Acta Geologica Sinica (English Edition), 2020, 94(5): 1711–1713

Research Advances

A New Infructescence of Angiosperms from the Early Cretaceous of China

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Citation: Han and Wang, 2020. A New Infructescence of Angiosperms from the Early Cretaceous of China. Acta Geologica Sinica (English Edition), 94(5): 1711–1713. DOI: 10.1111/1755-6724.14591

Objective

Angiosperms are the most diversified plant group in the current world. Studies on angiosperms, especially on their origin, evolution and systematics, are the major tasks and challenges for botanists. An increasing number of fossils from the Jurassic and Cretaceous have been interpreted as angiosperms, including *Chaoyangia, Archaefructus, Sinocarpus, Callianthus, Liaoningfructus, Baicarpus* and *Neofructus* from the Cretaceous of Liaoning, China, *Schmeissneria* from the Jurassic of northeastern China and southern Germany, *Euanthus*, *Juraherba*, *Yuhania, Zhangwuia, Nanjinganthus* from the Jurassic of China. These discoveries shed new light on the origin and early evolution of angiosperms.

Liaoningfructus from the Yixian Formation was published as the earliest ascidiate fruit. Thereafter there is no further confirming publication. Here we report a new fossil plant *Eofructus* gen. nov, an infructescence including a central axis and five fruits that more or less resemble *Liaoningfructus*, from the Yixian Formation. *Eofructus* gen. nov reinforces the existence of ascidiate fruits in Early Cretaceous, updating the current understanding of early angiosperms.

Methods

Besides early angiosperms (including *Chaoyangia*, *Archaefructus*, *Sinocarpus*, *Callianthus, Baicarpus, Liaoningfructus*, and *Neofructus*), the Yixian Formation of Liaoning, China has yielded various other fossil plants, including Bryophyta, Lycopodiales, Equisetales, Filicales, Pteridospermae, Cycadales, Bennettitales, Ginkgoales, Czekanowskiales, and Coniferales. There used to be some controversy regarding the age of the Yixian Formation, but there is now a general consensus on the age of Yixian Formation, namely, approximately 125 Ma (the Barremian, Early Cretaceous).

The material of *Eofructus* gen. nov includes a specimen preserved as compression with some coalified residue. The specimen is 74 mm long and 28 mm wide preserved on a slightly yellowish gray siltstone slab. The slab was recovered from the Liutiaogou, Dashuangmiao, Ningcheng, Inner Mongolia, China. The specimen was photographed using a Dual-LED dual-tone flash, panorama, HDR camera installed on Huawei Mate 8 and a Motic SMZ168 stereomicroscope equipped with a Moticam 282B digital camera. Sketches were drawn from the pictures using Photoshop 7.0. The specimen was deposited in the Palaeontological Center, Hainan Vocational University of Science and Technology, Haikou, China.

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Results

Type species: *Eofructus liutiaogouensis* gen. et sp. nov.

Generic diagnosis: A central axis bearing helically arranged fruits. Fruits including a decurrent smooth pedicel, an oval ovary, and an extended distal portion. Ovary opening at the subapical of the fruit. Seed inside the fruit, supplied by a vascular bundle arising from the ovary bottom.

Etymology: *Eo-*, for old in Latin; *-fructus,* for *fruit* in Latin.

Eofructus liutiaogouensis gen. et sp. nov (Fig. 1–2)

Specific diagnosis: the same as the genus.

Description: The specimen is 74 mm long and 28 mm wide, preserved as compression embedded in yellowish gray siltstone (Fig. 1a). There are five fruits attached to a central axis. The axis is 2.5 mm in diameter, tapering to 1.2 mm in the distal (Fig. 1a). Five fruits decrease in size distally, and their morphology is consistent although varying slightly (Fig. 1a). Each fruit includes a pedicel, an oval ovary with a seed inside, and a distal extension (Fig. 1a–b). The pedicel is decurrently inserted on the central axis, 5 mm long, 1.7 mm wide, with smooth profile, narrowing downward (Fig. 1a–b). The ovary is widest (3.3 –6.4 mm) in its middle, 5.5–10 mm long (Fig. 1a–b). Inside the fruit there is an oval seed (Fig. 1a–b, d). The seed is approximately 1.35 mm long, 0.9 mm wide, supplied by a basal vascular bundle (Fig. 1b, d–e). There is a depression on the subapical of the fruit, suggestive of a former ovary opening (Figs. 1b–c). The distal elongation has a smooth profile, tapering distally (Fig. 1a–b). A sketch of the fruit in Fig. 1b is shown in Fig. 2.

Etymology: *liutiaogou-*, for Liutiaogou, the fossil locality; *-ensis,* Latin ending.

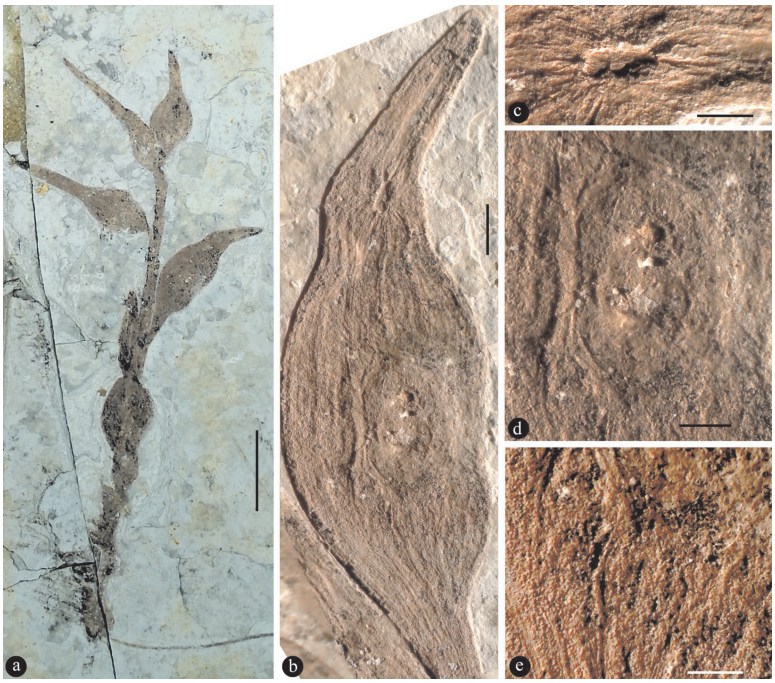

Fig. 1. Holotype of *Eofructus* gen. nov and its details. HGP039.
(a) Holotype including a central axis bearing five helically arranged fruits (bar = 1 cm). (b) Detailed view of one of the fruits with a tapering terminus, showing an *in situ* seed supported by a vascular bundle (bar = 1 mm). (c) Detailed view of the assumed ovary opening with radial texture (bar = 0.5 mm). (d) Detailed view of the *in situ* seed (bar = 0.5 mm). (e) Physical connection between the arising vascular bundle and *in situ* seed (bar = 0.5 mm).

Holotype: HGP039.

Type locality: Liutiaogou, Dashuangmiao, Ningcheng, Inner Mongolia, China (41º31′33"N, 118º55′29"E).

Stratigraphic horizon: the Yixian Formation, equivalent to the Barremian-Aptian, Lower Cretaceous (125 Ma).

Eofructus liutiaogouensis gen. et sp. nov. (Figs. 1–2)

Depository: Hainan Vocational University of Science and Technology, Haikou, China.

Remarks: We tried to make a peel to show the details of the fruit in Fig. 1b, but failed.

Conclusions

Before elucidating on the nature of its carpels, it is necessary to ascertain the angiospermous affinity of *Eofructus* gen. nov. Angiosperms are defined by their ovules enclosed before pollination. We currently have no information of *Eofructus* gen. nov before pollination. This makes our judgement more or less iffy. If the ovule in *Eofructus* gen. nov is indeed enclosed before its pollination, then *Eofructus* gen. nov is a *bona fide* angiosperm. In this case, the fruit morphology of *Eofructus* gen. nov suggests that it is most likely derived from an ascidiate carpel, as there is no evidence showing a conduplicate carpel developing into an ascidiate fruit like *Eofructus* gen. nov yet. The existence of an ovary opening at the subapical in *Eofructus* gen. nov suggests that its precursor carpel is most similar to that in *Ceratophyllum*. The current preservation is not good enough for us to determine whether there is a canal connected with ovary opening in *Eofructus* gen. nov. Were there such a canal, it would mean that early ascidiate carpels are not fully physically closed, just as ovaries in some living basal angiosperms are secluded only by liquid secretion. Were there no such a canal, then it would mean that *Eofructus* gen. nov had reached a carpel-closing degree higher than in some basal angiosperms, and thus the partial closure seen in extant basal angiosperms should have an earlier existence, a conclusion compatible with Triassic and Jurassic traces of angiosperms. However, if the ovary is

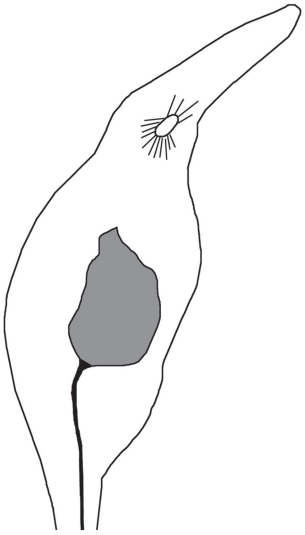

Fig. 2. Sketch of the fruit shown in Fig. 1b, showing the seed (gray) connected to an arising vascular bundle inside the fruit and the ovary opening with radial texture.

not fully closed before the pollination, *Eofructus* gen. nov becomes more intriguing in terms of carpel closing, as it may well represent the last step of pre-angiosperms in which the ovule-enclosing is not fully fulfilled, its morphology has already reached that of an ascidiate carpel in all other aspects and is distinct from any known reproductive organ of gymnosperms. Then *Eofructus* gen. nov may be taken as the precursor just before the birth of ascidiate carpels. Apparently, the seed of *Eofructus* is enclosed and supplied by a basal vascular bundle, implying that seed is borne on a vascularized funiculus (branch). This fact conflicts with the dominating megasporophyll doctrine, in which ovules were thought borne on leaf margins rather than branches. Recent works repeatedly confirm that all sporangia (including their derivatives, ovules/seeds) are all borne on branches, not leaves. Taking all information together, *Eofructus* gen. nov and existing evidence converge to the same conclusion that the traditional megasporophyll thinking (ovules are borne on leaf margins, and a carpel is a megasporophyll (leaf)) is far from botanical facts and fundamentally flawed.

An interesting phenomenon is that both coduplicate fruits and ascidiate fruits occurred in the Yixian Formation. As expected by the traditional botanical theory, fruits with conduplicate mrophology have been seen in *Archaefructus*, and *Nothodichocarpum*. However, this theory is apparently not favored by the non-conduplicate fruit morphology seen in *Chaoyangia*, *Callianthus*, *Baicarpus*, *Liaoningfructus*, *Neofructus*, and now *Eofructus*. Such a diversity of fruit morphology in the Yixian Formation makes it apparent that the origin time of angiosperms must be much older than the age of the Yixian Formation.

It is noteworthy that there is a long stipe below each ovary in *Eofructus*. The outline of the stipe is smooth, lacking of any scars of former any lateral appendages (Fig. 1a–b). This observation suggests that there are no parts (such as stamen, petals, sepals usually seen in flowers) missing in this fossil and that, before fruit maturation, the reproductive organ of *Eofructus* is female, unisexual, and perianthless. Similar lack of flower parts has previously been seen in *Archaefructus* and *Sinocarpus*. These consistent observations of fossil angiosperms in the Yixian Formation suggest that non-flower-like organization is a common existence for reproductive organs of angiosperms in the Yixian Formation. There appears to be a gap between such fossil reproductive organs and later typically bisexual flowers in eudicots. This gap is recently more or less bridged morphologically by *Dinganthus pentamera* found in the Miocene.

As an Early Cretaceous fossil angiosperm, *Eofructus* gen. nov sheds a unique light on the origin and evolution of ascidiate fruits in angiosperms. Consisting with the morphology of *Liaoningfructus*, *Eofructus* gen. nov confirms the existence of ascidiate fruits in the Early Cretaceous and favors a history of ascidiate fruits longer than assumed. Alternatively, *Eofructus* gen. nov may well represent the penultimate gymnosperm precursor of angiosperms with ascidiate fruits. The co-occurrence of both conduplicate and ascidiate fruits suggest that the angiosperms in the Yixian Formation are quite diversified.

Acknowledgements

This research is supported by the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (Grant No. XDB26000000), National Basic Research Program of China (973 Program 2012CB821901), and National Natural Science Foundation of China (91514302, 91114201) awarded to X.W., and the Key Discipline Construction Program of Hainan Provincial Department of Education in 2017-Marine Geology as well as the Research to Start Project 2018- Hainan Tropical Ocean University RHDXB201802 awarded to G.H.