Article

Mesozoic cupules and the origin of the angiosperm second integument

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The second integument of the angiosperm ovule is unique among seed plants, with developmental genetics that are distinct from those of the inner integument[1]. Understanding how the second integument should be compared to structures in other seed plants is therefore crucial to resolving the long-standing question of the origin of angiosperms[2–6]. Attention has focused on several extinct plants with recurved cupules that are reminiscent of the anatropous organization of the basic bitegmic ovules of angiosperms[1–6], but interpretations have been hampered by inadequate information on the relevant fossils. Here we describe abundant exceptionally well-preserved recurved cupules from a newly discovered silicified peat dating to the Early Cretaceous epoch (around 125.6 million years ago) in Inner Mongolia, China. The new material, combined with re-examination of potentially related fossils, indicates that the recurved cupules of several groups of Mesozoic plants are all fundamentally comparable, and that their structure is consistent with the recurved form and development of the second integument in the bitegmic anatropous ovules of angiosperms. Recognition of these angiosperm relatives (angiophytes) provides a partial answer to the question of angiosperm origins, will help to focus future work on seed plant phylogenetics and has important implications for ideas on the origin of the angiosperm carpel.

The extinct Mesozoic seed plant *Caytonia* (Fig. 1b, c) has been central in discussions of angiosperm origins[2–6], despite its gymnosperm pollination biology in which pollen grains directly access the developing ovule[7,8]. Phylogenetic analyses of living and extinct seed plants resolve *Caytonia* as the sister group to angiosperms[9,10] (Fig. 1e) and interpret the *Caytonia* cupule (Fig. 1c) as homologous to the angiosperm second integument (Fig. 1d), but how *Caytonia* cupules relate to the similar recurved cupules of other Mesozoic plants has remained uncertain. Descriptions of well-preserved recurved cupules from the Early Cretaceous[11,12], together with the absence of detailed anatomical information for the cupules of *Caytonia*, highlight the need for reassessment based on well-preserved material.

The new fossil material from Inner Mongolia that we describe here bears cupules similar to those of corystosperms (Umkomasiales)[11–15]. Lax seed cones comprise a central axis with helically arranged, deciduous lateral seed-bearing units (Figs. 1a, 2a, 3a, Supplementary Videos 1, 2). Each seed-bearing unit consists of a narrow, flattened, elongate bract, partially fused to a modified shoot—the cupule stalk—which bears a single recurved cupule near its tip (Figs. 1a, 2a, 3a, Extended Data Fig. 2a, d, g). Each cupule is formed by the flattened, curved, vascularized cupule stalk and three partly fused unvascularized flaps (Figs. 2b, c, 3a), the median of which forms a distal lip (Figs. 2d, e, 3a). The cupule stalk and flaps partially enclose two three-angled seeds. Each seed is in a near-terminal position on the cupule stalk but distal curvature of the stalk away from the bract results in the micropyles

being oriented back towards the base of the cupule stalk and cone axis (Figs. 2d, e, 3a).

Previous interpretations of the homologies of cupules in Mesozoic seed plants have relied heavily on details of vascular anatomy[10,11,14]. In the Inner Mongolia cupules there are two median bilaterally symmetrical vascular bundles at the base of the seed-bearing unit, with xylem towards the centre of the bract-cupule stalk complex in both bundles (Extended Data Fig. 3a, b). The abaxial bundle supplies the bract and the adaxial bundle supplies the cupule (Fig. 2f, g). Distally, the adaxial vascular bundle divides into two smaller bundles that each supply one of the two seeds (Extended Data Fig. 3c–f). Near the base of the cupule these two vascular bundles are flattened with the xylem towards the outer surface of the cupule (Extended Data Fig. 3e, f). Distally, as the cupule stalk becomes strongly curved, the xylem forms an inverted V shape, with poorly preserved phloem laterally (Extended Data Fig. 3g, h). Close to the point of seed attachment, the xylem is circular in transverse section and consists of radially aligned tracheids (Fig. 2h). In most seeds, the position of the phloem is inferred by a complete or incomplete ring of empty space around the xylem, but a few seeds show delicate, radially aligned, flattened cells that are probably sieve elements (Fig. 2h). Close to the seed base each vascular bundle expands into a disc of transfusion tissue, to which is attached a thin, pad of parenchyma on which the seed is borne (Fig. 2d).

Each seed is erect, sessile and borne near the tip of the strongly curved distal portion of the cupule stalk (Fig. 2d, e). Seeds are tetrahedral with

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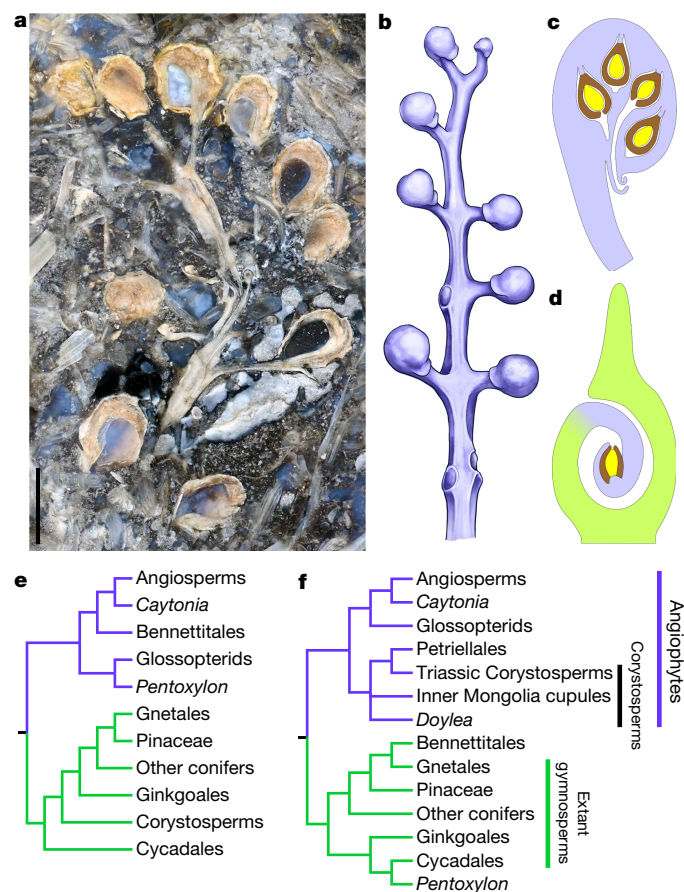
Fig. 1 | Recurved cupules of extinct seed plants; an angiosperm carpel; and the phylogenetic relationships of seed plants. a, Seed cone from the Early Cretaceous of Inner Mongolia, China. PB23663. Scale bar, 5 mm. **b**, Reconstruction of a *Caytonia* seed-bearing structure[5]. **c**, Reconstructed longitudinal section of *Caytonia* cupule[7] (blue), showing seeds, each with nucellus (yellow), single integument (brown) and micropylar canal. **d**, Longitudinal section of a syntropous angiosperm carpel[22], showing carpel (green), funiculus and second integument (blue), inner integument (brown) and nucellus (yellow). **e**, Partial cladogram of seed plants from a previous constrained parsimony analysis[10]. **f**, Partial cladogram of seed plants from a constrained parsimony analysis of a dataset (Supplementary Data 1) in which all recurved cupules are scored as homologous. The angiophyte clade is also recovered by constrained Bayesian and maximum likelihood analyses, although relationships among angiophytes differ (Supplementary Information).

a bifid micropyle (Extended Data Fig. 2h, i). The single integument is unvascularized and the nucellus is free from the integument except at the base (Extended Data Fig. 2i). In a few seeds, bisaccate pollen grains (*Alisporites* type) occur inside the integument at the tip of the nucellus (Extended Data Fig. 2l).

In the organization of the lateral seed-bearing units, the structure of individual cupules, the position of the three-angled seeds and the association with *Alisporites*-type pollen, the Inner Mongolia cupules closely resemble the previously described seed-bearing organ of *Doylea* from the Early Cretaceous of western Canada[11] and central Mongolia[12] (Extended Data Fig. 4). Anatomical details of *Doylea tetrahedrasperma*[11] also closely resemble those of the Inner Mongolia cupules, including the vascular supply to the bract and seeds, as well as the anatomical differentiation of the flaps and cupule stalk. However, in *Doylea* the cupule stalk bifurcates and each fork bears a cupule near the tip that contains a single seed and is formed by the cupule stalk and two unvascularized flaps[11].

The Inner Mongolia cupules are also fundamentally similar to the cupules of corystosperms from the Triassic of the Southern Hemisphere. In *Umkomasia resinosa* from Antarctica[14]—the only Triassic species for which anatomical details are known—the cupules are formed by the cupule stalk and two lateral flaps, enclose one or two seeds and are strongly curved back towards the base of the cupule stalk (Extended Data Figs. 5e, 7l–o). As in the Inner Mongolia cupules (Fig. 2d), the seeds are attached to a disc of transfusion tracheids, and there are two vascular bundles at the base of the cupule stalk with the xylem towards the outer surface of the cupule.

Silicified cupules of *Petriellaea* (Petriellales), from the Triassic of Antarctica, are formed by the cupule stalk and a recurved flap that encloses five or six tetrahedral seeds[16] (Fig. 3c, d, Extended Data Fig. 7a–f). Cupules are borne three-dimensionally (Fig. 3c), perhaps in a loose cone, but not clearly in pairs. In putatively synonymous compression fossils of *Kannaskoppia* (Petriellales)[13,17] (Extended Data Fig. 5b, d), the cupules are also formed by both the cupule stalk and three flaps.

The single vascular bundle at the base of the cupule stalk in *Petriellaea* divides into several bundles that each supply a seed[16]. The vascular bundle in the cupule stalk is described as collateral, with the xylem towards the inner side of the cupule—seemingly the reverse of the situation in *Doylea* and the cupules from Inner Mongolia—and this has been used to infer that the seeds are borne adaxially[16]. However, re-examination of the limited *Petriellaea* material shows that the arrangement of vascular tissue in the cupule stalk is not clear and in a few cases appears concentrically arranged (Extended Data Fig. 7g–j).

How the cupules of *Caytonia* compare to those from Inner Mongolia, as well as those of *Doylea*, *Kannaskoppia* and *Petriellaea* and those of *Umkomasia* and other corystosperms, is a critical issue. Cupules of *Caytonia* lack flaps and, like those of *Petriellaea*, are more completely closed at maturity than in *Doylea*, *Umkomasia* and the cupules from Inner Mongolia. However, similar cupules that are more completely closed also occur in compression fossils of *Ktalenia* from the Early Cretaceous of Argentina[18] (Extended Data Fig. 5g, h), and in *Geminispermum* from the Early Cretaceous of Virginia, USA[19] (Extended Data Fig. 8k), for which anatomy is known and in which the vascular supply to the cupule is very like that in *Doylea*, *Umkomasia* and the cupules from Inner Mongolia.

Caytonia cupules are borne suboppositely in two ranks and are recurved towards the inferred upper (adaxial) surface of a flattened axis-like structure[7,8] (Figs. 1b, 3e, f, Extended Data Fig. 6). As in *Umkomasia resinosa*, *Umkomasia uniramia* and many other corystosperms, as well as *Kannaskoppia* and *Doylea*, there is no bract subtending each cupule (Extended Data Fig. 8). At maturity each *Caytonia* cupule contains 8–30 flattened seeds and is completely closed except for a distinct, conspicuously papillate lip (Fig. 3f, g).

Caytonia, and similar forms such as *Reymanownaea* (Caytoniales)[20], are preserved only as compressions for which the anatomy is poorly known, but given that the cupules are recurved exactly as in those of better-understood Mesozoic plants, the most parsimonious explanation for the absence of bracts subtending individual cupules is that they are borne on proliferated seed-bearing structures rather than on a cone axis or highly modified leaf[2,10] (Extended Data Fig. 8f). Such proliferated seed-bearing structures with no bracts subtending individual seeds occur occasionally in extant *Ginkgo biloba* and also in *Doylea* and *Kannaskoppia*—as well as in many other corystosperms, including *U. resinosa* and *U. uniramia*[13–15]. As in the pollen organs of corystosperms, the structures bearing the cupules in these Mesozoic plants probably varied in being flattened or three-dimensionally branched[21].

We conclude that the new cupules from Inner Mongolia, as well as the cupules of *Caytonia*, *Doylea*, *Geminispermum*, *Ktalenia*, *Petriellaea*, *Reymanownaea*, *Umkomasia* and other corystosperms, are interpreted most straightforwardly as being fundamentally similar, and that they were produced by plants that shared a common organization of their ovulate reproductive structures. The evidence that there are two
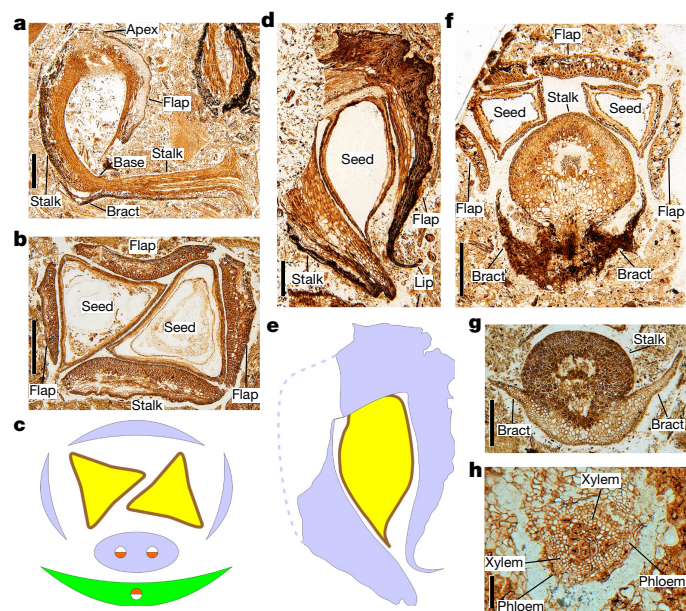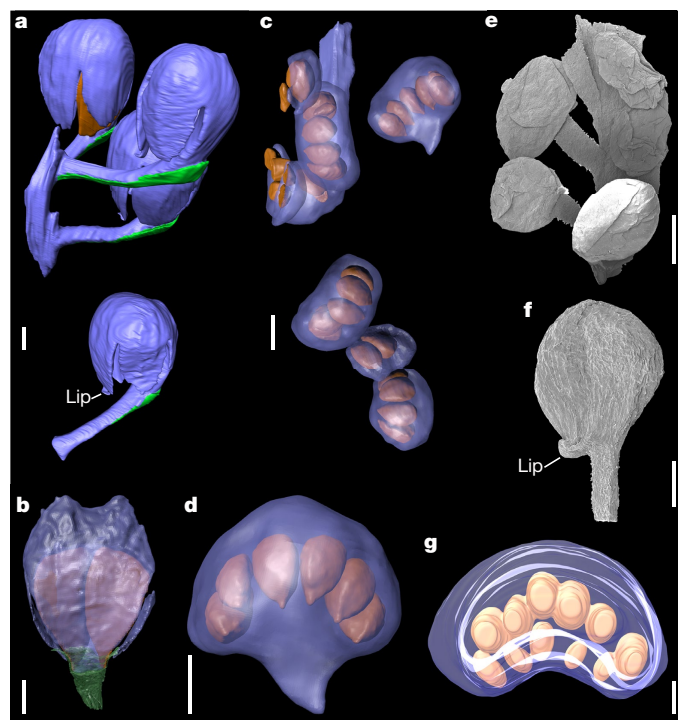
Fig. 2 | Fossil cupules from the Early Cretaceous of Inner Mongolia, China. **a**, Longitudinal section of a shed, empty seed-bearing unit. PB23664, showing terms used in description. **b**, Transverse section of a cupule. PB23665. **c**, Interpretive diagram of seed-bearing unit showing the bract (green), cupule stalk and flaps (blue), seeds with a single integument (brown), nucellus (yellow) and vasculature (xylem in orange; phloem in white). **d**, Longitudinal section of a cupule. PB23666. **e**, Line drawing of cupule in **d**. **f**, Transverse section of a seed-bearing unit near the base of the cupule. PB23667. **g**, Transverse section of the fused bract and cupule stalk. PB23668. **h**, Detail of vascular bundle of cupule stalk near the point of seed attachment, oriented as in **f**, with the lower side towards the outer side of the cupule. PB23671. Scale bars, 1 mm (**a**, **b**); 500 μm (**d**, **f**, **g**); 100 μm (**h**).

Fig. 3 | Three-dimensional reconstructions from segmented micro-computed tomography data, and scanning electron micrographs of cupules. a, **b**, Cupules from the Early Cretaceous of Inner Mongolia, China showing the bracts (green), stalked cupules (blue) and seeds (brown). **a**, Three cupules attached to a cone axis and one other cupule also in the same orientation. PB23672. **b**, Individual cupule tightly enclosing two three-angled seeds. PB23667. **c**, **d**, *Petriellaea triangulata* from the Triassic of Antarctica. 10025G. **c**, Cone fragment showing the orientation of the cupules and seeds relative to a fragmentary axis. **d**, Individual cupule. **e**, **f**, Small, possibly immature cupules of *Caytonia* sp. from the Jurassic of Yorkshire, UK. **e**, Cupules laterally attached to either side of a flattened axis. PP60604. **f**, Isolated, stalked cupule. PP60605. **g**, Cupule of *Caytonia* sp. from the Jurassic of Inner Mongolia, China. B0041. Scale bars, 1 mm (**a**–**e**, **g**); 500 μm (**f**).

different kinds of cupules among these plants is weak. As has previously been inferred for *Caytonia*[2–6], this group of plants with recurved cupules was probably also closely related to angiosperms. This is also consistent with results of phylogenetic analyses in which the cupules of corystosperms and *Caytonia* are scored as homologous, but the homology of the cupule with the outer integument of the angiosperm ovules is not assumed a priori (Fig. 1f, Extended Data Figs. 9, 10, Supplementary Information).

Variation among Mesozoic seed plants in the number of cupules per lateral unit, the number of seeds per cupule and the degree of seed enclosure (Extended Data Fig. 8) probably reflect differences relating to pollination, seed output and seed protection, as well as seed dispersal, for which there is evidence of zoochory in *Caytonia*[8]. The recurved cupule, which results in the micropyle of the seed being oriented back towards the base of the stalk on which it is borne, is likely to have been critical to allow the access of pollen grains to the micropyle via a pollination drop. Similarly, anatropy in angiosperms orients the micropyle towards the placenta through which the pollen tubes grow to reach the ovule[22].

Pervasive reduction of the second integument in orthotropous angiosperm ovules, analogy with the curved ovules of Podocarpaceae and overwhelming evidence from molecular developmental genetic studies indicate that curvature of the anatropous ovules of extant early diverging angiosperms is developmentally linked to the formation of the outer integument[1,22]. During ovule development, as a result of cell divisions towards the outside and near the base of the ovule, which are abaxial with respect to the nucellus, the outer integument grows asymmetrically, forming a hood or a cup. Especially important is the *YABBY* gene *INO*. In *ino* mutants there is no outer integument and the resulting ovule is erect[1].

Under the hypothesis that the cupule of *Caytonia* is homologous to the outer integument of angiosperms, but borne on a highly modified leaf, the origin of the carpel required expansion and folding of the flattened structure that bore lateral cupules[2,10]. Recognition that the cupules of the Inner Mongolia material and those of other Mesozoic plants, such as *Caytonia*, *Doylea*, *Geminispermum*, *Ktalenia*, *Petriellaea*, *Reymanownaea*, *Umkomasia* and other corystosperms, are all fundamentally the same no longer requires a singular focus on *Caytonia*. It also offers the more straightforward possibility that the carpel evolved by synorganization involving a recurved uniovulate cupule and a subtending bract or leaf, such as that seen in the Inner Mongolia cupules, *Doylea*, *Geminispermum*, *Ktalenia*, *Umkomasia* and other corystosperms[3]. Under this interpretation, the funiculus, which is highly conserved across angiosperms, is equivalent to the cupule stalk (Figs. 1c, d, 2e). Reduction of the proliferated cupule stalks seen in many corystosperms[13,15] and *Kannaskoppia* provides simple possibilities for the origin of a bitegmic ovule curved in the same direction as the curvature of the carpel (syntropous) (Fig. 1d), the probable plesiomorphic orientation in angiosperms[22].

The new fossil cupules from Inner Mongolia are similar to those of *Caytonia*, *Doylea*, *Geminispermum*, *Kannaskoppia*, *Ktalenia*, *Petriellaea*, *Reymanownaea*, *Umkomasia* and other corystosperms, and all are comparable in their organization to an anatropous angiosperm ovule. The fundamental similarities, and also the position of the best known of these groups relative to angiosperms in phylogenetic analyses that are

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neutral with respect to the homology of the cupule with the angiosperm second integument, allow recognition of a clade for which we use the previously proposed informal name angiophytes[23] (Fig. 1f, Extended Data Fig. 9). These extinct plants, and those that produced the cupules from Inner Mongolia, are stem angiophytes: extinct seed plants that are more closely related to angiosperms than to any other extant group and that possess one but not all of the synapomorphies of the angiosperm crown group[23]. The corystosperm fossil record suggests that the differentiation of angiophytes began in the Late Permian[24], considerably before fossil evidence of the angiosperm crown group. Other groups of extinct seed plants such as glossopterids are also probable Permian angiophytes[10] (Fig. 1f), but how angiophytes relate to other groups of seed plants—especially the Bennettitales–Erdtmanithecales–Gnetales group, and ginkgo-like plants—remains to be resolved (Supplementary Information).

The concept of angiophytes presented here partially resolves the long-standing question of angiosperm origins and suggests that the close fossil relatives of angiosperms exhibit considerable reproductive diversity and have been hiding in plain sight for almost a century. Further improvements in our knowledge of key fossil plants will be required to resolve relationships among angiophytes, identify the angiosperm sister group among stem angiophytes and understand the origin of two other diagnostic features of angiosperms that evidently came later, the carpel and the stamen.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-021-03598-w.

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Methods

Data reporting
No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Plant fossils from Inner Mongolia
The chert containing the silicified material described in this paper was discovered in 2017 at the Zhahanaoer open-cast coal mine (45° 21′ 38.5′′ N, 119° 25′ 04′′ E) (Extended Data Fig. 1a), Jarud Banner, eastern Inner Mongolia, China. Samples were collected during field expeditions in 2017, 2018 and 2019. The fossils occur in the Huolinhe Formation of the Huolinhe Basin. The Huolinhe Formation comprises a sequence of terrestrial and fluvio-lacustrine-swamp sediments that in addition to thick coal and lignite seams include conglomerates, sandstones, siltstones, and mudstones[25]. 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'[25]. Most of the exploitable coal and lignite seams are in the 'lower coal-bearing member', which is up to 720 m thick and has yielded rich assemblages of well-preserved plant fossil compressions[25].

Several massive and discontinuous layers of chert outcrop in a restricted area on the margin of the Zhahanaoer mine (Extended Data Fig. 1b, c). Boreholes and stratigraphic analyses show that these chert layers occur below a considerable thickness of coal towards the bottom of the 'lower coal-bearing member'. Associated with the cherts is a layer of ash that may be the source of the silica that impregnated the plant remains (Extended Data Fig. 1b). The fossil flora preserved in the chert includes lycopsids, ferns, pinaceous conifers and a variety of other plants that remain to be described. Especially distinctive and common in the chert are the cupules described here. Several hundred specimens have been examined for this study.

Uranium–lead (U–Pb) zircon dating shows that the ash layer below the cherts dates to 125.6 ± 1.0 million years ago[26] (Ma) (Extended Data Fig. 1b). The palynological assemblage associated with the chert, which contains rare *Clavatipollenites* but no tricolpate pollen, is also consistent with this U–Pb dating result[26]. We therefore regard the age of the flora of the Zhahanaoer chert as late Barremian–earliest Aptian. Permits for fieldwork were obtained from the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. All of the Zhahanaoer specimens, including the slabs, peels and microscopes slides illustrated in this study, are in the palaeobotanical collections (PB23663–PB23678) of the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences in Nanjing, China.

Caytonia material
Mesofossils of *Caytonia* were extracted from bulk samples collected from the type locality in the classic Gristhorpe Bed, which is exposed intertidally at Cayton Bay, Yorkshire, UK[27]. The Gristhorpe Bed occurs near the base of the Gristhorpe Member in the Cloughton Formation and is of Middle Jurassic (Lower Bajocian) age[27]. These specimens are deposited in the palaeobotanical collections (PP60604–PP60612) of the Field Museum, Chicago, IL, USA. We also examined new material of *Caytonia* from the late Middle–early Late Jurassic Daohugou Bed in eastern Inner Mongolia, northeastern China[28]. The new *Caytonia* cupules preserved as impressions (B0040, B0041) are deposited in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences in Beijing, China.

Petriellaea material
The type and illustrated material of *Petriellaea triangulata*, along with previously unprepared blocks, were examined in the collections of the Division of Paleobotany at the Natural History Museum and Biodiversity Institute, University of Kansas. The silicified peat containing *P. triangulata* was collected from the upper part of the Fremouw Formation at the Fremouw Peak in the Queen Alexandra Range, Antarctica[16]. The age of the silicified peat is considered to be late Middle or early Late Triassic[17].

Preparation of the fossil material
Peels of the silicified material were prepared using standard methods[29]. Blocks were slabbed with diamond-blade saws and the flat surfaces were polished on a ground glass plate with coarse, and then fine-grained, carborundum. Polished surfaces were etched with commercial-grade hydrofluoric acid. Peels were made using a cellulose acetate sheet and specimens for further examination were examined under a stereo microscope using reflected light on white background. Pieces of the peels containing key fossils were mounted on microscope slides with neutral balsam and measured and photographed using a Leica M205A stereomicroscope and Leica DMC5400 digital camera system with z-axis stacking and Leica Application Suite X software. Higher-magnification images were obtained using an Olympus BX53 microscope with an Olympus DP73 camera and Olympus cellSens software (standard 1.15).

The three-dimensional morphology of the Inner Mongolia cupules (PB23672, PB23667) and *Caytonia* (B0041) was examined using a General Electric dual-tube X-ray computed tomography scanner in the Department of Organismal Biology and Anatomy, University of Chicago. Scans were performed with 1,300–1,700 projections at a voltage of 67–70 kV and 80–250 μA. The settings for the scans varied according to the condition of specimens. *Petriellaea* (10025G) was scanned using a Nikon XTek XT H225 X-ray computed tomography scanner at Harvard University, with 3,142 projections at a voltage of 70 kv and 14 μA. Datasets were processed using Avizo software (v.2019.1; Lite v.2020.2; Lite v.9.2.0) to obtain successive virtual sections, translucent volumes and surface renderings.

Reporting summary
Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability
The data matrix for phylogenetic analyses is provided in Supplementary Data 1. Computed tomography data have been deposited in Dryad at https://doi.org/10.5061/dryad.5x69p8d2r.

Code availability
The MrBayes commands for Bayesian analysis are included in the NEXUS formatted file in Supplementary Data 2.

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