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## An edible fruit from the Jurassic of China

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### ABSTRACT

Frugivory is an important ecological tie between animals and angiosperms. It plays an important role in the evolution of food webs and energy flow networks in the ecosystem. However, little is known about how old this relationship can be due to lack of relevant fossil evidence. Here, the authors report a fossil fruit, *Jurafructus* gen. nov., a putative angiosperm from the Middle–Late Jurassic (>164 Ma) of Daohugou Village, Inner Mongolia, China, which provides the currently earliest evidence of frugivory. The fossil is a more or less three-dimensionally preserved coalified drupe that has been damaged by animals in two different ways. The pericarp, in addition to the seed coat surrounding parenchyma seed contents, is suggestive of an angiospermous affinity, as such a 3+3 structure is distinct from a three-layered seed coat in gymnosperms. The seed possesses a distal micropyle, attached on the base of the pericarp, suggestive of a former orthotropous ovule in the gynoeceum. The damaged pericarp of *Jurafructus* suggests that frugivory can be dated back to the Middle–Late Jurassic. Apparently, the ecological relationship between angiosperms and animals extends deep into the fossil record.

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## 1. Introduction

Frugivory plays an important role in forming food webs and energy flow network in the earth ecosystem, promoting diversification and evolution of related taxa in the present ecosystem (Elzinga JA and Bernasconi G, 2009; Chang SY et al., 2012; Onstein RE et al., 2017; Valido A and Olesen JM, 2019). But how early this important ecological coupling was established is an open question as relevant, especially earlier, fossil evidence has been lacking. Although angiosperms have been proposed to have an earlier origin (Hochuli PA and Feist-Burkhardt S, 2004, 2013; Wang X et al., 2007; Wang X, 2010; Prasad et al., 2011; Wang X, 2018; Wu Y et al., 2018; Fu Q et al., 2018) and many animal damage types have been documented and categorized in fossils (Labandeira CC et al., 2007), little information on early fruits and frugivory is

available. This lack of fossil evidence makes the origin and evolutionary history of frugivory mysterious. Here, the authors report a fossil drupe, *Jurafructus* gen et sp. nov., from the Jiulongshan Formation (the Middle–Late Jurassic) near Daohugou Village, Inner Mongolia, China, as the currently earliest evidence of frugivory. This three-dimensionally preserved coalified fossil fruit with 3+3 organization, which is rarely seen in gymnospermous seeds (except some seed ferns and gnetaleans), allows the authors to recognize it as a drupe with a pericarp damaged by animals. As a fruit typical of angiosperms, *Jurafructus* implies that the mother plant of *Jurafructus* is most likely an angiosperm. Two types of damage on a single drupe indicate that frugivory has a history dated back to the Jurassic. This discovery sheds new light on the evolution of early angiosperms and their relationship with coeval animals.

## 2. Material and methods

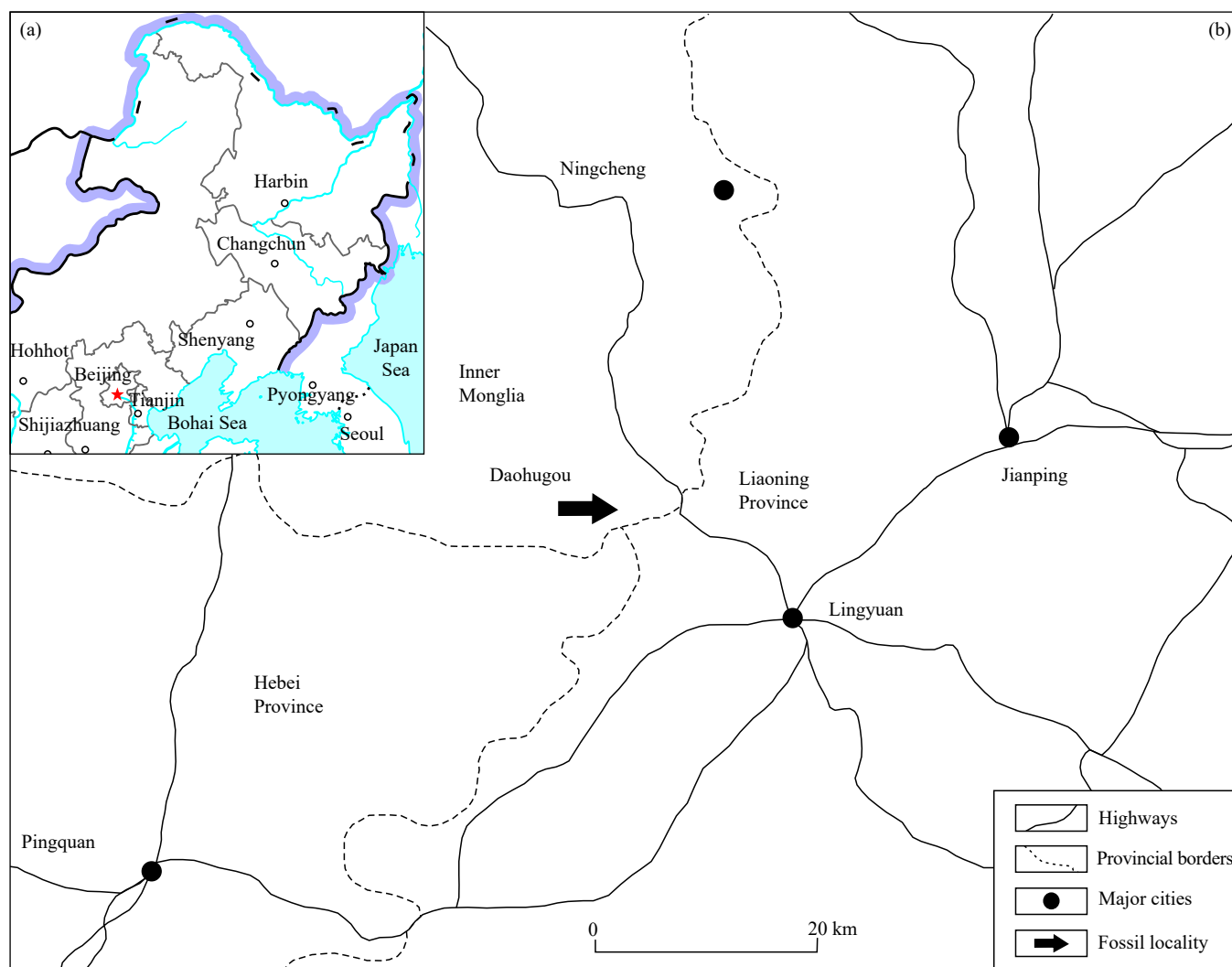
The fossil specimen was collected from Daohugou Village

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(119.24°E, 41.32°N) located at the junction among Inner Mongolia, Liaoning Province, and Hebei Province of China (Fig. 1). The fossiliferous strata belong to the Jiulongshan Formation that has been intensively dated by biostratigraphy and radiometric dating (Ren D et al., 2002, 2009, 2010; Zhang J, 2002; Zhang J et al., 2011; Shen YB et al., 2003; Zheng SL et al., 2003; Zhou Z and Zheng S, 2003; Zhou Z et al., 2007; Chen W et al., 2004; Li N et al., 2004; Liu YQ et al., 2004; Ji Q et al., 2005; Gao KQ and Ren D, 2006; Huang DY et al., 2006, 2009; Huang DY and Nel A, 2007, 2008; Petrulевичius J et al., 2007; Lin QB and Huang DY, 2008; Liu Y and Ren D, 2008; Selden PA et al., 2008; Chang SC et al., 2009, 2014; Liang J et al., 2009; Shih C et al., 2009; Wang B et al., 2009a, 2009b; Wang B and Zhang HC, 2009a, 2009b, 2011; Wang Y and Ren D, 2009; Zhang K et al., 2009; Zheng S and Wang X, 2010; Pott C et al., 2012; Na Y et al., 2014; Wang M et al., 2014). Currently, there is a general consensus that the fossiliferous strata are at least 164 Ma old, of the Middle–Late Jurassic boundary interval.

According to the studies by many researchers (Li N et al.,

2004; Zhou Z et al., 2007; Zheng S and Wang X, 2010; Wang X et al., 2010a, 2010b; Pott C et al., 2012; Heinrichs J et al., 2014; Dong C et al., 2016; Han G et al., 2016; Liu ZJ and Wang X, 2016), the Daohugou flora is very diversified. Various taxa including Algae 1 genus/species (Chlorophyceae), Bryophytes 4 genera, 6 species (*Daohugouthallus*, *Metzgerites*, *Muscites*, *Ningchengia*), Lycopodaceae 2 genera, 2 species (*Lycopodites*, *Selaginellites*), Sphenophytes 2 genera, 2 species (*Annularia*, *Equisetites*), Filicales 4 genera, 6 species (*Coniopteris*, *Osmunda*, *Eboracia*, *Sphenopteris*), Cycads 7 genera, 12 species (*Pterophyllum*, *Anomozamites*, *Nissoniopteris*, *Williamsonia*, *Weltrichia*, *Cycadolepis*, *Tyrmia*), Czekanowskiales 4 genera, 4 species (*Czekanowskia*, *Solenites*, *Leptostrobus*, *Ixostrobus*), Ginkgoales 4 genera, 6 species (*Yimaia*, *Ginkgoites*, *Baiera*, *Sphenobaiera*), Coniferales 13 genera, 20 species (*Pityocladus*, *Pityospermum*, *Schizolepis*, *Austrohamia* (*Yanliaoa*), *Brachyphyllum*, *Elatocladus*, *Amentotaxus*, *Taxus*, *Nageiopsis*, *Podocarpites*, *Cephalotaxopsis*, *Pseudofrenelopsis*, *Podozamites*), Caytoniales 2 genera, 2 species (*Caytonia*,



**Fig. 1.** Geographical information of the fossil locality of *Jurafructus* gen. nov., Daohugou Village, Inner Mongolia, China (b). The inset map shows northeastern China (a). The main map shows the junction region among Liaoning Province, Hebei Province and Inner Mongolia. The arrow points to the fossil locality of Daohugou Village.

*Sagenopteris*), Seeds/fruits with unknown affinities 3 genera, 3 species (*Conites*, *Problematospermum*, *Carpolithus*), Angiosperms 3 genera, 3 species (*Solaranthus*, *Juraherba*, *Yuhania*) have been documented in the flora. Now a new taxon, *Jurafructus* gen. nov., is appended to the list.

The fossil is a coalified compression embedded in tuffaceous siltstone, more or less in three dimensions. The specimen was observed and photographed using a Nikon SMZ1500 stereomicroscope equipped with a Digital Sight DS-Fi1 camera. One of the two facing parts (Fig. 2) was coated with gold and observed using a Leo 1530 VP scanning electron microscope (SEM) at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). X-ray micro-computerized tomography was performed on the same part (Fig. 4) using a 225 kV micro-computerized tomography developed by the Institute of High Energy Physics, Chinese Academy of Sciences (CAS) at the Key Laboratory of Vertebrate Evolution and Human Origins, CAS. The specimen was scanned with a beam energy of 100 kV and a flux of 120  $\mu$ A at a resolution of 7  $\mu$ m per pixel using a 360° rotation with a step size of 0.5°. A total of 720 projections were reconstructed in a 2048 $\times$ 2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics, CAS 43. All photographs were saved in TIFF format and organized together for publication using Photoshop 7.0.

### 3. Results

*Jurafructus* gen. nov.

Generic diagnosis: Fruit with a very short stalk, fleshy,

ellipsoid, about 11 mm long and 8 mm in diameter. An orthotropous seed surrounded by pericarp, attached to the bottom of the urceolate pericarp, about 7 mm long and 7 mm in diameter. Seed contents of parenchyma surrounded by a 3+3 structure (three-layered seed coat plus three-layered pericarp). Pericarp thickest near the top, with distal appendages.

Type species: *Jurafructus daohugouensis* gen. et sp. nov.

Etymology: *Jura-*, for Jurassic, the age of the fossil; *-fructus*, for fruit in Latin.

Type locality: Daohugou Village, Ningcheng, Inner Mongolia, China (119.24° E, 41.32°N).

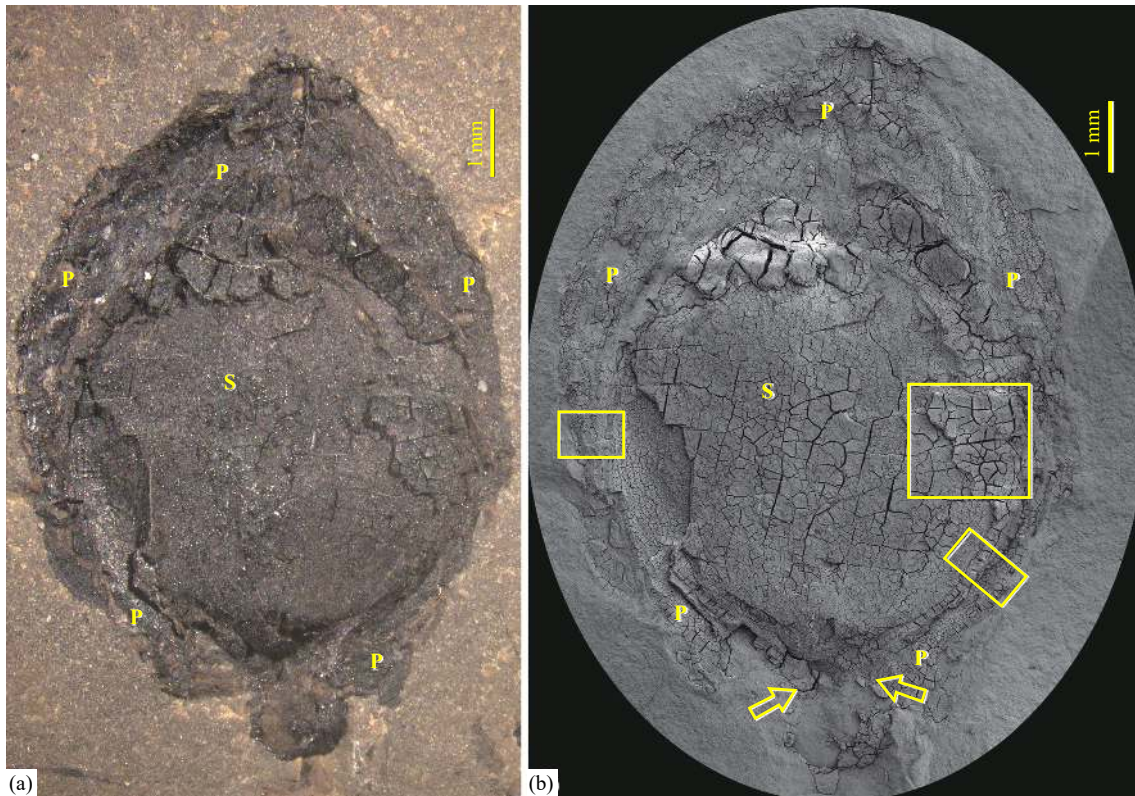
Horizon: Jiulongshan Formation, Middle–Upper Jurassic (>164 Ma).

*Jurafructus daohugouensis* sp. nov.

(Figs. 2–5)

Specific diagnosis: as of the genus.

Description: The fossil is preserved as a coalified compression embedded in grey tuffaceous siltstone (Figs. 2, 4a). The fossil is ellipsoid, more or less three-dimensionally preserved, about 11 mm long and 8 mm in diameter, with distal appendages (Figs. 2, 4a, 4g–h). The pericarp is thickest near the top, up to 2.5 mm thick, while it is thinnest near the bottom, only about 1 mm thick (Figs. 2, 4a), including three layers of tissues, namely, P1, P2, and P3 (Figs. 3d, 3f). P2 is conspicuous due to its single layer of sclerenchymatous cells, 50  $\mu$ m thick near the bottom and upper to 500  $\mu$ m thick near the tip, frequently interrupted. The sclerenchyma comprises a single layer of neatly, tightly packed cells oriented

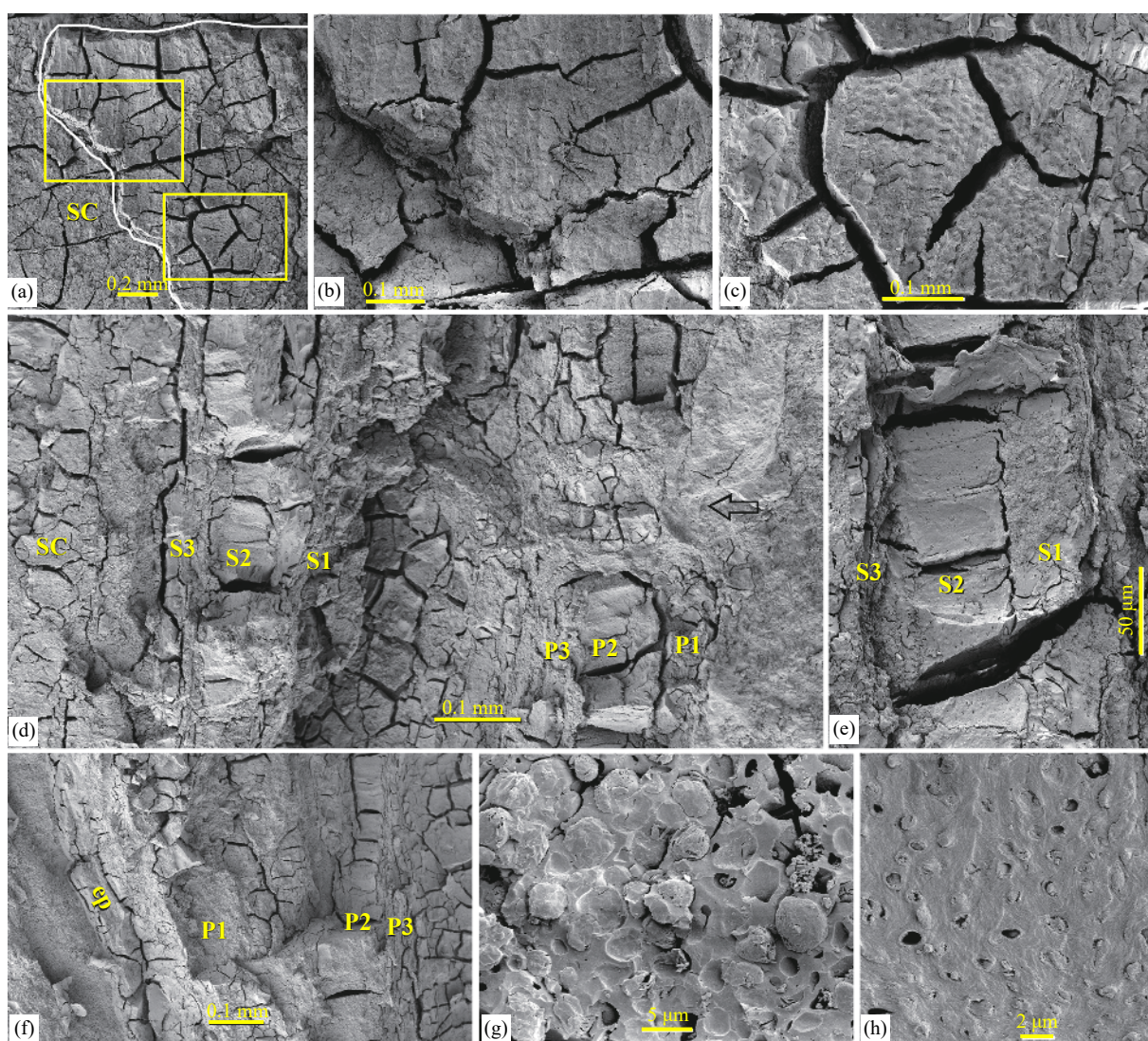


**Fig. 2.** General view of *Jurafructus*. a—coalified more or less three-dimensionally preserved fruit; b—the same as in Fig. 2a, but using SEM. Note the attachment (between arrows) of seed (S) on the bottom of the urceolate pericarp (P). The rectangular regions are shown in detail in Fig. 3.

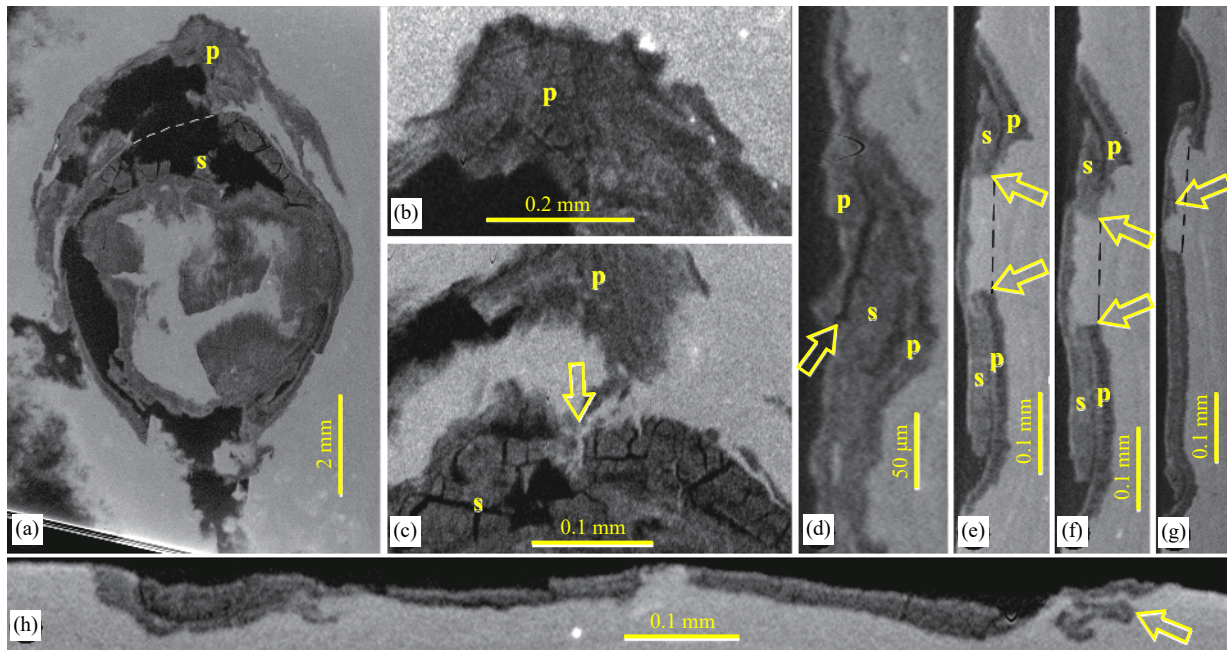
perpendicularly to the surface of the fruit. P2 is sandwiched between P1 and P3. Outside P2, P1 includes the epidermis and several cell layers, 0.35 mm thick near the bottom and 1.8 mm thick near the top, with some depression on its surface (Figs. 3d, 3f). Inside P2 layer, there are a couple of cell layers of P3, which is 25  $\mu\text{m}$  thick near the bottom but up to 2 mm near the fruit tip (Figs. 3d, 3f). The seed is fully enclosed by the pericarp, with its tip capped by the pericarp (Figs. 2, 4a–d). The seed is attached to the bottom of the pericarp, orthotropous with a micropyle oriented to the fruit tip (Figs. 2, 4a, 4c). Inside the P3 layer is the three-layered seed coat, which has variable surface texture (Figs. 3a–c). Some superficial cells are elongated and longitudinally oriented (Figs. 3a–b). Seed coat texture either reflects the profiles of longitudinally oriented cell or is rugose (Figs. 3a, 3c). The

seed coat includes three layers, namely, S1, S2, and S3 (Figs. 3d–e). Among them, the S2 layer is conspicuous due to its continuous single layer of sclerenchymatous cells neatly oriented perpendicularly to the seed surface, equivalent to the sclerotesta, 65–160  $\mu\text{m}$  thick, thinnest near the bottom, and with pit-like sculptures on their walls (Figs. 3d–e, 3h). S1, corresponding to the sarcotesta, includes layers of cells outside S2, is about 54–112  $\mu\text{m}$  thick (Figs. 3d–e). Inside the S2 layer is a 24–84  $\mu\text{m}$  thick layer of cells longitudinally oriented, namely, S3 (Figs. 3d–e). Inside the S3 layer is the seed contents, which comprises storage material preserved as spongy-appearing parenchyma (Fig. 3g).

The fruit surface is not fully even and sometimes irregular (Figs. 2, 3d, 4a, 4e–g). Some patches of the pericarp are missing (Figs. 4a, 4e–g). There is a depression on the surface



**Fig. 3.** SEM views of *Jurafructus*. a–detailed view of the upper-right rectangle in Fig. 2b, showing the surface view of the seed coat (white line) and seed contents (SC) inside; b–detailed surface view of the seed coat, showing longitudinally oriented elongated cells, enlarged from the upper rectangle in Fig. 3a; c–detailed view of the seed coat, showing rugose surface texture, enlarged from the lower rectangle in Fig. 3a; d–detailed view of the lower-right rectangle in Fig. 2b, showing the seed contents (SC) and surrounding 3+3 organization (three-layered seed coat (S3, S2, S1) PLUS three-layered pericarp (P3, P2, P1)). Note that the P2 is not continuous but interrupted at the position corresponding to the depression on fruit surface (arrow); e–detailed view of seed coat with three layers (S1, S2, S3); f–detailed view of the left rectangle in Fig. 2b, showing the epidermis (ep), three-layered pericarp (P1, P2, P3); g–spongy subcellular details of the parenchymatous cells in the seed contents; h–texture on the sclerenchymatous cells in S2 layer of seed coat.



**Fig. 4.** Micro-CT renderings of *Jurafructus*. a—longitudinal planar view of the fruit, showing the seed (s) separated from the enclosing pericarp (p) at its top. Note the missing patchy portion of pericarp and/or seed coat; b—detailed view of the pericarp at the fruit tip; c—longitudinal view of the fruit tip, showing the pericarp (p) and micropyle (arrow) at the seed top; d—longitudinal section of the fruit tip, showing seed tip (s) sandwiched by the pericarp (p). Note the separation (arrow) between the pericarp and seed; e–f—two longitudinal views of the fruit showing the damaged surface (broken lines between arrows) in seed (s) and pericarp (p); g—longitudinal view of the fruit showing tissue residue (arrow) after damaging and the original surface (broken line); h—longitudinal view of the fruit, showing the distal appendages (arrow). Bottom of the fruit is to the left of the figure.

of the pericarp (Fig. 3d).

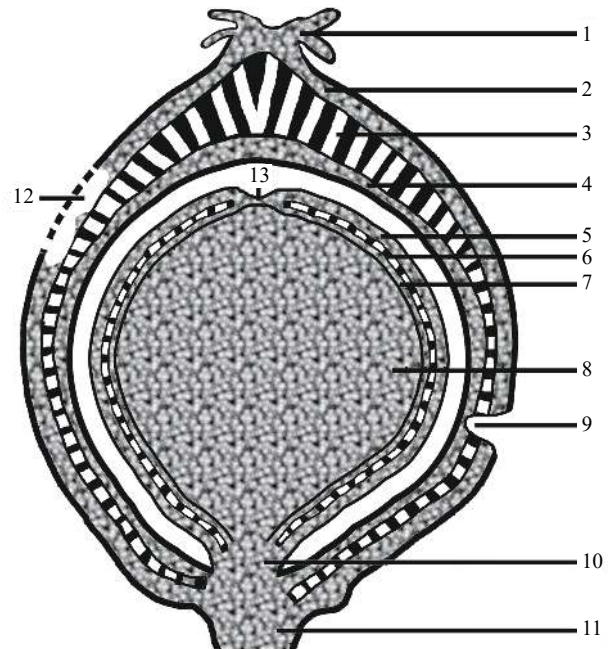
Etymology: *daohugouensis*, for the name of the fossil locality.

Holotype: DHG0258.

Depository: The Shenzhen Key Laboratory for Orchid Conservation and Utilization, National Orchid Conservation Center of China and Orchid Conservation & Research Center of Shenzhen, Shenzhen City, Guangdong Province, China.

#### 4. Discussions

Literally, angiosperms are defined by their enclosed seeds, although, more strictly, angiosperms are defined by ovules enclosed before pollination, namely, “angio-ovuly” (Tomlinson PB and Takaso T, 2002; Wang X, 2018). The occurrence of the 3+3 organization (pericarp and seed coat) in *Jurafructus* suggests that it is an angiosperm, as its seed is physically enclosed. Although the authors cannot ascertain the pollination mode in *Jurafructus*, excluding gymnosperm possibility can be achieved by comparing *Jurafructus* with known gymnosperms. Cycadales and Ginkgoales are frequently seen in the Jurassic (Taylor TN et al., 2009). A *Ginkgo* seed has a seed coat including a fleshy outer layer (sarcotesta) (Hori T et al., 1997), superficially similar to the fleshy pericarp of *Jurafructus*. But, actually, a *Ginkgo*'s seed only has three-layered seed coat homologous and comparable to S1, S2, and S3 of *Jurafructus*, and has no counterparts of P1, P2, and P3 of pericarp in *Jurafructus*. The seeds of Cycadales and Ginkgoales are all naked, namely, having



**Fig. 5.** Diagram of *Jurafructus* showing a section through the center of the fruit. Not to scale. Note the appendages (1) at the apex and stalk at the base (11), three-layered pericarp (2, 3, 4) fully enclosing three layered seed coat (5, 6, 7), which surrounds the seed contents (8), piercing damage (9) and patchy damage (12) on the fruit surface. The seed is attached at the base (10) and has a micropyle at the top (13).

nothing beyond have their three-layered seed coat, which is derived from the former integument, thus distinct from the

3+3 organization (seed coat + pericarp) seen in *Jurafructus* (Fig. 5). In addition, the distal appendages seen in *Jurafructus* (Figs. 4h, 5) are never seen in any Cycadales and Ginkgoales (Sporne KR, 1971; Biswas C and Johri BM, 1997; Meng et al., 2019). Some Corystospermales (including *Caytonia* and *Petriellaea*) have additional layer beyond seed coat, but these enclosing layers are fully devoid of distal appendages seen in *Jurafructus* and there are usually more than one seeds in each cupule (Taylor EL et al., 2006; Taylor EL and Taylor TN, 2009), thus distinct from *Jurafructus*.

The seeds in *Taxus* (Taxaceae) (Cope EA, 1998) and *Podocarpus* (Podocarpaceae) (Tomlinson PB, 1992) are only partially surrounded by a fleshy layer, thus distinct from the seed fully enclosed by pericarp in *Jurafructus*. The “fruit” of *Juniperus oxycedrus macrocarpa* is fleshy, with three basally attached seeds fully enclosed by the fleshy urceolate structure when mature. Judging by the appearance, this “fruit” appears like a typical drupe in angiosperm. However, this plant belongs to the Cupressaceae (Gymnosperms), since the seed enclosing is fulfilled only after pollination. The differences between this “fruit” and *Jurafructus* include the number of seeds per “fruit” and seed morphology. However, if the number of seeds per “fruit” in *Juniperus* was reduced from three to one, then *Jurafructus* and *Juniperus* would appear much more similar to each other.

The occurrence of three-layered pericarp in *Jurafructus* excludes most gymnosperms (except Gnetales) from consideration. Gnetales frequently have additional layers beyond seed coat, but micropylar tube characteristic of Gnetales is apparently lacking in *Jurafructus*, which instead has characteristic distal appendages fully lacking in Gnetales.

The lack of information about pollination mode in *Jurafructus* leaves two possible scenarios of evolution for *Jurafructus*. In the first scenario, assuming the ovule/seed is fully enclosed before pollination, then *Jurafructus* is a *bona fide* angiosperm. In the second scenario, assuming the seed is enclosed only after pollination, then *Jurafructus* is more comparable to *Juniperus* in Cupressaceae (Gymnosperms). But this scenario is no less intriguing, especially considering *Jurafructus* appears intermediate between a typical angiosperm and typical *Juniperus* in terms of pollination mode, and its only difference from angiosperms is the relative timing order of pollination and seed-enclosing. It is apparent either that *Jurafructus* is a *bona fide* angiosperm, or that *Jurafructus* may well provide a badly needed taxon intermediate between gymnosperms and angiosperms.

The irregular surface of *Jurafructus* (Figs. 2, 3d, 4a, 4e–h) is apparently not original but probably due to damage from unknown animals. This conclusion can be inferred from the views of the fruit rendered by micro-CT (Figs. 4e–g). Apparently, the supposedly original smooth surface of *Jurafructus* had been altered and damaged before fossilization (Figs. 4e–g). Although currently there is no information about which animals caused these damages on *Jurafructus*, a conclusion can be drawn: There are two types of damage on this single fruit, of which the patchy damage (Figs. 4a, 4e–h)

on the surface of the fruit may be caused by some chewing animals, while the depression on the fruit surface (Fig. 3d) may be caused by some other piercing animals. The latter type might appear similar to the ovioposition on *Yimaia*'s seed (Meng et al., 2019) while the former type (patchy damage) is apparently different from what documented by Meng et al. (2019). Considering the Jurassic age of *Jurafructus*, these observations mark the earliest record of frugivory. Apparently, the interaction between angiosperms and animals may well have started before the late Jurassic.

## 5. Conclusion

A three-dimensionally preserved coalified drupe, *Jurafructus*, from the Jurassic of China is damaged by animals in two different ways. Its 3+3 structure surrounding seed contents is distinct from a three-layered seed coat typically seen in gymnosperms. Even if its pollination mode were found gymnospermous later, *Jurafructus* still would shed a unique light on the transition from gymnosperms to angiosperms. Currently, available evidence suggests that *Jurafructus* marks the earliest record of frugivory and that the interaction between angiosperms and animals extends deep into the fossil record.

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