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Silicified cupulate seed-bearing structures from the Early Cretaceous of eastern Inner Mongolia, China: rethinking the corystosperm concept

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The group referred to informally as the corystosperms, described initially based on compression fossils from the Triassic of Gondwana, have long been considered critical extinct plants for understanding seed plant phylogeny, the evolution of seed plant reproductive structures and the relationships of angiosperms. Here we describe a new genus and species of corystosperm seed-bearing structure, *Jarudia zhoui* gen. et sp. nov., based on abundant silicified material collected from the newly discovered chert in the Early Cretaceous Huolinhe Formation of eastern Inner Mongolia, north-eastern China. *Jarudia zhoui* is a lax seed cone consisting of a flexible central axis bearing deciduous, helically arranged, lateral seed-bearing units. Individual seed-bearing units consist of an elongate bract partially fused to an unbranched cupule stalk that bears a single, reflexed cupule apically. Each cupule is formed by the strongly reflexed cupule stalk and one median and two lateral flaps. The cupule stalk supplied by two vascular bundles and three unvascularized flaps partially enclose two three-angled seeds. *Jarudia zhoui* bears a striking resemblance to *Doylea tetrahedrasperma* from the Early Cretaceous of Canada and similar plants from the Early Cretaceous of Mongolia. There are also strong similarities with ovulate structures of *Umkomasia* from the Triassic of Gondwana in the structure and anatomy of individual cupules, their axial nature, and the architecture of the entire seed-bearing structure that has two orders of branching. New information from *Jarudia zhoui*, together with information on other corystosperm ovulate organs from the Northern Hemisphere, significantly expands our understanding of this key group of extinct plants, suggests that the cupules of the Early Cretaceous and Triassic corystosperms are homologous, and raises critical questions about the definition and phylogenetic circumscription of the corystosperms, including how Early Cretaceous and Triassic corystosperms are related to each other and to other groups of seed plants, including angiosperms.

Keywords: silicified; corystosperm; cupule; anatomy; homology; seed plant

Introduction

Modern formulations of the long-debated question of flowering plant origins emphasize the importance of determining the phylogenetic position of angiosperms with respect to other extant and extinct groups of seed plants (Hill & Crane 1982; Crane 1985; Doyle & Donoghue 1986; Nixon *et al.* 1994; Rothwell & Serbet 1994; Doyle 2006, 2008, 2012; Hilton & Bateman 2006; Friis *et al.* 2007; Rothwell & Stockey 2016; Herendeen *et al.* 2017; Bateman 2020; Shi *et al.* 2021a). However, phylogenetic studies based on molecular data from extant taxa, and studies based on morphology and anatomy that include both fossil and extinct taxa, give results that remain to be reconciled. Results based on analyses of molecular data give a range of different topologies, but the most intensive studies based on large datasets resolve the four living groups of gymnosperms (cycads, *Ginkgo*, conifers and Gnetales) as part of a single clade (acrogymnosperms) that is the sister group to angiosperms (Bowe *et al.* 2000; Chaw *et al.* 2000; Nickrent *et al.* 2000; Rydin *et al.* 2002; Wickett *et al.* 2014; Li *et al.* 2017; Ran *et al.* 2018; Liu *et al.* 2022). Results based on analyses of morphological and anatomical data also give a range of different topologies (Hill & Crane 1982; Crane 1985; Doyle & Donoghue 1986; Nixon *et al.* 1994; Rothwell & Serbet 1994; Doyle 2006, 2008, 2012; Hilton & Bateman 2006; Friis *et al.* 2007; Rothwell & Stockey 2016; Coiro *et al.* 2018; Shi *et al.* 2021a; Klymiuk *et al.* 2022), but among the

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*Corresponding author. Email: glshi@nigpas.ac.cn several groups of extinct seed plants that have emerged as potential close angiosperm relatives, especially important are those plant fossils referred to informally as the corystosperms (Thomas 1933), as well as Caytoniaceae (Thomas 1925; Harris 1933, 1940, 1964), Petriellaceae (Taylor *et al.* 1994; Bomfleur *et al.* 2014), and other potentially related extinct plants in which the ovule or ovules are borne in recurved cupules (Crane 1985; Doyle 2006; Hilton & Bateman 2006; Taylor *et al.* 2006; Taylor & Taylor 2009; Rothwell & Stockey 2016; Shi *et al.* 2016, 2019, 2021a). These cupules have been hypothesized to be homologous to the second integument of a bitegmic anatropous ovule (Gaussen 1946; Stebbins 1974; Doyle 1978, 2006, 2008, 2012; Frohlich & Parker 2000; Frohlich 2003; Frohlich & Chase 2007; Shi *et al.* 2021a; Soltis 2021), a feature that is likely basic within angiosperms as a whole (Endress 2011).

The Corystospermaceae (=Umkomasiaceae) was first established by Thomas (1933) who named the family based on the helmet-like coverings that partially enclose the ovules (*corystos* = a helmet wearer in Greek). Thomas (1933) included seed-bearing organs of *Umkomasia*, *Pilophorosperma* and *Spermatocodon*, the pollen organ of *Pteruchus*, and forked, bipinnate leaves of *Dicroidium* in his concept of corystosperms, based on studies of compression fossils from the Upper Triassic Molteno Formation of South Africa. These isolated organs were considered to be produced by the same group of plants based on their consistent association in the same fossiliferous bed at the same locality, similarities in their cuticular anatomy, especially in the structure of their stomata, and the occurrence of the same type of bisaccate pollen within pollen sacs of *Pteruchus* and in the micropyles of *Umkomasia* seeds (Thomas 1933). *Pilophorosperma* and *Spermatocodon* were later regarded as not clearly distinguished from *Umkomasia*, and are now treated as synonyms of *Umkomasia* (Holmes 1987; Klavins *et al.* 2002; Anderson & Anderson 2003; Anderson *et al.* 2019a).

Corystosperms, especially as *Dicroidium* leaves, are abundantly preserved in the Middle and Late Triassic of Gondwana, and extensive collections of Gondwanan Triassic corystosperms have greatly expanded our understanding of these plants (e.g. Townrow 1962, 1965; Archangelsky 1968; Holmes & Ash 1979; Playford *et al.* 1982; Retallack 1983, 1995; Cantrill *et al.* 1995; Yao *et al.* 1995; Axsmith *et al.* 2000, 2007; Klavins *et al.* 2002; Anderson & Anderson 2003; Holmes & Anderson 2005; Bomfleur & Kerp 2010; Pattemore 2016a, b; Anderson *et al.* 2019a, b, 2020). However, a complete understanding of the structure and homology of their reproductive structures has been hindered by their preservation as compression or impression fossils. Recent discoveries of three-dimensional, lignified mesofossils (Shi *et al.* 2016, 2019), and anatomically preserved, permineralized fossils (Stockey & Rothwell 2009; Rothwell & Stockey 2016; Shi *et al.* 2021a) of corystosperm seed-bearing structures from the Early Cretaceous of the Northern Hemisphere have significantly expanded our view of the group. These fossils have contributed new morphological and anatomical information for understanding the structure and homology of corystosperm cupules. Among this newly available material especially important are the silicified corystosperm cupules from the Early Cretaceous of Inner Mongolia, China, because they are known from abundant, exceptionally well-preserved specimens (Shi *et al.* 2021a). The morphology and anatomy of these specimens, combined with re-examination of the cupules of Caytoniaceae, Petriellaceae and other related Mesozoic seed plants, strongly suggests that the recurved cupules of these groups are all fundamentally the same, and very likely homologous to the outer integument of angiosperm ovules (Shi *et al.* 2021a). In this paper we describe in detail these corystosperm seed-bearing structures from Inner Mongolia as a new genus and species, *Jarudia zhoui*. We also discuss the structure and homology of corystosperm seed-bearing structures and assess the concept of the corystosperms as a phylogenetically meaningful group.

Material and methods

The silicified material described here was collected from the Huolinhe Formation at the Zhahanaoer opencast coal mine (45°21′38.5″ N, 119°25′04″ E) in Jarud Banner, eastern Inner Mongolia, China during China–US joint field expeditions in the summers of 2017, 2018 and 2019 (Shi *et al.* 2021a). The Huolinhe Formation in the Huolinhe Basin is a non-marine Lower Cretaceous coal/lignite-bearing unit comprising a sequence of fluvio-lacustrine-swamp sediments (Li *et al.* 1982; Deng 1995). In ascending order, the formation is divided informally into a ‘conglomerate-sandstone member’, a ‘lower mudstone member’, a ‘lower coal-bearing member’, an ‘upper mudstone member’, an ‘upper coal-bearing member’, and a ‘top mudstone member’ (Li *et al.* 1982). The chert containing the silicified plant fossils occurs toward the bottom of the ‘lower coal-bearing member’ (Shi *et al.* 2021a, b). Below the chert is a thin layer of ash that may have been the source of the silica responsible for the formation of the chert and the silicification of the plants. U-Pb zircon dating using the Secondary Ion Mass Spectrometry (SIMS) method constrains the age of the ash layer to 125.6 ± 1.0 Ma (Shi *et al.* 2021b), corresponding to the middle Barremian in the latest version of the ICS International Chronostratigraphic Chart (Cohen *et al.* 2013, version 2022.02). The palynological assemblage associated with the chert also supports this age assignment (Shi *et al.* 2021b).

The assemblage of silicified plant fossils preserved in the chert is diverse. The plant fossils recognized so far include vegetative axes and leaves of lycopsids (Herrera *et al.* 2022) and ferns, leafy shoots, leaves and seed cones of cupressaceous and pinaceous conifers (Matsunaga *et al.* 2021), seeds of the Bennettitales-Erdtmanithecales-Gnetales (BEG) group (Bickner 2021), and the corystosperm seed-bearing structures described here (Shi *et al.* 2021a).

The silicified plant fossils were studied using cellulose acetate peels and micro-CT scanning. Acetate peels were prepared using standard methods (Joy *et al.* 1956; Galtier & Phillips 1999), and examined and sorted under a stereomicroscope. Selected pieces of peels were mounted on microscope slides with neutral balsam and photographed with a Leica M205A stereomicroscope and Leica DMC5400 digital camera system with Z axis stacking at the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences (NIGPAS). Higher magnification images were obtained using an Olympus BX53 microscope with an Olympus DP73 camera at NIGPAS. Micro-CT scanning was performed using a General Electric dual-tube X-ray computed tomography scanner in the Department of Organismal Biology and Anatomy, University of Chicago (for details of the settings see Shi *et al.* 2021a). The CT data were processed using Avizo software 2019.1 to obtain successive virtual sections and surface renderings.

All specimens, including slabs, peels and microscopes slides, are in the palaeobotanical collections of the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences.

Systematic palaeontology

Order **Umkomasiales** *sensu lato*

Genus ***Jarudia*** Shi, Herrera, Herendeen, Clark & Crane gen. nov.

Type species. *Jarudia zhoui* Shi, Herrera, Herendeen, Clark & Crane sp. nov.

Generic diagnosis. Seed cone lax, consisting of a flexible central axis bearing helically arranged lateral seed-bearing units that are shed at maturity. Each seed-bearing unit consisting of a narrow, elongate bract, subtending and partially fused to a terete axis (the cupule stalk) that bears a single cupule at the tip. Each cupule containing two seeds that are attached at, or very close to, the tip of the cupule stalk. Seeds shed at maturity. Cupules strongly inflexed (curved adaxially) relative to the cone axis, resulting in the micropyles of the two seeds being oriented back towards the base of the cupule stalk and the cone axis. Near the base, the fused bract-cupule stalk complex is supplied by two median vascular bundles, with their xylem opposite each other towards the centre of the complex. Distally the adaxial bundle divides into two small bundles that supply the cupule while the abaxial vascular bundle supplies the bract.

Each cupule formed by the strongly curved cupule stalk and three flaps, one median and two lateral, which together surround and partially enclose the two seeds. The two lateral flaps are fused to the cupule stalk and to the median flap at the apex of the cupule. Within the cupule, the cupule stalk and three flaps all consist of an outer cortical zone of parenchyma, and an inner cortical zone of sclerenchyma. In longitudinal section sclerenchyma cells of the inner cortical zone of the cupule are elongate with helical thickenings. The median and lateral cupule flaps are unvascularized.

Each cupule supplied by two vascular bundles, each of which supplies a seed. Vascular bundles flattened and bilaterally symmetrical where they enter the base of the cupule, with their xylem towards the outer surface of the cupule. Closer to the point of seed attachment the xylem is circular in transverse section and at the point of seed attachment it expands to form a disc of transfusion tissue that consists of short tracheids with helical or scalariform thickenings.

Seeds are ovate in lateral outline, three-angled in transverse section and have a truncate base resulting in a tetrahedral form. The three prominent lateral faces have weakly developed wings along the margins. The micropyle at the seed apex is bifid. Integument parenchymatous and unvascularized, consisting of an outer epidermis, an outer zone of 3–4 layers of isodiametric thick-walled cells, an inner zone of irregularly shaped thin-walled cells, and an inner epidermis. Nucellus free from integument except at the base where it is attached, consisting of a thin cuticle and a few layers of thin-walled parenchyma cells surrounding the megaspore membrane.

Derivation of generic name. From Jarud, the administrative region (Banner) in eastern Inner Mongolia Autonomous Region, China, where the fossil material of the new genus was collected.

Jarudia zhoui Shi, Herrera, Herendeen, Clark & Crane sp. nov.

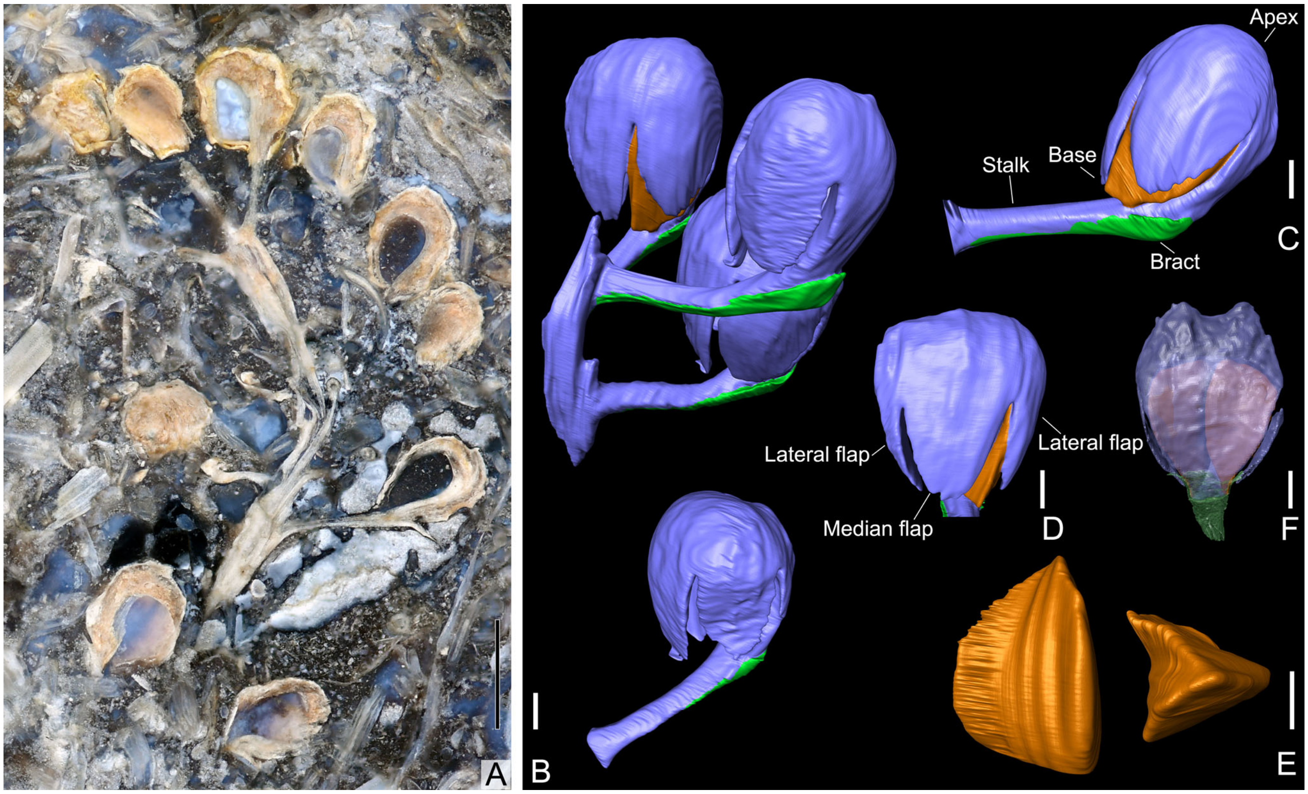


Figure 1. *Jarudia zhoui* gen. et sp. nov. **A,** seed cone with loose, helically arranged lateral seed-bearing units (Shi *et al.* 2021a). Note that the cupules are strongly inflexed (curved upwards and adaxially) relative to the flexible and curving cone axis but reflexed (curved downwards and abaxially) relative to the stalk on which the cupule is borne. PB23663. **B–F,** three-dimensional reconstructions of seed cone, cupules and seeds from segmented micro-CT data, showing the bracts (green), stalked cupules (blue) and seeds (brown). B–E, PB23672. **B,** seed cone with three cupules attached to the fragmentary cone axis and another cupule on the same alignment below (Shi *et al.* 2021a). Note that the cupules are strongly curved back towards the base of the cupule stalk but away from the bract. **C,** lateral view of individual seed-bearing unit from the cone in B (Shi *et al.* 2021a), showing the subtending bract and seed partially enclosed by the recurved cupule, and terms used to describe the seed-bearing unit and cupule. Note the micropyle of the seed is oriented back towards the base of the cupule stalk. **D,** ventral view of a cupule containing one remaining seed from the seed-bearing unit in **C,** showing terms used to describe the cupule. Note that each cupule is formed by the cupule stalk and one median and two lateral flaps, the two lateral flaps are fused to the median flap at the apex of cupule. **E,** lateral (left) and apical (right) view of the one remaining three-angled seed from the cupule in D. **F,** dorsal view of a cupule (Shi *et al.* 2021a) with transparent cupule stalk, two short apical projections and three flaps showing attachment and orientation of the two three-angled seeds. PB23667. Scale bars: A = 5 mm; B–F = 1 mm.

Specific diagnosis. As for the genus with the following additions. Cupule often with one or two short, apical protrusions formed mainly by transfusion tissue composed of short tracheids with helical or scalariform thickenings. Each cupule with a distinct lip at the tip of median flap. Small conical projections of variable size distributed irregularly over the outer surface of the cupule; protrusions formed by the epidermis, hypodermis and parenchyma tissue of the outer cortical zone, or by the epidermis and hypodermis alone.

Derivation of species name. In honour of Professor Zhiyan Zhou for his landmark contributions to understanding Mesozoic seed plants.

Material. Holotype: PB23663 (Fig. 1A). Other illustrated material: PB23672 (Fig. 1B–E), PB23667 (Figs 1F, 3A–D), PB23664 (Fig. 2A, C), PB23679 (Fig. 2B), PB23668 (Fig. 2D), PB23671 (Figs 2E, F, 6C), PB23680 (Figs 4A, 6B), PB23670 (Fig. 4B, F), PB23665 (Figs 4C, 8D), PB23681 (Fig. 4D), PB23673 (Figs 4E, 7E), PB23682 (Fig. 5A), PB23674 (Fig. 5B), PB23666 (Figs 5C, 7D), PB23683 (Fig. 5D), PB23684 (Fig. 5E), PB23669 (Fig. 6A), PB24571 (Fig. 6D), PB24572 (Fig. 6E), PB24573 (Fig. 6F), PB24574 (Fig. 6G), PB24575 (Fig. 6H), PB24576 (Fig. 7A), PB24577 (Fig. 7B, C), PB23678 (Fig. 7F), PB23675 (Fig. 8A), PB24578 (Fig. 8B), PB24579 (Fig. 8C), PB24580 (Fig. 8E, F). Additional unfigured material: PB24581–PB24600. All specimens are in the palaeobotanical collections of the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences.

Type locality. Zhahanaoer open-cast coal mine (45°21′38.5″ N, 119°25′04″ E), Jarud Banner, eastern Inner Mongolia, north-eastern China.

Stratigraphy and age. Bottom of the 'lower coal-bearing member' of the Huolinhe Formation, middle Barremian (125.6 ± 1.0 Ma), Lower Cretaceous.

Description and comments on the species. *Jarudia zhoui* gen. et sp. nov. is known from two seed cones (Fig. 1A, B) and more than 100 isolated seed-bearing units (Figs 2A, B, 3B) and/or isolated cupules (Fig. 4A–E). The seed cone consists of a flexible central axis bearing helically and loosely arranged lateral seed-bearing units at angles of *c.* 50° (Fig. 1A, B). The abundance of isolated seed-bearing units in the collection suggests that they are shed from the cone axis at maturity. The more completely preserved seed cone (Fig. 1A) is *c.* 17 mm in diameter, and 36 mm long; the cone axis is *c.* 2 mm in diameter, slender and curved, perhaps suggesting that the cone was pendulous in life rather than held erect (Fig. 9). Both seed cones (Fig. 1A, B) are highly opalized with few anatomical details preserved, but the cone axis consists of a more transparent central region that appears to be a parenchymatous pith, surrounded by a thick, less transparent ring that comprises the bulk of the cone axis and appears to be a sclerenchymatous cortex.

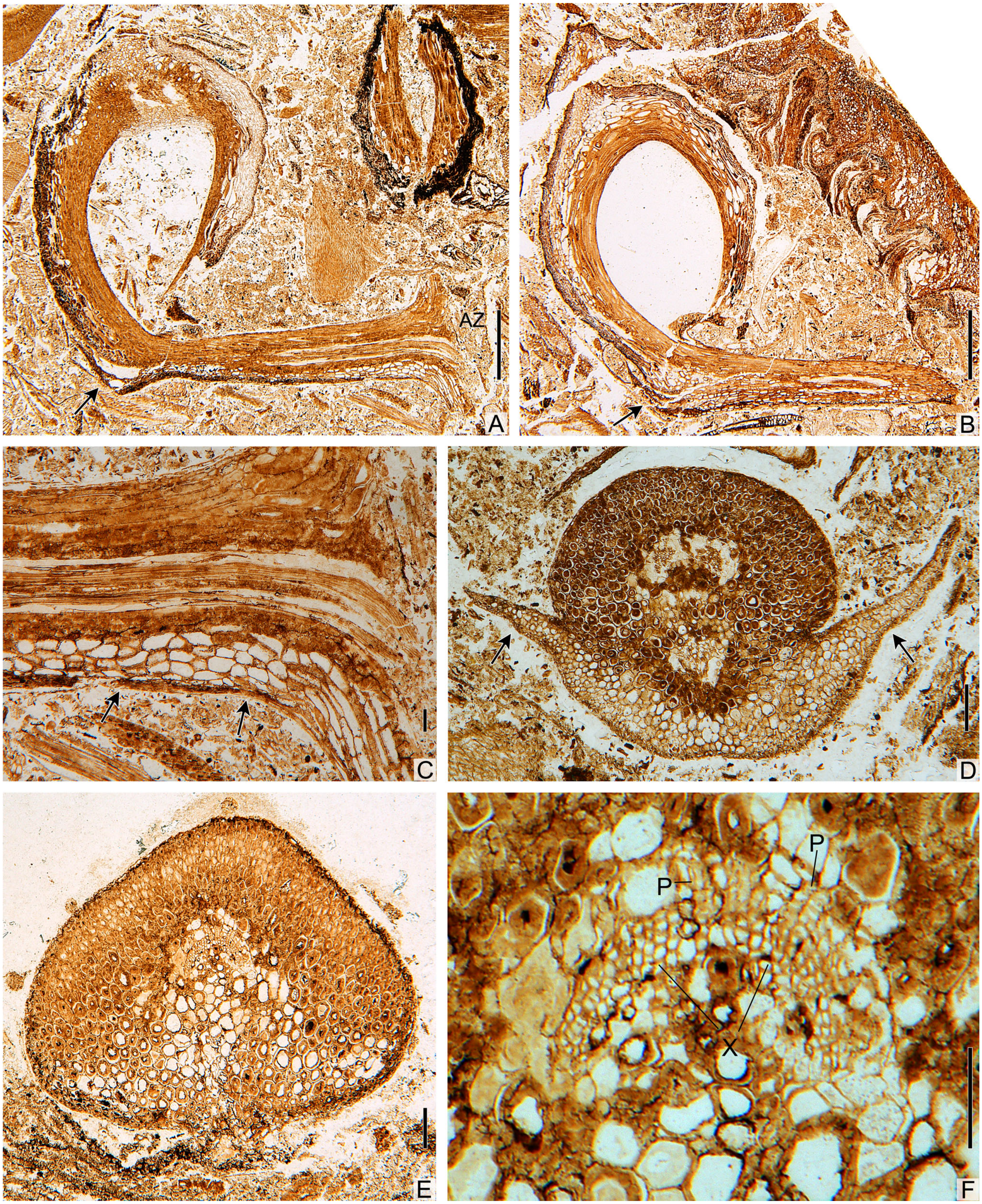
Each seed-bearing unit consists of a narrow elongate, flattened bract subtending, and partially fused to, a terete fertile axis (the cupule stalk) that bears a single cupule at the tip (Fig. 1C). The cupules are strongly inflexed (curved adaxially) relative to the cone axis, but reflexed (curved abaxially) relative to the cupule stalk (Fig. 1A, B). Each cupule is formed by a flattened, strongly curved, vascularized cupule stalk and three unvascularized flaps (Fig. 1C, D). Each cupule contains two three-angled seeds that are usually shed at maturity (Fig. 1F).

At the base of isolated seed-bearing units, there is a distinct, elongated abscission zone (Fig. 2A). The bract remains attached to the shed seed-bearing units but extends from the abscission zone at the base (Fig. 2A, C), indicating that it was borne directly on the main axis of the cone, and thus the cupule stalk arises in the axil of the bract. The degree of fusion of bract and cupule stalk decreases gradually distally. Near the base of the seed-bearing unit the bract is almost entirely fused with the cupule stalk (Fig. 3A) but in its middle and upper regions it is fused only along the midrib. Along its lateral margins (Figs 2D, E, 3B) and near its tip (Figs 1A, B, 2A, B) the bract is free.

The bract is narrowly elongate, shallowly 'U'-shaped in transverse section (Figs 2D, 3B) and broadens gradually towards its free apex (Fig. 1B, C). The bract is *c.* 6 mm long, 1.2–2.2 mm wide, and is fused with the proximal portion of the cupule stalk for up to *c.* 4.5 mm. The cupule stalk is more - less circular, to broadly elliptical or ovate, in transverse section (Figs 1B, C, 2E, 3B), and *c.* 1.0–1.6 mm in diameter. The fused bract-cupule stalk complex is composed mainly of the sclerenchymatous cortex of the cupule stalk and the parenchyma of the bract mesophyll (Figs 2C, D, 3A). The epidermis is very thin, often poorly preserved, and overlays a sclerotic hypodermis one or two cells thick (Figs 2D, 3B). The sclerenchyma cells that comprise the cortex of the cupule stalk are more or less isodiametric in transverse section with dark internal contents (Figs 2D, E, 3A, B). They are up to *c.* 80 µm in diameter and become gradually larger towards the centre of the bract-cupule stalk complex. In longitudinal section these sclerenchyma cells are elongate (Fig. 2C), *c.* 350–650 µm long and 25–60 µm wide, with a length/width ratio up to about 14. The parenchyma cells comprising the bract mesophyll are tightly packed, more or less isodiametric in transverse section, and lack dark internal contents (Fig. 2D). They are 20–55 µm in diameter and become larger toward the midline and also near to the fusion of the bract with the cupule stalk (Fig. 2D). In longitudinal section these parenchyma cells are rectangular to elongate rectangular in outline (Fig. 2C), 100–260 µm long and 20–55 µm wide, with a length/width ratio of 1.5–6.5. In many cases, the parenchyma tissue of the bract mesophyll is degraded (Figs 2E, 3B). Resin bodies or secretory cavities have not been observed in the seed-bearing unit.

Details of the vascularization of several seed-bearing units have been traced through serial sections. Near the base of the bract-cupule stalk complex there are two median bilaterally symmetric vascular bundles embedded one above the other in the cortical sclerenchyma tissue with their xylem facing each other toward the centre of the bract-cupule stalk complex (Figs 3A, 10A). In both bundles the empty space toward their outer sides, most likely created in part by the shrinkage of delicate tissues during preservation, is inferred to indicate the former position of the phloem (Fig. 3A). The adaxial vascular bundle supplies the cupule stalk, while the abaxial bundle supplies the bract (Fig. 3A, B). The vascular bundle supplying the bract is smaller and more flattened (Fig. 3A) than that supplying the axis, and its xylem is composed of only a few tracheids.

The xylem of the adaxial vascular bundle, which supplies the cupule stalk, consists of 3–5 rows of tracheids arranged in radial files; the tracheids are more-or-less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isodiametric to slightly elliptical in transverse section and *c.* 7–16 µm in diameter (Fig. 2F). Proximally, the adaxial vascular bundle forms a shallow inverted 'U' (Figs 2F, 3A, B), but distally, close to the point where the bract separates from the axis, it gradually becomes two-lobed (Figs 3C, D, 10B) and then divides into two separate smaller vascular bundles (Figs 2D, 10C). In these two vascular bundles, the xylem, which consists of 3–4 rows of tracheids arranged in radial files, is toward the lower side of the bract-cupule stalk complex: abaxial relative to the cone axis. The associated empty space, which is inferred to indicate the former position of poorly developed phloem, is toward the upper side of the bract-cupule stalk complex: adaxial relative to the cone axis (Fig. 2D).

Cupules are typically obovoid in lateral (Fig. 1C) and ventral (Fig. 1D) view, and *c.* 4.5–5.5 mm high. In median transverse section they are ovate to elliptical to more-or-less rectangular in outline (Fig. 4C), *c.* 4.2–6.0 mm long and 3.5–5.2 µm wide. Each cupule is formed by the flattened vascularized cupule stalk that is strongly curved distally (Figs 1B, C, 2A, B), and three unvascularized flaps, one median and two lateral (Fig. 4A–C). The three flaps are borne on the tip of the cupule stalk (Figs 1C, 5A–C).

Within the cupule the flattened cupule stalk is commonly thicker than the median and lateral flaps. In transverse section it is thickest in the median region and gradually becomes thinner laterally (Fig. 4A–C). The median flap is about as broad as the cupule stalk when seen in transverse section and both are slightly broader than the lateral flaps (Fig. 4A–C), resulting in the cupule being more or less rectangular to obovoid in median transverse section. Near the apex of the cupule, where the flaps are borne, the two lateral flaps are generally fused to the flattened cupule stalk, and also to the median flap (Figs 1C, D, 4A, B), but near their tips the two lateral flaps are separate from both the cupule stalk and the median flap (Figs 1A–D, 3B, C); as a result the cupule forms a helmet-like structure surrounding and partially enclosing the two seeds (Fig. 1C–F). All three flaps gradually become thinner towards their tip. The median flap is often curved upwards at the tip to form a distinct small lip (Figs 1B, 5C, E).

The cupule stalk and the lateral and median flaps all have a thin, poorly preserved outer epidermis with a sclerotic hypodermis two or three cells thick immediately beneath. Towards the outside the cupule stalk and the lateral and median flaps all have an outer cortical zone composed of parenchyma tissue, while towards the inside there is an inner cortical zone of sclerenchyma tissue and an inner epidermis (Fig. 4A–C). There are no trichomes on either the inner or outer surface of the cupule, but the outer surface of many cupules has irregularly distributed tooth-like conical projections that vary in size and have a more-or-less sharp apex (Figs 4C, 5B, E). Larger teeth are formed by the epidermis, hypodermis and parenchyma tissue of the outer cortical zone; smaller teeth are formed by only the epidermis and hypodermis (Fig. 5B, E). On its dorsal side the cupule stalk is often extended into one or two short apical protrusions (Figs 1F, 2A, B, 5A, E). This protrusion is formed mainly by transfusion tissue composed of short tracheids with helical or scalariform thickenings (Figs 2A, B, 5E).

In well-preserved and well-developed cupules, the inner and outer cortical zones of the cupule stalk and three flaps are similar in thickness as seen in transverse and lateral sections (Figs 4A, B, F, 5A, B). In a smaller cupule, which was perhaps aborted or preserved at an early stage of development, the cupule stalk and three flaps are composed mainly of parenchyma tissue (Fig. 4D), suggesting that the sclerenchyma tissue of the inner cortical zone might form later during cupule development.

The thick parenchyma of the cupules indicates that they were probably originally fleshy (Fig. 9). However, in many cupules the parenchyma tissue towards the outside is more-or-less degraded (Fig. 4E) or crushed forming a darker layer (Figs 4C, 5C). In transverse section

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Figure 2. *Jarudia zhoui* gen. et sp. nov., isolated seed-bearing units. **A, B,** median longitudinal sections of empty seed-bearing units, showing the free tip (arrows) of the bract subtending and partially fused with the cupule stalk, and the straight profile of the elongate abscission zone (AZ) at the base. In B note the short apical protrusion of the cupule and the irregularly distributed projections on the outer cupule surface. **A,** PB23664 (Shi *et al.* 2021a). **B,** PB23679. **C,** longitudinal section of the partially fused bract and cupule stalk, enlarged from A, showing the bract (arrows) composed mainly of slightly elongated parenchyma cells that lack dark contents, and the cupule stalk composed mainly of elongate sclerenchyma cells with dark contents and the central vascular tissue. **D,** transverse section of the partially fused bract and cupule stalk (Shi *et al.* 2021a) showing the well-preserved bract (arrows) composed mainly of parenchyma cells and the cupule stalk composed mainly of sclerenchyma cells. Note the three separate vascular bundles close to the midline (two above and one below) and conspicuous, free lateral margins of the bract (arrows). PB23668. **E,** transverse section of the partially fused bract and cupule stalk, showing cupule stalk with one bilaterally symmetric vascular bundle, and degraded bract that is fused with the cupule stalk in the midrib region. PB23671. **F,** detail of vascular bundle from the cupule stalk in E, showing radial files of xylem tracheids (X) that are toward the lower side of the seed-bearing unit and sparse, partially decayed probable phloem cells (P) that are toward the upper side of the seed-bearing unit. Scale bars: A, B = 1 mm; C–E = 200 µm; F = 100 µm.

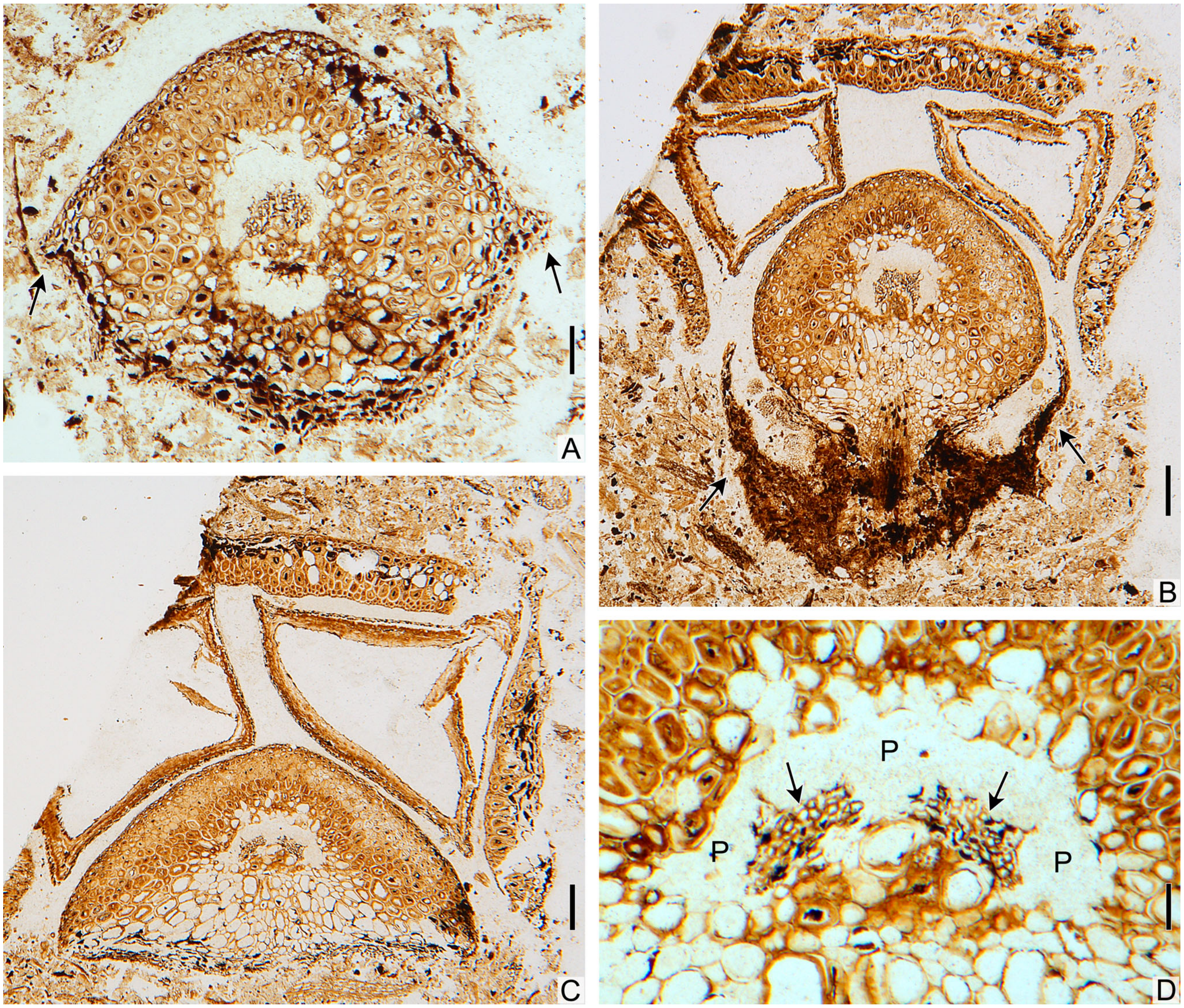


Figure 3. *Jarudia zhoui* gen. et sp. nov., isolated seed-bearing units. **A–C,** transverse sections of seed-bearing unit from serial sections of the specimen in Figure 1F from the base to the apex with the upper (inner) surface of the cupule stalk uppermost. PB23667. **A,** transverse section of the fused bract and cupule stalk near the base of the cupule stalk (Shi *et al.* 2021a), showing two bilateral symmetric (collateral) vascular bundles; the upper bundle with the xylem (toward lower side of the seed-bearing unit) partly surrounded by a space above probably reflecting the partially decayed or torn phloem cells; the lower bundle with the xylem (toward upper side of the seed-bearing unit) partly surrounded by a space below probably reflecting the partially decayed or torn phloem cells. Note the two incipient lateral margins of the bract (arrows). **B,** transverse section of the seed-bearing unit near the base of the cupule (Shi *et al.* 2021a), showing the bract (arrows) partially fused with the cupule stalk in the midrib region, but free along its margins. Note that the bract, which is mainly composed of parenchyma tissue (Fig. 2D), is easily degraded. **C,** transverse section of cupule with two seeds, showing flattened cupule stalk composed of inner cortical zone of sclerenchyma tissue, and outer cortical zone of parenchyma tissue. Note two partially contiguous flattened vascular bundles embedded between the inner and outer cortical zones, with the xylem (for detail see D) towards the outer surface of the cupule. **D,** detail of vascular bundles in cupule stalk in C (Shi *et al.* 2021a), showing radial files of xylem tracheids (arrows) and the empty space that may represent partially decayed or torn phloem cells (P). Scale bars: A = 100 µm; B, C = 200 µm; D = 50 µm

the parenchyma cells in the outer cortical zone are irregular in shape with curved to sinuous cell walls and lack dark contents (Fig. 4A, B, F). They vary considerably in size, generally become larger, up to *c.* 80 µm in diameter, toward the centre of the cupule stalk and flaps (Fig. 4F). In longitudinal section these parenchyma cells are isodiametric to longitudinally elongated (Fig. 5A, B).

The sclerenchyma cells of the inner cortical zone are more-or-less isodiametric in transverse section, commonly have dark contents, and become larger, up to *c.* 110 µm in diameter, from the inner surface towards the centre of the cupule stalk and flaps (Fig. 4A, B, F). In longitudinal section these sclerenchyma cells are isodiametric to longitudinally elongated, and have distinct, helical to reticulate secondary wall thickenings (Fig. 6E, F).

Most of the larger cupules are empty (Figs 1A, B, 2A, B, 5E), indicating that the seeds were shed at maturity. Empty cupules are usually open along the four corners between the cupule stalk and the flaps (Fig. 1B, D), but the two lateral flaps are still fused with the cupule stalk at the apex of cupule, as in cupules where the two seeds are still present (Figs 1F, 4A, B). Where two seeds are still tightly enclosed in the cupule, transverse sections show that they fit closely together with one of their three flattened faces facing each other so that in transverse section they together form a rectangle (Fig. 4A–C). This organization, with one seed with one flat face adjacent to the cupule stalk, and the other seed with one flat face adjacent to the median flap, is consistent in all of our material (Fig. 4A–C). In the few cupules that contain only one seed nearly half of the cupule is empty, but the presence of two vascular bundles in the flattened cupule stalk indicates that two seeds were originally present.

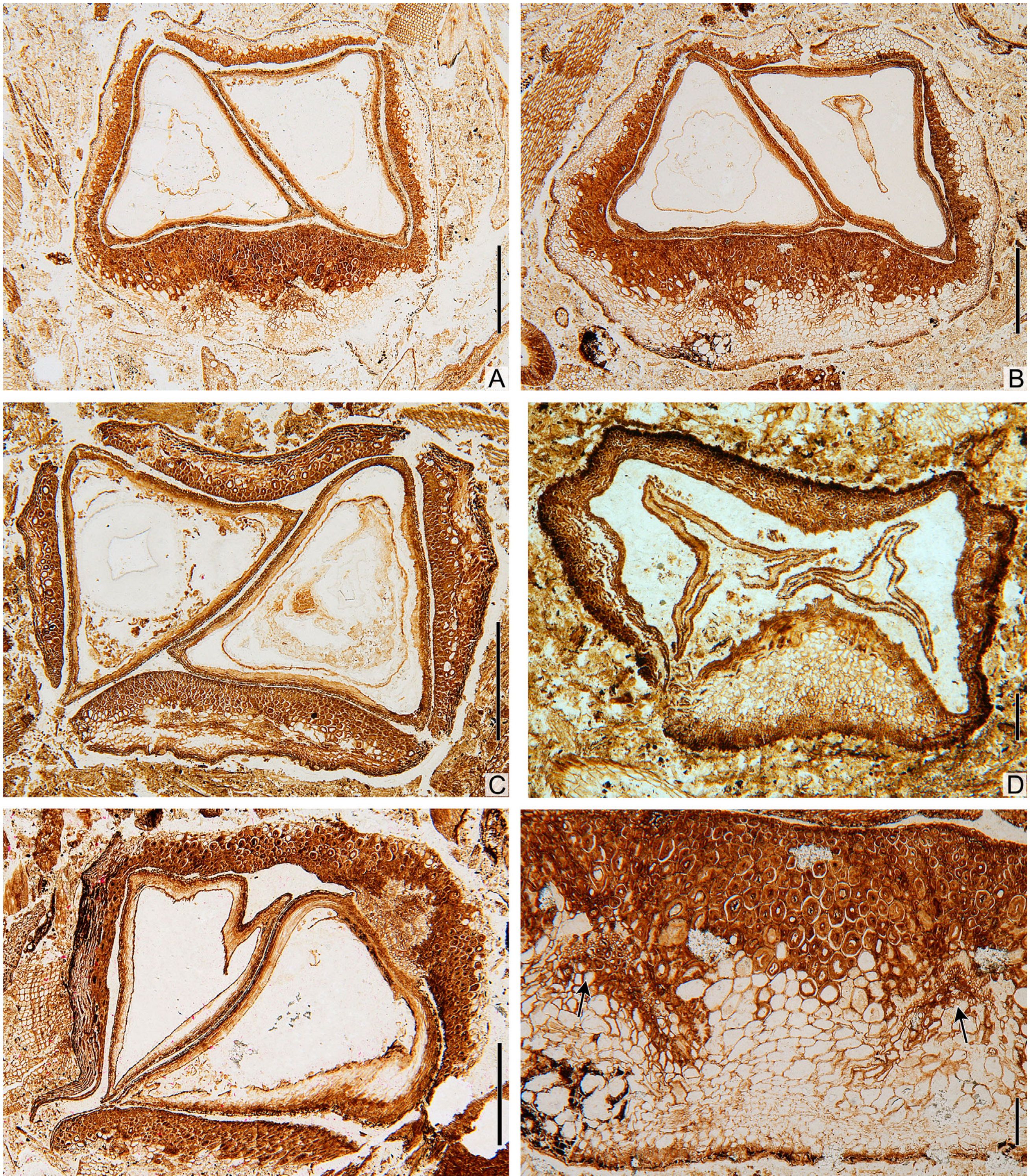
The two vascular bundles present in the cupule stalk continue distally into the cupule to supply the two seeds. These two vascular bundles are flattened, more-or-less bilaterally symmetric, and are embedded between the outer cortical parenchyma zone and the inner cortical sclerenchyma zone, but a bundle sheath is not seen (Fig. 6A). The two bundles become further apart closer to the points of seed attachment. At this level the xylem is composed of 3–5 rows of radially aligned tracheids and is toward the outer surface of the cupule: abaxial relative to the cone axis (Figs 6A, 10D). In most cupules the phloem is not preserved, and its position is inferred by an empty space, but in some cupules radially aligned sieve elements, which are thinner walled and more flattened than tracheids in transverse section, are present (Fig. 6A). These phloem cells are positioned toward the inner surface of the cupule relative to the xylem: adaxial relative to the cone axis (Fig. 6A).

Towards the apex of the cupule, near to the point where the cupule stalk becomes strongly curved (Fig. 4A, B), the xylem of the two vascular bundles forms an inverted ‘V’ (Figs 4F, 6B, 10E). The xylem composed of 3–4 rows of tracheids in radial files is toward the outer surface of the cupule: abaxial relative to the cone axis (Figs 4F, 6B). Poorly preserved phloem, or the space inferred to represent the former position of the phloem, occurs lateral to the inverted ‘V’-shaped xylem and toward the inner surface of the cupule relative to the xylem (Figs 4F, 6B). The open part of the inverted ‘V’-shaped vascular bundle surrounds several smaller thick-walled, sclerenchyma cells, and is itself surrounded by transfusion tissue consisting of short tracheids with helical thickenings (Fig. 6B).

Near the tip of the strongly curved distal part of the cupule stalk, close to the points of seed attachment, the two vascular bundles are completely embedded in the inner cortical sclerenchyma zone (Fig. 4E). At this level, the xylem of each vascular bundle, as seen in its transverse section, is circular and consists of radially aligned rows, each of three to five tracheids (Figs 6C, D, 10F). In the centre of the circle formed by the tracheids are a few smaller very thick-walled sclerenchyma cells (Fig. 6C, D). The tracheids are more-or-less isodiametric to slightly elongate in transverse section, *c.* 10–15 µm wide tangentially and 12–22 µm wide radially, with helical or scalariform secondary wall thickenings (Fig. 6G, H). In most cupules the phloem is not preserved and its position is inferred by a complete or incomplete ring of empty space around the xylem (Figs 4E, 6D). However, in a few cupules, there are delicate, flattened cells, aligned radially around the xylem that may be sieve elements (Fig. 6C).

Each of the two vascular bundles ends in, and expands into, a vascular disc of transfusion tissue that is 0.6–1 mm in diameter, at the point of seed attachment (Figs 2A, 4E, 5B, C, 7B–D). The vascular disc consists of short, irregularly arranged transfusion tracheids with helical or scalariform secondary wall thickenings (Fig. 7D, E). Each seed is borne on a thin pad of parenchyma, 1.0–1.2 mm in diameter and 150 µm thick, that is attached to the vascular disc of transfusion tissue (Figs 4E, 5A–C, 7A, B). The pad is formed by *c.* 5–7 layers of thin-walled cells that are more-or-less isodiametric in longitudinal sections of the cupule (Fig. 7D). The parenchyma tissue of the pad fits into a shallow depression in the base of the seed. The parenchyma tissue is often degraded (Figs 5B, 7A), but also occurs in cupules from which the seeds have been shed (Fig. 2A). Shedding of the seeds occurred along an abscission layer between the seed base and the surface of the parenchyma pad.

The seeds are erect, sessile and borne near the apex of the strongly curved distal portion of the cupule stalk (Figs 1C, 5A–C, 8A). Curvature of the stalk of more than 90° results in the micropyle of the seed being oriented back towards the base of the cupule stalk and the central axis of the cone (Figs 1B, C, 5A–C, 9). The seeds are ovate in lateral outline, 3.2–3.8 mm high, 2.7–3.3 mm wide and three-angled in transverse section (Figs 1E, 4A–C, 8B). The three more or less flattened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lateral faces have narrow, weakly developed, lateral wings (Figs 4A–C, 8B, D). The base of the seed is flattened and sunken. It accommodates the pad of parenchyma through which it is attached to the cupule prior to shedding of the seed (Figs 4E, 5A–C, 7A, B, 8A). As a result of its flattened basal attachment area the seed has an overall tetrahedral shape (Fig. 1E). At the apex of the seed is a short bifid micropyle (Fig. 8A).

The single integument is parenchymatous and consists of an outer epidermis, an outer zone of isodiametric thick-walled cells, an inner zone of irregularly shaped thin-walled cells, and an inner epidermis with a probable inner cuticle (Fig. 8C–E). The seed coat is not vascularized. The carbonized outer epidermis of the integument consists of delicate rectangular cells that are dark in colour (Fig. 8C–E). The epidermal cells are 15–20 µm wide in transverse sections of the seed. The outer zone of the integument is composed of 3–4 layers of isodiametric thick-walled cells that lack dark internal contents and are *c*. 15–25 µm in diameter in transverse sections of the seed. The weakly developed seed wings are formed mainly by these thick-walled parenchyma cells, and a small group of sclerenchyma cells beneath each wing where it joins the body of the seed (Fig. 8D). In most seeds the inner zone of the integument is crushed or degraded into a thinner, dark-coloured layer lacking cellular details (Fig. 8C). However, in a few seeds the inner zone is up to 120 µm thick and well preserved (Fig. 8E). It is composed of irregularly shaped, isodiametric to elongate thin-walled parenchyma cells with anticlinal walls that appear sinuous in transverse section (Fig. 8E). The inner epidermis is carbonized and consists of dark-coloured, rectangular cells similar to those of outer epidermis (Fig. 8C, D). In some specimens there is a probable inner cuticle immediate beneath the inner epidermis (Fig. 8E), or separated from the inner epidermis (Fig. 8A). The bifid micropyle is formed by extension of the entire integument, including the outer epidermis, the outer zone of thick-walled cells and the inner zone of thin-walled cells (Fig. 8A).

The nucellus is free from the integument except at the base and is generally shrunken to varying degrees (Figs 4B, C, 5A, B, 7A, B, 8A, B). The nucellus is unvascularized and consists of a thin outer cuticle and a thin megaspore membrane separated by a few layers of parenchyma cells (Fig. 8F). In most seeds the layers of parenchyma are either crushed or not preserved (Fig. 8A, B), but in a few seeds the parenchyma is better preserved and is five to six cells thick (Fig. 8F). The individual parenchyma cells are thin-walled, variously shaped, irregularly arranged, generally slightly elongate, and lack dark internal contents (Fig. 8F). In longitudinal sections of a few seeds, the tip of the nucellus forms a short nucellar beak (Fig. 8A). The megagametophyte is rarely preserved and even in the best specimens all that remains is the variously shrunken megaspore membrane with no distinct internal contents (Figs 4B, 8A, B).

Bisaccate pollen grains of the *Alisporites*-type occur inside the integument of a few seeds at the tip of the nucellus (Fig. 7F). Similar pollen grains are common adhering to the outer surface of cupules or seeds. The pollen grains are elliptical in polar view and 50–70 µm long (saccus to saccus). The corpus is circular to elliptic in polar view, *c*. 45 µm wide and usually more than half of the length of the grain. The corpus is non-striate with an elliptical to oblong sulcus transverse to the equatorial diameter of the grain on the presumed distal surface (Fig. 7F). Sacci are weakly developed, attached laterally to the corpus, and do not protrude from the elliptical outline of the grain (Fig. 7F). They are crescent-shaped with fine endoreticulations (Fig. 7F).

Comparisons and nomenclature. Comparisons undertaken previously for lignitic material from Mongolia with species of *Umkomasia* from the Triassic of

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Figure 4. *Jarudia zhoui* gen. et sp. nov., cupules. **A–D,** median transverse sections of individual cupules showing two tightly enclosed seeds that are triangular in transverse section. In A and B the cupule stalk and flaps are more or less equally anatomically differentiated into an outer cortical zone of parenchyma tissue, and an inner cortical zone of sclerenchyma tissue. Note the two vascular bundles in the cupule stalk (below) that supply the two seeds. In A the two lateral flaps are fused to the cupule stalk (below) while the median flap has torn free, in B the two lateral flaps are fused with the cupule stalk (below) and the median flap, and median flap is torn in the middle. **A,** PB23680. **B,** PB23670. **C,** cupule with the lateral flaps torn free from the cupule stalk (below) and from the median flap (Shi *et al.* 2021a), but note the clean untorn lower edge of the flap to the left. Note also the weakly defined projections on the outer surface of the lateral flaps, that the cupule stalk has two vascular bundles, and the strongly crushed cells of the outer parenchyma zone. PB23665. **D,** transverse section of smaller cupule with two shrivelled, probably aborted, triangular seeds, showing that the cupule stalk and flaps are mainly composed of parenchyma tissue. PB23681. **E,** oblique transverse section of cupule (Shi *et al.* 2021a) showing the attachment of one of the two seeds (right) in each cupule to the pad of parenchyma tissue and the vascular bundle with a ring of xylem. PB23673. **F,** detail of cupule stalk in transverse section enlarged from B, showing a distinct outer cortical zone (below) composed of parenchyma cells that lack internal contents, and inner cortical zone composed of sclerenchyma cells with dark internal contents reflecting the thick cell walls and small cell lumens. Note the two vascular bundles (arrows) embedded in between the parenchyma and sclerenchyma zones. PB23670. Scale bars: A–C, E = 1 mm; D, F = 200 µm.

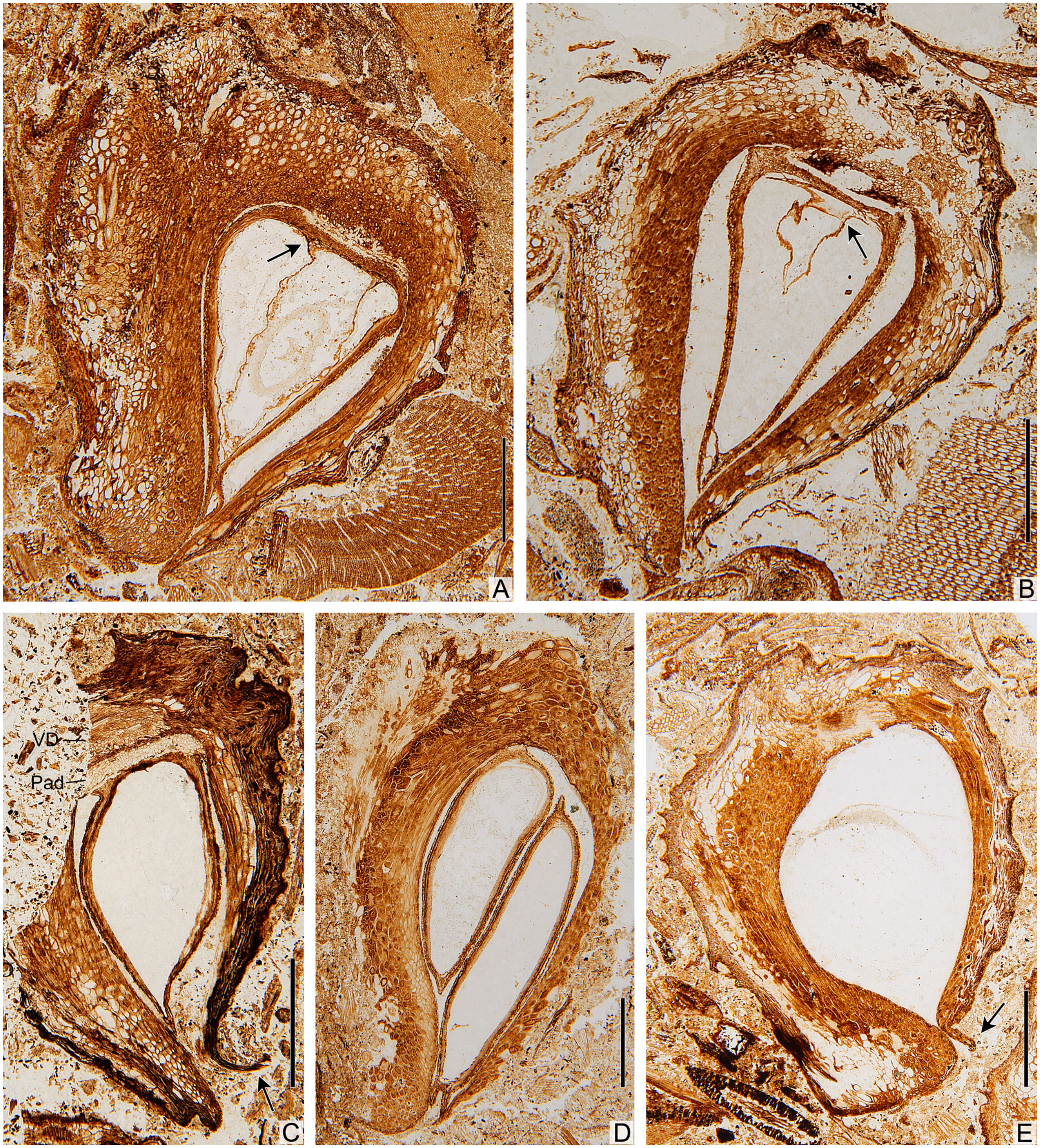
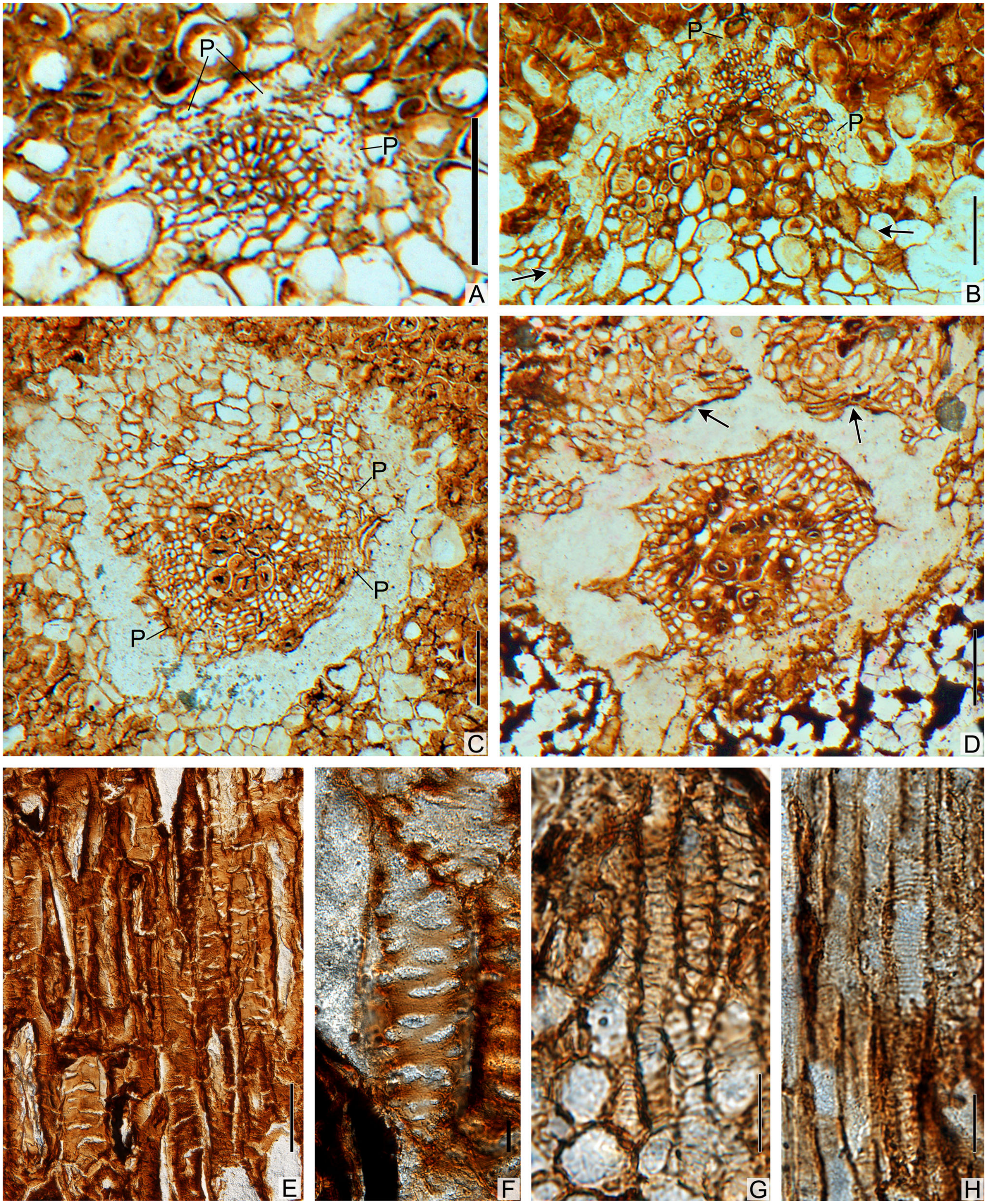


Figure 5. *Jarudia zhoui* gen. et sp. nov., cupules. **A–C,** median longitudinal section of cupules showing one of the two seeds attached at the tip of the strongly reflexed cupule stalk, which results in the micropyle being oriented toward the base of the cupule stalk. Note that seeds are attached only to the cupule at the base, and the remains of the nucellus within the seeds are attached only to the integument at the base. Note also the irregularly distributed and variably-sized tooth-like conical projections on the outer surface of the cupules. **A,** PB23682. **B,** note the distinct outer cortical zone composed of parenchyma cells that lack internal contents, and inner cortical zone composed of sclerenchyma cells with dark internal contents reflecting the thick cell walls and small cell lumens (Shi *et al.* 2021a). PB23674. **C,** partially broken cupule (Shi *et al.* 2021a) showing the vascular disc (VD) of short tracheids that supplies one of the two seeds, and the corresponding pad of parenchyma tissue (Pad) on the inner surface of cupule at the point of seed attachment. Note the upturned lip of the median cupule flap (arrow). PB23666. **D,** oblique longitudinal section of cupule showing two tightly enclosed seeds. PB23683. **E,** longitudinal section of an empty cupule, showing the upturned lip of the median cupule flap (arrow), and distinct irregular teeth on the cupule surface. Note that the larger teeth are formed by the epidermis, hypodermis and parenchyma tissue of the outer cortical zone; the smaller teeth are formed by only the epidermis and hypodermis; compare also A and B. PB23684. All scale bars = 1 mm.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Gondwana (Shi *et al.* 2016, 2019) apply equally to *Jarudia zhoui*, and are not repeated here. The similarities and differences from the Triassic material are considered in more detail below, but *Jarudia zhoui* is clearly distinct from any previously described corystosperm material. Most similar to *Jarudia zhoui* are *Umkomasia mongolica* (= *Doylea mongolica*) from the Early Cretaceous Tevshiin Govi locality in central Mongolia (Rothwell & Stockey 2016; Shi *et al.* 2016, 2019) and *Doylea tetrahedrasperma* from the Early Cretaceous Apple Bay locality, northern Vancouver Island, western Canada (Stockey & Rothwell 2009; Rothwell & Stockey 2016). These similarities require consideration of the most appropriate nomenclatural treatment of these and similar species.

Umkomasia mongolica and *Doylea tetrahedrasperma* both resemble *Jarudia zhoui*, in having a compound seed cone consisting of a central axis bearing helically arranged seed-bearing units, each of which consists of an elongate bract subtending and partially fused to a cupule-bearing axis. In all three species individual cupules are formed by a strongly curved cupule stalk together with flaps that enclose one or two three-angled seeds. The seed is borne at or near the tip of the strongly curved portion of the cupule stalk and that curvature results in the micropyle of the seed being oriented back toward the base of the cupule stalk and the axis of the cone. However, *Jarudia zhoui* is distinct in having an unbranched cupule-bearing axis that bears a single cupule at the tip. Each cupule is formed by the cupule stalk and three flaps and contains two seeds. In *U. mongolica* and *D. tetrahedrasperma* the cupule-bearing axis bifurcates, each branch bears a cupule. Each cupule is formed by the cupule stalk and two lateral flaps and contains a single seed. These differences justify placement of the silicified material from Inner Mongolia in the new genus *Jarudia.*

In his description of the original corystosperm material from South Africa, Thomas created three genera, *Pilophorosperma*, *Spermatocodon* and *Umkomasia*, for which separate diagnoses were provided. Subsequently, Holmes (1987) subsumed *Pilophorosperma* within *Umkomasia*. Anderson & Anderson (2003) supported this approach and further subsumed *Spermatocodon* under *Umkomasia* on the basis of more extensive collections from the type locality than Thomas had available (Anderson & Anderson 2003; Anderson *et al*. 2019a). Holmes (1987) provided an emended diagnosis.

Umkomasia mongolica was described based on exceptionally well-preserved three-dimensional lignitic material, which was assigned to *Umkomasia* because it corresponded in all essential features to the diagnosis of the genus as emended by Holmes (1987) based on material from the Triassic of the Southern Hemisphere (Shi *et al.* 2016, 2019). The only differences appeared to relate to details of the seeds. The emended diagnosis of Holmes (1987, p. 166) notes that each cupule bears “a single platyspermic ovule with a recurved micropyle”, whereas in *Umkomasia mongolica* and *Doylea tetrahedrasperma* the ovules are triangular in cross-section and there is no conspicuous recurved micropyle in *U. mongolica*.

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Figure 6. *Jarudia zhoui* gen. et sp. nov. **A–D,** detail of vascular bundles in cupule stalk at different levels, all oriented as the vascular bundles in Figures 3, 4, with the upper side of each bundle toward the inner side of the cupule, and the lower side of each bundle toward the outer side of the cupule. **A,** vascular bundle near the base of the cupule, showing xylem, composed of radially aligned files of tracheids, toward the outer side of cupule, and flattened, poorly preserved, partly torn sieve cells (P) toward the inner side of cupule. Note that the vascular bundles are embedded in between the thinner walled cells of the parenchyma zone (below) and the thick walled cells of the sclerenchyma zone. PB23669. **B,** vascular bundle near the apex of cupule, showing inverted ‘V’-shaped organization of weakly developed and poorly aligned xylem toward the outside of the cupule and poorly preserved phloem (P) laterally and toward the inside of the cupule. Note the transfusion tissue (arrows) composed of cells with helical thickenings around the vascular bundle. PB23680. **C,** vascular bundle close to the point of seed attachment (Shi *et al.* 2021a) showing an almost complete xylem cylinder composed of three to five layers of tracheids, some of which are arranged in discrete radial files surrounding a small group of about eight sclerenchyma cells with very thick walls, dark internal contents and small lumens. The xylem is surrounded by possible flattened, poorly preserved sieve cells (P) and a space that may represent the torn former position of the phloem and that is most prominent toward the outer side of cupule in contrast to A and B (and perhaps D) where the space indicating the possible former position of the phloem is toward the inner side of cupule. PB23671. **D,** vascular bundle close to the point of seed attachment showing circular arrangement of xylem composed of three to five layers of tracheids, a few of which are arranged in discrete radial files, surrounded by empty space that may represent the former position of phloem. Note that the xylem surrounds a small group of sclerenchyma cells, and the transfusion tissue (arrows) composed of tracheids with helical thickenings around the vascular bundle. PB24571. **E,** detail of sclerenchyma cells in longitudinal section from the inner cortical zone of the cupule stalk, showing strongly thickened secondary walls with prominent transverse pits. PB24572. **F,** detail of sclerenchyma cell in longitudinal section from the inner cortical zone of the cupule stalk, showing helical to reticulate secondary wall thickenings and prominent transverse pits. PB24573. **G,** detail of tracheids in cupule stalk showing helical secondary wall thickenings. PB24574. **H,** detail of tracheids in cupule stalk showing scalariform secondary wall thickenings. PB24575. Scale bars: A = 50 µm; B–E = 100 µm; F–H = 20 µm.

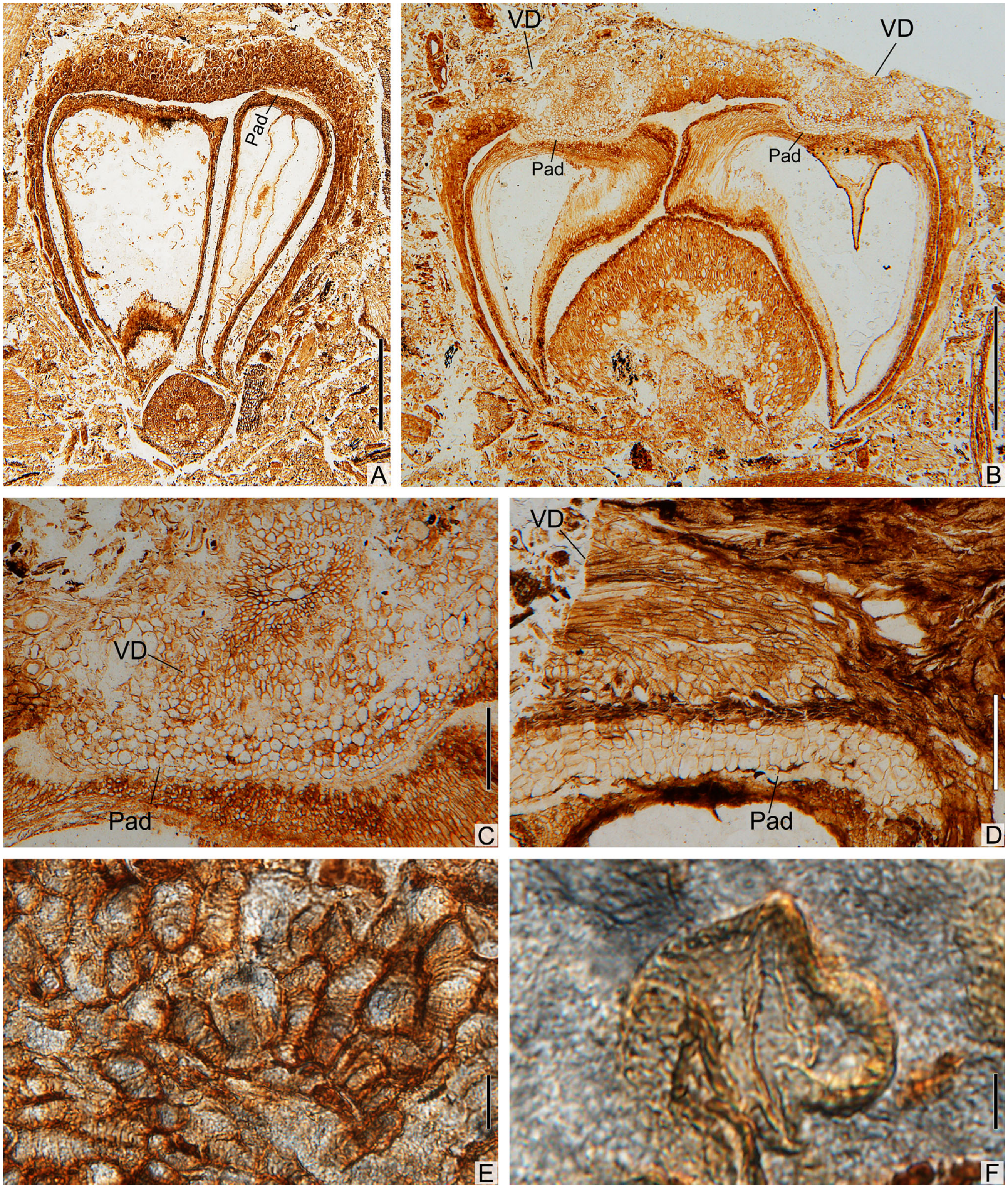
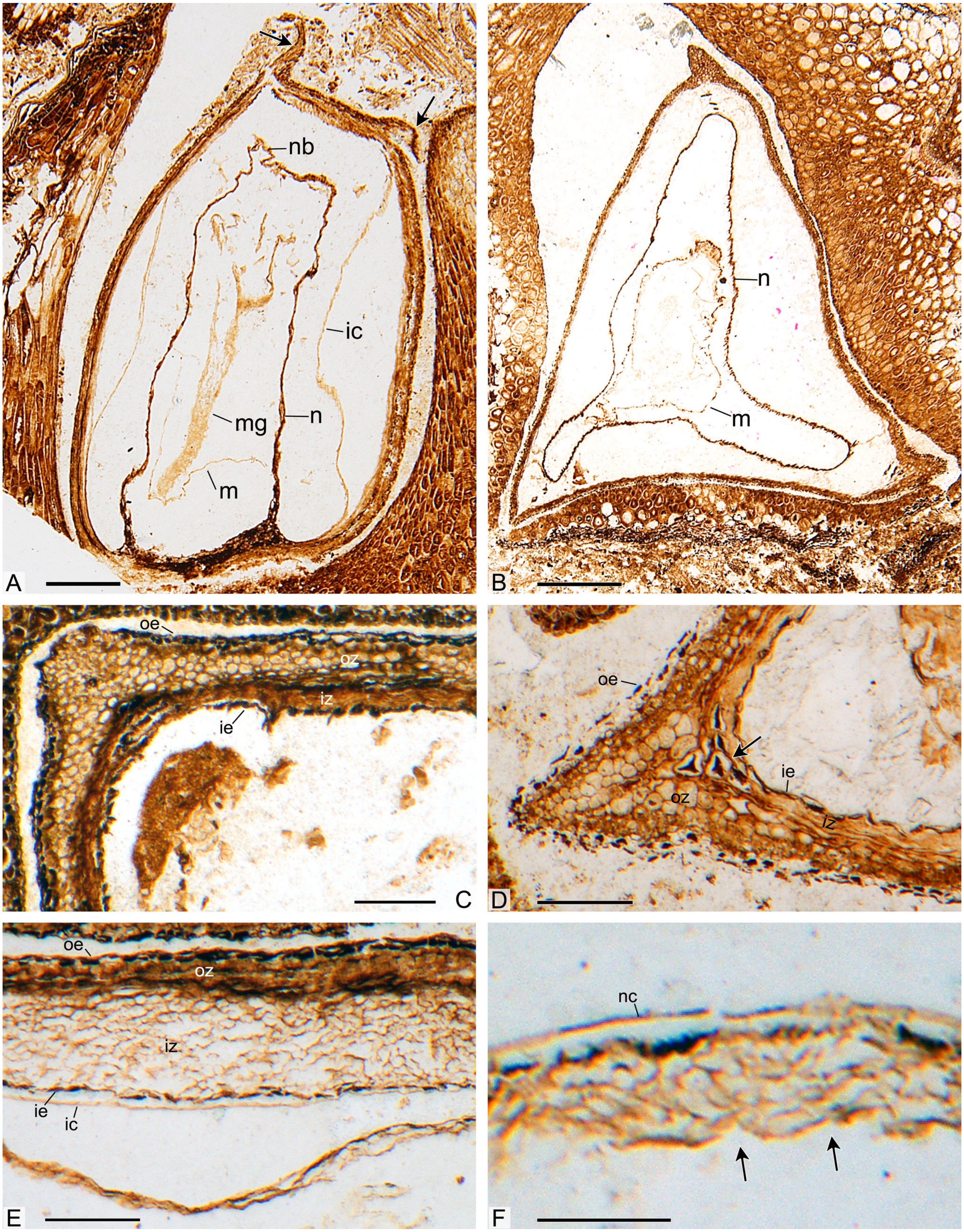


Figure 7. *Jarudia zhoui* gen. et sp. nov. **A, B,** oblique transverse section of seed-bearing units, showing cupule containing two seeds each attached to the pad of parenchyma tissue (Pad) that is borne on the vascular disc of transfusion tissue composed of short transfusion tracheids (VD). Note the fusion of the cupule stalk and bract in the lower part of both sections (below). **A,** PB24576. **B,** PB24577. **C,** detail of the vascular disc (VD) of transfusion tissue continuous with the pad-like structure of parenchyma tissue (Pad) at the point of seed attachment, enlarged from B. **D,** longitudinal section showing the vascular tissue merging into the transfusion tracheids that comprise the vascular disc (VD) and the pad of isodiametric parenchyma cells to which the seed is attached (Pad), enlarged from Figure 5C. PB23666. **E,** detail of the short transfusion tracheids with helical or scalariform secondary wall thickenings that comprise the transfusion tissue of the vascular disc in the cupule stalk at the point of seed attachment, enlarged from Figure 4E. PB23673. **F,** bisaccate pollen grain adhering to the tip of nucellus within the integument (Shi *et al.* 2021a). PB23678. Scale bars: A, B = 1 mm; C, D = 200 µm; E = 20 µm; F = 10 µm.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In assigning the material from Mongolia to *Umkomasia*, as *Umkomasia mongolica*, Shi *et al.* (2016, 2019) took the same approach as other authors who have assigned seed-bearing organs with reflexed cupules to *Umkomasia* from a variety of late Paleozoic and Mesozoic localities. These include material from the late Permian of India (Chandra *et al.* 2008) and Jordan (Blomenkemper *et al.* 2020), the Late Triassic of northern China (Zan *et al.* 2008), and the Late Triassic and Early Jurassic of Germany (Kirchner & Müller 1992; Kelber & van Konijnenburg-Van Cittert 1997).

Doylea tetrahedrasperma was described based on permineralized material (Stockey & Rothwell 2009; Rothwell & Stockey 2016). Originally considered a possible corystosperm based on the structure and anatomy of individual cupules (Stockey & Rothwell 2009), *D. tetrahedrasperma* was later regarded as distinct from the corystosperms and placed in a separate order Doyleales (Rothwell & Stockey 2016). This revised interpretation was heavily influenced by the discovery that *Doylea* seed-bearing units were borne in a compact compound cone, a conifer-like feature not recognized in corystosperm material from the Triassic of the Southern Hemisphere (Rothwell & Stockey 2016). This led to the conclusion that the cupules of the Early Cretaceous material from Canada and Mongolia were different from the cupules of corystosperms from the Triassic (Rothwell & Stockey 2016; Klymiuk *et al.* 2022). The hypothesized non-homology of the Triassic and Early Cretaceous cupules was also incorporated into a phylogenetic analysis of seed plants, and the results suggested that *Doylea* and corystosperms were only very distantly related (Rothwell & Stockey 2016; Klymiuk *et al.* 2022).

Based on the clear similarities between *Umkomasia mongolica* and *Doylea tetrahedrasperma*, Rothwell & Stockey (2016) transferred *U. mongolica* to *Doylea* as *D. mongolica*. Shi *et al.* (2016) had previously recognized and acknowledged the same similarities between *U. mongolica* and *D. tetrahedrasperma* in the overall organization of individual seed-bearing units and structure of individual cupules, and these were further confirmed with the discovery that the seed-bearing units of *U. mongolica*, like those of *D. tetrahedrasperma*, were borne in compound cones (Shi *et al.* 2019).

Consideration of whether or not the recognition of *Doylea* as distinct from *Umkomasia* is warranted could take into account a variety of factors but seems critically dependent on three considerations: (1) the weighting of similarities in the cupules versus apparent differences in the axes on which the cupules are borne; (2) the weight given to the other organs believed to be associated with the seed-bearing structures; and (3) whether a broad or narrow concept of *Umkomasia* is preferred. In assigning the material from Mongolia to *Umkomasia*, Shi *et al.* (2019) emphasized similarities in the structure of the cupules in the Triassic and Early Cretaceous material and also noted that recognizing *Doylea* renders a broad concept of *Umkomasia* paraphyletic. However, they also noted that as the seed-bearing organs of these extinct plants became better understood an appropriate solution might be to create several new and clearly defined genera of seed-bearing organs within a broader concept of Umkomasiales.

In their recent review Anderson *et al.* (2019a) take the opposite approach to Shi *et al.* (2019); they weight differences in the axes on which the cupules are borne more than similarities in the structure of the cupules, they emphasize the different leaves associated with the Triassic and Early Cretaceous material, and they favour a narrow concept of *Umkomasia.* They support the transfer of *Umkomasia mongolica* to *Doylea* by Rothwell & Stockey (2016). They also create a new genus (*Kirchmuellia*) for the material from the Early Jurassic of Germany (Kirchner & Müller 1992), assign the Chinese Triassic material (Zan *et al.* 2008) to

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Figure 8. *Jarudia zhoui* gen. et sp. nov., seeds attached to cupules. **A,** longitudinal section of seed (Shi *et al.* 2021a), showing the remains of the bifid micropyle (arrows), the nucellus (n) attached to the integument only at the base, the probable nucellar beak (nb), megaspore membrane (m) and remains of presumed megagametophyte (mg). Note that a probable inner cuticle of the integument (ic) has separated from the rest of the developing seed coat. PB23675. **B,** oblique transverse section of a seed showing the triangular outline, the free shrunken nucellus (n) and megaspore membrane (m). PB24578. **C,** detail of integument in transverse section, showing the carbonized outer epidermis (oe), the outer zone (oz) composed of 3–4 layers of isodiametric, thick-walled parenchyma cells that lack dark internal contents, the inner zone (iz) of crushed parenchyma tissue, and the carbonized inner epidermis (ie). PB24579. **D,** detail of integument in transverse section, showing the carbonized outer epidermis (oe), the outer zone (oz) of isodiametric thick-walled cells, the inner zone (iz) of thin-walled cells, and the inner epidermis (ie). Note the small group of sclerenchyma cells with very thick cell walls and dark internal contents beneath the short wing at the seed angle (arrow). PB23665. **E,** detail of integument in transverse section, showing the carbonized outer epidermis (oe), the outer zone of crushed parenchymatous tissue (oz), the inner zone (iz) of irregularly shaped thin-walled parenchyma cells, the carbonized inner epidermis (ie), and a probable detached inner cuticle (ic). PB24580. **F,** detail of nucellus, showing the thin nucellar cuticle (nc) and irregularly shaped parenchyma cells (arrows) internal to the nucellar cuticle (external to the megaspore membrane, not included in this image). PB24580. Scale bars: A, B = 0.5 mm; C–E = 100 µm; F = 50 µm.

Figure 9. *Jarudia zhoui* gen. et sp. nov., restoration of seed cone. The seed cone is reconstructed as pendulous on the basis of the flexible and curving axis of the cone.

Stenorachis and treat the cupules from the Permian of India (Chandra *et al.* 2008) as cf. *Arberiopsis* sp. Anderson *et al.* (2019a) also exclude *Umkomasia uniramia* from the Late Triassic of Antarctica (Axsmith *et al.* 2000) and create the new genus *Axsmithia*. The goal of the revision by Anderson *et al*. (2019a) is to demonstrate that *Umkomasia* "should be retained in the more narrow sense as the fertile organ of the plants bearing *Dicroidium* leaves" to which they also affiliate the pollen organ *Pteruchus* (Anderson *et al.* 2019b, p. 2). In later reviews of the *Dicroidium* leaves and the *Pteruchus* pollen organs Anderson *et al.* (2019b, 2020) also exclude all Northern Hemisphere and Gondwanan Permian records.

Anderson *et al.* (2019a) provide a revised diagnosis for *Umkomasia* that differs from the original one provided by Thomas (1933) and the emended one by Holmes (1987), most significantly in the treatment of the manner in which the cupules are borne. The original diagnosis for the family Corystospermaceae states, "Seed bearing inflorescence with lateral branches produced in the axils of bracts and pedicellate cupules" (Thomas 1933, p. 199). The Holmes diagnosis for *Umkomasia* states "An ovulate inflorescence comprising an axis with branches arising from axils of bracts" (Holmes 1987, p. 166). The Anderson *et al.* diagnosis states "Strobilus of lax paniculate form with helically attached megasporophylls" (Anderson *et al.* 2019a, p. 45). Emphasizing the "lax paniculate form" of the strobilus excludes *Doylea tetrahedrasperma*, which has been interpreted as a "compact compound seed cone" (Rothwell & Stockey 2016, p. 924), but omitting "branches arising from axils of bracts" obscures an important point of similarity between Triassic and Early Cretaceous forms that we consider in more detail below. Bracts and bracteoles are also not included in the comparative diagrams of *Umkomasia* seed-bearing structures in Anderson *et al.* (2019a, fig. 3), although they are clearly present and are included in the drawings and diagnoses of *Umkomasia* seed-bearing structures in Anderson & Anderson (2003).

The effect of the taxonomical changes described above is that the distinctiveness of the seed-bearing organs of *Umkomasia sensu* Anderson *et al.* (2019a) from the equivalent organs in the Early Cretaceous material rests almost entirely on the morphology of the 'lax paniculate strobilus' to which the cupules are attached. We think that in seeking to define *Umkomasia* as 'more natural' in this way Anderson *et al.* (2019a) may have had the opposite effect, because as Anderson *et al.* themselves note, the reconstruction of *Umkomasia resinosa* from the Triassic of Antarctica (Klavins *et al.* 2002), which is associated with *Dicroidium* leaves (Klavins *et al.* 2002), conflicts with their emended diagnosis in that cupules are borne helically and alternately on a shoot.

Revising the taxonomical treatment of Permian and Triassic corystosperms is beyond the scope of this paper. It will require detailed study of the original material of the cupules themselves and structures to which the cupules are attached. However, given the clear similarities between the bicupulate seed-bearing units of *Umkomasia mongolica* and *Doylea tetrahedrasperma* from the Early Cretaceous of Mongolia and Canada respectively, and to avoid further taxonomical and nomenclatural distractions, we accept the transfer of *U. mongolica* to *Doylea* as *Doylea mongolica* (Rothwell & Stockey 2016). The bicupulate seed-bearing units of *Umkomasia corniculata* (Shi *et al.* 2019) are also very similar to those of *D. tetrahedrasperma* and *D. mongolica* and we therefore also transfer the species to *Doylea* as *Doylea corniculata*.

The third kind of corystosperm seed bearing unit from the Early Cretaceous Tevshiin Govi locality, *Umkomasia trilobata*, is distinct from *Doylea tetrahedrasperma*, *D. mongolica* and *D. corniculata* in its tricupulate, trilobed, flattened seed-bearing units (Shi *et al.* 2019). We therefore assign the species to a new genus as *Tevshiingovia trilobata.* Also distinct are the perminerализed, unicupulate seed bearing units of *Jarudia zhoui.*

Genus ***Doylea*** Stockey & Rothwell, 2009

Type species. *Doylea tetrahedrasperma* Stockey & Rothwell 2009.

Doylea corniculata (Shi, Crane, Herendeen, Ichinnorov, Takahashi & Herrera) Shi, Herrera, Herendeen, Clark & Crane comb. nov.

2019 *Umkomasia corniculata* Shi, Crane, Herendeen, Ichinnorov, Takahashi & Herrera in J. Syst. Palaeontol. 17: 1002, figs 1E–H, 3–6.

Material. Holotype: PP56618, (Shi *et al.* 2019, fig. 4A), deposited in the Paleobotanical Collections, The Field Museum, Chicago, Illinois, USA.

Species diagnosis. As given for *Umkomasia corniculata* in Shi *et al.* (2019).

Remarks. *Doylea corniculata* is known from three-dimensionally preserved, isolated seed-bearing units and cupules that are strikingly similar to those of *D. tetrahedrasperma*, the type species of the genus. The organization of the bicupulate seed-bearing units is almost identical. The individual cupules are formed by a strongly recurved cupule stalk and two lateral flaps that partially enclose a single three-angled seed with a bifid micropyle. Especially characteristic is the prominent, corniculate protrusion at the apex of the cupule, which is present in *D. corniculata* and *D. tetrahedrasperma*, but inconspicuous in *D. mongolica* and *Jarudia zhoui.* The distinct elongated abscission zone at the base of each seed-bearing unit in *D. corniculata* also suggests that they were deciduous lateral units shed from a cone-like structure as in *D. tetrahedrasperma*, *D. mongolica* and *Jarudia zhoui. Doylea corniculata* and *D. tetrahedrasperma* are distinguished mainly by the extent of seed enclosure at maturity. At maturity the seed is completely or nearly completely enclosed by the cupule in *D. tetrahedrasperma* (Stockey & Rothwell 2009), but only partially enclosed by the cupule in *D. corniculata*, *D. mongolica* and *J. zhoui* (Shi *et al.* 2019, 2021a). *Doylea corniculata* also differs from *D. tetrahedrasperma* in having minute teeth on the outer surface of cupule (Shi *et al.* 2019).

Type locality. 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), Lower Cretaceous.

Genus *Tevshiingovia* Shi, Herrera, Herendeen, Clark & Crane gen. nov.

Type species. *Tevshiingovia trilobata* (Shi, Crane, Herendeen, Ichinnorov, Takahashi & Herrera) Shi, Herrera, Herendeen, Clark & Crane comb. nov.

Generic diagnosis. Individual seed-bearing units consisting 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 bearing a single cupule. Each cupule formed by the lamina of the lobe and two or three flaps, and containing a single seed. Each lobe is recurved, resulting in the micropyle of the seed being oriented back towards the base of the seed-bearing unit. Seeds ovate in lateral outline, three-angled, with a flat basal triangular attachment scar.

Derivation of generic name. The generic name derives from the Tevshiin Govi open-cast lignite mine in central Mongolia where the specimens were collected.

Tevshiingovia trilobata (Shi, Crane, Herendeen, Ichinnorov, Takahashi & Herrera) Shi, Herrera, Herendeen, Clark & Crane comb. nov.

2019 *Umkomasia trilobata* Shi, Crane, Herendeen, Ichinnorov, Takahashi & Herrera in J. Syst. Palaeontol. 17: 1008, figs 1I–L, 8–11.

Material. Holotype: PP56946 (Shi *et al.* 2019, fig. 9A), deposited in the Paleobotanical Collections, The Field Museum, Chicago, Illinois, USA.

Type locality. 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), Lower Cretaceous.

Derivation of the species name. The species name derives from the three-lobed structure.

Species diagnosis. As the specific diagnosis given for *Umkomasia trilobata* in Shi *et al.* (2019).

Remarks. *Tevshiingovia trilobata* is known from three-dimensional, lignified, isolated tricupulate and trilobed seed-bearing units that are distinctly different from the bicupulate seed-bearing units of *Doylea* and the unicupulate seed-bearing units of *Jarudia*. Also distinctive is the flattened, scale-like cupule-bearing axis with a central lobe in which the cupule, which contains a single seed, is formed by the flattened cupule stalk and three flaps. However, there are also strong similarities with *Doylea* and *Jarudia* in the strongly reflexed cupules containing a single, three-angled seed, and a flattened bract that subtends and is partially fused to the cupule-bearing axis. The distinct abscission zone at the base of each seed-bearing unit in *T. trilobata* also suggests that they were deciduous, lateral units shed from a cone-like structure as in *D. tetrahedrasperma*, *D. mongolica*, *Jarudia zhoui* and probably *D. corniculata.*

Homology of Triassic and Early Cretaceous corystosperm cupules

The formal nomenclatural adjustments made above are independent of whether the cupules of Triassic and Early Cretaceous corystosperms are homologous. However, non-homology, and assumed parallelism, is implied by Anderson *et al.* (2019a) and is incorporated explicitly into the approach and phylogenetic analyses of Klymiuk *et al.* (2022). We take the opposite view. We regard the cupules of Triassic and Early Cretaceous corystosperms as homologous because: (1) there are no significant features of the cupules themselves that differ between the material known from the Triassic of the Southern Hemisphere and the Early Cretaceous of the Northern Hemisphere; and (2) the cupule-bearing shoots in both the Triassic and Early Cretaceous material are consistently borne in the axil of a bract and therefore are morphologically branches rather than leaves.

With regard to the cupules themselves, we do not regard the difference in size mentioned by Anderson *et al.* (2019a) as either clear or significant, and the suggestion of differences in stomatal structure deserve more detailed examination. Neither the Triassic nor the Early Cretaceous material has been carefully analysed for this character using a modern approach or similar techniques. More interesting are two other features of the cupules, the presence or absence of a short protrusion at the apex of the cupule and the extent to which the cupule stalk contributes to enclosure of the seed.

Anderson *et al.* (2019a) note that there is often a protrusion at the apex of the cupule in *Doylea mongolica* but that this is not seen in Triassic *Umkomasia* species. This is a significant point because this protrusion is an especially well-developed characteristic feature of *D. tetrahedrasperma* and *D. corniculata*. It is also often present, but only weakly developed, in *Jarudia zhoui*. In cupules of *Doylea mongolica* the presence or absence of this protrusion and the extent of its development is variable (compare Shi *et al.* 2016, fig. 1 and fig. S1i–l with fig. 2a, b, c, e and fig. S1a–h, m–p). Therefore, while the absence of the protrusion in Triassic *Umkomasia* species is an interesting issue to follow up, in our view it does not constitute a basis for regarding the cupules of Triassic and Early Cretaceous plants as fundamentally different.

A further potential difference between the cupules of Triassic and Early Cretaceous plants not addressed by others, but that deserves careful study in well-preserved Triassic material, is the extent to which the cupule stalk participates in enclosing the seed; in other words, whether the cupule stalk is separate from, or integral to, the structure of the cupule. In *Doylea*, *Tevschingovia* and *Jarudia* the cupule stalk is distinctly flattened, has the same tissue differentiation as the cupule flaps, and is integral to the enclosure of the seeds. In contrast, in much of the Triassic material (Anderson & Anderson 2003) the enclosing cupule appears to be borne on the reflexed tip of a more distinct cupule stalk. The incorporation of the cupule stalk into the cupule itself is often less marked, particularly in the 11 ‘pedicellate’ species of *Umkomasia* recognized by Anderson *et al.* (2019a). A more distinct cupule stalk than in the Early Cretaceous species is also consistent with the circular, rather than flattened, cross-section of the cupule stalk in the permineralized material of *Umkomasia resinosa* (Klavins *et al.* 2002). However, while the cupule stalk in the three-dimensionally preserved cupules of *Umkomasia uniramia* (*Axsmithia sensu* Anderson *et al.* 2019a) also appears to be terete, there does not appear to be a flap of tissue separating the interior of the cupule from the stalk. This also appears to be the case in *U. macleani* (Thomas 1933, figs 1, 2) and *U. verrucosa* (=*U. macleani sensu* Anderson, Thomas 1933, fig. 6). Also, in the three species of *Umkomasia* recognized by Anderson *et al.* (2019a) as having ‘sessile’ cupules (*Umkomasia grandis*, *Umkomasia sessilis* and *Umkomasia decussata*), the cupule stalk appears to be more fully integrated into the cupule structure, which is also consistent with the open cupule of *Umkomasia grandis* figured by Anderson & Anderson (2003, p. 245, fig. 1). Future studies of this feature, based on well-preserved material, would be worthwhile to establish the extent of similarities and differences, but based on current knowledge we do not regard this apparent difference as a sufficiently strong basis for regarding the cupules of the Triassic and Early Cretaceous material as non-homologous.

Most discussions that favour non-homology of the cupules in Triassic and Early Cretaceous corystosperms (Stockey & Rothwell 2009; Rothwell & Stockey 2016; Anderson *et al.* 2019a; Rothwell *et al.* 2021; Klymiuk *et al.* 2022) are based not on the cupules themselves, but on the long-standing and widely adopted conventional interpretation that the seeds of Triassic corystosperms are borne on leaves (megasporophylls; Crane 1985; Doyle & Donoghue 1986; Klavins *et al.* 2002; Doyle 2006; Hilton & Bateman 2006; Stockey & Rothwell 2009; Rothwell & Stockey 2016; Anderson *et al.* 2019a; Rothwell *et al.* 2021; Klymiuk *et al.* 2022), whereas that is clearly not the case for the Early Cretaceous material.

The cupule of *Doylea tetrahedrasperma* was interpreted initially as a leaf-derived structure with the seed borne on the abaxial surface (Stockey & Rothwell 2009; Rothwell & Stockey 2016), but the description of *Jarudia* from Inner Mongolia, and additional material of *Doylea* from Mongolia, makes the morphological situation in the Early Cretaceous material very clear: the seed is borne terminally or nearly terminally on a stem (Shi *et al.* 2019, 2021a). Klymiuk *et al.* (2022) acknowledge that in *Doylea* the seed is borne on a fertile shoot, but they interpret the lateral cupule-bearing structure in Triassic *Umkomasia* as a leaf homologue. In our view the structures on which the seed is borne in the Triassic material is a modified stem because in all material of *Umkomasia* from the Late Triassic Molteno flora the lateral cupule-bearing structure arises from the axil of a bract (Thomas 1933; Anderson & Anderson 2003). We also see no evidence to support the suggestion of Townrow (1962) that the ‘bracteoles’ associated with the cupule-bearing axes of *Umkomasia* are reduced pinnules.

In addition to long standing morphological orthodoxy, which can be traced back to Goethe and that gives morphological primacy to the leaf in plant comparative morphology, the idea that the cupule-bearing structures of Triassic *Umkomasia* are highly modified leaves was given some credence by the early observation of slight dorsiventrality in the cuticles prepared from the cupule-bearing axes. This was noted by Thomas (1933) in his initial careful assessment and description of the original material from the Triassic of South Africa and led him to suggest that the cupule-bearing structures may have been flattened in life. However, he nevertheless strongly favoured the interpretation that the cupules are borne on proliferated axes and he regarded the positional relationship of the cupule-bearing axes to their subtending bract as decisive. He noted that while these "branches appear at first sight like the pinnae of a sporophyll, they are generally seen to arise in the axils of bracts." (Thomas 1933, p. 200). The bracts are seen clearly in Thomas' material including in the holotype (specimen U11), which is often re-illustrated (Klavins *et al.* 2002; Anderson & Anderson 2003) and which we have examined. The bracts are also clearly visible in Thomas' photograph and line drawings of specimen U11 in which all three of the lateral cupule-bearing axes arise in the axil of a bract (Thomas 1933, fig. 1, see also the detail in Thomas 1933, fig. 4). While bracts are not seen subtending the cupule-bearing axes of all specimens, most likely due to poor preservation, they are clear in several other of Thomas' figures (Thomas 1933, figs 5, 8, 12, 14, 18, 22, 25). Contrary to Rothwell *et al.* (2021) we do not believe these structures were 'misinterpreted' by Thomas.

Bracts subtending the axes on which the cupules are borne are clearly visible in the very extensive collections of *Umkomasia* made from several localities in the Triassic Molteno Formation of South Africa by Anderson & Anderson (2003). The line drawings and reconstructions of all the *Umkomasia* species considered by Anderson & Anderson (2003) clearly show the bract subtending each lateral cupule-bearing axis (Anderson & Anderson 2003, e.g. p. 244, p. 246, figs 3, 5, 6, p. 247, figs 2–4, p. 248, figs 2, 5, p. 249, figs 2, 4), and they also include the features of bracts (as bracteoles) in the diagnosis of the genus and individual species. While it may be the case that compared to the Early Cretaceous material the bracts (bracteoles of Thomas 1933; Anderson *et al.* 2019a) are relatively short in relation to the length of the axis they subtend (Anderson *et al.* 2019a) it is their presence, not their size, that is important. The presence of bracts is unequivocal and the paired bracteoles that are often present midway along the axis just distal to the point of attachment are classic features of proleptic growth.

Also relevant, as noted above, is the emended diagnosis of *Umkomasia* provided by Holmes (1987, p. 166) which includes the character "branches arising from axils of bracts". Further, the description of *Umkomasia polycarpa* from the Middle Triassic Esk Formation of Queensland notes the presence of a "narrow subtending bract" at the base of two of the 10 cupule-bearing branches, one of which is clearly visible in his illustration (Holmes 1987, fig. 1).

In assessing the relationship between the Triassic and Early Cretaceous material a further key feature to consider is the architecture of the branching system on which the cupule-bearing axes are borne. The most recent emended diagnosis of *Umkomasia* states "Strobilus of lax paniculate form with helically attached megasporophylls" (Anderson *et al.* 2019a, p. 45), but based on the material illustrated by Anderson & Anderson (2003) it is not clear that any species of *Umkomasia* has a true panicle in the sense that the lateral axes themselves have the potential for indeterminate branching. Six of the 14 species of *Umkomasia* diagrammed by Anderson *et al.* (2019a, fig. 3) have cupule-bearing units that consist of only one pair of cupules bifurcated from a common cupule stalk, and in all cases the cupule-bearing axis arises in the axil of a bract (Anderson & Anderson 2003, p. 244) exactly as in *Doylea*, and often without the additional pair of bracteoles (e.g. *U. bracteolata*, *U. gracilliaxis*, *U. cupulata*, *U. grandis*) (Anderson & Anderson 2003, p. 246, figs 5, 6; p. 248, fig. 5, p. 249, figs 1–4) that are also absent in *Doylea*. In the other eight species the lateral units have two or more pairs of cupules, but all appear strictly determinate with no evidence of additional buds or of additional growth to produce third order axes. All the strobili of *Umkomasia* illustrated by Anderson & Anderson (2003) are basically racemes with determinate lateral units each in the axil of a bract. Furthermore, several of the six species of *Umkomasia* that have cupule-bearing units consisting of an axis that bifurcates and bears only one pair of cupules, as is the case in *Doylea* (e.g. Anderson & Anderson 2003, p. 248, figs 1, p. 249, figs 1, 3), appear to be aggregated in a loose cone that differs from the cone of *Doylea mongolica* and *Jarudia zhoui* (Fig. 9) only in the slightly wider spacing of the lateral seed-bearing units.

To go beyond morphology to anatomical comparisons of the Early Cretaceous and Triassic material, *Doylea tetrahedrasperma* and *Jarudia zhoui* provide information on the anatomy of the Early Cretaceous material, whereas anatomical information for the Triassic material is based entirely on *Umkomasia resinosa* from the upper

Middle or Late Triassic of the Fremouw Peak locality, Antarctica (Klavins *et al.* 2002). *Doylea tetrahedrasperma* is known from a seed cone and nine isolated cupules and *J. zhoui* is known from more than 100 specimens. Unfortunately, *U. resinosa* is based only on a single permineralized cupulate axis and several isolated cupules, and the material is not well preserved (Klavins *et al.* 2002).

Umkomasia resinosa is described and reconstructed as a short determinate cupule-bearing axis, up to 15 mm long, bearing up to five helically arranged, strongly recurved cupules (Klavins *et al.* 2002). There is no evidence of a bract subtending the individual cupules and the base of the cupule-bearing axis is not preserved. The main axis has 'stem-like anatomy' with a radially symmetrical vascular cylinder of three vascular bundles all of which have the xylem positioned toward the centre of the cupule-bearing axis (Klavins *et al.* 2002). Paired bilaterally symmetrical vascular traces arise from the vascular tissue in the main axis and supply the seeds within the cupule.

The cupules of *Umkomasia resinosa* are formed by the cupule stalk, which is circular in cross-section, and either two lateral flaps or a single unlobed flap (Klavins *et al.* 2002). The cupules contain one or two unitegmic, orthotropous ovules. Based on the interpretation that the cupules were foliar the seeds were interpreted as borne abaxially because the curvature of the cupule is towards the phloem side of the vascular bundles in the cupule stalk, as in *Jarudia zhoui* and *Doylea tetrahedrasperma*. However, as shown in the reconstruction (Klavins *et al.* 2002, figs 18, 20), the seeds are borne very near the tip of the cupule stalk, which is curved back toward its base. The seeds have a bilobed micropyle that projects beyond the cupule (Klavins *et al.* 2002).

For comparisons with the anatomically preserved specimens from the Early Cretaceous the key features of *Umkomasia resinosa* are: (1) the apparent absence of bracts subtending each cupule (the presence or absence of a bract at the base of the cupule-bearing axis is unknown); (2) each cupule is on a single stalk rather than in pairs; (3) each cupule commonly contains two seeds; and (4) that the cupule-bearing axis has stem-like anatomy and that the vascular bundles supplying the cupules are more leaf-like in being collateral (bilateral) with the curvature of the cupule towards the phloem side of the vascular bundles (abaxially relative to the cupule-bearing axis).

In the absence of its attachment to its parent axis it is hard to be certain how *U. resinosa* should be compared to the compression/impression species of *Umkomasia*, the ovulate reproductive architecture of which is much better known (e.g. Anderson & Anderson 2003; Anderson *et al.* 2019a). Klymiuk *et al.* (2022) consider that individual stalked cupules of *U. resinosa* are homologous to the lateral cupule-bearing axis of the more completely preserved *Umkomasia* species from the Molteno flora. However, we agree with the original interpretation by Klavins *et al*. (2002) that the specimen of *U. resinosa* is more likely a determinate lateral seed-bearing structure of a compound cone, which is also consistent with the absence of bracts subtending each cupule. A corollary is that the whole structure is a stem that would have been borne in the axil of a bract, which is also consistent with its stem-like anatomy. One potential problem with this interpretation, as pointed out by Anderson *et al.* (2019a), is that the arrangement of cupules in *U. resinosa* is helical, rather than in opposite pairs (see Anderson *et al.* 2019a, fig. 3). Nevertheless, we think that the morphological interpretation of Klavins *et al.* (2002) is most likely correct. We also note a partial precedent in that the cupules of *U. decussata* are decussate rather than in a single plane (Anderson & Anderson 2003, p. 247, figs 3, 4; Anderson *et al.* 2019a, fig. 3). Under this interpretation the entire cupule-bearing axis of *U. resinosa* is homologous not to the cone of *Jarudia zhoui* and *Doylea tetrahedrasperma* but to the lateral cupule-bearing axis that arises in the axil of a bract.

This interpretation finds further support in similarities of the vascular supply to the cupules in *Umkomasia resinosa* to what occurs in *Jarudia zhoui* and *Doylea tetrahedrasperma.* Under the interpretation of Klavins *et al.* (2002) the portion of the cupule bearing axis on which *U. resinosa* is based is distal to its corresponding bract. Taking that into account the vascular supply to the cupules in *U. resinosa*, with two collateral bundles, is the same as the vascular supply to the cupule-bearing axis of *D. tetrahedrasperma* proximal to its bifurcation. It is even more similar to the vascular structure of unbifurcated cupule-bearing stalk in *Jarudia*, because *U. resinosa* and *J. zhoui* both have two seeds per cupule; consistently in *Jarudia*, commonly in *U. resinosa.* Notable in homologizing the entire cupule-bearing axis of *U. resinosa* to the bract-cupule-bearing axis complex of *J. zhoui* and *D. tetrahedrasperma* is that the vasculature of the main axis in *U. resinosa* is stem-like. This is not surprising since it is morphologically most likely a stem (Klavins *et al.* 2002) and is proliferated. The cupule-bearing axis is much more substantial and bears more cupules than the small, simple cupule-bearing axes of *J. zhoui* and *D. tetrahedrasperma.*

The vascular supply to the ultimate cupule-bearing stalks of *Umkomasia resinosa*, *Jarudia zhoui* and *Doylea tetrahedrasperma* is very similar. It is also similar to the vascular supply to the ovules in proliferated ovule-bearing axes of extant *Ginkgo biloba* (Shi *et al.* 2016). Previous suggestions that these ultimate ovule-bearing stalks are leaf homologues place great weight on the presence of bilaterally symmetric vascular bundles as evidence for their foliar nature. However, this feature is not a reliable indicator for foliar structure (Kaplan 1981; Shi *et al.* 2016) as is clear from their presence in the ovuliferous scales of conifers that are usually interpreted as modified shoots (Florin 1951). Our investigation of the anatomy of *J. zhoui*, based on abundant well-preserved material, also indicates the complexity of the relationship between vascular anatomy and leaf/shoot homologues. The ovule-bearing stalk of *J. zhoui* has two bilaterally symmetric vascular bundles but morphologically it is a shoot homologue because it is borne in the axil of a bract. Also significant is that in *J. zhoui* the arrangement of xylem and phloem in the vascular bundle varies through the ovule-bearing stalk. Near the tip of the strongly curved distal part of the ovule-bearing stalk, each of the two vascular bundles are shoot-like with circular xylem that consists of radially aligned tracheids.

In the details of its anatomy *Umkomasia resinosa* exhibits minor similarities and differences to *Jarudia zhoui* and *Doylea tetrahedrasperma.* In all three cupules the cupule wall has distinct inner and outer cortical zones, and the inner cortical cells are thicker walled and often with dark contents. Also, as in *J. zhoui* and *D. tetrahedrasperma,* the two vascular bundles supplying cupules of *U. resinosa* are collateral with the xylem towards the outer surface of the cupule, and each seed is supplied by one bundle that expands into a disc of short transfusion tracheids (Klavins *et al.* 2002). In all three species the integument of ovule is composed of mainly parenchymatous tissues and lacks a distinct sclerenchymatous layer. *Umkomasia resinosa* differs from *J. zhoui* and *D. tetrahedrasperma* in the vascularization of the two lateral flaps that form part of the cupule in *U. resinosa*, which is not the case in the generally smaller cupules of *J. zhoui* and *D. tetrahedrasperma. Umkomasia resinosa* also has secretory cavities in the cupule wall and integument, which are not seen in *J. zhoui* and *D. tetrahedrasperma*.

In conclusion, we believe that the facts currently available support the interpretation that the cupule-bearing axes of Triassic *Umkomasia*, including of *Umkomasia sensu* Anderson *et al.* (2019a), are fundamentally homologous to the cupule-bearing axes of Early Cretaceous *Doylea*, *Jarudia* and *Tevshiingovia*. In no case does the structure to which the cupules are attached resemble a typical leaf, neither do the small bracts that subtend the cupule-bearing axes, or the pairs of bracteoles that are often present near the base of those axes, resemble the pinnules of a pinnately compound leaf as suggested by Townrow (1962).

The ovulate structures of both the Early Cretaceous and Triassic fossils are basically lax or compact racemes with lateral cupule-bearing axes that are always borne in the axil of a bract. We know of no example, in well-preserved material, where the bract at the base of a cupule-bearing axis is absent. In Early Cretaceous *Doylea* and also in several Triassic species of *Umkomasia* the cupule-bearing axis bifurcates with each branch bearing a cupule, which results in a pair of cupules at the tip of each cupule-bearing axis. In other Triassic species of *Umkomasia* the cupule-bearing axis is proliferated and may bear up to seven pairs of cupules aligned in a single plane, but these cupule-bearing axes are strictly determinate, never have orders of branching beyond the primary axis and its laterals, and the cupules themselves are never subtended individually by a bract. Also, while the cupule-bearing axes of many *Umkomasia* species show dorsiventrality in the planar arrangement of the pairs of cupules, in other species the cupules are three-dimensionally arranged in an opposite and decussate manner (e.g. *U. decussata*) and apparently also helically (*U. resinosa*).

Based on these similarities we think that the Triassic and Early Cretaceous plants that produced the fossil cupulate reproductive structures described in this paper were closely related, and that their respective cupules are homologous rather than independent, parallel evolutionary developments as suggested by Klymiuk *et al.* (2022). The proliferated cupule-bearing structures of Triassic corystosperms likely reflect the form of plants that flourished in favourable growing conditions, as evidenced by the rich and varied Triassic plant assemblages, with many large leaves, in which they occur. In contrast, the much less elaborated reproductive structures of the Early Cretaceous forms, based on the fossil assemblage from the Tevshiin Govi lignite mine, Mongolia, likely reflect the limitations on growth in a depauperate swamp community, with many small leaves (Leslie *et al.* 2013; Shi *et al.* 2014, 2016, 2018, 2019; Herrera *et al.* 2015, 2016, 2017a, b, c, 2018, 2020, 2021).

Information about the whole-plant morphology of the Triassic plants is more complete than what we know about the morphology of the Early Cretaceous plants, but the reverse is true with respect to the detailed architecture and anatomy of the cupulate reproductive structures. *Doylea* and *Jarudia* provide more, unequivocal detailed morphological and anatomical information about the Early Cretaceous cupulate reproductive structures than *U. resinosa* does about the Triassic material. Nevertheless, irrespective of the complexities created by different degrees of knowledge, two groups can be recognized provisionally within this complex of plants based mainly on the leaves and other organs with which they are associated: the Triassic umkomasioids and the Early Cretaceous doyleoids. Given active research on the homologies and hierarchical patterns of relationship among these groups and other angiophytes (Shi *et al.* 2021a) we think it prudent to treat these groups informally rather than applying names that imply a particular hierarchy or taxonomical rank.

Doyleoids as a natural group

Jarudia zhoui from the middle Barremian of eastern Inner Mongolia, China, closely resembles *Doylea mongolica*, *D. corniculata* and *Tevshiingovia trilobata* from the Aptian–Albian of central Mongolia (Shi *et al.* 2016, 2019), and *D. tetrahedrasperma* from the Valanginian of western Canada (Stockey & Rothwell 2009; Rothwell & Stockey 2016). All five species have the cupules borne on lateral seed-bearing units that have apparently been shed from a central axis, and in *J. zhoui*, *D. mongolica* and *D. tetrahedrasperma* the lateral structures are known to have been helically attached in a lax (*J. zhoui* and *D. mongolica*) (Fig. 9) or compact (*D. tetrahedrasperma*) cone. *Doylea mongolica* has also been linked to leaves of *Pseudotorellia palustris.* The prediction is that the leaves of *J. zhoui*, *D. tetrahedrasperma*, *D. corniculata* and probably *T. trilobata* will also be strap-shaped, parallel-veined and similar to those of *Pseudotorellia*. Leaves of this kind are common in the Inner Mongolia chert (Shi *et al.* 2021a). We would also expect that *D. corniculata* and *T. trilobata* would be borne in cone-like structure as in *J. zhoui*, *D. tetrahedrasperma* and *D. mongolica*.

In all five species the lateral structures consist of an elongate bract subtending and partially fused with a cupule-bearing axis. In *Doylea tetrahedrasperma*, *D. corniculata* and *D. mongolica* the lateral seed-bearing units are bicupulate (Fig. 11B, C): the cupule-bearing axis bifurcates and each branch bears a cupule at the tip. In *Jarudia zhoui* the lateral seed-bearing units are unicupulate and although the cupule-bearing axis (cupule stalk) is not branched the vascular bundle divides to supply the two seeds (Fig. 11A). In *Tevshiingovia trilobata* the lateral seed-bearing units are tricupulate (Fig. 11D): the cupule-bearing axis is flattened, three-lobed and has three

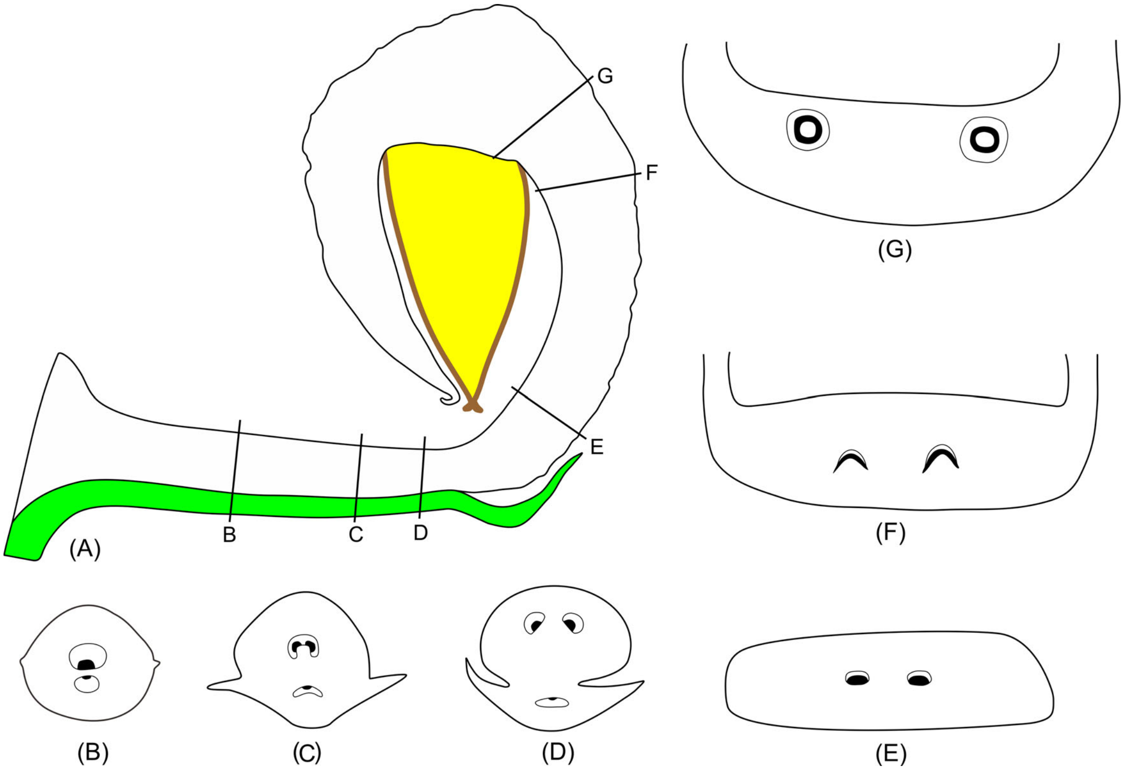

Figure 10. *Jarudia zhoui* gen. et sp. nov. **A,** interpretative line drawing of median longitudinal section of seed-bearing unit, showing the bract (green) subtending and partially fused with the cupule stalk with a free apex, and a seed which consisting of the nucellus (yellow) with a single integument (brown). **B–D,** interpretative line drawings of proximal to distal transverse sections of the fused bract and cupule stalk in A showing organization and orientation of xylem (black) in vascular bundles. **E–G,** interpretative line drawings of proximal to distal transverse sections of the cupule stalk in A showing organization and orientation of xylem (black) in vascular bundles.

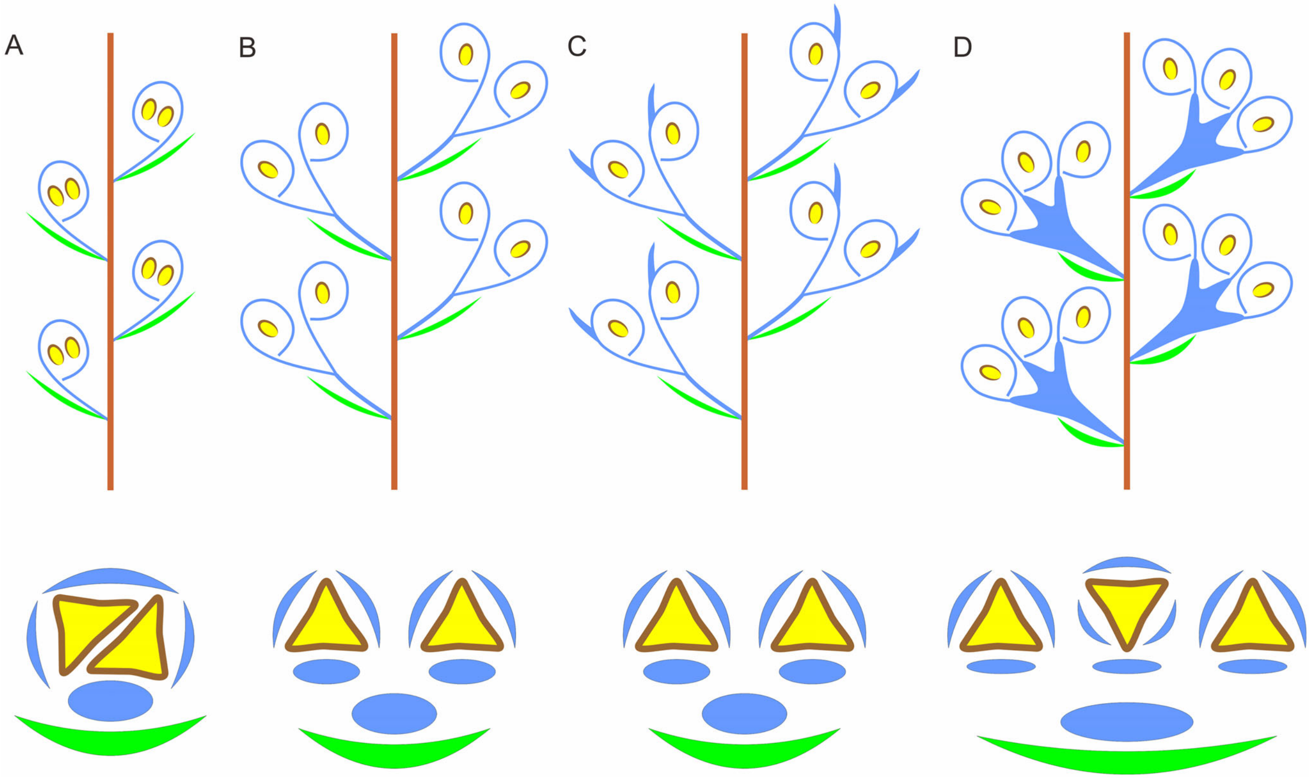

Figure 11. Interpretative diagrams of Early Cretaceous corystosperms, the bract (green), the stalked cupules (blue) and the axis on which they are borne (red brown), and seed consisting of the nucellus (yellow) with a single integument (brown). **A,** *Jarudia zhoui* gen. et sp. nov. Each lateral seed-bearing unit consists of a bract subtending an axis (the cupule stalk) that bears a single cupule at the tip; each cupule contains two three-angled seeds, and is subtended by a bract. **B,** *Doylea mongolica*. Each lateral seed-bearing unit consists of a bract subtending an axis that bifurcates into two cupule stalks; each cupule stalk bears one cupule that contains a single three-angled seed. Individual cupules are not subtended by a bract. **C,** *Doylea corniculata* and *Doylea tetrahedrasperma*. Each lateral seed-bearing unit consists of a bract subtending an axis that bifurcates into two cupule stalks; each cupule stalk bears one cupule that contains a single three-angled seed. Individual cupules are not subtended by a bract. Note the prominent projection at the apex of the cupule. **D,** *Tevschingovia trilobata*. Each lateral seed-bearing unit consists of a bract subtending a flattened axis that is divided distally into three flattened cupule stalks; each cupule stalk bears one cupule that contains a single three-angled seed. Individual cupules are not subtended by a bract.

cupules. In all cases each cupule is formed by the strongly curved cupule stalk with two or three flaps that may be fused to varying degrees. The cupule contains and partially encloses one or two seeds.

The vasculature of the seed-bearing axis with its fused bract and cupule-bearing portion is known only for *Jarudia zhoui* and *Doylea tetrahedrasperma*. The subtending bract is almost completely fused to the cupule-bearing axis near the base, and the whole complex is supplied by three vascular bundles, one supplying the bract and two supplying the axis.

A close relationship among the five species is also supported by other features that *Jarudia zhoui* shares with *Doylea* and *Tevshiingovia trilobata*. These include the irregular teeth on the outer surface of the cupules of *J. zhoui* and *D. corniculata*, as well as the short, apical protrusion on the back of the cupule in some specimens of *Jarudia zhoui* and *D. mongolica*, which is especially well developed in *D. corniculata* and *D. tetrahedrasperma*. The cupules of *J. zhoui* also resemble the central cupule of *T. trilobata* in being formed by the cupule stalk, two lateral flaps and a median flap.

All these similarities of both morphology and anatomy strongly suggest that *Jarudia zhoui*, *Doylea mongolica*, *D. corniculata*, *Tevshiingovia trilobata* and *D. tetrahedrasperma* comprise a closely related group of plants. So far they are known only in the Early Cretaceous of the Northern Hemisphere. We treat them informally as the doyleoids, broadly equivalent to the order Doyleales (Rothwell & Stockey 2016).

Umkomasioids as a natural group

In their recent reviews Anderson *et al.* (2019a, b, 2020) define the three corystosperm genera *Umkomasia*, *Pteruchus* and *Dicroidium* narrowly and exclude all records from the Northern Hemisphere. They also exclude all records from the Jurassic and Permian of Gondwana. The intent was to restrict *Umkomasia*, as well as *Pteruchus* and *Dicroidium*, to create a whole-plant concept approximating a living biological entity. This is a worthy objective, although we consider the apparent weighting of geographical and temporal considerations as inappropriate, and the exclusion of *Axsmithia* is also at variance with this approach.

The concept that *Umkomasia*, *Pteruchus* and *Dicroidium* were produced by the same plants was recognized originally by Thomas (1933) and has been amply supported subsequently by evidence from many localities on four continents (Townrow 1965; Playford *et al.* 1982; Retallack 1983, 1995; Pole & Raine 1994; Cantrill *et al.* 1995; Holmes & Anderson 2005; Anderson & Anderson 2003; Pattemore 2016a). The reconstruction is also supported by the similar secretory cavities that occur in tissues of the permineralized cupules of *Umkomasia resinosa*, the pollen organ of *Pteruchus fremouwens* (Yao *et al.* 1995) and leaves of *Dicroidium fremouwensis* (Pigg 1990) from the upper Middle or Late Triassic Fremouw Peak locality in the Central Transantarctic Mountains, Antarctica. The same secretory cavities also occur in small stems of *Kykloxylon fremouwensis* (Meyer-Berthaud *et al.* 1993), although not in probable larger *Kykloxylon* stems from the same locality (Decombeix *et al.* 2010, 2014).

Even though it is rarely possible to correlate individual species of *Umkomasia*, *Pteruchus* and *Dicroidium* and assemble them into ‘whole plants’ (Anderson & Anderson 2003), there is no doubt that taken together these three genera comprise a useful concept and we refer to them informally as the umkomasioids. However, as is normally the case, even for the most well-defined groups of fossil plants, there is a penumbra of other fossils surrounding the core umkomasioids that may or may not belong in the group (Crane *et al.* 2004). For a deeper understanding of the limits of the umkomasioids, and their potential relationships to other groups, careful assessment of the ovulate structures that Anderson *et al.* (2019a) excluded from *Umkomasia* is likely to be especially critical. It needs to be established whether the cupulate structures of *Axsmithia uniramia* (=*Umkomasia uniramia*) from the Late Triassic of Antarctica (Axsmith *et al.* 2000), *Umkomasia aequatorialis* from the late Permian of the Middle East (Blomenkemper *et al.* 2018, 2020), *Kirchmuellia franconica* (=*Umkomasia franconica*) from the Jurassic of Germany, *Stenorachis asiatica* (=*Umkomasia asiatica*) from the Late Triassic of north-eastern China (Zan *et al.* 2008), and cf. *Arberiopsis* sp. (=*Umkomasia polycarpa* plus *Umkomasia uniramia*) from the late Permian of India (Chandra *et al.* 2008) are fundamentally different from those of core umkomasioids or are more likely homologous. It seems unlikely that the classic *Dicroidium-Umkomasia-Pteruchus* assemblage as defined by Anderson *et al.* (2019a, b, 2020), which was abundant and widespread in the Southern Hemisphere during the Middle and Late Triassic, was the only member of the umkomasioid group.

Angiophytes as a natural group

The recognition and description of *Jarudia* from the Early Cretaceous of Inner Mongolia, China, adds to the significant expansion of knowledge about corystosperms that has occurred over the past two decades, as a result of research on material from the Permian and Triassic (Thomas 1933; Holmes 1987; Kirchner & Müller 1992; Axsmith *et al.* 2000, 2007; Klavins *et al.* 2002; Anderson & Anderson 2003; Chandra *et al*. 2008; Zan *et al.* 2008; Blomenkemper *et al.* 2018, 2020; Anderson *et al.* 2019a, b, 2020) as well as from the Early Cretaceous (Stockey & Rothwell 2009; Rothwell & Stockey 2016; Shi *et al.* 2016, 2019, 2021a). Based in part on these discoveries, including the new information provided by the well-preserved material of *Jarudia*, we have proposed that the reflexed cupules of the doyleoids, umkomasioids, *Caytonia* and *Petriellaea*, perhaps also including the ovule-bearing structures of glossopterids, are all fundamentally similar (Shi *et al.* 2021a). Also, consistent with previous interpretations, we regard these cupules as homologous to the outer integument of angiosperms (Gaussen 1946; Stebbins 1974; Crane 1985; Doyle 1978, 2006, 2008; Frohlich & Parker 2000; Frohlich 2003; Frohlich & Chase 2007; Shi *et al.* 2021a). Based on this potential homology, which is also (weakly) supported as a synapomorphy based on the totality of available characters, the doyleoids, umkomasioids, *Caytonia*, *Petriellaea*, glossopterids and angiosperms have been grouped together as the angiophytes (Shi *et al.* 2021a).

These comparisons are not pursued further here but the precise pattern of relationships among the doyleoids, umkomasioids and other groups of angiophytes will have a significant bearing on the utility of retaining the corystosperms as a meaningful evolutionary group. In particular, while the cupules of doyleoids and umkomasioids are more similar to each other than to the cupules of other angiophytes, this similarity may not reflect a close relationship if cupules of that kind are basic for angiophytes as a whole (Fig. 12). It may be the case that doyleoids and umkomasioids are not especially closely related, not because their one or two seeded

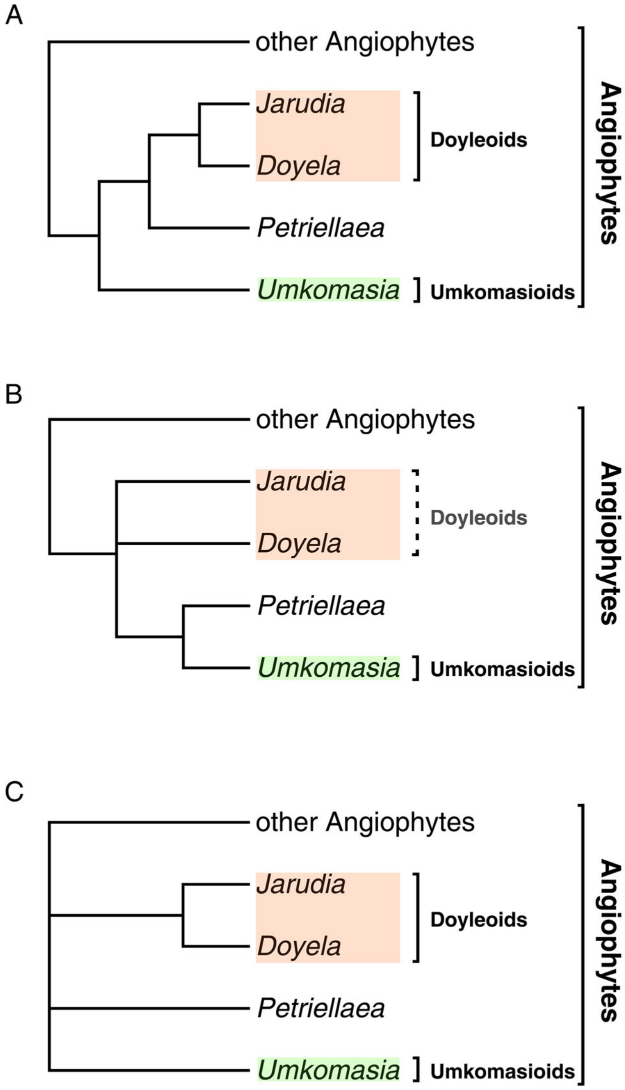

Figure 12. Relationships within angiophytes, simplified from cladograms of seed plants from analyses with relationships among extant taxa constrained to be compatible to a molecular-backbone tree (Shi *et al.* 2021a, extended data fig. 9), showing the relationships of Doyleoids and Umkomasioids. **A,** result from a constrained maximum likelihood (ML) analysis, in which *Jarudia* and *Doylea* form the Doyleoids, and Doyleoids plus *Petriellaea* and *Umkomasia* form a clade. **B,** result from a constrained maximum parsimony (MP) analyses, in which *Umkomasia* plus *Petriellaea*, *Jarudia* and *Doylea* form a clade. **C,** result from a constrained Bayesian analysis, in which *Jarudia* and *Doylea* form the Doyleoids, and Doyleoids, *Umkomasia* and *Petriellaea* form a polytomy with other angiophytes.

cupules are non-homologous, but because cupules of that kind may be plesiomorphic in the context of other angiophytes (Fig. 12). Current phylogenetic analyses interpose *Petriellaea* between the doyleoids and umkomasioids, suggesting that *Petriellaea* is especially relevant to this question (Shi *et al.* 2021a). Additional analyses that include other well-preserved fossil material, especially of *Petriellaea*, are needed to test this pattern of relationships.

Conclusions

Jarudia differs from *Doylea* in having a non-bifurcated cupule-bearing axis that bears a single cupule containing two seeds. However, *Jarudia* is united with *Doylea* and *Tevshiingovia* by the fundamentally similar architecture of the cupule, which is formed from the cupule stalk with enclosing flaps, and the terminal or almost terminal position of the seed on a branch that arises in the axil of a bract. It seems very likely that *Jarudia*, *Doylea* and *Tevshiingovia* are closely related and we refer to them here as the doyleoids.

The doyleoids are distinguished from the Triassic plants with ovulate reproductive structures assigned to *Umkomasia*, which we refer to as the umkomasioids, by their associated leaves and minor differences in architecture of the cupulate structures. However, we reject the interpretation that the ovulate reproductive structures of the doyleoids and umkomasioids are fundamentally different: the seeds of the former being stem-borne and the seeds of the latter being leaf borne, as has been argued by Klymiuk *et al.* (2022). On the contrary we think that the cupules of the two groups are homologous because they share fundamental structural, positional and anatomical similarities that likely reflect similar pollination and dispersal biology. In both groups the cupules are formed from the cupule stalk and enclosing flaps and are borne on branches that arise in the axils of bracts. In the doyleoids the cupules are borne on axes that are either unbranched, or only sparsely branched and consequently bear only one, two, or three terminal cupules. In contrast, in many, but not all, umkomasioids the cupules are borne on proliferated axes and consequently bear multiple cupules, usually in pairs and often in a planar arrangement.

Beyond the similarities of their cupules, differences between doyleoids and umkomasioids in other features are to be expected. For example, it has been suggested that the absence of secretory cavities is a significant difference between the Early Cretaceous and Triassic material (Rothwell & Stockey 2016), but the extent to which secretory cavities are a widespread feature of Triassic umkomasioids is by no means clear (Decombeix *et al.* 2010, 2014). More significant may be the difference between the platyspermic seeds thought characteristic of umkomasioids (Anderson *et al.* 2019a), and seeds of doyleoids that are three-angled in transverse section. This feature needs more careful study given that Thomas (1933, pp. 227–228, fig. 33) noted and figured three-angled, isolated seeds associated with his original material of *Umkomasia*. Similar isolated seeds from the late Permian of Jordan, which have been assigned to *Umkomasia* sp., have a clear longitudinal ridge (Blomenkemper *et al.* 2020, pl. XI, 4, 5, 7), which suggests these compressed seeds were originally three-angled. Three-angled seeds also occur in the putative corystosperms from the Late Triassic of Zimbabwe (Barale *et al*. 2009) and in *Petriellaea triangulata* from the Triassic of the Fremouw locality in Antarctica (Taylor *et al.* 1994).

Whether or not these the apparent differences are confirmed, doyleoids and umkomasioids differ most obviously and most significantly in the other plant fossils with which they have been linked. The cupules of umkomasioids are linked with leaves of *Dicroidium* and pollen organs of *Pteruchus*. The cupules of doyleoids are so far linked only with leaves of *Pseudodotorellia* and their corresponding pollen organs are unknown.

Against this background, grouping the doyleoids and umkomasioids together as two subgroups of the corystosperms, which recognizes the homology of the cupules, is a logical approach, but with the proviso that the potential relationships of doyleoids and umkomasioids to other group of angiophytes, notably the Caytoniaceae, Petriellaceae (*Kannaskoppia*), glossopterids and angiosperms, require further investigation and analysis.

Also important to this question, but not so far considered in detail, are extant and fossil conifers. For example, the bilobed compound cone scales of Early Cretaceous and Triassic *Schizolepidopsis*, a putative stem group member of Pinaceae (Leslie *et al.* 2013; Matsunaga *et al*. 2021), have interesting similarities with the cupule-bearing structures of *Doylea tetrahedrasperma* and *Doylea mongolica*. Understanding the basic condition of the ovulate cone scale in Pinaceae and other groups of conifers will be important for such comparisons, especially given that conifers are not monophyletic based on some analyses of molecular data (Wickett *et al.* 2014; Li *et al.* 2017; Ran *et al.* 2018).

Petriellaceae is of interest because like the umkomasioids it is present in the Molteno Formation, and although relatively little is known about the detailed structure of its cupules they appear to be borne on bifurcated proliferated axes (Anderson & Anderson 2003). Glossopterids are also potentially relevant because there is ample evidence that their ovulate units were borne in an axillary position, and among glossopterid reproductive structures there are several in which the seeds seem to be borne terminally or near terminally (e.g. *Arberia*, Mcloughlin & Prevec 2019), and in some (e.g. *Lidgettonia*) there are potential homologues to the cupule flaps of corystosperms (e.g. *Lidgettonia*, Mcloughlin & Prevec 2019).

Also, potentially relevant to the phylogenetic relationships of doyleoids and umkomasioids are *Umaltolepis* and *Ginkgo. Umaltolepis* is especially interesting because the leaves of *Pseudotorellia resinosa*, with which the cupules of *Umaltolepis* are associated (Herrera *et al.* 2017b), are very similar to *Pseudotorellia palustris*, the leaves linked with *Doylea mongolica* (Shi *et al.* 2019). *Ginkgo biloba*, along with its diverse extinct relatives, is potentially relevant because the ovules are borne terminally on an ovule-bearing shoot that is borne in the axil of a normal leaf. Usually there are only two ovules at the apex of the ovule-bearing shoot, but sometimes there are more, and the shoot itself may be three-dimensionally branched with terminal ovules (Shi *et al*. 2016). Also relevant are the ovule-bearing structures of the fossil ginkgoid *Karkenia* Archangelsky, which are cone-like with compact recurved ovules, and also have *Ginkgo*-like, but more deeply divided, leaves (Archangelsky 1965; Del Fueyo & Archangelsky 2001; Nosova *et al.* 2021). Understanding these and other potential connections among doyleoids, umkomasioids and potentially related seed plants will ultimately determine the utility of the corystosperms as a useful group for phylogenetic purposes. Essential to that process will be identifying similarities, rather than differences, and determining whether they can be supported as secure hypotheses of homology.

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