

# *Geminispermum*, an Early Cretaceous (early–middle Albian) cupulate unit from the angiosperm-dominated Puddledock flora of eastern North America

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**ABSTRACT.** A new genus and species, *Geminispermum virginense*, is described based on a well-preserved coalified cupulate reproductive unit recovered from the Early Cretaceous (early–middle Albian) Puddledock locality, Virginia, U.S.A. The reproductive unit is bisymmetrical and consists of an axis that bifurcates into two cupule-bearing stalks, each in the axil of a bract. Each cupule stalk bears a single non-valvate cupule recurved towards the center of the reproductive unit. The cupule opens distally by a short transverse slit with a distinct upper margin. Each cupule almost completely encloses a single orthotropous seed that is free from the cupule except at the base. The nucellus is also free from the integument except at the basal point of attachment. *Geminispermum* combines features of the ovulate structures of Caytoniales, Umkomasiales (= Corystospermales, including Doyleales) and Petriellales, but cannot be included in any of these existing orders as they are currently understood. The recurved, closed, non-valvate cupules are particularly similar to those of *Caytonia*, *Petriellaea* and *Reymanownaea* in external morphology, but differ in being one-seeded. The cupules of *Geminispermum* differ from the one-seeded cupules of Umkomasiales in being non-valvate and in having only a single cupule per bract. *Geminispermum* is perhaps most similar to the one- or two-seeded non-valvate cupules of *Ktalenia* from the Early Cretaceous of Argentina, but *Ktalenia* is poorly preserved, details of cupule architecture are uncertain, and the cupules appear to be associated with a single strongly dissected bract. *Geminispermum* is currently the only unequivocal seed plant cupule recovered from the Early Cretaceous Potomac Group and is distinct from all previously described cupulate reproductive structures.

**KEYWORDS:** Caytoniales, Corystospermales, Doyleales, Petriellales, seed ferns, synchrotron radiation X-ray tomographic microscopy, Umkomasiales

## INTRODUCTION

Several decades of intensive palaeobotanical work focused on the Early Cretaceous have provided new insights about the reproductive structures of early angiosperms and their relationships to extant taxa (e.g. Friis et al. 2011), but an important ancillary development has been the emergence of significant new information on a surprising diversity of non-angiosperm

seed plants. Especially notable has been the recognition of a diverse group of seeds related to the Bennettitales Engl., Erdtmanithecales E.M.Friis & K.R.Pedersen and Gnetales Luer ss. (BEG group of Friis et al. 2009, 2013, 2019). Another significant advance has been the recognition of Early Cretaceous ovulate reproductive structures with strong similarities to the cupules of Umkomasiales Doweld (= Corystospermales H.H.Thomas, including

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Doyleales G.W.Rothwell & Stockey) (Stockey & Rothwell 2009, Rothwell & Stockey 2016, Shi et al. 2016, 2019), a group often regarded as characteristic of the Late Triassic in the Southern Hemisphere (Anderson & Anderson 2003, Pattenmore 2016, Anderson et al. 2019).

*Doylea tetradrasperma* Stockey & G.W. Rothwell (2009), preserved as a calcareous permineralization from the Valanginian–Hauterivian of Apple Bay, Vancouver Island, was tentatively assigned to Umkomasiales but was subsequently assigned to a new order Doyleales G.W.Rothwell & Stockey (2016). Several kinds of ovulate reproductive structures very similar to *Doylea* Stockey & G.W.Rothwell, and also to typical *Umkomasia* H.H.Thomas emend. W.B.K.Holmes from the Triassic, have been described from lignites of Aptian–Albian age from south-central Mongolia (Shi et al. 2016, 2019). These discoveries, based on superbly well-preserved lignitic compressions, suggest that cupules of Umkomasiales and Doyleales are identical in their major structural features.

The excellent preservation of both the North American and the Mongolian material has added new and detailed information on the morphology and anatomy of these cupule-bearing reproductive structures, which together with other records from the Northern Hemisphere (e.g. Krassilov & Bugdaeva 1988, Cao 1992, Kirchner & Müller 1992, Zan et al. 2008) have helped transform perspectives on the diversity and palaeogeographic distribution of the Umkomasiales. In addition, early umkomasialean leaves (*Dicroidium* Gothan) have been documented in the Late Permian (Kerp et al. 2006), and studies of lignitic material from Mongolia have shown that at least some Early Cretaceous umkomasialeans bore narrowly elliptical leaves with several parallel veins (Shi et al. 2016, 2019), very different from the typically pinnate *Dicroidium* leaves of their Triassic relatives from the Southern Hemisphere (Anderson & Anderson 2003).

In this paper we describe a new gymnosperm cupulate reproductive structure from the early–middle Albian Puddledock assemblage collected in the Potomac Group of eastern North America. This new cupulate organ is unusual in occurring in an angiosperm-dominated assemblage. As in *Doylea*, and also in other Northern Hemisphere forms assigned to *Umkomasia* (Umkomasiales: Shi et al. 2016, 2019), the new cupulate organ is a modified seed-bearing branch

borne in the axil of a bract, but the cupules are non-valvate. Externally, the new fossil resembles cupules of *Caytonia* H.H.Thomas, *Reymanownaea* Barbacka & Bóka (Caytoniales H.H.Thomas), *Petriellaea* T.N.Taylor, Fueyo & Ed.L.Taylor (Petriellales T.N.Taylor, Fueyo & Ed.L.Taylor) and apparently also *Ktalenia* S.Archang., but there are also differences that warrant the establishment of a new genus. In the new cupulate organ each cupule contains one ovule, rather than several.

## MATERIAL AND METHODS

The specimen described here was extracted from sediment sample Puddledock 185 collected at the former Tarmac Lone Star Industries (now Vulcan Materials Co.) sand and gravel pit, south of Richmond and east of the Appomattox River in Prince George County, Virginia, U.S.A. (37°15'52"N; 77°22'10"W). Sediments at the Puddledock locality are of early to middle Albian age and contain rich assemblages of plant mesofossils in which angiosperm flowers, fruits and seeds are particularly common (Friis et al. 2011). The mesofossils are preserved as charcoal or lignite and typically have their three-dimensional shape intact. The specimen described here is lignitic and preserved in three dimensions.

The fossil was extracted from the sediments and cleaned with HF, HCl and water for further analysis. It was studied using attenuation-based synchrotron radiation X-ray tomographic microscopy (SRXTM) at the TOMCAT beamline of the Swiss Light Source of the Paul Scherrer Institute, Villigen, Switzerland (Stampanoni et al. 2006, Friis et al. 2014). For SRXTM analyses the fossil was mounted on a brass stub using nail polish and the analysis was carried out at 10 keV with a sCMOS detector over 180° using a 10× objective and 17 µm thick LSO:Tb scintillator screen (isotropic pixel size 0.65 µm) and a 20× objective and 20 µm thick LuAg:Ce scintillator (isotropic pixel size 0.325 µm).

The fossil specimen is housed in the Paleobotanical Collections of the Field Museum, Chicago. Raw data from the SRXTM analysis are stored at the Swedish Museum of Natural History, Stockholm.

## SYSTEMATIC PALAEONTOLOGY

Caytoniales-Umkomasiales-Petriellales  
(CUP) group

Genus. *Geminispermum* gen.nov.

Derivation of generic name. From the paired arrangement of the cupules.

Generic diagnosis. Reproductive (ovulate) unit bisymmetrical consisting of a short axis bifurcating into two cupule-bearing stalks.

Cupule-bearing stalks above bifurcation narrowly elliptical and bilaterally symmetrical in transverse section. Each cupule stalk in the axil of, and partially fused to, a prominent bract. Bract several cell layers thick and supplied by a single central vascular bundle. Each cupule stalk bearing a single one-seeded cupule and continuing distally beyond the attachment of the seed to form a broad transverse crest over the cupule apex. Cupule stalk supplied by two vascular bundles. Cupules recurved towards the center of the reproductive unit. Cupule non-valvate, with parallel longitudinal ridges on its exposed surface and opening by a short transverse slit. Seed almost completely enclosed in the cupule, basally attached, orthotropous, free from cupule except at the base, triangular in transverse section. Micropyle positioned at the transverse slit and projecting only slightly. Nucellus free from the integument except at base. Resin bodies present in axes and bracts.

Remarks on the genus. *Geminispermum* is distinct from all previously described cupulate seed-bearing organs, justifying the establishment of a new genus. However, in its major structural features, and in having the seeds borne in recurved cupules, *Geminispermum* is very similar to the seed-bearing structures of Caytoniales, Petriellales and Umkomasiales, as well as *Ktalenia* from the Early Cretaceous of Argentina that is unassigned at the ordinal level. These fossils are often included together in the informal grouping “Mesozoic pteridosperms” (“Mesozoic seed ferns”). This grouping is poorly defined, but based on the clear similarities of their cupulate ovulate reproductive structures we informally refer to this subset of “Mesozoic pteridosperms” comprising Caytoniales, Petriellales, Umkomasiales and *Ktalenia* as the CUP (Caytoniales, Umkomasiales, Petriellales) group.

In external morphology the cupules of *Geminispermum* are similar to those of *Caytonia*, *Ktalenia*, *Petriellaea* and *Reymanownaea* in being non-valvate, in almost completely enclosing the seeds, and in having a transverse opening that takes the form of a slit (unknown for *Ktalenia*). However, *Geminispermum* differs from *Caytonia*, *Petriellaea* and *Reymanownaea* in having one seed rather than many seeds in each cupule. In *Caytonia*, *Petriellaea* and *Reymanownaea* there also is no evidence of any associated bract, but in *Reymanownaea* the cupulate stalk broadens towards the cupule

and appears to be extended distally to form a broad crest similar to the stalk extension in *Geminispermum*.

*Geminispermum* is more like the cupules of *Doylea*, *Ktalenia* and *Umkomasia* in being one-seeded (sometimes two-seeded in *Ktalenia*). Also, as in *Doylea* and several *Umkomasia* species, the cupule stalk is in the axil of a bract. However, in *Geminispermum* the cupulate axes are more compact, and in *Doylea* and most *Umkomasia* species the cupules are valvate and only partly enclose the seeds. In *Ktalenia* the cupules appear to be in the axil of a single, free, strongly dissected bract. See Discussion for a more detailed assessment of similarities and possible systematic relationships.

Type species designated here. ***Geminispermum virginense*** gen. et sp. nov.

Plant Fossil Names Registry. PFN000591 (for new genus).

***Geminispermum virginense*** gen.  
et sp. nov.

Figs 1A–G, 2A–H, 3A–C

Derivation of specific epithet. From the state of Virginia, U.S.A., where the fossil was collected.

Specific diagnosis. As for the genus.

Holotype, designated here. PP56588 (Puddledock sample 185; illustrated here, Figs 1A–G, 2A–H, 3A–C).

Plant Fossil Names Registry. PFN000592 (for new species).

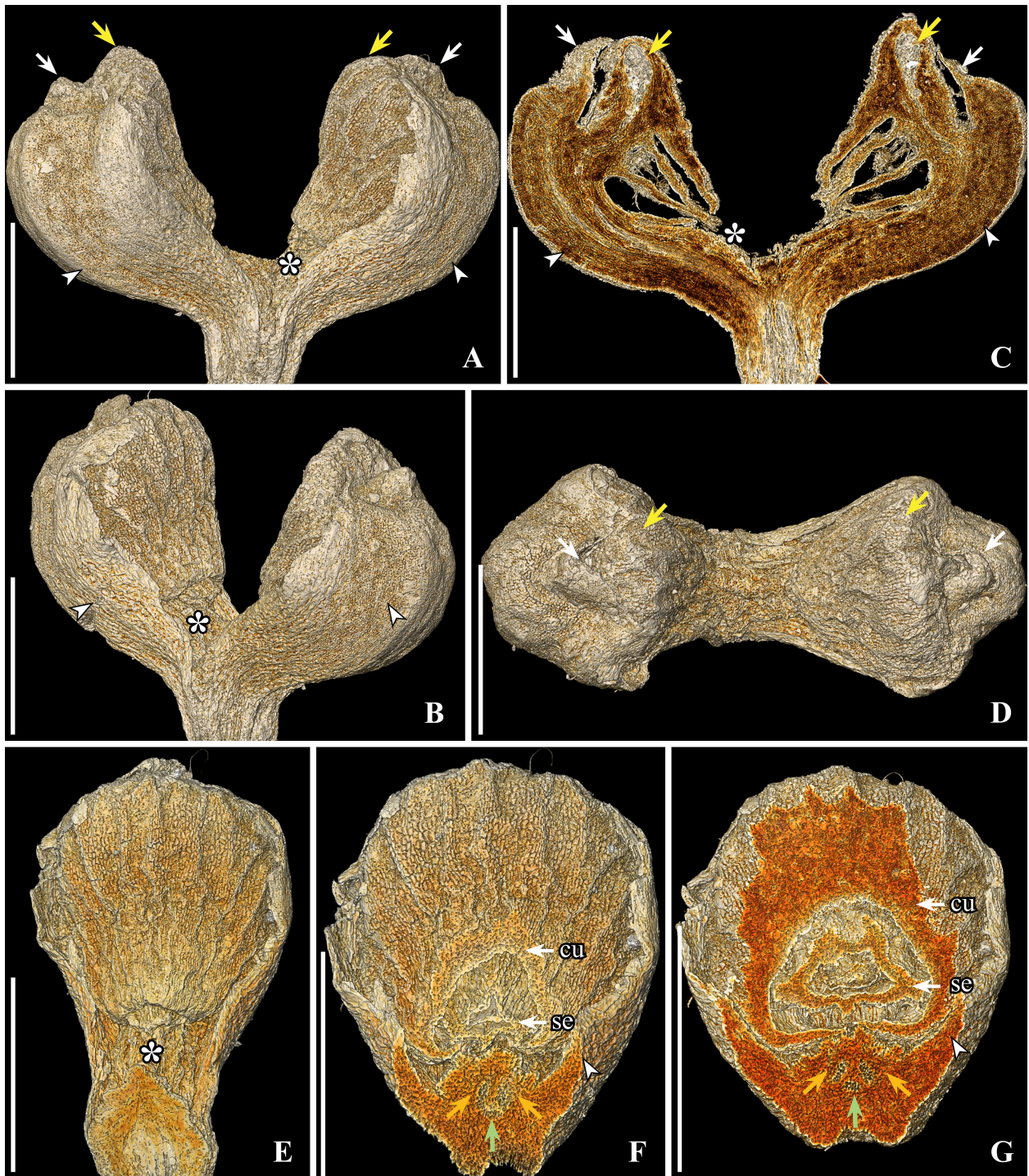
Repository. Paleobotanical Collections, Department of Geology, Field Museum, Chicago, Illinois (PP).

Type locality. Puddledock locality, former Tarmac Lone Star Industries (Vulcan Materials Co.) sand and gravel pit, located south of Richmond and east of the Appomattox River in Prince George County, Virginia (lat. 37°15'52"N, long. 77°22'10"W).

Type stratum and age. Basal part of Subzone IIB, Potomac Group; Early Cretaceous (early to middle Albian).

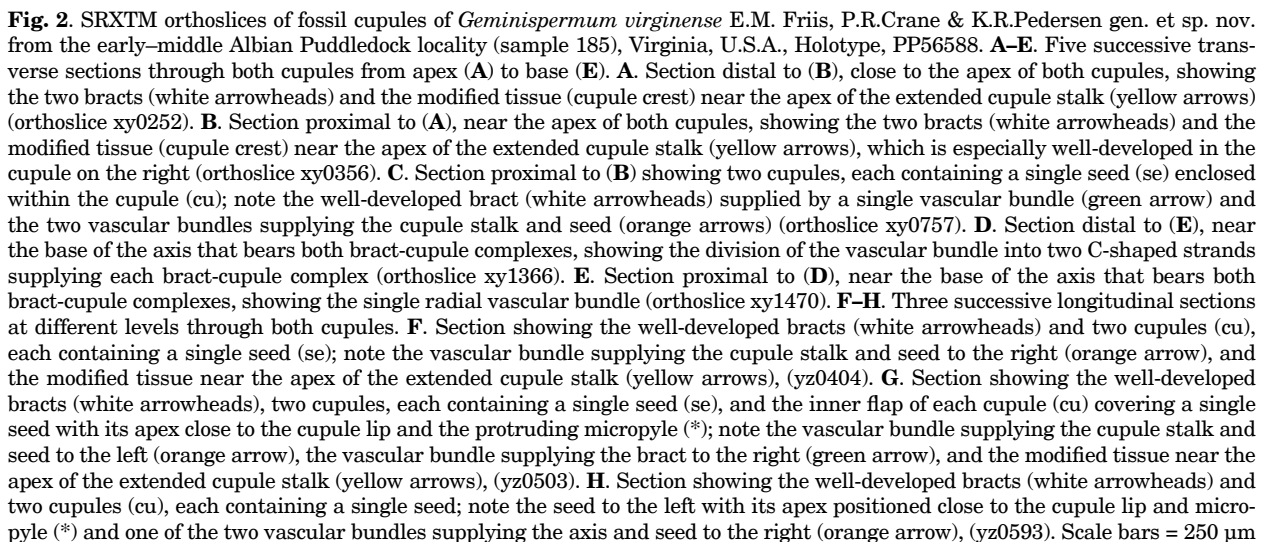
Description and remarks. The specimen is a reproductive (ovulate) unit consisting of an axis that branches into two cupule-bearing stalks, each of which bears a single



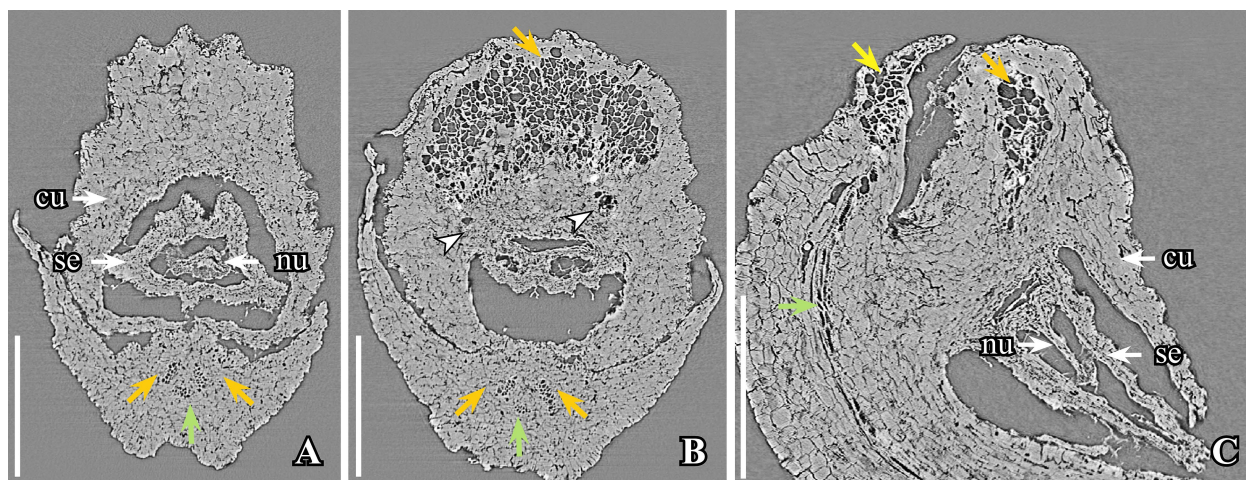


**Fig. 1.** SRXTM volume renderings of fossil cupules of *Geminispermum virginense* E.M. Friis, P.R.Crane & K.R.Pedersen gen. et sp. nov. from the early–middle Albian Puddledock locality (sample 185), Virginia, U.S.A., Holotype, PP56588. **A, B.** Pair of cupules in slightly oblique lateral view (**A**, inclined slightly away to the right; **B**, turned and inclined slightly away to the left) showing two bracts (white arrowheads), each partially covering a cupule: note the weakly developed lip on the cupule, the protruding micropyle (\*), the epidermal surface texture of the bracts, the modified apices of the bracts (white arrow) and the extended cupule stalk (cupule crest; yellow arrows). **C.** Pair of cupules in lateral view, cut longitudinally between orthoslices yz0610 and yz0650, showing both cupules, each of which is supported by a bract (white arrowheads) and contains a single seed; note the modified apices of the two bracts (white arrows), the modified tissues of the extended cupule stalk (cupule crest; yellow arrows) and the protruding micropyle (\*). **D.** Pair of cupules viewed from above, showing their directly opposite positions with both cupule lips directed toward the center; note the modified apices of both bracts (white arrows) and the extended cupule stalk (cupule crest; yellow arrows). **E.** Cupule in dorsiventral view (specimen cut at orthoslice xz1242), showing exposed surface of cupule with irregular longitudinal ridges and micropyle (\*) extending slightly beyond the transverse slit of the cupule. **F, G.** Cupule in dorsiventral view cut at orthoslice xz1590 (**F**) and xz1735 (**G**), showing longitudinal-transverse sections of bracts (white arrowhead), cupule stalk, cupule (cu) and seed (se); note the central vascular bundle to bract (green arrow) and the two lateral vascular bundles supplying the cupule stalk and seed (orange arrows). Scale bars = 500  $\mu$ m









**Fig. 3.** SRXTM orthoslices of fossil cupules of *Geminispermum virginense* E.M. Friis, P.R.Crane & K.R.Pedersen gen. et sp. nov. from the early–middle Albian Puddledock locality (sample 185), Virginia, U.S.A., Holotype, PP56588. **A, B.** Longitudinal-transverse sections perpendicular to sections in 2F–H through bract, cupule axis, cupule (cu) and seed (se) with remains of nucellus (nu) close to micropyle (**A**, xz1742) and close to seed attachment (**B**, xz1900); note the central vascular bundle to bract (green arrow) and the two lateral vascular bundles supplying the cupule stalk and seed (orange arrows); note larger cells of the modified tissue near the apex of the cupule stalk (orange arrow); note also larger, rounded cells scattered in the ground tissue of the cupule (white arrowheads) that are probable secretory/resin cells. **C.** Longitudinal section parallel to sections in 2F–H through bract, cupule stalk, cupule (cu) and seed (se) with remains of nucellus (nu); note larger cells near the apex of the bract (yellow arrow) and the expanded modified tissue near the apex of the extended cupule stalk (orange arrow); also note the micropyle extending beyond the cupule. Scale bars = 250  $\mu$ m

one-seeded cupule (Figs 1A–G, 2A–H, 3A–C). The specimen is about 1.15 mm long, 1.8 mm wide (broadest dimension) and 0.87 mm wide (shortest dimension). The specimen is broken immediately below the point of branching and there is no indication that the axis continued above the level of branching. The bisymmetric rather than bilaterally symmetric form suggests that the specimen is probably the apical proportion of larger compound seed-bearing axis rather than a single lateral unit.

In transverse section, below the point of branching the main axis is rounded, with a slightly ribbed surface and with a central, almost radially symmetrical stele (Fig. 2E). Distally the main axis branches to form the two cupule stalks, each of which is in the axil of a bract. The stele divides into two C-shaped traces (Fig. 2D), each of which supplies a bract and cupule stalk. Each C-shaped trace then divides to produce two lateral bundles that supply the cupule stalk, and a single abaxially positioned central bundle that supplies the bract (Figs 2C, F, G, 3A–C).

Each cupule stalk is narrowly elliptical in transverse section and partially fused to the bract near the base (Figs 2A–C, F–H, 3A–C). The bract is curved, about 1 mm long and 0.6 mm wide, and terminates in a small protrusion (Figs 1C, D, 3C). The cupule stalk is short, about 0.25 mm long from the point of

branching to the point at which it is recurved and forms part of the cupule (Figs 2F–H, 3C). The cupule stalk is mainly composed of small, isodiametric, thick-walled cells, similar to the cells of the bract and cupule. The cupules on each cupule stalk are recurved towards the center of the reproductive unit, which results in the two cupules facing each other (Figs 1A–D, 2A–C, F–H). The cupule stalk extends for a short distance beyond the cupule, forming a transverse crest (Fig. 1A, B, D). In this extension, and bordering the vascular bundle, the cells are larger, equiaxial and thin-walled (Figs 1C, 2A, B, F–H, 3B, C).

The single cupule on each stalk is about 0.6 mm long and about 0.5 mm in maximum diameter. In the median plane the cupule wall is composed of the recurved cupule stalk with additional enclosing tissues towards the inside of the reproductive unit (Figs 2G, H). The cupule wall is about 0.06 mm thick and consists of small, equiaxial, thick-walled cells (Figs 2 C, F–H). The cupule is almost completely closed, but opens towards the center of the unit by a short transversely elongate slit with a distinct margin. Neither the margin of the slit nor the adjacent part of the cupule stalk is papillate (Figs 1A, B, E). About ten irregular ridges extend longitudinally on the exposed surface of the cupule (Fig. 1E–G). This surface pattern may reflect some shrinkage

but may also indicate slight structural differences in the cupule tissues.

A single, basally attached, orthotropous seed is present in each cupule (Figs 1C,G, 2C, F–H, 3A). The seed is almost completely enclosed by the cupule and projects only slightly through the slit-like opening (Figs 1B, C, E, 2G, H, 3C). The seed is free along almost its full length and is attached to the cupule only at the base (Figs 2G, H, 3C). It is ovate to elliptical in longitudinal section (Figs 1C, 2G, H, 3C) and triangular in transverse section (Figs 1F, G, 3A). The integument is about 0.06 mm thick except near the micropyle, where it is thinner (Figs 2G, H). The micropylar region of the seed is positioned at the distal cupule opening and projects only slightly (Figs 1B, 2G, H, 3A). The micropyle is apparently slightly bifid at the very tip, and triangular immediately proximal to the tip (Fig. 1F). Remains of tissues inside the integument, interpreted as the nucellus, suggest that the nucellus is free along its full length (Fig. 2H). Resin bodies are present in the cupule stalk and bracts but not in the seed.

## DISCUSSION

### CUPULES OF *GEMINISPERMUM* AND COMPARISON WITH SIMILAR MESOZOIC PLANTS

The radial symmetry of the main axis of *Geminispermum*, and also the radial symmetry of its stele, strongly suggests that the single specimen is the tip of a larger cupule-bearing axis. From the Early Cretaceous of North America and Mongolia, cupule-bearing organs assigned to *Doylea* and *Umkomasia* are aggregated into a cone-like structure in which lateral, bilaterally symmetrical, cupule-bearing units are each borne in the axil of a bract (Rothwell & Stockey 2016, Shi et al. 2016, 2019). The material from Mongolia was assigned originally to a broadly defined *Umkomasia* as *U. mongolica* G.Shi, A.B.Leslie, Herend., F.Herrera, Ichinnorov, Mas.Takah., P.Knopf & P.R.Crane, *U. corniculata* G.Shi, P.R.Crane, Herend., Ichinnorov, Mas.Takah. & F.Herrera and *U. trilobata* G.Shi, P.R.Crane, Herend., Ichinnorov, Mas.Takah. & F.Herrera. *Umkomasia mongolica* was later transferred to *Doylea* (Rothwell & Stockey 2016), and a revision of the other umkomasiacean species from Mongolia is underway (Shi et al., pers. comm.;

see also Anderson et al. 2019). Notwithstanding these nomenclatural transfers, the structure of the cupules in these plants is fundamentally similar. Furthermore, the single bract subtending the lateral cupule-bearing units of *Doylea* and the Mongolian umkomasiaceans, which may have two or three cupules, suggests that each lateral unit is homologous to one bract and its axillary cupule-bearing stalk in *Geminispermum*. The situation in *Petriellaea*, *Reymanownaea* and *Caytonia* is less clear.

Petriellales, including permineralized *Petriellaea* and compression/impression fossils of Kannaskoppiaceae J.M.Anderson & H.M.Anderson (Bomfleur et al. 2014), are widespread in the Gondwanan Triassic. The ovulate structure of *Petriellaea* is reconstructed as having cupules in pairs (Taylor et al. 1994), similar to Early Cretaceous *Doylea tetraedrasperma*, *D. mongolica* and *Umkomasia corniculata*, but the illustrations and descriptions provide no indication of a bract (Taylor et al. 1994). There is also no evidence of a bract in *Caytonia* and *Reymanownaea*, either subtending the entire cupule-bearing axis, or subtending the individual cupules (Thomas 1925, Barbacka & Bóka 2000). However, in *Geminispermum* the cupule stalk is very broad laterally, similar to the situation in *Reymanownaea*, and the distinct crest distal to the cupule stalk in *Reymanownaea* may be equivalent to the crest formed from the distally expanded stalk in *Geminispermum*.

Cupules of *Ktalenia* described from the Early Cretaceous of Argentina (Archangelsky 1963, Taylor & Archangelsky 1985) appear similar to those of *Geminispermum* in fully enclosing one (or sometimes two) seeds. The cupules are also reconstructed as sometimes occurring in pairs, as in *Geminispermum*. The material is not well preserved, however, and the structure of the cupules, and their precise relationship to what appears to be a single, strongly dissected bract, is not clear.

In *Doylea tetraedrasperma*, *D. mongolica* (formerly *Umkomasia mongolica*) and *Umkomasia corniculata* the lateral axis in the axil of the bract divides to produce two stalks, each of which bears a cupule that contains a single seed (Stockey & Rothwell 2009, Rothwell & Stockey 2016, Shi et al. 2016, 2019). In *Umkomasia trilobata* the axis in the axil of the bract is flattened and three-lobed, and each lobe bears a cupule that contains a single

seed (Shi et al. 2019). An important difference between *Geminispermum* and *Doylea*, and also the Mongolian species of *Umkomasia*, is that the axis in the axil of the bract does not divide and that the cupule is non-valvate. Further, the bisymmetry of the ovulate structure of *Geminispermum* differs from the bilateral symmetry of the equivalent structure in *Doylea* and the umkomasialean species from Mongolia.

The fundamental similarity of *Geminispermum* to *Doylea* is also reflected in identical vascularization of the lateral cupule-bearing units. In *Geminispermum* three vascular bundles supply the ovulate structure; one supplies the bract while the other two supply the cupule stalk. In *Doylea* the pattern is identical, with a single bundle “dividing into collateral bract trace and two collateral axillary shoot bundles” (Rothwell & Stockey 2016).

The recurved form of the cupules in *Geminispermum* is very similar to that seen in *Caytonia*, *Doylea*, *Ktalenia*, *Petriellaea*, *Reymanownaea* and *Umkomasia*, but *Geminispermum* resembles especially closely the cupules of *Caytonia*, *Ktalenia*, *Petriellaea* and *Reymanownaea* in the almost complete enclosure of the seed or seeds. With regard to *Caytonia*, *Petriellaea* and *Reymanownaea*, the only major difference is that the cupules of *Geminispermum* contain only one seed rather than many. A more minor difference from *Caytonia* and *Reymanownaea* is the absence of papillae around the opening of the cupule in *Geminispermum*. Seeds of *Doylea*, *Petriellaea* and *Umkomasia* are triangular in transverse section, which is also the case for those of *Geminispermum*, while seeds of *Caytonia* and *Reymanownaea* are elliptical in cross section. Seeds of *Ktalenia* are preserved as compressions and their original shape is uncertain.

In its uniovulate cupules, *Geminispermum* is more similar to *Doylea*, the three umkomasialean species from Mongolia and *Ktalenia*, than *Caytonia*, *Petriellaea* and *Reymanownaea*. However, *Geminispermum* differs from *Doylea* and *Umkomasia* in that the cupule is not valvate and almost completely encloses the seed, which is more like the situation in the one- to two-seeded cupules of *Ktalenia*. Nevertheless, the detailed information available from SRXTM shows that the manner in which the cupule stalk participates in enclosing the seed and forming the cupule in *Geminispermum* is fundamentally similar to the situation

in *Doylea* and *Umkomasia*. Unfortunately, these details are unknown for *Ktalenia*.

The way in which the cupule is formed in *Doylea*, *Umkomasia* and similar plants is especially well seen in *Doylea mongolica*, in which the seed is borne on the cupule stalk and the recurved cupule stalk contributes to orienting the seed micropyle back towards the main axis of the cupule-bearing structure (Shi et al. 2016). In this way the cupule stalk is integral to the formation of the cupule and to creating the inner part of the structure in which the seed is enclosed. The situation in *Doylea tetrahedrasperma* and in *Umkomasia corniculata* is the same, but in these species, as also in *Geminispermum* and perhaps *Reymanownaea*, the cupule stalk is also extended apically beyond the point of cupule attachment (Barbacka & Bóka 2000, Stockey & Rothwell 2009, Rothwell & Stockey 2016, Shi et al. 2019).

Less clear in *Geminispermum*, and also in *Caytonia*, *Ktalenia*, *Petriellaea* and *Reymanownaea*, is how the outer part of the cupule is formed. In *Doylea*, and in the Mongolian umkomasialean species, the outer parts of the cupule are formed by two or more flaps of tissue that arise from the cupule stalk (Shi et al. 2016, 2019). As a result, the cupule has a valvate structure in which the seeds are only partly enclosed and from which they are easily shed. How the more complete enclosure of the seeds is achieved in *Geminispermum*, and also in *Caytonia*, *Ktalenia*, *Petriellaea* and *Reymanownaea*, is uncertain, but enclosure most likely involves some lateral expansion of the cupule stalk and perhaps synorganization with flaps of the kind seen in *Doylea* and *Umkomasia*.

In summary, the cupules of *Geminispermum* are distinct from all previously described Early Cretaceous cupules of the CUP group including *Doylea*, *Ktalenia* and the Mongolian umkomasialeans. They are also significantly smaller. However, the clear similarities of cupule architecture among these Early Cretaceous species make it likely that they are all homologous. Broader comparisons also suggest that the cupules of *Geminispermum* are fundamentally similar to umkomasialean cupules from the Triassic of the Southern Hemisphere (Klavins et al. 2002). Except for the occurrence of one seed rather than several, the strongest similarities are with the non-valvate cupules of *Caytonia*, *Petriellaea* and *Reymanownaea*.



There is also a resemblance to the non-valvate cupules of *Ktalenia*, but these differ in having the cupules along an axis associated with large, strongly dissected leaf-like bracts. The small size of *Geminispermum* cupules is matched most closely by the cupules of *Petriellaea* and the small (presumed immature) cupules of *Caytonia* (Thomas 1925). Taken as a whole, however, the clear similarities in the construction of the cupules of all these genera, which range in age from Late Permian to Late Cretaceous, provide a strong indication that they are homologous.

#### THE CRETACEOUS RECORD OF *GEMINISPERMUM* AND SIMILAR PLANTS

*Geminispermum virginianense* is currently the only unequivocal seed plant cupule recovered from the many mesofossil samples that we have studied intensively from the Early Cretaceous Potomac Group. In contrast to seeds related to Bennettitales, Erdtmanithecaceae and Gnetales (Friis et al. 2009, 2013, 2019), *Geminispermum* or similar plants were not common in the vegetation sampled by the mesofloras recovered from the Potomac Group. Nevertheless, other evidence suggests that these kinds of plants may have been widespread during Potomac Group times. Among the dispersed pollen reported by Brenner (1963) and Robbins (1991) from the Early Cretaceous of Maryland, U.S.A., *Platysaccus megasaccus* G.J.Brenner was assigned to Corystospermaceae by Robbins (1991) and to Pinaceae-Podocarpaceae by Brenner (1963), while *Vitreisporites pallidus* (Reissinger) T.Nilsson was assigned to the Caytoniales. Similarly, leaves of *Sagenopteris* C.Presl, generally assigned to Caytoniales, have also been reported from Potomac Group sediments, although they are not common (Fontaine 1889). Also interesting is the pollen organ *Brenneria potomacensis* K.R.Pedersen, E.M.Friis & P.R.Crane, described from sediments of Barremian or Early Aptian age from Drewry's Bluff and Dutch Gap, southeast of Richmond, Virginia (Pedersen et al. 1993). *Brenneria* contains saccate striate pollen similar to dispersed grains assigned to *Decussosporites* G.J.Brenner. *Brenneria*, *Decussosporites*, and the associated seeds *Brennerispermum potomacensis* K.R.Pedersen, E.M.Friis & P.R.Crane may have been produced by a CUP plant, although a relationship

to extant conifers cannot be excluded (Pedersen et al. 1993).

Despite their relatively sparse record in the Early Cretaceous of eastern North America, evidence from northwestern North America (Stockey & Rothwell 2009, Rothwell & Stockey 2016), Mongolia (Shi et al. 2016, 2019) and also northeastern China (Shi et al. pers. comm.), indicates that CUP plants similar to *Geminispermum* were important in Early Cretaceous vegetation elsewhere in the Northern Hemisphere at that time. Based on occurrences of distinctive *Sagenopteris* leaves in northeastern Asia and Alaska, these kinds of plants may have persisted through much of the Late Cretaceous (e.g. Hollick 1930, Krassilov 1979).

#### CONCLUSION

The sparseness of information about the reproductive structures of Cretaceous plants related to the CUP group has been an impediment to understanding their systematic relationships, including how they may relate to angiosperms or to earlier seed plants from the Permian, Triassic and Jurassic. New information from *Geminispermum*, as well as informative permineralized and lignified material (Stockey & Rothwell 2009, Rothwell & Stockey 2016, Shi et al. 2016, 2019), have revealed basic architectural similarities among the recurved cupules of more ancient plants and those of *Doylea* and *Umkomasia* from the Early Cretaceous. Recurved cupules of the kind found in *Geminispermum* have been described from a range of plant fossil assemblages in both the Northern and Southern Hemispheres and have been assigned to at least three different orders of fossil plants: Caytoniales, Petriellales and Umkomasiales (= Corystospermales including Doyleales), as well as *Ktalenia*. Data from *Geminispermum*, along with emerging data from other sources (Rothwell & Stockey 2016, Shi et al. 2016, 2019), suggest that the cupules of these plants may be much less distinct than has previously been supposed, with the corollary that these groups may be much more closely related than previously envisaged. Further studies aimed at understanding probable homologies among the other organs of these plants, including especially their pollen organs, will be crucial to understanding their interrelationships and placing them in

the broader context of seed plant evolution. Similarly, understanding how these ovule-bearing cupules should be compared with the ovule-bearing structures of non-cupulate gymnosperms will be central to resolving the question of how the major groups of extinct and extant seed plants are related. In this regard, further comparisons with plants such as *Ginkgo*, Gnetales and conifers, in which the ovules are also borne on a modified branch in the axil of a bract or a leaf, and in which there are also potential cupule homologues (Crane 1985, Gordenko & Broushkin 2015, Shi et al. 2016), will be of particular interest.

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