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A Fruit-Bearing Angiosperm from the Jurassic of Inner Mongolia, China

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Abstract

Although pre-Cretaceous angiosperms were rejected or suspected by some palaeobotanists, their existence in the Jurassic appears increasingly plausible, especially when recent palaeobotanical progress and phylogenomic studies are taken into consideration. An herbaceous whole plant of an angiosperm has been reported from the Jurassic Jiulongshan Formation, but its implication for angiosperm evolution is under-appreciated. Here, from exactly the same fossil locality, we report a fruit-bearing angiosperm, *Daohugoufructus sinensis* gen. et sp. nov, which was previously wronged as a gnetalean plant. The unique fruits on elongated scapes distinguish *Daohugoufructus* from all known gymnosperms and suggest an angiospermous affinity. With physically connected fruits, leaves, and a branch, *Daohugoufructus* sheds an otherwise unavailable light on early angiosperms and their evolution.

Keywords

Fruit, Angiosperm, China, Jurassic, *Daohugoufructus*

1. Introduction

The diversity of angiosperms in the Early Cretaceous (Archangelsky et al., 2009; Wang, 2018; Coiffard & Bernardes-de-Oliveira, 2020) would appear unusually high, if there were no pre-Cretaceous angiosperms. Molecular clock estimates and recent fossil evidence congruously suggest that angiosperms must have occurred in the Jurassic (Hochuli & Feist-Burkhardt, 2004; Wang et al., 2007; Wang, 2009, 2010; Prasad et al., 2011; Hochuli & Feist-Burkhardt, 2013; Han et

al., 2016; Liu & Wang, 2016; Liu & Wang, 2017; Fu et al., 2018; Wang, 2018; Wu et al., 2018; Li et al., 2019; Fu et al., 2020; Zuntini et al., 2024). But this conclusion does not extinguish the controversy over the origin time of angiosperms. To resolve the controversy, the only reliable way is to test various hypotheses using independent fossil evidence. Here we report *Daohugoufructus sinensis* gen. et sp. nov, a fruit-bearing angiosperm from the Jiulongshan Formation (the Middle-Late Jurassic, >164 Ma) of Inner Mongolia, China. The morphology of *Daohugoufructus* fruits distinguishes them from all known gymnosperm seeds and conjures to some fruits in angiosperms. With physically connected fruits, leaves, and a branch, *Daohugoufructus* unveils an unexpected morphology of early angiosperms. This plant apparently falls out of the expectations of all known hypotheses, calling for a refreshing review of the existing angiosperm evolution theories.

2. Materials and Methods

Our fossil was uncovered from an outcrop of the Jiulongshan Formation near Daohugou Village (119.236727˚E, 41.315756˚N) at the southeast corner of Inner Mongolia, China (**Figure 1(a)**, **Figure 1(b)**). A Jurassic angiosperm, *Juraherba*, has been previously reported from the same outcrop (Han et al., 2016). Stratigraphic works and isotopic datings (Chen et al., 2004; Ji et al., 2005; Huang et al., 2006; Zhang, 2006; Huang & Nel, 2007; Petrulevicius et al., 2007; Huang & Nel, 2008; Huang et al., 2008a; Huang et al., 2008b; Lin et al., 2008; Liu & Ren, 2008; Selden et al., 2008; Zhang et al., 2008; Fang et al., 2009; Huang et al., 2009; Liang et al., 2009; Shih et al., 2009; Wang et al., 2009a; Wang et al., 2009b; Wang & Zhang, 2009a, 2009b; Wang et al., 2009a, 2009b, 2009c; Wang & Ren, 2009; Zhang et al., 2009; Wang, 2018) suggest an age of over 164 Ma old (the Middle-Late Jurassic) for our fossil. The specimen was a compression with some coaly residue embedded in a siltstone. It was observed and photographed using a Nikon SMZ1500 stereomicroscope equipped with a DS-Fi1 digital camera and using a TESCAN MAIA3 scanning electron microscope (SEM) housed at the Nanjing Institute of Geology and Palaeontology, Nanjing, China. The specimen was observed using a Phoenix v|tome|x m scanner using a voltage of 230 Kv and a current of 170 μA at the State Key Laboratory of Continental Dynamics (Northwest University), Xi'an, Shaanxi Province, China. The specimen was stabilized using a self-adhesive tape. 1500 projections were obtained, and the data set had a resolution of 18.03 μm. Three-dimensional reconstruction was generated by using a VG studio 3.2. All images were saved in TIFF or JPEG format, and organized for publication with a Photoshop 7.0 software.

3. Results

***Daohugoufructus* gen. nov**

Synonym

Daohugoucladus, Yang et al. 2023, *Plants*, 12, 1749, page 2-8, Figures 1-5.

Diagnosis: Distal portion of a plant, including a branch, leaves and fruits. Leaves lanceolate, smooth margined, with a midvein, decussately arranged at nodes. Fruits elongated-scaped, vertically ridged, with a dimpled cap as well as a persistent perianth.

Type species: *Daohugoufructus sinensis* gen. et sp. nov.

Etymology: *Daohugou* or the fossil locality, Daohugou Village, *fructus* for fruit in Latin.

Horizon: the Jiulongshan Formation, Middle-Late Jurassic (>164 Ma).

Locality: Daohugou Village, Ningcheng, Inner Mongolia, China (119.236727˚E, 41.315756˚N).

Remarks: Exactly the same specimen as of *Daohugoufructus sinensis* gen. et sp. nov was previously published as *Daohugoucladus sinensis*, a gnetalean plant, by Yang et al. (2023) in *Plants*. Article 8.4 of ICBN states, "Type specimens of names of taxa must be preserved permanently". Yang et al. (2023) failed to deposit and secure their specimen in the Herbarium of Nanjing Forest University, as they stated in their paper. Therefore name for the fossil given by Yang et al. (2023) is illegitimate.

Furthermore, the fossil specimen shows none of the "unusual morphological characters" of Gnetophytes listed by Yang et al. (2023), which Yang et al. listed as "bisexual cones, flower-like reproductive organs, style-like micropylar tube, unique chlamydosperms with additional envelope(s) partially enclosing the inner ovule and exposing an apical micropylar tube, vessels in the wood anatomy, double fertilization and archegonia" (Yang et al., 2023). Placing a fossil plant lacking either of these "unusual" features characteristic of Gnetophytes and being "different from other known gnetalean macrofossils" indicate that the treatment given by Yang et al. was spurious. Therefore here we propose a new genus for the fossil, *Daohugoufructus* gen. nov.

***Daohugoufructus sinensis* gen. et sp. nov**

(**Figures 1-3**)

Synonym

Daohugoucladus sinensis, Yang et al. 2023, *Plants*, 12, 1749, page 2-8, figs. 1-5.

Diagnosis: the same as the genus.

Description: The fossil is 40 mm wide, 75 mm long, including a branch, leaves and fruits (**Figure 1(a)**). The branch includes at least six nodes (**Figure 1(a)**). The length of internodes ranges from 3.3 to 5.8 mm, decreasing distally (**Figure 1(a)**). At each node, there are decussately arranged leaves (**Figure 1(a)**, **Figure 1(b)**). The leaves are lanceolate, smooth-margined, constricted at decurrent bases, with rounded or pointed tips, with a midrib, 14 - 41 mm long, 1.9 - 2.4 mm wide, frequently damaged (**Figure 1(a)**, **Figure 1(b)**, **Figures 1(d)-(h)**, **Figures 2(d)-(i)**). The midrib is up to 0.18 mm wide (**Figure 1(b)**, **Figures 1(d)-(g)**). Epidermal cells are longitudinally oriented, 18 - 26 μm wide (**Figure 1(d)**). Seven fruits of various developmental stages are in the axils of leaves, elongated-scaped, longitudinally ridged, oval-shaped, 4.2 - 6.2 mm in length and

Figure 1. General view and details of *Daohugoufructus sinensis* gen. et sp. nov. (a) General view of the fossil, showing a physically connected branch, leaves, and seven fruits (numbers). Scale bar = 1 cm. (b) Detailed view of the basal portion of the fossil, showing a short-shoot at base (black arrow) and leaves decussately arranged at nodes (white arrows). Scale bar = 5 mm. (c) Detailed view of the short-shoot like structure with scaly leaves. Scale bar = 1 mm. (d) Detailed view of a leaf, showing smooth margin (black arrows), longitudinally oriented epidermal cells, and the midrib (white arrows). SEM. Scale bar = 0.5 mm. (e) Detailed view showing the rounded leaf tip and midrib (arrows) of the leaf shown in **Figure 1(g)**. Scale bar = 1 mm. (f) Detailed view of a constricted leaf base (arrow). Scale bar = 1 mm. (g) A basal leaf with a round tip, a mdrib (arrows), and smooth margins. Scale bar = 1 mm. (h) A distal leaf with a pointed tip (arrow), and smooth margins. Scale bar = 1 mm.

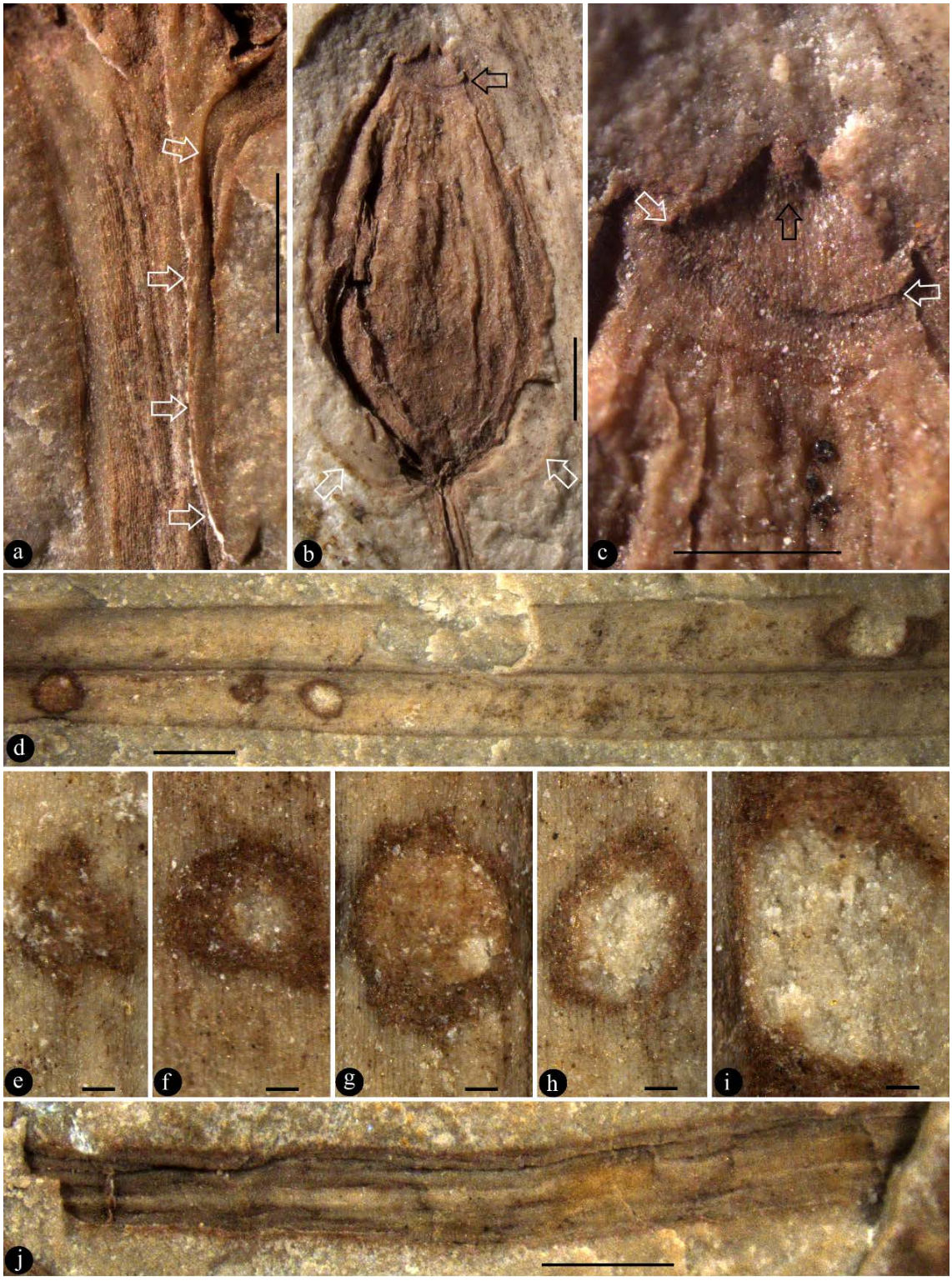

Figure 2. Details of the fruits and leaf damages. (a) Details of a branch and a decurrent leaf base (arrows). Scale bar = 1 mm. (b) General view of Fruit 1 with persistent perianth (white arrows), longitudinal ridges, and a terminal cap (black arrow). Scale bar = 1 mm. (c) Detailed view of the fruit tip shown in **Figure 2(b)**, showing the rim of the cap (white arrows) and a central dimple on the cap (black arrow). Scale bar = 0.5 mm. (d) Four damages on a single leaf. Scale bar = 1 mm. (e)-(i) Five varying damages. Scale bar = 0.1 mm. J. Detailed view of a fruit scape with longitudinal ridges. Scale bar = 1 mm.

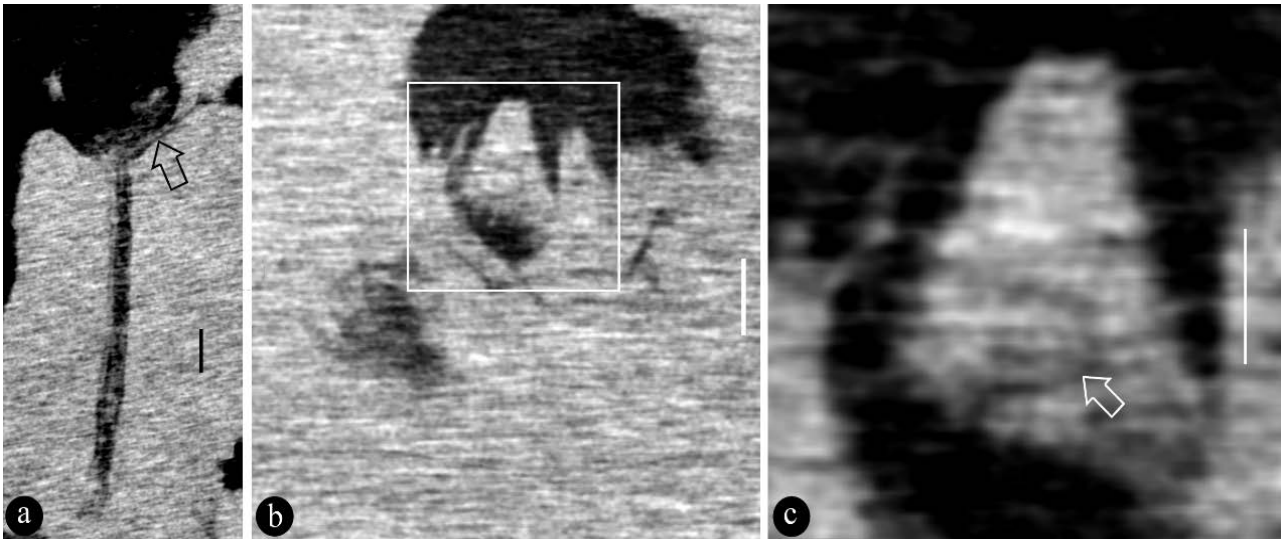

Figure 3. Micro-CT virtual sections of fruits. (a) Fruit 7 with a subtending perianth (arrow) on the terminal of its elongated, longitudinally ridged scape. Scale bar = 1 mm. (b) Fruit 6 bracketed by the perianth. Scale bar = 1 mm. (c) Detailed of Fruit 6 in the rectangle in **Figure 3(b)**, showing an oval body (arrow) attached to the internal wall of the fruit. Scale bar = 0.5 mm.

2.9 - 3.8 mm in diameter (**Figure 1(a)**, **Figure 2(b)**, **Figure 2(c)**). The scape ranges from 17.0 to 23.5 mm long, approximately 0.6 mm in diameter, longitudinally ridged (**Figure 1(a)**, **Figure 2(b)**, **Figure 2(j)**). Under each fruit, there are foliar appendages (perianth) (**Figure 2(b)**, **Figure 3(a)**). A conic cap is on each fruit tip, with a central dimple (**Figure 2(b)**, **Figure 2(c)**). There appears to be a stalked oval body connected to a side wall of fruit (**Figure 3(b)**, **Figure 3(c)**).

Etymology: *sinensis*, species epithet conserved from former name of the specimen, *Daohugoucladus sinensis*.

Holotype: HKD-PF-0001.

Depository: The Geological and Palaeontological Center, Hainan Vocational University of Science and Technology, Haikou, China.

Remark: The general morphology of *Daohugoufructus sinensis* gen. et sp. nov appears similar to that of *Juraherba* (Han et al., 2016), especially when the leaf morphology and general outline of the fruits are taken into consideration. However, these two plants are distinct in leaf arrangement (*Juraherba* has helically arranged, clufted leaves, while *Daohugoufructus* has decussately arranged leaves) and fruit morphology (the fruit scape bears scaly leaves in *Juraherba* while the fruit scape is smooth in *Daohugoufructus*; the fruit has a terminal breakage in *Juraherba* while the fruit has a well-defined conical-formed, dimpled cap in *Daohugoufructus*). These differences justify *Daohugoufructus* as a new genus.

4. Discussions

Daohugoufructus has various organs physically connected, including a branch, leaves, and fruits. The assemblage of these organs has never been seen in all known gymnosperms (**Table 1**). Based on its morphology, we have the following discussion on *Daohugoufructus*.

Table 1. Comparison between *Daohugoufructus* and other taxa.

	Fruit or seed-subtending parts	Escape/ pedicel	Pyxidium	Longitudinal ridges	Circumscissile dehiscence	Leaf midrib	Decurrent leaf base	Leaf venation
Daohugoufructus	+	long	+	+	+	+	+	
Ginkgo biloba	collar	long	–	–	–	–		
Taxus	aril	none	–	–	–	+		
Podocarpus	aril	none	–	–	–	–		
Berberis	–	long	+	+?	+	+	–	Pinnate, reticulate
Bertholletia	–	short	+	+?	+	+	–	pinnate, reticulate
Couratari	–	short	+	+?	+	+	–	pinnate, reticulate
Cariniana micrantha	–	short	+	+?	+	+	–	pinnate, reticulate
Amaranthus	–	short	+	+?	+	+	–	pinnate, reticulate
Actinostemma	–	long	+	–	+	+	–	pinnate, reticulate
Plantago	–	short	+	–	+	–?	–	parallel, reticulate
Scopolia	–	short	+	–	+	–	–	pinnate, reticulate
Hyoscyamus	–	short	+	–	+	–	–	pinnate, reticulate
Anisodus	–	short	+	–	+	–	–	pinnate, reticulate
Sphenoclea	–	short	+	–?	+	+	–	pinnate, reticulate
Eucalyptus	–	short	+	–	+	+	–	pinnate, reticulate
Sphenostemon	–	long	–	–	–	+	–	pinnate, reticulate
Sesuvium	–	short	+	+	+	?	–	?

The presence of seven fruits in various developmental stages (**Figure 1(a)**, **Figure 2(b)**, **Figure 2(c)**) strengthens our conclusion on the affinity of *Daohugoufructus*. The fruits' morphology excludes the possibility of their being sporangia, seeds, or cones. Each of these fruits has an elongated shape, longitudinal-

ly-ridged, up to 6.2 mm long, excluding the possibility of sporangia in ferns and seeds in various gymnosperms (including Cycadales, Coniferales, Gnetales, Corystospermales, Peltaspermales, Bennettitales, and Pentoxylales), leaving two alternatives in non-angiosperms: sporangia of bryophyte and seeds of Ginkgoales (**Table 1**). However, these two alternatives can be easily excluded: The decussately arranged leaves of *Daohugoufructus* are distinct from Bryophytes and Ginkgoales; the persistent perianth of *Daohugoufructus* (**Figure 2(b)**, **Figure 3(a)**) is never seen in Bryophytes and Ginkgoales. Especially, each fruit of *Daohugoufructus* has a characteristic elongated scape and a cap with a central dimple, both of which have so far never been seen in any known gymnosperm seeds. Micro-CT outcome shows that there is a stalked oval body attached to the side wall of the fruit (**Figure 3(b)**, **Figure 3(c)**), which is comparable to the ovule seen in ovary of some angiosperms, *e.g.* Tapisciaceae (Xin et al., 2019). Apparently, the ovule/seed is enclosed in the fruit of *Daohugoufructus*. This feature, in combination with others, pins down an angiospermous affinity for *Daohugoufructus*, as ovule/seed enclosed is the defining feature of angiosperms (Tomlinson & Takaso, 2002; Wang, 2018).

The leaves of *Daohugoufructus* are smooth-margined, lanceolate, with a midrib and a decurrent base (**Figure 1(a)**, **Figure 1(b)**, **Figures 1(d)-(h)**, **Figure 2(d)**). Among the known Jurassic fossil plants, similar leaves have been seen in *Juraherba*, which is from the same fossil locality (Han et al., 2016). However, *Juraherba* is an herbaceous plant that includes hairy roots and elongated fruit scape with scaly leaves (Han et al., 2016), thus differing from *Daohugoufructus*' no root and a smooth scape documented here (**Figure 1(a)**, **Figure 2(j)**, **Figure 3(a)**). The foliar features (**Figures 1(a)-(h)**, **Figure 2(d)**) exclude a eudicot affinity for *Daohugoufructus*. Instead, they suggest a possible monocot affinity. The lack of further information about whole plant of *Daohugoufructus* prevents us from elaborating on the affinity of *Daohugoufructus*. It is noteworthy that 1) *Juraherba* and *Daohugoufructus* are from the same fossil locality of the Jurassic (Han et al., 2016), 2) *Herbifolia*, a monocot leaf from the Middle Jurassic of eastern Siberia, Russia (Frolov & Enushchenko, 2022), 3) Poaceous epidermis and phytolith from the Early Cretaceous of China (Wu et al., 2018), 4) a rice tribe fossil from the latest Cretaceous of India (Prasad et al., 2011), and a re-studied angiosperm fossil from the Early Permian (Wang & Fu, 2023) all suggest an pre-Cretaceous origin for angiosperms and favor the Monocot-first hypothesis (Burger, 2012). Although this conclusion appears to contradict the mainstream thinking (Herendeen et al., 2017), it is at least a fact-based hypothesis and is rather compatible with recent molecular and phylogenomic studies (Li et al., 2019; Zuntini et al., 2024). It may be decent to test which, this hypothesis or so-called mainstream theories about angiosperm origination, is closer to the truth.

It is noteworthy that the fruit of *Daohugoufructus* includes a terminal dimpled cap and basal foliar appendages (**Figure 2(b)**, **Figure 2(c)**). Similar confi-

gurations have been seen in the fruit of *Nelumbo* and other pyxidia. However, the deployment and general morphology, especially its dimple on the cap and non-aggregated fruits, of *Daohugoufructus* lack their counterparts in *Nelumbo*, therefore we exclude it from our further consideration. Pyxidium is a circumscissile capsule rarely seen in angiosperms, in at least 17 families (*Amaranthus* (Amaranthaceae), *Berberis* (Berberidaceae), *Actinostemma* (Cucurbitaceae) (Schaefer & Renner, 2010), *Bertholletia, Couratari, Cariniana micrantha* (Lecythidaceae), Myrtaceae, *Plantago* (Plantaginaceae (Hassemer et al., 2021), *Scopolia, Hyoscyamus, Anisodus* (Solanaceae) (Kadereit & Bittrich, 2016), *Sphenoclea* (Sphenocleaceae), *Eucalyptus* (Eucalyptaceae)). Our comparison with these plants excludes the possibility that *Daohugoufructus* can be related to either of them. It appears that *Daohugoufructus* represents a Jurassic pyxidia-bearing angiosperm, although its whole plant and more details remain to be understood. The unique morphology of *Daohugoufructus* implies that it may well represent an extinct group with a combination of characters absent in all extant taxa.

It is also noteworthy that some leaves of *Daohugoufructus* are damaged (**Figures 2(d)-(i)**). These damages are of variable sizes and damaging degrees, and appear in a single piece of leaf (**Figures 2(d)-(i)**). It is intriguing that more or less similar insect damages have been previously reported in *Juraherba* (**Figure 2(f)**, **Figure 2(g)** of (Han et al., 2016)), a fossil angiosperm from the same locality. According to Labanderia (Labandeira et al., 2007), these leaf damages belong to DT01. This type of damage is assumed to be caused by insects with chewing mouthparts. The co-occurrence of similar damages in both *Daohugoufructus* and *Juraherba* from the Jurassic of Inner Mongolia, China suggests that the nowadays well-recognized interaction between angiosperms and insects may be traced back at least to the Middle-Late Jurassic. This places a solid foundation for the later complication of the angiosperm-related ecosystem in the Late Cretaceous (Han et al., 2024).

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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