Biosis: Biological Systems (2021) 2(4), 416-422
https://doi.org/10.37819/biosis.001.04.0160

ORIGINAL RESEARCH

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The Currently Earliest Angiosperm Fruit from the Jurassic of North America

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ABSTRACT

Angiosperms are the single most important plant group in the current ecosystem. However, little is known about the origin and early evolution of angiosperms. Jurassic and earlier traces of angiosperms have been claimed multiple times from Europe and Asia, but reluctance to accept these records remains. To test the truthfulness of these claims, palaeobotanical records from continents other than Europe and Asia constitute a crucial test. Here I document a new angiosperm fruit, *Dilcherifructus mexicana* gen. et sp. nov, from the Middle Jurassic of Mexico. Its Jurassic age suggests that origin of angiosperms is much earlier than widely accepted, while its occurrence in the North America indicates that angiosperms were already widespread in the Jurassic, although they were still far away from their ecological radiation, which started in the Early Cretaceous.

ARTICLE HISTORY

Received: 24-08-2021
Revised: 14-11-2021
Accepted: 15-12-2021

KEYWORDS

Earliest
Fruit
Origin
Angiosperm
North America
Mexico

1 Introduction

Increasing number of fossils indicate that angiosperms existed in the Jurassic(Fu *et al.* 2018; Wang 2018), although this conclusion was frequently challenged by some palaeobotanists(Friis *et al.* 2011; Herendeen *et al.* 2017). Among all, *Nanjinganthus* is recognized based on by far the most numerous specimens (over two hundred flowers) recovered from the Lower Jurassic of China (Fu *et al.* 2018). However, the morphology of *Nanjinganthus* is at odds with the mainstream hypotheses of angiosperm evolution. Such a conflict between hypotheses and fossil evidence has to be resolved. One way to resolving this conflict is to see whether there are other Jurassic fossil angiosperms in continents other than Asia, where most of the pre-Cretaceous angiosperms were claimed (Wang 2018). Here I report an angiosperm fruit, *Dilcherifructus* gen. nov, from the Simón Formation (Middle Jurassic) of Tezoatlán, Oaxaca, Mexico. The Jurassic age of the Simón Formation seems to suggest the presence of angiosperms in the Jurassic, a period earlier than expectation of the mainstream thinking. Angiosperm records scattered in North America (Mexico, *Dilcherifructus*), Europe (Germany, *Schmeissneria*)(Wang *et al.* 2007; Wang 2010), and

Asia (China, *Nanjinganthus*) (Fu *et al.* 2018; Taylor and Li 2018) suggest that angiosperms were already intercontinentally widespread at least over the North Hemisphere in the Jurassic, refuting the obsolete "No Angiosperms Until the Cretaceous" conception(Scott *et al.* 1960; Friis *et al.* 2011; Herendeen *et al.* 2017).

2 Geological Settings

The fossil was collected from an outcrop of the Simón Formation near Tezoatlán, nine miles south of the city Tezoatlán, Oaxaca, Mexico. Previously, from this fossil locality, Wieland collected fossils of Cycadophytes in the early 1900s, later Delevoryas collected more fossil plants(Delevoryas 1968), and in November, 1968 Dr. David L. Dilcher collected the present and other specimens. Fossil plants and ammonites indicate an age of the Middle Jurassic for the Formation(Delevoryas 1968; 1969; Delevoryas and Person 1975).

The fossils are coalified compressions embedded in a yellowish siltstone. The specimens were photographed using a Sony ILCE-1 digital camera. Details of the fossils were observed and photographed using a Nikon SMZ-10 stereomicroscope equipped with a Canon EOS Rebel XSi digital camera. All photographs were saved in TIFF format and organized together for publication using a Photoshop 7.0.

3 Results

Dilcherifructus gen. nov.

Generic diagnosis: Fruit with depressions at both top and base, with a style in apical depression. Exocarpic epidermal cells polygonal or rectangular in shape, with straight cell walls. Stomata anomocytic, level with neighboring cells. Single seed enclosed by a pericarp

Type species: *Dilcherifructus mexicana* gen. et sp. nov.

Etymology: *Dilcher-*, for the collector, Dr. David L. Dilcher; *-fructus*, for fruit in Latin.

Type locality: Tezoatlán, nine miles south of the city Tezoatlán, Oaxaca, Mexico.

Horizon: The Simón Formation, Tecocoyunca Group, the Middle Jurassic.

Dilcherifructus mexicana gen. et sp. nov

(Figure 1-3)

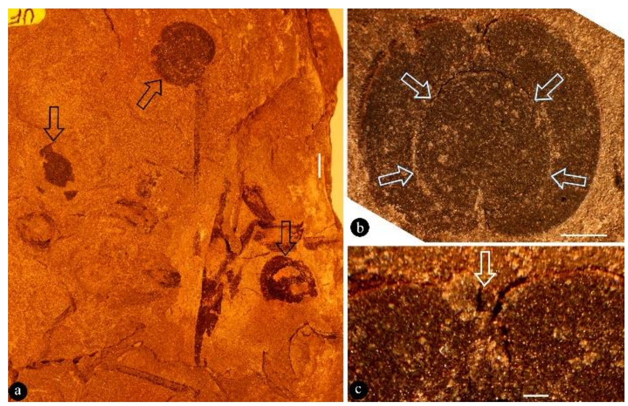

Fig. 1. General morphology of *Dilcherifructus mexicana* gen. et sp. nov and its details. UF18481-38859. **Notes**: A. Three fruits (arrows) preserved on the same specimen, associated with unidentified branches and leaf. Bar = 5 mm. B. Detailed view of the top fruit in Fig. 1a, showing its round shape, smooth exocarp, depressions at the top and bottom, and outline (arrows) of the seed within the fruit. Bar = 250 μm. C. Detailed view of the apical depression and persistent style (arrow) within. Bar = 50 μm.

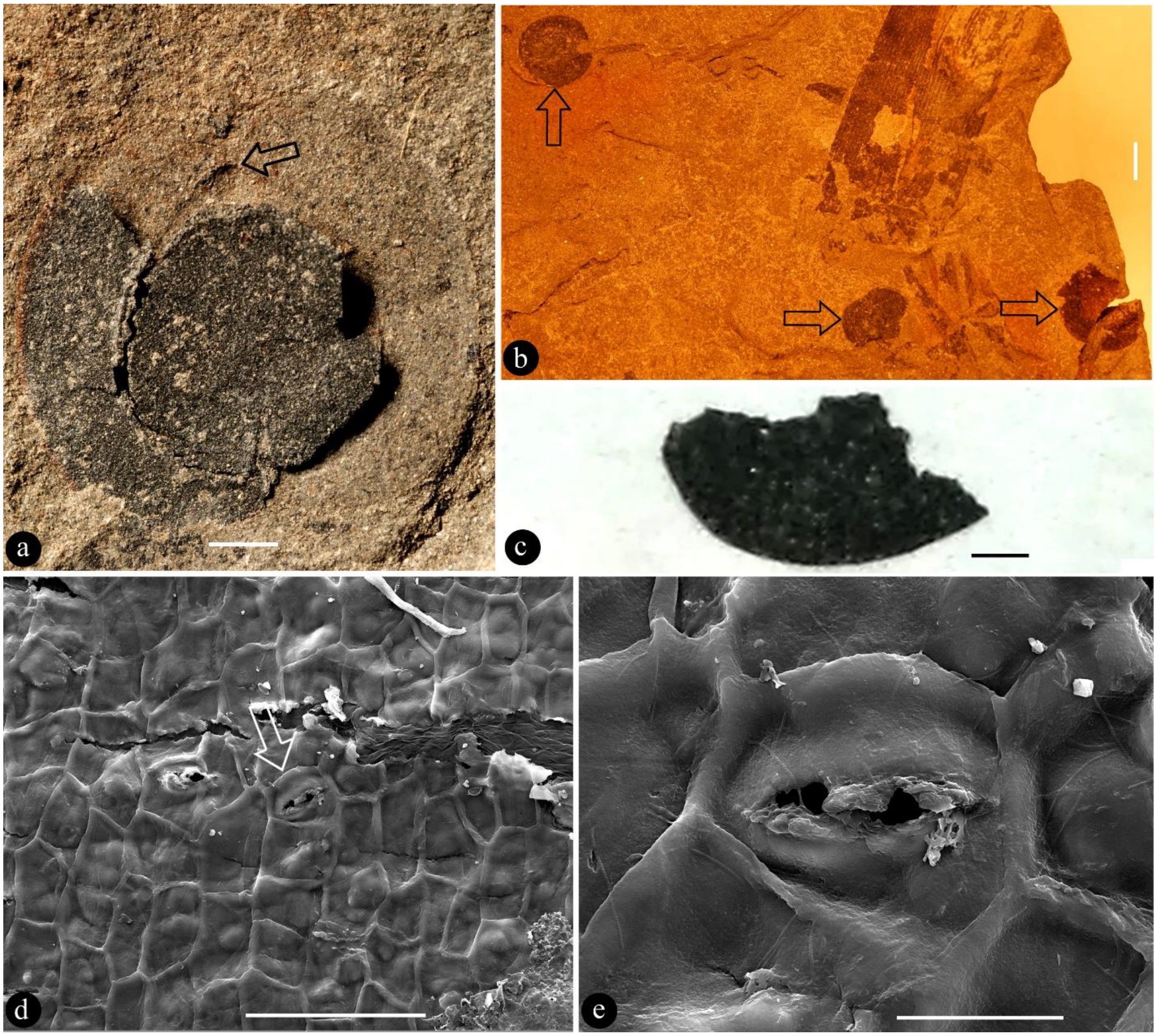

Fig. 2. Details of *Dilcherifructus mexicana* gen. et sp. nov. UF18481-38859. **Notes**: A. Another fruit with partially preserved organic material, showing the contrast between the central seed (white arrows) and surrounding pericarp due to their difference in hardness, apical depression, and tip of the seed (black arrow). The apical depression is visible but less obvious in this specimen than in Fig. 1c, due to the missing organic material. Bar = 2 mm. B. Three fruits (arrows) in another region of the same specimen shown in Fig. 1a, associated with an unidentified leaf with parallel venation. Bar = 5 mm. C. A piece of organic material of a fruit, whose cuticular details are shown in Figs. 2d and 2e. Bar = 2 mm. D. Exocarpic cuticle with polygonal or rectangular epidermal cells, straight anticlinal cell walls, and stoma. Bar = 100 μm. E. Detailed view of the anomocytic stoma in Fig. 2d, level with five neighboring epidermal cells. Bar = 20 μm.

Specific diagnosis: as of the genus.

Description: The fossils are preserved as coalified compressions embedded in yellowish siltstones (Fig. 1a). There are at least six fruits preserved on the same specimen (Figs. 1a, 2b). The fruits are round-shaped, with an apical and a basal depressions, 10-13.6 mm long, 10-13 mm wide, including a seed and an enclosing pericarp (Figs. 1a-b, 2a-b, 3a). The pericarp has a smooth surface, 2 mm thick at the bottom, 2.9-3.1 mm thick near the shoulder, 0.9-1.4 mm thick below the apical depression (Figs. 1b, 2a, 3a). The seeds are inside the fruits, round in shape, approximately 8 mm long and 6-9 mm wide (Fig. 1a-b, 2b, 3a). A persistent style 76 µm long and 30 µm wide is in the apical depression (Fig. 1b-c, 3a). Epidermal cells of the exocarp are polygonal or rectangular in shape, 20-60 µm long, 13-38 µm wide (Figs. 2d-e, 3b). Anomocytic stoma is surrounded by approximately five epidermal cells, 36 µm long, 36 µm wide, with a slit 25 µm long, 5.4 µm wide, level with neighboring epidermal cells (Figs. 2d-e, 3b).

Etymology: *mexicana,* for Mexico, the country in which the fossil was collected.

Holotype: UF18481-38859, deposited in the Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA.

Remarks: *Dilcherifructus* is not a homologue of a seed. If *Dilcherifructus* were taken as a seed, less hard seed content enclosed by a hard seed coat should not be visible for an observer. The situation in *Dilcherifructus* (Figs. 1b, 2a) is on the contrary: the inside content is obvious. This observation suggests that the internal body in *Dilcherifructus* is harder than the enclosing layer, a case frequently seen in angiosperm fruits: seeds inside ovary usually are harder than the enclosing fleshy ovarian wall and thus visible when squashed. The distal projection in *Dilcherifructus* is interpreted as a persistent style on the tip of a fruit, as frequently seen in angiosperms. Thus I interpret *Dilcherifructus* as a fruit rather than a seed.

There are unidentified branches and leaf closely associated with *Dilcherifructs*, but they are not physically connected with *Dilcherifructus*. Their biological relationship with *Dilcherifructus* requires further investigation.

There is uncertainty about the form of *Dilcherifructus*. If *Dilcherifructus* were of radial symmetry in the top view, then the apical depression and the persistent style within in Figs. 1b-c and 2a should not be visible. My observation makes it more likely that *Dilcherifructus* is more or less flattened in form. However, this inference is open to debate.

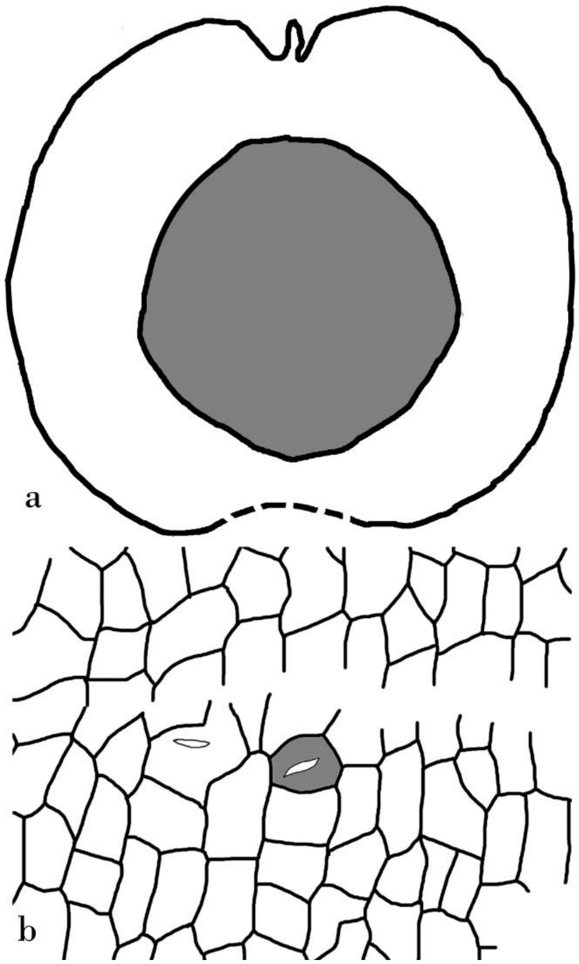

Fig. 3. Sketches of *Dilcherifructus mexicana* gen. et sp. Nov. **Notes**: A. Fruit with apical persistent style and enclosed seed (gray in color) inside, drawn after Fig. 1b. B. Anomocytic stoma (gray) and epidermal cells with straight cell walls, drawn after Fig. 2d.

4 Discussions

As angiosperms were frequently thought to be restricted to the Cretaceous and later ages(Scott *et al.* 1960; Friis *et al.* 2011; Herendeen *et al.* 2017), I have to be cautious on the angiospermous affinity of *Dilcherifructus* because of its Middle Jurassic age. However, the risk of misidentifying another Jurassic angiosperm is reduced when the Early Jurassic age of *Schmeisseria* (Wang *et* *al.* 2007; Wang 2010) and *Nanjinganthus* (Fu *et al.* 2018) is taken into consideration.

Morphology plays an important role in my treatment of *Dilcherifructus*. Among the frequently seen Mesozoic plant groups, including Pentoxylales, Cycadales, Bennettitales, Ginkgoales, Coniferales, and Gnetales, apical projections are seen only in seeds of Bennettitales and Gnetales. Thus, apparently, Pentoxylales, Cycadales, Ginkgoales, and Coniferales are out of the question here. Bennettitales characterized by seeds with micropylar tubes and interspersed among interseminal scales (Wieland 1906; Harris 1941; Foster and Gifford 1974; Stevenson 1990; Biswas and Johri 1997; Rothwell *et al.* 2009) are distinct from *Dilcherifructus* in general morphology, such lack of fleshy peripheral layers, small size and elongated form of seeds surrounded by interseminal scales (Rothwell *et al.* 2009). It is of special interest that *Juniperus oxycedrus* var. *macrocarpa* (Cupressaceae, Coniferales) demonstrates a great resemblance to *Dilcherifructus*, as it has a fleshy layer fully surrounding its three seeds when mature, but there is no apical projection in *Juniperus oxycedrus* var. *macrocarpa*. After the above comparison, it is clear that *Dilcherifructus* does not fall in the morphological scope of any known gymnosperms. Most importantly, the seed fully enclosed by the pericarp (ovarian wall), as suggested by the presence of apical limit of the former ovarian locule and persistent style in *Dilcherifructus* (Figs. 1b, 2a), suggests that the enclosure of ovule is completed most likely before pollination, favoring that *Dilcherifructus* is a *bona fide* angiosperm, as ovule enclosed before pollination is a feature restricted to angiosperms(Tomlinson and Takaso 2002; Wang 2018).

The exocarpic cuticular feature of *Dilcherifructus* further strengthens its angiospermous affinity. Stomata are usually expected on leaves, but they are frequently present on carpel or ovary surface(Paulino *et al.* 2014). In strong contrast to the stomata in gymnosperms, which are usually sunken and with subsidiary cells, the stoma in *Dilcherifructus* is anomocytic and level with neighboring epidermal cells (Figs. 2d-e, 3b). Although similar stomata have been documented in, besides angiosperms, Caytoniales(Barbacka and Boka 2000), the fruit morphology and lack of basal opening in *Dilcherifructus* annihilate any relationship to Caytoniales, leaving only one affinity alternative for *Dilcherifructus*: Angiosperms.

The occurrence of six fruits of *Dilcherifructus* on the same specimen indicates that, at least locally, *Dilcherifructus* was abundant and flourished in the vegetation of Mexico during the Middle Jurassic. Previous reports of various Jurassic angiosperms are restricted to Asia and Europe(Wang *et al.* 2007; Wang 2010; Fu *et al.* 2018; Wang 2018), now the occurrence of *Dilcherifructus* in Mexico, for the first time, expands the distribution of Jurassic angiosperms into North America. It appears that angiosperms were already widespread in the North Hemisphere during the Jurassic, a period well before the widely accepted Cretaceous origin of angiosperms (Friis *et al.* 2011; Herendeen *et al.* 2017).

5 Conclusions

Dilcherifructus mexicana gen. et sp. nov is an angiosperm fruit from the Middle Jurassic of Oaxaca, Mexico. The fruit has a persistent style, a seed enclosed by a pericarp, and anomocytic stomata on exocarp. Such a character assemblage implies that *Dilcherifructus* is a *bona fide* angiosperm. This is the currently earliest record of angiosperms in the North America, and its geographical position indicates that angiosperms were already widespread in the North Hemisphere during the Jurassic. This new information prompts a rethinking on the history of angiosperms and related hypotheses.

6 Acknowledgments

I thank Dr. Prof. David L. Dilcher for collecting the important fossil material five decades ago and his comments on the manuscript, Dr. Hongshan Wang at the Florida Museum of Natural History for help accessing the valuable fossil collection and photographing specimens, and Dr. Yan Fang for help with SEM. This research was supported by the Strategic Priority Research Program (B) of Chinese Academy of Sciences (Grant No. XDB26000000) and the National Natural Science Foundation of China (41688103, 91514302, 41572046).

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