

THE BIGGEST SEED FROM THE MESOZOIC AND ITS EVOLUTIONARY IMPLICATIONS

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Abstract

Seed plants are the dominant and most important group in the Earth's terrestrial ecosystem. In extant angiosperms, seeds vary greatly in dimensions, ranging from 50 µm long to 50 cm long (Bellot 2020, Bellot, et al. 2020). In contrast, seed dimension variation is limited in gymnosperms: although Palaeozoic seeds might be much bigger, their Mesozoic peers are much less variable and smaller. Here we report a permineralized gigantic seed with an embryo preserved, *Dinospermum* gen. nov, from the Lower–Middle Jurassic of Xinjiang, China. As it is the currently largest seed in the Mesozoic, the large size of *Dinospermum* alone distinguishes it from all known Mesozoic fossil gymnosperms. This makes the affinity and ecology of *Dinospermum* mysterious. The huge size of *Dinospermum* suggests that its mother plant had adopted a survival strategy distinct from all known Mesozoic gymnosperms, probably representing a dead end of evolution in the history of plants. The extinction of *Dinospermum* is a failed K–selection experiment in the evolutionary history of seeds.

Keywords: seed, biggest, Jurassic, plant, evolution

1. Introduction

Seed plants have existed on the Earth over 360 Ma, and they constitute the major components of current terrestrial ecosystem and supply most of the food for land animals (including the humans). Therefore it is not an over-statement that the human beings cannot occur on the Earth without seed plants. Seeds vary in dimensions, especially greatly in angiosperms. The currently known largest seed is *Lodoicea maldivica* (Arecaceae, Angiosperms), which may be up to 50 cm long and very voluminous. Seed plants diversified rapidly soon after their origin in the Late Devonian. Gymnosperm seeds culminated in their size in the Late Palaeozoic. For example, a gigantic seed, *Pachytesta gigantea*, was documented from the Upper Carboniferous of France and USA, and one of the specimens was reported (not figured) to be up to 11 cm long (Brongniart 1881, Taylor, et al. 2009). However, gigantic seeds are hitherto missing in Mesozoic plants. Here

we document the largest Mesozoic seed, *Dinospermum* gen. nov., from the Lower–Middle Jurassic of Xinjiang, China. This discovery unveils an otherwise unknown aspect of seed evolution in the Mesozoic.

2. Materials and Methods

The specimen was collected from an outcrop of the Sangonghe Formation (the Lower–Middle Jurassic) in the Kelameili area (N44.9018°, E89.2226°) on the northeast edge of the Junggar Basin in Xinjiang, China in 1984 by HL. The Sangonghe Formation is 30–300 m thick in the region, conformably overlying the Badaowan Formation (the Lower Jurassic) and overlain unconformably by the Xishanyao Formation (the Middle Jurassic). The fossiliferous strata are greenish gray lamina of siltstones and mudstones, with red stripes, calcareous concretions as well as cross beddings. The fossils associated with *Dinospermum* include plants (*Equisetites* cf. *gracilis*, *Coniopteris* sp., *Phoenicopsis* sp., *Carpolithus* sp. 1), spores (*Cyathidites minor*, *Duplexisporites gyrates*, *Calamospora mesozoica*, *Concavisporites toralis*, *Cibotiumspora paradoxa*, *Apiculatisporis spiniger*, *Neoraistrickia gristhorpensis*, *Khukisporites pseudoreticulatus*, *Laevigatosporites ovatus*), pollen (*Psophosphaera tenuis*, *Chasmatosporites hians*, *Classopollis annulatus*, *Ginkgocycadophytus nitidus*, *Perinopollenites elatoides*, *Callialasporites dampieri*, *Cerebropollenites mesozoicus*, *Protohaploxypinus samoilovichii*, *Protopinus latebrosa*, *Quadraeculina anellaeformis*, *Alisporite australis*, *Pseudopicea variabiliformis*, *Abietinaepollenites* sp., *Pinuspollenites* sp., *Podocarpidites multesimus*), insects (*Chaoborites*), bivalves (*Ferganoconcha* sp., *Margaritifera delunshanensis*) (Cheng and Qi 1994, Lu 1995). Although the plant assemblage includes elements frequently seen in the Middle Jurassic (e.g., *Phoenicopsis* and *Coniopteris*), the presence of *Protohaploxypinus*, a relic element of the Permian and Triassic, suggests an Early Jurassic age for the formation, a conclusion favored by bivalves and conchostracans (Lu 1995, Cheng, et al. 2009). Thus a compromising conclusion is that the Sangonghe Formation, which yields *Dinospermum*, belongs to the Lower–Middle Jurassic (Cheng and Qi 1994, Lu 1995, Cheng, et al. 2009).

The specimen was preserved as a compression. The specimen was observed and photographed using a Nikon SMZ1500 stereomicroscope equipped with a digital camera. The specimen was scanned using a 225 kV micro–computerized tomography (developed by the Institute of High Energy Physics, Chinese Academy of Sciences), housed at the Key Laboratory of Vertebrate Evolution and Human Origin of Chinese Academy of Sciences. The data set has a resolution of 56.46 µm and the scan was carried out at 140 kV and 120 µA. One frame per projection was acquired by a timing of 1000 ms for a total of 1440 projections. To double check the truthfulness of micro–CT outcome, the specimen was physically cut transversely near the bottom. A thin section was made, and observed using a Nikon SMZ1500 stereomicroscope equipped with a digital camera and a Zeiss Lab A1 microscope equipped with an AxioCam ERc 5s digital camera. All images were recorded in TIFF or JPEG format, and organized for publication with a Photoshop 7.0.

3. Systematic Palaeobotany

Gymnosperms

Genus *Dinospermum* gen. nov.

Type species: *Dinospermum kelameiliensis* gen. et sp. nov.

Type specimen: PB23888.

Etymology: *Dino*– Latin word for “terrible” and dinosaur age of the seed, *–spermum* Latin word for seed.

Generic diagnosis: Seed three-dimensional, elongated conic in form, with longitudinal ridges, 11 cm long and 3.4–3.5 cm wide near the base, including seed coat, perisperm, and embryo. Embryo pentagonal in cross view, with a feeder in perisperm.

Species *Dinospermum kelameiliensis* gen. et sp. nov.
(Figure 1–4)

Etymology: *kelameili*, for Kelameili, Xinjiang, the fossil locality.

Holotype: PB23888.

Diagnosis: The same as that of the genus.

Description: The seed is three-dimensionally permineralized, elongated conic in form, constricted at both ends, 11 cm long and 3.4–3.5 cm wide near the base (Figs. 1A, 3A–B). The preservation allows us to identify three layers of different tissues in the seed (Figs. 1B–G, 2A–B, 3H–R). The outermost one is the seed coat (Figs. 1B–E, 2A–B, 3D–S). The seed coat is variable in thickness, ranging from 1 mm to 4 mm, partially lost, of dark color (Figs. 1B, E, 2A–B, 3E–S), with approximately 10 longitudinal ridges on the surface of the seed (Figs. 1A, E–F, 2A–B, 3A–B). Inside to the seed coat is a perisperm of light color (Figs. 1E, 2D). The innermost is the embryo, of dark color, pentagonal in cross view, with two lobes in cross view, with a feeder in the perisperm near the base, preserved with cellular details (Figs. 1B–F, 2C–E, 3E–F, H–R). The volume of the preserved part of the seed is 61.3 cm³, the seed content is 38.6 cm³, including the embryo 9.3 cm³ (Fig. 4).

Type locality: Kelameili, Xinjiang, China (N44.9018°, E89.2226°).

Stratigraphic horizon: The Sangonghe Formation (the Lower–Middle Jurassic).

Depository: The Nanjing Institute of Geology and Palaeontology, Nanjing, China.

4. Discussions

Cellular details within fossil seeds have been previously reported in some well-preserved conifer fossils (Taylor 1965, Stockey 1975). Therefore the cellular preservation in *Dinospermum* (Figs. 2C–E) is not a surprise for palaeobotanists, instead it is a proxy of good preservation of *Dinospermum*. The huge size of *Dinospermum* distinguishes itself from all known Mesozoic fossil seeds as well as all known extant gymnosperm seeds (Table 1). Hitherto Mesozoic seeds reported are rather smaller than or similar to their living peers. This fact implies that, despite various survival pressures driving the evolution, extant gymnosperms and their ancestors seem to have been living similar environments and adopting basically similar strategies in their evolution.

However, *Dinospermum* appears to be an exception for this generalization: the large size of *Dinospermum* suggests a previously ignored or rarely adopted strategy in gymnosperm evolution. Apparently, not all Mesozoic gymnosperms converged to similar sizes, instead they radiated and adopt various strategies to explore various potentials to survive during the Mesozoic, although not all of such trials (for example, *Dinospermum*) led to success.

Seeds in gymnosperms do not have endosperm, which is a product of second fertilization in double fertilization (a feature frequently taken as characteristic of angiosperms) (Linkies, et al. 2010, Li, et al. 2022). The nutrition (perisperm) allocated to future seedling in gymnosperm seeds is derived from the nucellus and integument. Embryos in these seeds usually have a special structure termed “feeder” to absorb nutrition from the peripheral perisperm. The embryo with a feeder seen in Figs. 1B–D, F, 3J–O and 4C is surrounded by perisperm in *Dinospermum*. According to the data generated by Micro-CT, the E : S ratio (embryo to seed ratio) is 0.15 in *Dinospermum*. According to Linkes et al. (Linkies, et al. 2010), there is a general trend of increasing E : S ratio in seed plant evolution. The low E : S ratio of *Dinospermum* seems to suggest that *Dinospermum* prepares abundant nutrition for its embryo.

The occurrence of an embryo with a feeder in *Dinospermum* suggests that *Dinospermum* is a gymnosperm seed. Although most seeds are round in shape, having smooth surface, and without longitudinal ridges, there are abundant examples of seeds with longitudinal ridges, for example, fossil seeds of *Trigonocarpus* (fig. 13.103, p573), *Pachytesta illinoensis* (fig. 14.111, p577), *Hexapterospermum delevoryii* (fig. 14.122, p581), *Petriellaea triangulata* (fig. 15.50, p637), *Vardekloeftia sulcata* (fig. 17.87–88, p737) in Taylor et al. (Taylor, et al. 2009), and extant angiosperm seeds of *Rumex crispus* (fig. 52), *Chrysanthemum leucanthemum* (fig. 294), *Lactuca scariola* (fig. 404), *Zostera marina* (fig. 542), *Ostrya virginiana* (fig. 688), *Verbena* (figs. 234–236) (Martin and Barkley 2000). The occurrence of longitudinal ridges on these seeds justifies our interpreting *Dinospermum* as a seed. In addition, petrified wood is usually cylindrical in form, invariably radial in anatomy, uniform in dimensions within limited range. These expectations for fossil wood are not honored by the profile (constrictions at both ends as shown in Figs. 1A–C, 3A–D) and internal anatomical details (Figs. 1B–G, 2B–D, 3E–S, 4B–C) of *Dinospermum*. Therefore we exclude fossil wood from our discussion.

One general rule for sexual reproduction is ODC (offspring development conditioning), in which parents tend to enhance physical protection and provide abundant nutrition for the development of their offsprings (Fu, et al. 2021). In general, a seed and its developmental precursor (ovule) are provided with increased protection through evolution, in contrast to their peer spore plants. This accounts for the great increase of seed dimensions in the late Palaeozoic (Brongniart 1881, Taylor 1965). Palynological analysis of the Sangonghe Formation indicates that the local vegetation was mainly composed of conifers (Wang 2000). The innate nutrition gave *Dinospermum* some initial developmental advantage against its conifer peers: at least, it provided more nutrition supply so that its seedling could develop well during the initial development. The volume of *Dinospermum* is up to 61.3 cm³, implying that its mother tree must have invested an enormous (several orders of magnitude greater) amount nutrition in its seed to guarantee a nutrition

supply enough for its future seedling. This becomes an advantage for *Dinospermum* in its survival struggle, especially in a niche where competition is intensive or nutrition supply is limited. Its big embryo (up to 9.3 cm³) is much bigger than those in most angiosperm seeds, and is also conducive to its seedling's survival. The occurrence of such features in *Dinospermum* seems to suggest that *Dinospermum* adopts a strategy similar to that adopted by gymnosperms in Late Palaeozoic and extant world (Brongniart 1881, Taylor 1965, Leslie and Boyce 2012).

Despite the above mentioned advantages, the large seed of *Dinospermum* apparently did not bring enough benefits against its Mesozoic peers, and did not prevent itself from extinction. Apparently, *Dinospermum* has no comparable living relatives in the current world, implying that *Dinospermum* and its relatives have gone extinct. The huge size of *Dinospermum* means that its mother plant have to allocate its limited resources and nutrition to a few offspring (seeds) at the expense of offspring population. Studies of living plants (including both gymnosperms and angiosperms) indicated that “smaller seeds were proportionally more expensive for gymnosperms to produce. In particular, costs of abortions and packaging structures were significantly higher in gymnosperms..... the carpel was a key evolutionary innovation reducing accessory costs in angiosperms by allowing sporophytic control of pre- and post-zygotic mate selection and timing of resource allocation” (Lord and Westoby 2012), and that “extensive megagametophyte growth prior to fertilization” in gymnosperms contrasted strongly against “ovules are generally less developed than other groups of seed plants prior to fertilization” in angiosperms (Leslie and Boyce 2012). Apparently, *Dinospermum* demonstrates an evolutionary trend opposite to that of these successful angiosperms, in terms of nutrition allocation. Although the thicker seed coat with longitudinal ridges suggests that *Dinospermum* provided stronger protection for the embryo inside, the large size made it difficult to be efficiently dispersed far away from its mother plant, and challenged its animal disperser. Adopting such an outdated strategy made its extinction rather expected, just as its Palaeozoic gigantic peers.

There are two opposite selection strategies, *R*-selection and *K*-selection, in plant evolution. Against *R*-selection, *K*-selection species tend to produce lower number of larger offspring with longer life spans, which are the result of longer gestation, longer parental care, and slower maturation. A familiar example of *R*-selection is mice, while that of *K*-selection is elephants. *Dinospermum* reported here apparently adopts *K*-selection in its survival struggle. Its extinction in the Jurassic indicates that *Dinospermum* represents a failed example of *K*-selection experiment in the evolutionary history of seed plants.

Seed size, plant body size, genome size as well as polyploidy are interrelated in living plants (Linkies, et al. 2010). The huge size of *Dinospermum* suggests that its mother plant may be a rather big plant, and its genome may be huge. This inference sounds plausible as living gymnosperms have much bigger genomes, compared to their angiosperm peers (Nystedt, et al. 2013, Liu, et al. 2021). The largest seed in angiosperms, that of *Lodoicea maldivica*, is found related to large plants, shady habitat, and large seed-dispersing animals (Bellot, et al. 2020). Whether *Dinospermum* lived in a scenario similar to that of *Lodoicea*, and whether *Lodoicea* is facing a fate similar to that of *Dinospermum*, are questions to answer.

5. Conclusions

Dinospermum represents the currently biggest Mesozoic gymnosperm seed. Its mother plant was likely to be huge in size and woody. Although its systematic position requires further effort to determine, its extinction in the Jurassic suggests that it had adopted a failing strategy, K-selection, in the evolution of gymnosperm seeds.

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Author contributions HL and XW designed the project, HL collected the specimen, YH, PY carried out the Micro-CT observation, XZ, XW analyzed the data, XW drafted the manuscript, and all authors finalized and approved the manuscript.

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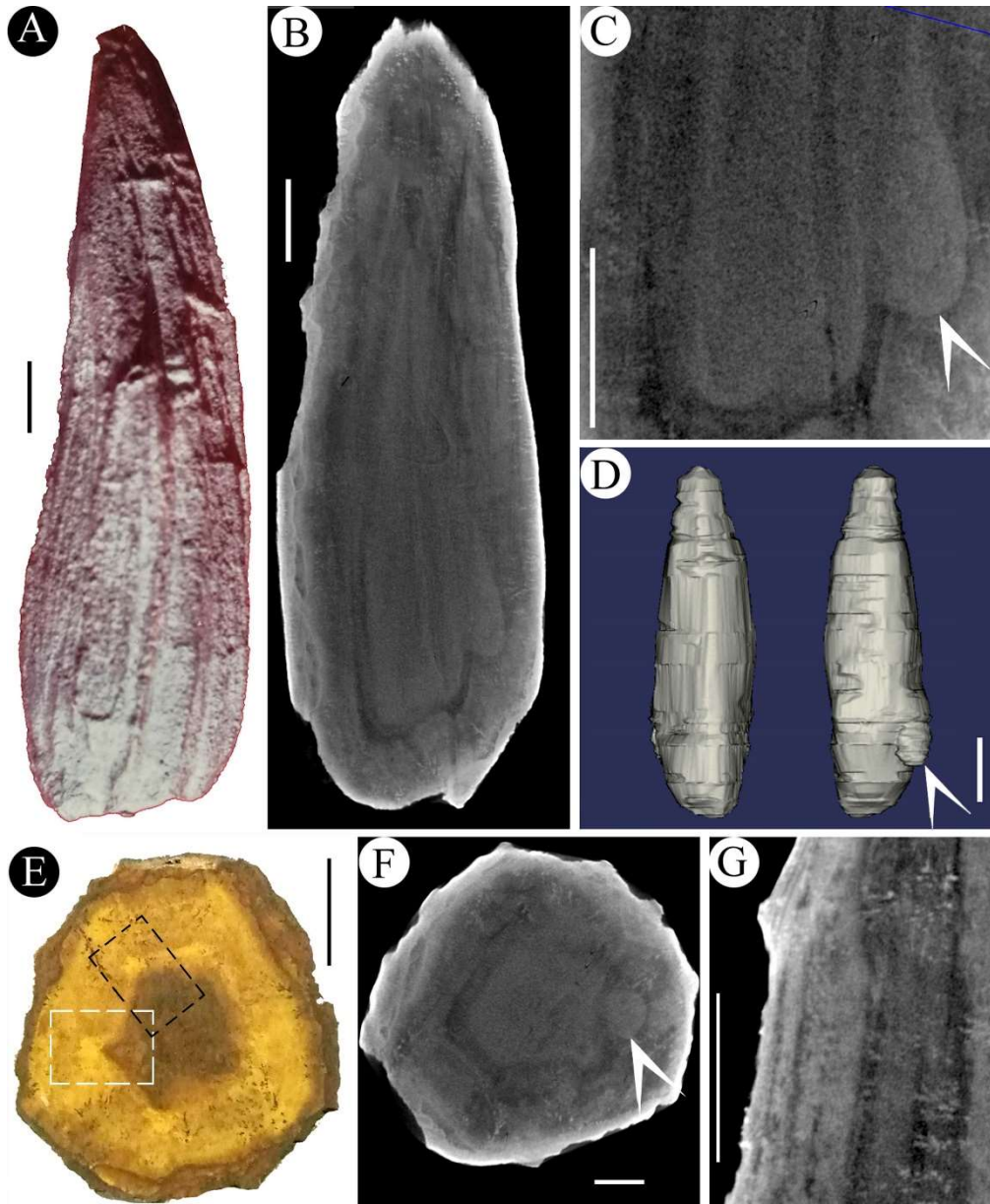


Fig. 1 *Dinospermum* gen. nov and its anatomical details.

A. Side view of the seed, showing longitudinal ridges. Scale bar = 1 cm.

B. Micro-CT virtual longitudinal section of the seed, showing profile of the seed and seed coat surrounding its content. Scale bar = 1 cm.

C. Detailed view of lower portion of the seed, showing embryo with a feeder (arrow). Scale bar = 1 cm.

D. Two longitudinal lateral views of the embryo with a feeder (arrow). Scale bar = 1 cm.

E. Cross section view of the seed, showing seed coat (peripheral dark color), perisperm (light color) with pentagonal embryo (dark color in center). Stereomicrography. Scale bar = 1 cm.

F. Micro-CT virtual section of the seed showing the embryo with a feeder (arrow) in perisperm. Scale bar = 5 mm.

G. Micro-CT virtual longitudinal section showing layered seed coat (left) and perisperm (right).
Scale bar = 1 cm.

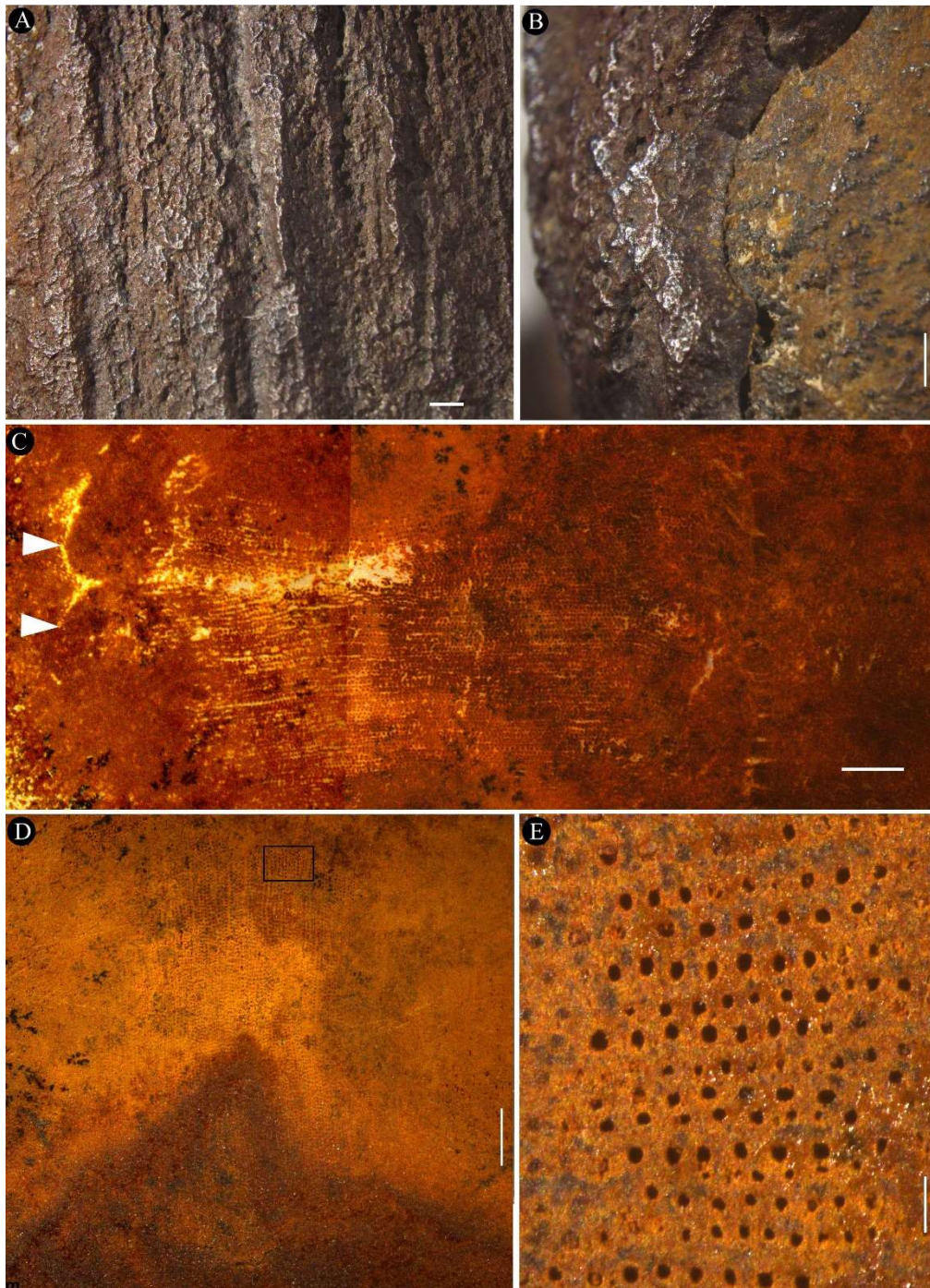


Fig. 2 *Dinospermum* and its further anatomical details.

A. Longitudinal ridges on seed surface. Scale bar = 1 mm.

B. Detailed view of the seed coat (left) and perisperm (right). Stereomicrography. Scale bar = 1 mm.

C. Two embryo lobes (triangles), enlarged from the position corresponding to the black rectangle in Fig. 1E. Transmission light microscopy. Scale bar = 1 mm.

D. Detailed view of the white rectangle in Fig. 1E, showing embryo and cellular details restricted to the middle region. Scale bar = 1 mm.

E. Detailed view of the rectangular area in Fig. 2D, showing cellular details. Scale bar = 0.1 mm.

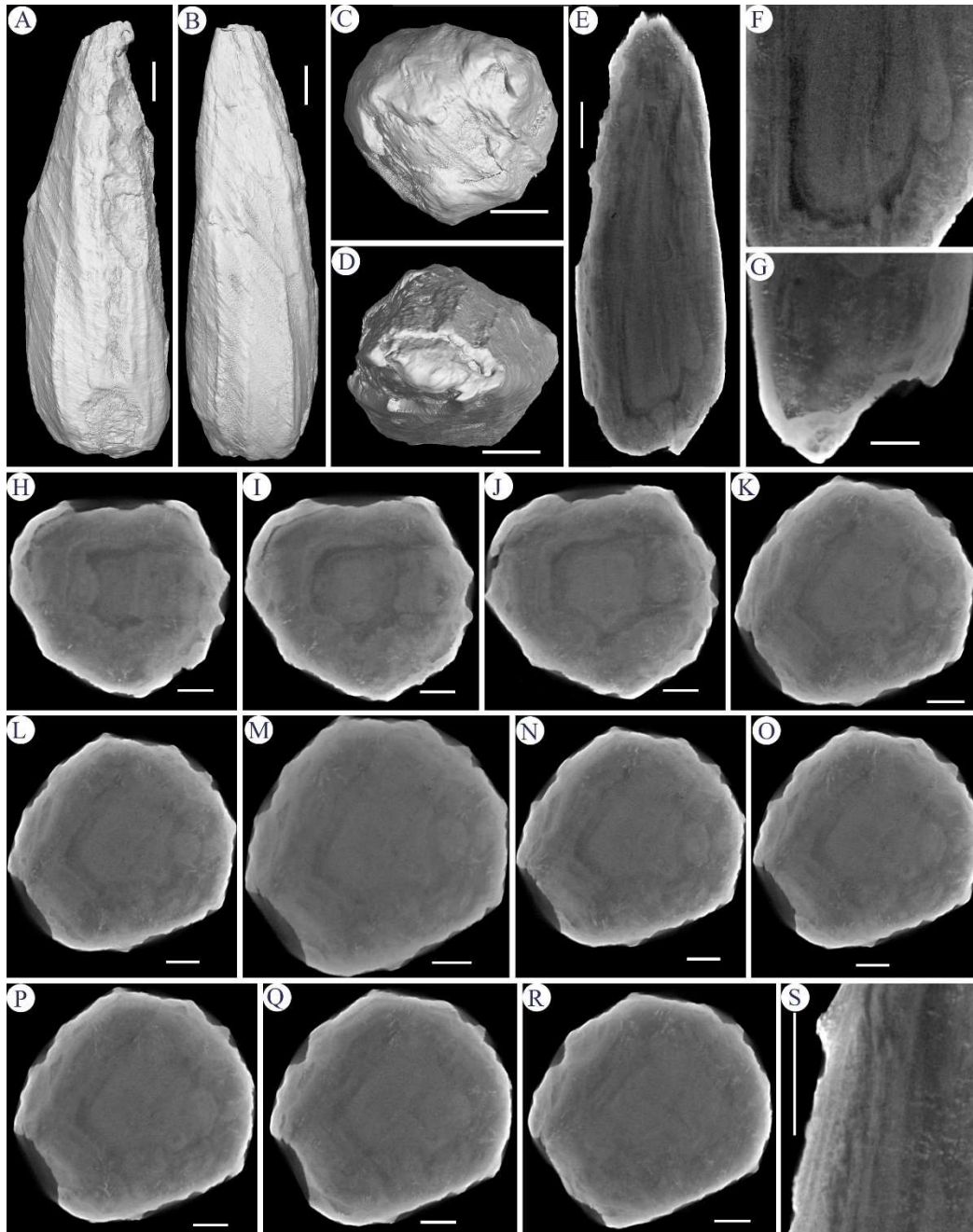


Fig. 3 Micro-CT sections of *Dinospermum*.

A–B. Two side views of the seed. Scale bar = 1 cm.

C. Bottom view of the seed. Scale bar = 1 cm.

D. Top view of the seed. Scale bar = 1 cm.

E. Longitudinal section of the seed, showing profile of the seed and seed coat enclosing its content. Scale bar = 1 cm.

F. Detailed longitudinal view showing embryo within the seed coat. Scale bar = 1 cm.

G. Detailed view of umbo. Scale bar = 5 mm.

H–R. Serial sections of the seed showing the embryo with varying outlines within the perisperm. Scale bar = 5 mm.

S. Detailed longitudinal section showing layered seed coat (left) and perisperm (right). Scale bar = 1 cm.

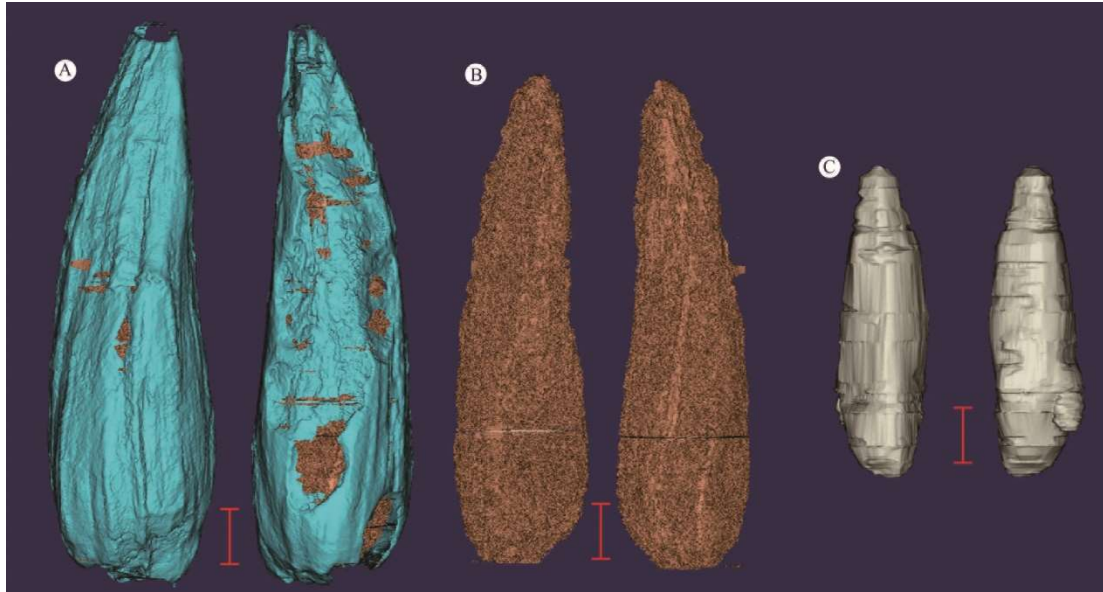


Fig. 4 Three dimensional renderings of the whole seed (a), seed content (b), and embryo (c) of *Dinospermum*. Scale bar = 1 cm.

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