the lateral flaps, while the other is covered by the flattened cupule stalk (Figs 9A, C, 10A).

In the few specimens in which the seed is preserved within a cupule, it is only loosely and partially enclosed (Figs 9A, C, 10A, 11A, B), or in some cases is only enclosed near the base (Fig. 9B). The single seed is erect and borne on a short stalk (Fig. 10B, G) that is strongly reflexed, with the result that the micropyle of the seed is oriented towards the base of the seed-bearing unit (Figs 9A–C, 10A, B).

The cupules of most seed-bearing units are empty, indicating that the seeds were shed at maturity (Figs 8A–L, 9D–G). In empty cupules a short, reflexed stalk to which the seed was attached is clearly visible (Fig. 10C–E) and has a terminal scar *c.* 0.5 mm across, indicating the point at which the seed was attached (Fig. 10C, D). The size and triangular shape of the scar corresponds to the size and shape of the scar on the base of each three-angled seed.

Cuticles of the seed-bearing units are delicate, poorly preserved and the external cell outlines of epidermal cells are only visible using SEM. The epidermal cells of the bract, axis and lateral flaps of the cupule are generally similar in form and size. They are rectangular in outline with straight anticlinal walls and are arranged in longitudinal files.

Seeds remaining attached to the cupules are ovate in lateral outline (Fig. 10F, G), with three large lateral faces, weakly developed lateral wings, and a basal triangular attachment scar. The outer cuticle of the seeds is thin, lacks stomata and consists of elongated rectangular cells with straight anticlinal walls and smooth periclinal walls that are arranged in more or less regular longitudinal files (Fig. 10H). Beneath the seed cuticle, the seed coat is formed by an outer zone of sclerenchyma and an endotesta (Fig. 11G). In most seeds, the outer seed cuticle has been lost, exposing the outer surface of the sclerenchymatous zone. The sclerenchymatous zone is composed of more or less isodiametric cells on the outer surface (Fig. 10I); each cell bears an angular pit (Fig. 10I), which probably indicates the former presence of a cuboidal crystal.

Seeds attached to the cupules of *Umkomasia trilobata* and *U. corniculata* are very similar and when micropyles are not preserved they are indistinguishable from one another. Both are very similar to the isolated three-angled seeds described under *U. corniculata* (Fig. 7A–F). In samples where *U. trilobata* and *U. corniculata* co-occur (PSH 286, 287, 288) these isolated seeds could have been produced by either species. The basal triangular attachment scars (Fig. 7B, D) of these isolated seeds are the same size and shape as the triangular scar at the tip of the of short seed stalks seen in cupules of *U. trilobata.*

Putative leaves of *Umkomasia mongolica*

We have collected very extensively at the Tevshiin Govi coal mine and have sieved and sorted about 100 samples (each of several kg) from 49 different parts of the exposure. Specimens of *Umkomasia mongolica* occur in many of the lignitic samples (PSH179, 180, 181, 247, 250, 254, 258, 259, 261, 281, 289), but *U. corniculata* occurs only in six samples: two from the lignite (samples PSH281, 295) and four from the less extensively sampled, poorly consolidated carbonaceous sandy siltstones (samples PSH177, 286, 287, 288). In just one lignite sample (PSH281), *U. corniculata* occurs together with *U. mongolica*. *Umkomasia trilobata* occurs only in three samples from the sandy siltstones (PSH 286, 287, 288), and always together with *U. corniculata*.

Judging from the almost complete absence of sedimentary input, the Tevshiin Govi lignites appear to have accumulated more or less autochthonously. Although never abundant, *Umkomasia mongolica* is widespread in the lignitic samples and we would therefore expect the leaves of the *U. mongolica* plant to be present and similarly widely distributed.

Samples from the Tevshiin Govi lignite that yield *Umkomasia mongolica* contain abundant and well-preserved leaf material, but the only pinnate leaves recovered to date are the minute membranous leaves of *Hymenophyllum iwatsukii* (Herrera *et al.* 2017a). All the other leaves recovered fall into three main groups. They can be: (1) simple, linear, often needle-like and with a single vein, e.g. leaves of unequivocal Pinaceae (Herrera *et al.* 2016a) and the probable Pinaceae stem-group species, *Schizolepidopsis* Doweld (Leslie *et al.* 2013); (2) narrow with a single vein but falcate and awl-shaped, e.g. leaves of unequivocal Cupressaceae, *Elatides* Heer (Shi *et al.* 2014) and *Stutzeliastrobus* F. Herrera, G. Shi, Knopf, A. B. Leslie, Ichinnorov, Takahashi, P. R. Crane & Herend. (Herrera *et al.* 2016b); or (3) narrowly elliptical, strap-shaped and multiveined with a broad lamina, e.g. leaves of *Podozamites* and *Pseudotorellia* (Shi *et al.* 2018).

Careful analysis of the strap-shaped, multiveined leaves in the Tevshiin Govi lignite has discriminated three species: *Podozamites harrisii* G. Shi, F. Herrera, Herend., A. B. Leslie, Ichinnorov, Takahashi, & P. R. Crane, *Pseudotorellia resinosa* G. Shi, F. Herrera, Herend., A. B. Leslie, Ichinnorov, Takahashi, & P. R. Crane and *Pseudotorellia palustris* (Shi *et al.* 2018).

Figure 12. Reconstruction of a shoot of *Umkomasia mongolica* showing the cone with lateral seed-bearing units, each with two cupules. The cone is attached to leaves of *Pseudotorellia palustris* and is reconstructed as pendulous based on the thin cone axis, which appears to be insufficiently robust to support an erect cone. We reconstruct the seed cones as borne on a long shoot but it is equally possible that they were borne on short shoots.

There is strong evidence from stomatal and cuticular structure that *Podozamites harrisii* is the leaf of *Krassilovia mongolica* (Herrera *et al.* in progress) and there is also good evidence that *Pseudotorellia resinosa* is the leaf of *Umaltolepis mongoliensis* F. Herrera, G. Shi, Ichinnorov, Takahashi, Bugdaeva, Herend. & P. R. Crane (Herrera *et al.* 2017b; Shi *et al.* 2018). This process of elimination points towards *Pseudotorellia* *palustris* being the leaf of *Umkomasia mongolica.* While the stomata of *P. palustris* have fewer subsidiary cells than the stomata of *U. mongolica*, their stomatal structures are not fundamentally different. Similarly, although the cuticle of *P. palustris* is thick compared to the thin and delicate cuticle of *U. mongolica*, this is not unusual in the corystosperm material from Gondwana (Thomas 1933; Holmes 1987; Axsmith *et al.* 2000).

The only other possibility for the leaf of the *Umkomasia* species at Tevshiin Govi appears to be the leaves of *Nilssoniopteris*, fragments of which occur with *Pseudotorellia* leaves and *U. corniculata* and *U. trilobata* seed-bearing structures, in four samples (PSH177, 286, 287, 288) collected from the carbonaceous sandy siltstones at Tevshiin Govi. However, *Nilssoniopteris* does not occur in any of the many lignite samples from which *U. mongolica* has been recovered. We therefore favour the conclusion that *P. palustris* is the leaf of *U. mongolica* and present this hypothesis in our reconstruction of the plant (Fig. 12).

This preliminary conclusion requires more direct and definitive evidence, but we think it very likely because of the similar stomatal pattern of *Dicroidium* and *Pseudotorellia palustris* leaves, and the similarities in venation between *Pseudotorellia palustris* and the pinnae of *Dicroidium bandelii* Abu Hamad, Blomenkemper, Kerp & Bomfleur described recently from the Upper Permian of Jordan (Abu Hamad *et al.* 2017).

In the Southern Hemisphere *Dicroidium* is considered to be the leaf of the plants that produced *Umkomasia*, based on their consistent association in the same bed and similarities in cuticular structure (Thomas 1933; Anderson & Anderson 1983, 2003). The normal form of *Dicroidium* is a frond with a characteristic basal bifurcation and a pinnate or bipinnate arrangement of pinnules that have odontopteroid venation (Townrow 1957; Abu Hamad *et al.* 2008, 2017; Bomfleur & Kerp 2010; Bomfleur *et al.* 2012). Such leaves are very different from the simple, linear leaves of *Pseudotorellia palustris*, and *Pseudotorellia* has long been thought to be the leaf of an extinct ginkgoalean (Shi *et al.* 2018). However, basal frond elements of *Dicroidium* resemble ginkgophyte leaves in their shape and venation and in this respect also resemble leaves of *Pseudotorellia* (Bomfleur *et al.* 2012). It is also interesting that *D. bandelii* (Abu Hamad *et al.* 2017) has strap-shaped pinnae with parallel venation resulting from repeated vein dichotomies near the leaf base. *Dicroidium* has thick cuticle and characteristic brachyparacytic or incompletely cyclocytic stomatal complex with two to five differentiated lateral subsidiary cells and one or two unspecialized polar cells (Townrow 1957; Abu Hamad *et al.* 2008, 2017; Bomfleur & Kerp 2010). Similar stomatal patterns are also described in *Pseudotorellia palustris* (Shi *et al.* 2018).

Discussion

Comparison of the Tevshiin Govi species of *Umkomasia*

All three species of *Umkomasia* are fundamentally similar in the organization of the seed-bearing units, which all appear to have been deciduous. Each seed-bearing unit consists of a modified bract, which subtends an axis that either bifurcates (*U. mongolica* and *U. corniculata*) or expands into a three-lobed, flattened scale (*U. trilobata*) (Figs 13, 14). Each fork of the axis (cupule stalks), or each lobe of the scale in *U. trilobata*, bears a single-seeded cupule that is reflexed (curved abaxially) relative to the axis of the seed-bearing unit, and inflexed (curved adaxially) relative to the cone axis (Figs 13, 14). The seed is erect within the cupule, but because the stalk on which it is borne is reflexed the micropyle is directed back towards the base of the seed-bearing unit and the point of attachment to the axis (Fig. 13). This is seen clearly in *U. mongolica* and is especially obvious in *U. trilobata.*

Seeds of the three *Umkomasia* species from Mongolia are also very similar. Isolated seeds *of U. corniculata* and *U. trilobata* occur together, and cannot be definitively separated (Fig. 7), but they are very similar to the seeds of *U. mongolica*. The seeds are distinctively three-angled, with a basal triangular attachment scar and three major faces separated by weakly developed lateral wings. The seed coat has a thin cuticle that apparently lacks stomata, and an outer sclerenchymatous zone composed of cells with a single central angular pit. These shared characters suggest strongly that *U. mongolica*, *U. corniculata* and *U. trilobata* all belong to a single group of plants.

The three species appear to have grown in slightly different habitats that are preserved in the different facies of the Tevshiin Govi mine. *Umkomasia mongolica* is known only from the lignites, occurring in 11 of the 30 lignite samples that we have examined. *Umkomasia corniculata* is much more restricted, occurring in just six samples; four samples from the carbonaceous sandy siltstones above the lignites (PSH 177, 286, 287, 288) and only two lignite samples (PSH 281, 295). *Umkomasia trilobata* is even more restricted, occurring in just three of clastic (non-lignite) samples that also yield *U. corniculata.*

Among the three species, *Umkomasia trilobata* is clearly distinct from *U. mongolica* and *U. corniculata* in having the cupule stalks modified into a flattened three-lobed scale, bearing three cupules (one central, two

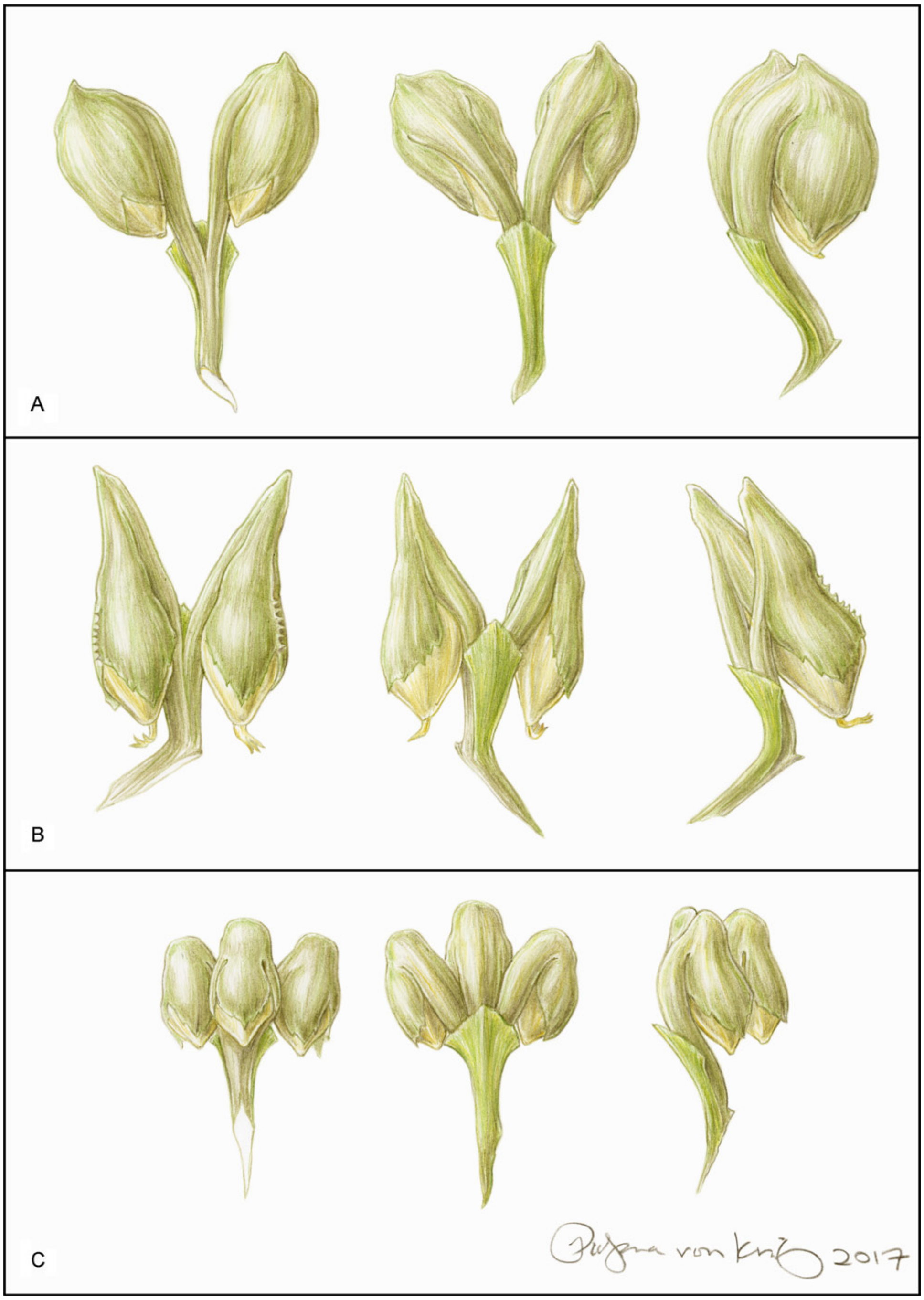

Figure 13. Reconstructions of the seed-bearing units of three species of *Umkomasia* from the Lower Cretaceous of Tevshiin Govi, central Mongolia in adaxial (left), abaxial (centre) and lateral (right) views. **A,** *Umkomasia mongolica*; **B,** *Umkomasia corniculata* sp. nov.; **C,** *Umkomasia trilobata* sp. nov.

lateral) each with a single seed (Figs 13C, 14C). The short, persistent and clearly reflexed seed stalk is also a distinctive feature of *U. trilobata*. *Umkomasia mongolica* (Figs 13A, 14A) and *U. corniculata* (Figs 13B, 14B) are more similar to each other. In both the axis of the seed-bearing unit bifurcates with each branch bearing one cupule, each containing a single sessile seed. Each cupule is formed by the cupule stalk and two lateral flaps.

Umkomasia corniculata differs from *U. mongolica* in being much more robust, with a stout axis, stout cupule stalk, a pronounced extension at the tip of cupule and

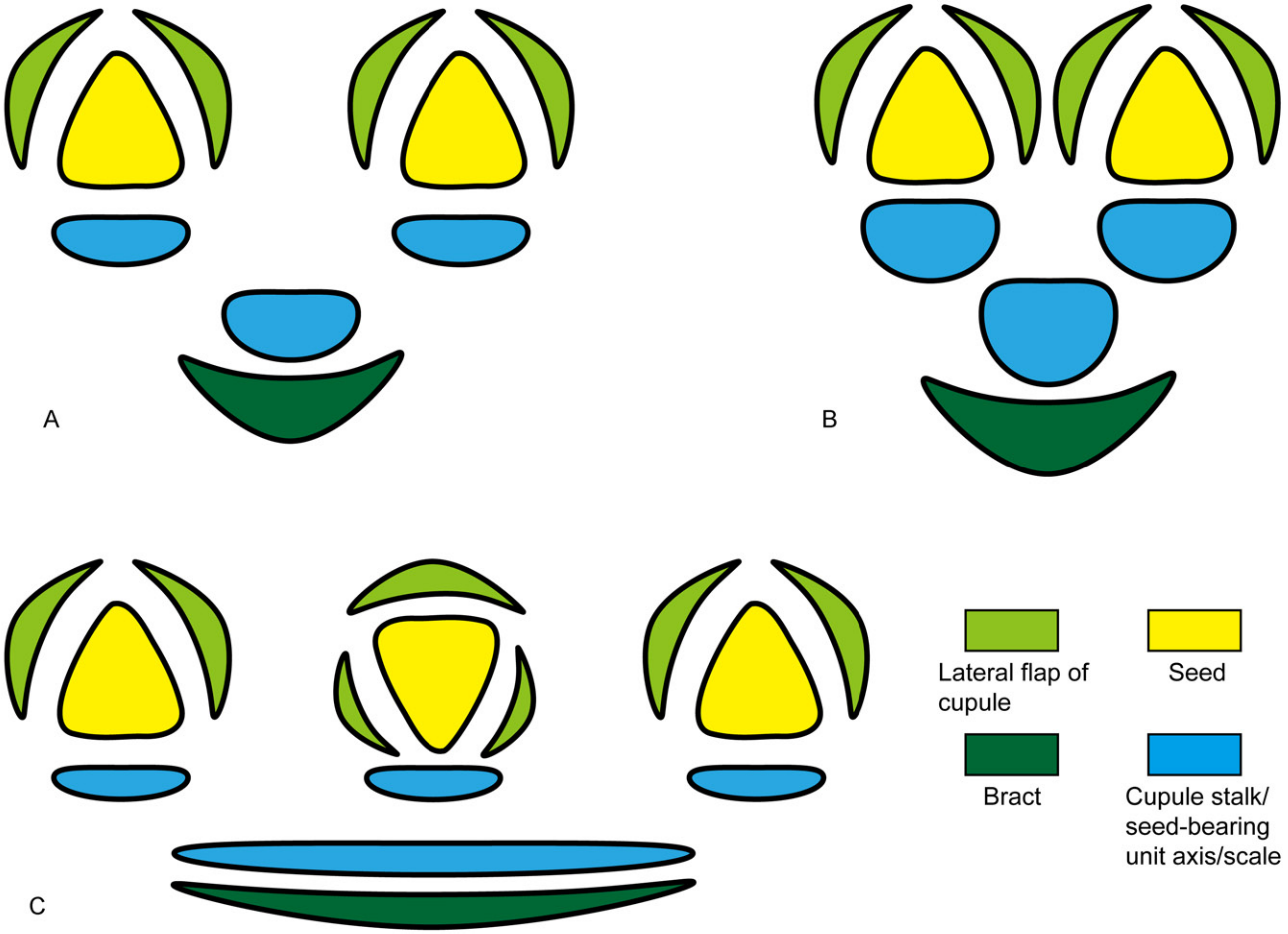

Figure 14. Interpretive diagrams of the three species of *Umkomasia* seed-bearing units from the Lower Cretaceous of Tevshiin Govi, central Mongolia, showing the bract (dark green), cupule stalk (blue), seed-bearing axis/scale (blue), lateral flap of cupule (light green) and seed (yellow). **A,** *Umkomasia mongolica*. **B,** *Umkomasia corniculata* sp. nov.; note that the axis and cupule stalks are more robust than in *U. mongolica*, and that the two cupules are borne very close to one another. **C,** *Umkomasia trilobata* sp. nov.; note the flattened, laminar seed-bearing axis/scale and the central cupule, which is formed by the cupule stalk and three flaps (one median and two lateral).

an especially pronounced attachment scar (Figs 13B, 14B). The cupule also has minute teeth and the seed has a distinctive bifid micropyle. In *U. mongolica* (Figs 13A, 14A), the cupules lack teeth, have a very short extension at the tip, and the micropyle of seed is elongated but a bifid micropyle has not been observed (Shi *et al.* 2016). Moreover, our abundant and well-preserved material suggests that *U. corniculata* also differs from *U. mongolica* in cupule development. In small cupules of *U. corniculata*, which are presumed to have been preserved early in development, the lateral flaps are not well developed and only loosely enclose the base of the seed (Fig. 4E, F). They are easily broken or abraded exposing the entire seed (Fig. 4D). In the larger cupules, apparently preserved at a more mature stage, the lateral flaps are well developed and loosely enclose almost the entire seed (Fig. 4A–C, I). This suggests significant growth of the lateral flaps during seed (or ovule) development in *U. corniculata*. In *U. mongolica*, in both small and large cupules the lateral flaps are well developed and loosely enclose the seed. The lateral flaps do not appear to grow disproportionately during seed (or ovule) development (Shi *et al.* 2016).

Comparison with *Doylea* and other species of *Umkomasia*

A full comparison of *Umkomasia mongolica* with previously described species of *Umkomasia* was provided when the species was established (Shi *et al.* 2016). Most of the previously described species are not well preserved and none are sufficiently similar to *U. corniculata* and *U. trilobata* to preclude the establishment of two new species (Table 1).

Table 1. Comparison of *Umkomasia mongolica*, *U. corniculata* sp. nov. and *U. trilobata* sp. nov. with *Doylea tetrahedrasperma* and selected well-known *Umkomasia* species (Thomas 1933; Axsmith *et al.* 2000; Klavins *et al.* 2002; Anderson & Anderson 2003; Stockey & Rothwell 2009; Rothwell & Stockey 2016; Shi *et al.* 2016).

Characters	***Umkomasia mongolica***	***Umkomasia corniculata***	***Umkomasia trilobata***	***Umkomasia macleanii***	***Umkomasia uniramia***	***Umkomasia resinosa***	***Doylea tetrahedrasperma***
Arrangement of lateral seed-bearing units	Helical on axis of a loose cone	Very likely on a cone axis	Very likely on a cone axis	Alternate on axis of a flattened, lax branching system	In groups of at least three near the apex of short shoot	?	Helical on axis of a compact cone
Bract of lateral seed-bearing units	One linear bract	One broad, linear bract	One narrowly obovate bract	Two pairs of opposite bracts	One pair of opposite bracts	?	One triangular bract
Bract fused with seed-bearing axis	Partially fused with a free apex	Partially fused with a free apex	Partially fused with a free apex	Probably not fused	Probably not fused	?	Partially fused with a free apex
Lateral seed-bearing units deciduous	Yes	Yes	Yes	Possibly no	Yes	?	Possibly no
Arrangement of cupules on lateral seed-bearing units	In a terminal pair	In a terminal pair	Three cupules on a flattened axis	Opposite/subopposite in 2–3 pairs	In a subapical whorl of 4–8	Helical	In a terminal pair
Cupule formation	Cupule stalk and two lateral flaps	Cupule stalk and two lateral flaps	Cupule stalk and two lateral flaps (lateral cupules); cupule stalk and three lateral flaps (central cupule)	Cupule stalk and two lateral flaps	Cupule stalk and two lateral flaps	Cupule stalk and two lateral flaps, or cupule stalk and an unlobed laminar structure	Cupule stalk and two lateral flaps
Cupule size (mm)	2.3–3.5 × 1.5–2.7	3.0–4.2 × 2.1–2.6	1.8–3.0 × 1.3–2.0	4–6 × 2.5–5*	4.1–14 × 4.0–13	7 × 2.7–5.5	Up to 5.5 × 3–4
Seed enclosure by cupule	Cupule partially encloses seed	Cupule partially encloses seed	Cupule partially encloses seed	Cupule partially encloses seed	Completely except a small distal opening at immaturity, open at maturity	Cupule partially enclosing seed	Cupule partially encloses seed when immature, nearly completely closed at maturity
Cupule toothed	No	Yes	No	No	No	No	No
Extension at tip of cupule	Short	Prominent and corniculate	Prominent and flattened	Absent	Absent	Absent	Prominent, up to 1–2 mm long
Secretory cavities in cupules	Absent	Absent	Absent	?	?	Present	Absent
Seed number per cupule	One	One	One	One	?	One or two	One
Seed orientation	Micropyle towards base of cupule stalk	Micropyle towards base of cupule stalk	Micropyle towards base of cupule stalk	Micropyle towards base of cupule stalk	Micropyle towards base of cupule stalk	Micropyle towards base of cupule stalk	Micropyle towards base of cupule stalk
Seed stalk	Absent	Absent	Present	Absent	Absent	Absent	Absent

(*Continued*)

Table 1. (*Continued*).

Characters	***Umkomasia mongolica***	***Umkomasia corniculata***	***Umkomasia trilobata***	***Umkomasia macleanii***	***Umkomasia uniramia***	***Umkomasia resinosa***	***Doylea tetrahedrasperma***
Seed shape	Three-angled	Three-angled	Three-angled	Possibly three-angled	?	Flattened	Three-angled
Seed base	Triangular	Triangular	Triangular	?	?	?	Triangular
Seed wing	Weakly developed	Weakly developed	Weakly developed	Weakly developed*	?	Absent	Weakly developed
Micropyle	Elongated	Bifid	Elongated	Bifid	?	Bifid	Bifid

Note: data measured or derived based on the original figures by the present authors are indicated by asterisk mark; unknown characters are indicated by question marks.

More relevant is *Doylea tetrahedrasperma* from the Early Cretaceous of Apple Bay, British Columbia, Canada (Stockey & Rothwell 2009; Rothwell & Stockey 2016; Shi *et al.* 2016), to which both *Umkomasia mongolica* and especially *U. corniculata* are very similar. *Doylea* was initially tentatively referred to the corystosperms based on the structure and anatomy of individual cupules (Stockey & Rothwell 2009) but was later transferred to a separate family Doyleaceae and order Doyleales. Rothwell & Stockey (2016) considered *U. mongolica* sufficiently similar to *D. tetrahedrasperma* that they transferred it to *Doylea*, recognizing it as a second species, *Doylea mongolica* (G. Shi, A. B. Leslie, Herend., F. Herrera, Ichinnorov, Takahashi, Knopf & P. R. Crane) G. W. Rothwell & Stockey.

Based on the new material described here it is clear that *Umkomasia mongolica* and *Doylea tetrahedrasperma*, and most probably *U. corniculata* and *U. trilobata*, are compound seed cones with helically arranged, lateral seed-bearing units. As recognized by Rothwell & Stockey (2016) the overall architecture of the cone is very conifer-like. In *U. mongolica* and *U. corniculata*, as well as *D. tetrahedrasperma*, the overall morphology of the lateral seed-bearing units is identical. Each consists of a bract subtending and partially fused to a fertile axis that bifurcates, and each fork of the axis bears a cupule that is formed by the cupule stalk and two lateral flaps. Each cupule contains a single, three-angled seed with weakly developed lateral wings and a basal triangular attachment scar (Stockey & Rothwell 2009; Rothwell & Stockey 2016). The cupule and the seed are reflexed (curved abaxially) relative to the cupulate axis, but inflexed (curved adaxially) relative to the cone axis. Both *U. mongolica* and *D. tetrahedrasperma* are associated with bisaccate pollen grains of the *Alisporites*-type (Stockey & Rothwell 2009; Shi *et al.* 2016). The three-lobed scale-like seed-bearing units of *U. trilobata* have their own distinctive features, but again the overall form, with a bract subtending and partially fused to a fertile axis, is the same.

Among the three *Umkomasia* species from Mongolia, *Doylea tetrahedrasperma* most closely resembles *U. corniculata*. In both species the seed-bearing axis and the two cupule stalks are stout, with a long, robust extension at the cupule apex. Also, in both the seed has a prominent, bifid micropyle. There are also similarities in development. In smaller, presumed immature, cupules of *D. tetrahedrasperma* the lateral flaps are less developed and only fully enclose the seed later in development (Stockey & Rothwell 2009; Rothwell & Stockey 2016). This is also the case in *U. corniculata*. In addition, while *U. corniculata* is known only from dispersed seed-bearing units, the long abscission zone suggests they are deciduous lateral units of a cone-like structure, just as in *D. tetrahedrasperma.*

There are, however, sufficient differences between the seed-bearing units of *Doylea tetrahedrasperma* and *Umkomasia corniculata* to justify recognition of the latter as a separate species (Table 1). The cupules (up to 5.5 mm long and 3–4 mm wide) of *D. tetrahedrasperma* are slightly larger than those of *U. corniculata.* In the larger, presumed mature, cupules of *D. tetrahedrasperma* the lateral flaps are completely fused to one another and also to the cupule stalk forming a closed cupule that completely envelops the seed. In contrast, in *U. corniculata* and *U. mongolica*, even in the larger and presumed mature cupules, the seed is only partially and loosely enclosed by the bilobed structure that is formed by partial fusion of the two lateral flaps. The bilobed structure is also free from the cupule stalk except at the point of attachment. *Umkomasia corniculata* also differs from *D. tetrahedrasperma* in the minute teeth on the cupule surface.

Systematic and nomenclatural considerations

Three genera of corystosperm seed-bearing organs were established by Thomas (1933) based on his material from South Africa: *Umkomasia*, *Pilophorosperma* and *Spermatocodon*. All are compound, branching systems with lateral seed-bearing units, each of which has an axillary fertile axis that bears reflexed cupules. The lateral seed-bearing units are developed to varying extents and may bear multiple cupules. In *Umkomasia* and *Pilophorosperma*, the lateral seed-bearing units are arranged in one plane, but in *Spermatocodon* they are helical on the main axis.

Holmes (1987) treated *Pilophorosperma* as a synonym of *Umkomasia* and while he considered *Spermatocodon* to be problematic, he nevertheless emended the diagnosis of *Umkomasia* to also include helical branch insertion. Based on his consideration of Thomas' work and also on his study of material from the Middle Triassic of eastern Australia, Holmes (1987, p. 166) presented the following emended diagnosis of *Umkomasia*. "An ovulate inflorescence comprising an axis with branches arising from axils of bracts. Branches arranged spirally or in one plane (?), bearing one or more opposite pairs of sessile or pedicellate cupules and terminated by a pair of cupules or a single cupule. Cupules cap-, basin- or helmet-shaped, margin entire or divided into lobes by one to several clefts; each cupule bearing a single platyspermic ovule with a recurved micropyle."

With regard to their overall construction, the three species of seed-bearing organs now known from Tevshiin Govi correspond in every respect with the diagnosis of *Umkomasia* as emended by Holmes (1987). The only point of difference concerns the seeds, which are three-angled in all three species of *Umkomasia* from Mongolia. Compressed seeds of *Umkomasia* from its type locality were generally described as 'ovoid' with pronounced bifid micropyle. However, Thomas (1933, p. 227) also noted "a prominent ridge is seen running down one surface of the seed, and in another example a similar ridge is seen in a central position, suggesting that this form may have been more or less triangular in section". Three-angled seeds have also been described in corystosperms from other localities, for example in the Upper Triassic of Zimbabwe (Barale *et al.* 2009).

Characters that distinguish *Doylea* from the type material of *Umkomasia* from the Triassic of Gondwana were listed by Rothwell & Stockey (2016) as the basis for recognizing *Doylea* as a distinct genus and establishing the new family Doyleaceae and order Doyleales. These characters were: (1) the cupule almost completely enveloping seed at maturity; (2) the absence of secretory cavities in tissues of the cupule; and (3) the conifer-like, compact, compound seed cone. By implication, Rothwell & Stockey (2016) also used these features to argue that *U. mongolica* should be separated from the genus *Umkomasia.* Together with the obvious similarities between *U. mongolica* and *D. tetrahedrasperma* this was also the basis for transferring *U. mongolica* to *Doylea* as *Doylea mongolica*.

Umkomasia Thomas *sensu* Holmes, including the three species described here, shares sufficient similarities with *Doylea tetrahedrasperma* that together they form a natural systematic unit (a putative clade) defined by the presence of distinctive lateral seed-bearing units that are borne in the axil of a bract, and which bear reflexed cupules. Whether the compound seed cone is compact or not seems much less fundamental. Our new material shows that the seed cones of *U. mongolica* are loose, unlike the compact, immature cone of *D. tetrahedrasperma*, but more or less similar to *U. macleanii* H. H. Thomas, the type species of the genus from the Upper Triassic of South Africa (Thomas 1933; Anderson & Anderson 2003).

The other two features cited by Rothwell & Stockey (2016) as a basis for separating *Doylea* and *Umkomasia mongolica* from *Umkomasia* (cupule almost completely enveloping seed at maturity; absence of secretory cavities in tissues of the cupule) are also not compelling. In larger, presumed mature, cupules of *U. mongolica*, *U. corniculata* and *U. trilobata* the cupule only partially and loosely encloses the seed, with lateral flaps that are fused to one another at the base, but that are free from the cupule stalk except at the point of attachment. The more complete enclosure of the seed in *D. tetrahedrasperma* is different from all of the Mongolian species.

Secretory cavities are absent from the cupules of *Doylea* and the three *Umkomasia* species from Tevshiin Govi. However, the feature is only known in *U. resinosa* among *Umkomasia* species from the Triassic of Gondwana, and thus it is inappropriate to consider the presence of secretory cavities as a feature that defines corystosperms.

The similarities between the three *Umkomasia* species from the Upper Cretaceous of Mongolia, the original material of *Umkomasia* from the Upper Triassic of South Africa (Thomas 1933; Anderson & Anderson 2003), and *Doylea tetrahedrasperma* are striking (Table 1). This suggests that *Umkomasia* Thomas *sensu* Holmes from the Triassic of Gondwana, as well as the three species described here and *D. tetrahedrasperma*, form a natural systematic unit (a putative clade) corresponding to the Umkomasiales (= Corystospermales). We therefore reject the assessment that *D. tetrahedrasperma* and *U. mongolica* are only distantly related to corystosperms as proposed by Rothwell & Stockey (2016). We regard Doyleales as a taxonomic synonym of Umkomasiales, and Doyleaceae a taxonomic synonym of Umkomasiaceae.

We place the three Mongolian species of corystosperms in *Umkomasia*, rather than in *Doylea* or a new genus of Umkomasiales because to do otherwise, while also retaining systematic units that can be justified as potentially monophyletic, would require more information on the many other species of *Umkomasia*, most of which are relatively poorly understood. It is also interesting that of the three Mongolian species described here, *U. mongolica* is especially similar to the original material of *Umkomasia* from South Africa, which is a fertile branch system with two orders of branching. Meanwhile, some *Umkomasia* species from the Triassic of Gondwana are different in their construction. For example, in *U. uniramia* from the Upper Triassic of Schroeder Hill, Shackleton Glacier area, central Antarctica (see Bomfleur *et al.* 2014b), the seed-bearing units consist of an axis borne near the apex of a dwarf shoot; the axis bears a whorl of four to eight cupules at the tip (or perhaps as a contracted spiral, Benjamin Bomfleur, pers. comm.).

Given current systematic treatments, and different levels of knowledge about different species of *Umkomasia*, removing *U. mongolica* from *Umkomasia* would render *Umkomasia* paraphyletic. This would not be helpful. We therefore retain *U. mongolica* in *Umkomasia* Thomas *sensu* Holmes, and also assign the two new species in that genus. We recognize that future work may allow the recognition of several genera of ovulate reproductive structures within Umkomasiaceae and Umkomasiales. At a future date, as our knowledge of these plants increases, an appropriate solution may be to transfer *D. tetrahedrasperma* to *Umkomasia*, or to create several new genera to accommodate the different forms of ovulate reproductive structures now grouped together as *Umkomasia* Thomas *sensu* Holmes.

An interesting difference between new material of *Umkomasia mongolica* and the compact cone of *D. tetrahedrasperma* is that in *U. mongolica* the central axis is very slender and the cone is more lax (Fig. 12). This is more similar to the original material of *Umkomasia* from the Triassic of South Africa (Thomas, 1933, figs 1, 56). Also interesting is that some of the lateral seed-bearing units in the original material of *Umkomasia* bear multiple (many more than two or three) cupules. We interpret this situation as analogous (and potentially homologous) to the situation that occurs in some aberrant specimens of *Ginkgo* in which the ovulate shoots are proliferated and bear more than two ovules, with each ovule on a simple stalk (Shi *et al.* 2016, fig. S7).

Comparisons with other fossils

Documentation of unequivocal and diverse corystosperms in the Early Cretaceous of Mongolia raises the question as to whether the group has previously been overlooked in fossil floras from the Northern Hemisphere. Four species based on compression/impression fossils originally referred to other taxa are of particular interest: *Meeusella proteiclada* Krassilov & Bugdaeva from the Lower Cretaceous of the Russian Far East (Krassilov & Bugdaeva 1988), *Toretzia shunfaensis* Z. Cao from the Lower Cretaceous of eastern Heilongjiang, north-eastern China (Cao 1992), *Dirhopalostachys rostrata* Krassilov from the Upper Jurassic–Lower Cretaceous of the Russian Far East (Krassilov 1975) and *Swedenborgia junior* Krassilov from the Lower Cretaceous of Mongolia (Krassilov 1982).

Meeusella proteiclada is known from a single specimen from the Lower Cretaceous of Transbaikal in the Russian Far East (Krassilov & Bugdaeva 1988). It was described as a loose pollen cone with helically arranged, bifurcate, lateral units bearing two ovoid ‘recurved sporangial heads’. These heads were interpreted as a group of fused pollen sacs although pollen was not recovered (Krassilov & Bugdaeva 1988). The lateral units of *Meeusella* strikingly resemble the cupules of *Umkomasia mongolica*, and several of the original illustrations (Krassilov & Bugdaeva 1988, figs 1D, 3B) clearly show the bract subtending the bifurcate axis. *Baikalophyllum* Bugdaeva, the putative leaf of *Meeusella* as suggested by Krassilov & Bugdaeva

(1988), is quite different from *Pseudotorellia* in having a distinct midrib, but more work is needed to reliably establish the link between the two organs. Interestingly, *Pseudotorellia* leaves are dominant in the Lower Cretaceous Kharanor mine of Transbaikal (Bugdaeva 1995), although they are not recorded in the same bed as *M. proteiclada*.

The genus *Toretzia* Stanislavsky was established for ovulate organs borne on a short shoot with attached leaves from the Upper Triassic of the Donetz Basin, Ukraine (Stanislavsky 1973). The genus has long been thought to be part of the *Ginkgo* lineage and perhaps closely related to *Umaltolepis* (Stanislavsky 1973; Zhou 1991, 2009). The type species of *Toretzia*, *T. angustifolia* Stanislavsky, has long and short shoots bearing helically arranged, linear to strap-shaped leaves with two indistinct, more or less parallel, veins. Seed-bearing organs of *T. angustifolia* are borne on short shoots and each is subtended by a ribbon-like leaf. Each seed-bearing organ consists of a stalk bearing a whorl of several inverted seeds (up to six) at the tip (Stanislavsky 1973). While the resemblance of *T. angustifolia* to the *Umkomasia* species from Mongolia is not strong, it is relevant because of the similarities to *U. uniramia* from the Triassic of Antarctica (Axsmith *et al.* 2000). Like *T. angustifolia*, the seed-bearing structures of *U. uniramia* consists of an axis, attached near the apex of a short shoot, that bears a whorl of four to eight reflexed cupules (Axsmith *et al.* 2000).

Toretzia shunfaensis from the Lower Cretaceous of eastern Heilongjiang, north-eastern China (Cao 1992) comprises a bifurcating axis with two inverted seeds. Although the seeds of *T. shunfaensis* are larger than those of *Umkomasia mongolica*, they are well within the size range of *Umkomasia* seeds from the Late Triassic Molteno flora (Anderson & Anderson 2003). In the form of the axis, the way in which it branches, the angle at which the two branches diverge and the form of the probable cupules (interpreted as seeds by Cao 1992), the illustrated specimens of *T. shunfaensis* are very similar to *U. mongolica.*

Dirhopalostachys rostrata Krassilov from the Upper Jurassic–Lower Cretaceous of the Russian Far East is a lax seed cone (gynoclad *sensu* Krassilov 1975) with helically arranged lateral seed-bearing organs, each of which consists of a stalk that bifurcates, with each branch bearing ‘capsule’ *sensu* Krassilov (1975). Each ‘capsule’ contains a single seed, which is completely enclosed and that has the micropyle oriented back towards the cone axis (Krassilov 1975). Krassilov interpreted the ‘capsule’ as shedding the seed at maturity by dehiscence along a ventral suture (Krassilov 1975).

Although *Dirhopalostachys rostrata* is not well preserved, its overall form is similar to *Umkomasia corniculata* and *Doylea tetrahedrasperma*, especially in the long, corniculate extension (= ‘beak’ in Krassilov 1975) at the tip of the ‘capsule’, which may be a cupule like that of *Doylea tetrahedrasperma*. Seeds of *Dirhopalostachys rostrata* are also described as ovate and flattened with a median groove, which suggests that their original form was three-angled. *Dirhopalostachys rostrata* has resin bodies in the cupule walls, a characteristic seen in some Gondwana Triassic corystosperms (Klavins *et al.* 2002) and the cupule cuticle is very thin and delicate like *Umkomasia* (Axsmith *et al.* 2000; Shi *et al.* 2016). However, the complete enclosure of the seed is more like *Doylea tetrahedrasperma*.

In *Dirhopalostachys* Krassilov (1975) did not describe a bract subtending each lateral seed-bearing unit, which is a critical feature that needs to be assessed. Also important is Krassilov’s hypothesis regarding the leaf of *Dirhopalostachys*, which he interpreted to be *Nilssonia schmidtii* (Heer) Seward because of their close field association (Krassilov 1975). If the pinnate leaves of *Nilssonia schmidtii* are part of the *Dirhopalostachys* plant this would be evidence that *Dirhopalostachys rostrata* is not closely related to *Doylea tetrahedrasperma*, *U. corniculata*, and other *Umkomasia* species. However, while Krassilov (1975, p. 105) noted that “The most constant associates of *Dirhopalostachys* are the gymnosperm leaf-genera *Phoenicopsis* (*Stephenophyllum*), *Pityophyllum* and *Nilssonia*”, he also noted the presence of *Pseudotorellia* at the locality with the best-preserved specimens of *Dirhopalostachys* (Krassilov 1975, p. 101). Definitive resolution of this and other questions will likely require better preserved material of *Dirhopalostachys rostrata* and recollecting at the key *Dirhopalostachys* localities.

The similarities of *Meeusella proteiclada*, *Toretzia shunfaensis* and *Dirhopalostachys rostrata* are with *Umkomasia mongolica* and *U. corniculata*, but comparisons of *U. trilobata* with previously described fossils open new and intriguing similarities with fossil plants previously assumed to be conifers, including several taxa among the large complex of plants assigned to the genus *Swedenborgia* (see Herrera *et al.* 2015, fig. 8). Of particular interest is the compact seed cone, *Swedenborgia junior* Krassilov from the Upper Jurassic–Lower Cretaceous of Mongolia (Krassilov 1982, fig. 84). The cone is 30 mm long and 13 mm wide, with trilobed cone scales up to 3 mm long. Key details are not visible, but several of the isolated cone scales (Krassilov 1982, figs 85, 86, 91) seem to show additional appendages potentially corresponding to the flaps that form part of the cupule in *U. trilobata.*

Swedenborgia megasperma Stanislavsky and *S. tyttosperma* Stanislavsky (Stanislavsky 1976) are two better understood species of *Swedenborgia* that have distinctive three-lobed seed-bearing units resembling those of *Umkomasia trilobata.* Both species also have distal projections that resemble those seen in *U. corniculata*. Unfortunately, poor preservation makes it impossible to determine if the seeds were borne in a cupule and partially covered by the bilobed structures in the same way as in *Umkomasia.* Even in our much better-preserved material these parts of the cupule are sometimes broken, exposing the complete seed, and this is especially the case in *U. corniculata* (Fig. 4D, G).

The possibility that some species of *Swedenborgia*, which have been assigned previously to conifers, are likely corystosperms again highlights the fundamental similarities between compound ovulate seed-bearing structures (cones and cone scales) of conifers and corystosperms already noted by Rothwell & Stockey (2016). The way in which *Doylea* is scored in the phylogenetic analysis of Rothwell & Stockey (2016) also implies homology and is a key feature that influences the placement of *Doylea* in a clade with *Ginkgo*, conifers, cordaites and Gnetales rather than corystosperms.

Detailed comparison of corystosperm seed-bearing structures with the cones of conifers is beyond the scope of this paper, but we previously noted the basic similarities between the seed-bearing units of *Umkomasia mongolica* and the seed-scale complexes of *Podocarpus totara* D. Don. in which the seeds are partly enclosed by an epimatium (Shi *et al.* 2016, fig. S8). The bract-scale complexes of the extinct conifer family Cheirolepidiaceae are also of interest. In Cheirolepidiaceae a broad, flattened bract subtends a lobed ovuliferous scale bearing one or two seeds (variable within a single species) with their micropyles directed towards the cone axis (Kvaček 2000; Escapa *et al.* 2012, 2013). Unusually among conifers, in Cheirolepidiaceae the seeds are also covered by a flap. Such enclosure in a pocket of ovuliferous scale tissue (pocket-forming tissue) (Kvaček 2000; Escapa *et al.* 2012, 2013) highlights issues of potential homology (or merely analogy) with corystosperm cupules that require closer examination.

Organography and homology

Thomas (1933) considered the entire corystosperm seed-bearing organ to be a fertile branch system with two orders of branching, in which the ultimate and penultimate fertile axes are subtended by one or more bracts. Even though the seed-bearing organ in some of his material was flattened and showed dorsiventral differentiation of the cuticles, Thomas (1933) was convinced that the seeds were borne on axes rather than leaves. Permineralized material of *Umkomasia resinosa* from the upper Middle or Upper Triassic of Antarctica (see Bomfleur *et al.* 2014a) is also consistent with this interpretation because the axis that bears helically arranged cupules has typical cauline anatomy (Klavins *et al.* 2002) and even though the cupules are supplied by collateral bundles this is not a definitive indication of foliar structure (Shi *et al.* 2016).

The discovery of seed cones of *Doylea tetrahedrasperma* and *Umkomasia mongolica* adds further weight to Thomas's original interpretation of the entire seed-bearing organ of corystosperms as a branch system (Thomas 1933) as well as previous interpretations of the homology of corystosperm cupules, which suggested that the seed is borne directly on a shoot, rather than on a surface of a leaf-derived structure (Shi *et al.* 2016). That the seed is borne directly on a shoot is also clearly demonstrated by the short seed stalk that is clearly visible in empty cupules of *U. trilobata* (Fig. 10C, D, E).

Comparing Thomas's material with *Doylea tetrahedrasperma* and the three species of *Umkomasia* from Mongolia, it is clear that the form of the ultimate seed-bearing units varies considerably among species. In *U. mongolica* and *U. corniculata* the seed-bearing unit branches just once and bears only two cupules. In *U. trilobata* branching is presumed to be similarly sparse but in this case the homologue of the seed-bearing axis is flattened, scale-like and bears three cupules. In other species, such as *U. quadripartita* J. M. Anderson & H. M. Anderson and *U. decussata* J. M. Anderson & H. M. Anderson, both from the Late Triassic Molteno flora (Anderson & Anderson 2003), the individual seed-bearing units may be more extensively branched and bear many cupules in a helical or planate arrangement. *Umkomasia uniramia* is distinct from all other known *Umkomasia* species. Its seed-bearing units consist of an axis borne near the apex of a dwarf shoot. The axis bears a pair of bracts and has a whorl (or condensed spiral) of four to eight cupules at the tip (Axsmith *et al.* 2000).

In *Doylea tetrahedrasperma* and the three species of *Umkomasia* from Mongolia the cupule is a complex organ formed by both the seed stalk and the lateral flaps, which are morphologically different structures. In *Doylea*, the cupules of which are morphologically very similar to *U. corniculata*, the cupule stalk has a single vascular bundle but the two lateral flaps are unvascularized and it is possible that they are leaf homologues.

In impression fossils of corystosperm reproductive structures, as well as in poorly preserved compressions, it is difficult to be certain about details of cupule architecture, but the number of cupule lobes has frequently been used as an important systematic feature (Thomas

1933; Holmes & Ash 1979; Holmes 1987; Anderson & Anderson 2003). For example, Thomas (1933) described the cupules of *Umkomasia* as a bilobed, while cupules of *Pilophorosperma* and *Spermatocodon* were described as unlobed. Similarly, among the corystosperm species from the Late Triassic Molteno flora, *U. bracteolata* J. M. Anderson & H. M. Anderson, *U. quadripartita*, *U. decussata* and *U. grandis* J. M. Anderson & H. M. Anderson mainly have bilobed cupules; *U. monopartita* J. M. Anderson & H. M. Anderson and *U. gracilliaxis* J. M. Anderson & H. M. Anderson have four-lobed cupules; *U. cupulata* J. M. Anderson & H. M. Anderson has four- or five-lobed cupules, and *Fanerotheca* Freng. mainly has four-lobed cupules (Anderson & Anderson 2003). *Karibacarpon* Lacey, another ovulate organ referred to the corystosperms from the Triassic of Zimbabwe (Lacey 1976) and Australia (Holmes & Ash 1979), has ribbed cupules that when open are star-shaped with five to nine lobes.

However, all the corystosperm species mentioned above are based on compression/impression fossils. The three-dimensionally preserved ovulate organs of corystosperms including *Umkomasia uniramia*, *U. resinosa*, *U. mongolica*, *U. corniculata* and *Doylea tetrahedrasperma* consistently suggest that the cupules of *Umkomasia* are formed by part of the cupule stalk and two lateral flaps of a bilobed structure born on the stalk (Axsmith *et al.* 2000; Klavins *et al.* 2002; Stockey & Rothwell 2009; Rothwell & Stockey 2016; Shi *et al.* 2016). The cupules either partially enclose (*U. resinosa*, *U. mongolica*, *U. corniculata*) or (nearly) completely envelop the seeds (*U. uniramia*, *D. tetrahedrasperma*) at maturity. The closed cupules of *U. uniramia* and *D. tetrahedrasperma* dehisce at maturity to shed the seeds. The exceptionally well-preserved material of *U. trilobata* demonstrates a new morphological pattern for corystosperm cupules, in which the median cupule includes part of the cupule stalk as well as three lateral flaps. The three lateral flaps correspond to the three lateral faces of the single, three-angled seed but the two inner flaps are small and the flattened cupule stalk is also morphologically and functionally part of the seed enclosing structure. The three flaps are all free from the cupule stalk except at the point of attachment, although they may be partly fused together. The two inner flaps, for example, may be slightly fused at the base to the outer flap.

Evolutionary implications

Corystosperms attained their greatest diversity and widest distribution in the Southern Hemisphere during the Middle and Late Triassic (Retallack 1977; Anderson & Anderson 1983, 2003; Bomfleur & Kerp 2010; Pattemore 2016a). They were apparently less prominent through the Jurassic and Cretaceous, although a few relicts may have persisted as late as the Eocene (McLoughlin *et al.* 2008). In the Northern Hemisphere corystosperms were present as early as the Late Triassic (Zan *et al.* 2008) and apparently persisted through the Jurassic (Harris 1964; Kirchner & Müller 1992). Evidence from Mongolia and Canada shows that in the Northern Hemisphere corystosperms persisted into the Early Cretaceous and were likely contemporaneous with early angiosperms, although no angiosperm mesofossils have been recognized so far in any samples from Tevshiin Govi. Whether corystosperms were eventually driven to extinction by competition with angiosperms, or were impacted by changes in the broader environment, remains to be determined.

The presence of unequivocal (Shi *et al.* 2016) and probable (Krassilov 1975, 1982; Krassilov & Bugdaeva 1988; Cao 1992) corystosperm seed-bearing reproductive structures in the Lower Cretaceous of Asia, together with *Doylea tetrahedrasperma* from the Lower Cretaceous of Canada (Stockey & Rothwell 2009; Rothwell & Stockey 2016), shows that corystosperms were more important in the late Mesozoic vegetation of the Northern Hemisphere than has been recognized previously. The popular view that corystosperms were predominantly an early Mesozoic group, more or less confined to the Southern Hemisphere, needs to be revised. Evidence from Tevshiin Govi also suggests that the group was once much more diverse. In addition to species with bifurcate pinnately compound *Dicroidium*-type fronds, there were also species with simple laminar leaves of the *Pseudotorellia* type.

The occurrence of different corystosperm species in different facies at the Tevshiin Govi locality also shows that different corystosperm species most likely grew in different environments on the same landscape, ranging from peat swamps (*Umkomasia mongolica*) to fluvio-lacustrine settings with higher clastic input (*U. corniculata* and *U. trilobata*). Ecological differentiation was also accompanied by morphological differentiation, especially with regard to the form of the individual ovulate units, which are elaborated in various ways.

The different elaborations of corystosperm seed-bearing structures suggest new opportunities for instructive comparisons with the seed-bearing structures of other seed plants. Most immediately, information from the Lower Cretaceous of Mongolia suggests that corystosperms and Petriellales (Taylor *et al.* 1994; Anderson & Anderson 2003; Bomfleur *et al.* 2014a) may be more closely related than previously thought (Doyle 2006). For example, empty cupules of *Kannaskoppia* J. M.

Anderson & H. M. Anderson (Petriellales) from the Late Triassic Molteno flora (Anderson & Anderson 2003) appear to consist of the cupule stalk and three lateral flaps, like the central cupules of *U. trilobata*. Separating corystosperms from Petriellales based on the direction of curvature of the cupules (Doyle 2006) is also complicated by the realization that the cupules of *Umkomasia mongolica*, *U. corniculata* and *U. trilobata* are reflexed (curved abaxially) relative to the secondary axis on which they are borne, but inflexed (curved adaxially) relative to the primary axis of the cone of which they are part.

More broadly within seed plants, a case has been made for a possible close relationship of *Umkomasia mongolica* to *Ginkgo* (Shi *et al.* 2016), which is consistent with Meyen's concept of the Ginkgoopsida (Meyen 1984; Gordenko & Broushkin 2015), and is supported by resemblances of *Pseudotorellia palustris*, the leaf of *U. mongolica* (Fig. 12), to *Ginkgo*.

More surprising are the potential similarities between conifers and corystosperms, also noted by Rothwell & Stockey (2016). For example, the pronounced distal extension of the two cupules in *Umkomasia corniculata* results in a situation resembling the deeply bilobed cone scales of the extinct putative pinaceous conifer *Schizolepidopsis* (Leslie *et al.* 2013), while in *U. trilobata* the flattening and presumed fusion of three ovule bearing stalks into a three-lobed cone scale results in a situation resembling the cone scales of extinct voltzialean conifers (Herrera *et al.* 2015). A close relationship between corystosperms and conifers would be surprising, but the fundamental similarities of seed-bearing structures comprising a bract subtending a variously modified axis/axes bearing ovules is striking. The same arrangement is also seen in *Ginkgo* (Shi *et al.* 2016; Rothwell & Stockey 2016), as well as in Gnetales (Crane 1985). These observations, together with the potential similarities of corystosperm cupules to those of other extinct Mesozoic seed plants, such as *Caytonia* and *Petriellaea*, highlight interesting questions about the homologies of the reproductive structures among major groups of seed plants and imply architectural commonalities that are currently underappreciated and require further exploration.

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