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A Novel Angiosperm from the Early Cretaceous and Its Implications for Carpel-Deriving

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Abstract: The Yixian Formation (Lower Cretaceous) of China is famous for its fossils of early angiosperms, and these fossils have shed otherwise unavailable light on the evolution of angiosperms. The seeds in *Archaefructus* and *Nothodichocarpum* are inserted along the dorsal of the fruits while those in *Sinocarpus* are along the ventral of the fruits, suggesting different Bau-plans and pathways deriving the carpels in these plants of the Early Cretaceous. Adding further fossil evidence, here we report a novel fossil angiosperm, *Neofructus lingyuanensis* gen. et sp. nov, with its seeds inserted on both ventral and dorsal sides of the fruits documented through light microscopic and SEM observations, suggesting a novel way forming gynoecium in the Yixian Formation. These fossil angiosperms indicate that angiosperm gynoecia in the Yixian Formation (the Barremian to Aptian) are derived in obviously different ways, implying an evolutionary scenario for angiosperms quite different from formerly assumed.

Key words: angiosperm, *Neofructus*, gynoecium, Yixian Formation, Early Cretaceous, Liaoning

1 Introduction

The systematics and evolution of angiosperms can be reliably recognized and established only when based on real history, which is otherwise ambiguous except when supported by fossil evidence. Among all, interpreting the provenance and evolution of gynoecium characteristic of angiosperms is the core question in angiosperm systematics. A carpel, the basic unit of gynoecium, used to be thought derived from a megasporophyll bearing ovules along its margins, and thus the ovules were supposed to be inserted along the ventral margin of fruits, as seen in the Magnoliaceae (Arber and Parkin, 1907). However, this sound and long-held idea is not favored by living Magnoliaceae and other angiosperms (Rounsley et al., 1995; Roe et al., 1997; Skinner et al., 2004; Mathews and Kramer, 2012; Guo et al., 2013; Liu et al., 2014; Zhang et al., 2017), and *Archaefructus* and *Nothodichocarpum* from the Early Cretaceous have ovules inserted along the dorsal of the fruits, apparently refuting the classical theory. The specious support for the classical theory of angiosperm evolution by the assumed "ventral" ovules in *Archaeanthus* (Dilcher and Crane, 1984) and *Archaefructus* (Sun et al., 1998) is found false as at least some of the ovules are actually attached to the dorsal fruit margin (Ji Qiang et al., 2004; Wang Xin and Zheng Xiaoting, 2012; Wang Xin, 2018b). The Yixian Formation has yielded various early fossil angiosperms and shed unique light on the early evolution of angiosperms (Duan Shuying, 1998; Sun et al., 1998, 2001, 2002; Leng and Friis, 2003, 2006; Ji Qiang et al., 2004; Wang Xin and Zheng Shaolin, 2009; Wang Xin and Han Gang, 2011; Wang Xin and Zheng Xiaoting, 2012; Han Gang et al., 2013, 2017). To shed more light on this question, here we report a new angiosperm *Neofructus* gen. nov. from the Yixian Formation, which is unique in that its ovules are inserted along both the ventral and dorsal sides of the fruits. Apparently, the gynoecia of early angiosperms in Yixian Formation are unexpectedly diversified, suggesting various provenances for the angiosperm gynoecia and a

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longer history for angiosperms, if a monophyly is assumed for angiosperms.

2 Geological Settings

An Yixian Formation of Liaoning, China is worldwide famous for its early angiosperm fossils (Duan Shuying 1998; Sun et al., 1998, 2001, 2002; Leng and Friis, 2003, 2006; Ji Qiang et al., 2004; Dilcher et al., 2007; Wang, 2010, 2018a; Wang Xin and Zheng Xiaoting, 2012; Han Gang et al., 2013, 2017) and animal fossils (including insects) (Wang Wuli et al., 1989; Li and Luo, 2006; Liu Yushuang et al., 2007, 2008), which constitute the unique Jehol Biota and the biological background for early angiosperm diversification in the Early Cretaceous. Despite former controversy over the age of the Yixian Formation (Sun et al., 1998; Swisher et al., 1998), there is now an increasing consensus on the age of Yixian Formation, namely, approximately 125 Ma (the Barremian -Aptian, Early Cretaceous) (Dilcher et al., 2007).

3 Samples and Methods

The material of *Neofructus* gen. et sp. nov includes a specimen preserved as compression / impression with some coalified residues on two facing slabs. The specimen is 95 mm long and 26 mm wide, preserved on yellowish gray siltstone slabs approximately 20 cm × 17 cm. The slabs were recovered from the outcrop of the Yixian Formation at Dawangzhangzi, Lingyuan, Liaoning, China (Fig. 1), the locality yielding *Archaefructus sinensis, Sinocarpus decussatus*, and *Nothodichocarpum lingyuanensis*. The specimen was photographed using a Nikon D200 digital camera, a Leica M205A stereomicroscope equipped with DFC450c digital camera and a Nikon SMZ1500 stereomicroscope with a Nikon DS -Fi1 digital camera. *In situ* seeds were removed and cleaned, coated with gold, and observed using a Leo 1530 VP SEM (scanning electron microscope) at the Nanjing Institute of Geology and Palaeontology, CAS. All figures were organized using a Photoshop 7.0. The specimen was deposited in the National Orchid Conservation Center of China, Shenzhen, China.

4 Results

Neofructus gen. nov.

Type species: *Neofructus lingyuanensis* gen. et sp. nov.

Generic diagnosis*:* Distal portion of plant, including a long peduncle terminating in a cluster of fruits. Peduncle slender, straight, without evident nodes. Fruits probably helically arranged on the peduncle. Fruits pedicellate, lanceolate-shaped, enclosing about ten seeds, with tapering termini. Seeds elongated oval, inserted on the dorsal and/or ventral side of the fruit.

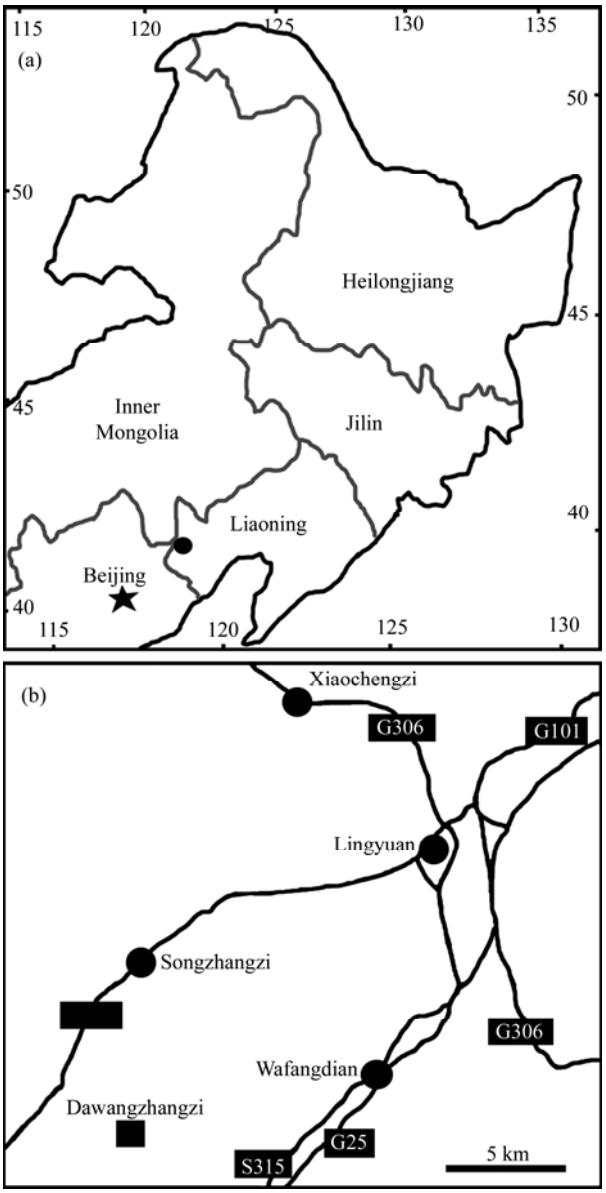

Fig. 1 Geographical position of the fossil locality of *Neofructus* in Liaoning, China. Reproduced from Han et al. (2017), with permission and courtesy of *Acta Geologica Sinica* (English Edition).
(a), fossil locality (black dot) in northeastern China; (b), detailed position of fossil locality (black square) in suburb of city Lingyuan, Liaoning.

Etymology: *Neo-*, for new in Latin; *-fructus,* for fruit in Latin.

Neofructus lingyuanensis gen. et sp. nov.
(Figs. 2–3)

Specific diagnosis: the same as the genus.

Description: The specimen is 95 mm long and 26 mm wide, including a long peduncle and at least 16 fruits (Fig. 2a). The peduncle is 47.5 mm long and 1.1 mm wide,

Fig. 2. Infructescence, fruits and seeds of *Neofructus*.
(a), Holotype, including a long peduncle bearing at least 16 fruits (numbers). DWZZ001B. Bar = 1 cm. (b), Probably helically arranged fruits (numbers) with *in situ* seeds. Note one (arrow) of the elongated pedicels. Bar = 1 mm. (c), Three seeds (1-3) in a row, in Fruit 14 in Fig. 2a. Bar = 1 mm. (d), Two adjacent seeds in the same fruit attached to the dorsal and ventral, respectively, fruit margins by the funiculi (arrows). Bar = 1 mm. (e), The counter part of Fruit 13 in Fig. 2a, with about 10 seeds inside. Bar = 1 mm. (f), Two adjacent seeds in the counter part of Fruit 10, note the stub of the funiculus (black arrow) and possible embryo (white arrows, em) inside the seed. Bar = 0.5 mm. (g), (g), Sinuous cell walls (probably of seed coat) in a seed. Bar = 10 μm. (h), Imprint left by a seed coat. Note the funiculus (bottom-right) attached to the fruit margin. Bar = 1 mm.

smooth and free of lateral appendages and nodes proximally (Fig. 2a). Each fruit includes a stalk and fruit body, 13–22 mm long and 1.4–2.2 mm wide (Fig. 2a–b). The fruit stalk is about 5 mm long, 0.4–0.8 mm wide, smoothly connected with fruits, narrowing proximally (Fig. 2a–b). Each fruit encloses 10–12 seeds (Fig. 2a–e). The seeds are arranged along both the ventral and dorsal margins, even in a single fruit (Figs. 2a-e, h). Seed is about 2 mm long and 1 mm wide, connected with either the dorsal or ventral placenta by a funiculus, probably anatropous (Fig. 2b–f, 3a-e). The epidermal cells on the seed probably have sinuous cell walls (Figs. 2g). The embryo-like structure is seen in a seed, near to micropyle, about 1 mm long and 0.45 mm wide (Fig. 2f).

Etymology: *lingyuan*-, for Lingyuan, where the fossil was collected.

Holotype: DWZZ001A (not shown), DWZZ001B (Fig. 2a).

Type locality: Dawangzhangzi, Lingyuan, Liaoning, China (41º15′N, 119º15′E).

Stratigraphic horizon: the Yixian Formation, equivalent to the Barremian-Aptian, Lower Cretaceous

(125 Ma).

Depository: the National Orchid Conservation Center of China, Shenzhen, China.

5 Discussion

Angiosperms can be defined, and thus distinguished from other seed plants, by ovule(s)/seed(s) enclosed in gynoecium or carpels (Sun et al., 1998). The seeds of *Neofructus* are apparently enclosed by its fruit wall, suggesting its angiospermous identity. The morphology of *Neofructus* distinguishes it from previously reported angiosperms from the Yixian Formation (Table 1) (Duan Shuying 1998; Sun et al., 1998, 2001, 2002; Leng and Friis, 2003, 2006; Ji Qiang et al., 2004; Wang Xin and Zheng Shaolin, 2009; Wang Xin and Zheng Xiaoting, 2012; Han Gang et al., 2013, 2017). Therefore the discovery of *Neofructus* adds to the existing list of early angiosperms in the Yixian Formation.

There are two competing hypotheses on the derivation of carpels in angiosperms. The first one says that the carpels in angiosperms are derived from the so-called "megasporophylls" bearing ovules along their margins (Arber and Parkin, 1907). The evidence from Bennettitales, which lack the wanted "megasporophylls", does not favor this hypothesis. The ovules inserted along the dorsal side of fruits in *Archaefructus* and *Nothodichocarpum* from the Yixian Formation (Ji Qiang et al., 2004; Wang Xin and Zheng Xiaoting, 2012; Han Gang et al., 2017; Fig.3f) undermine the hypothesis further. The second hypothesis says that each carpel comprises two parts, namely, placenta and ovarian wall (Taylor, 1991; Wang, 2010, 2018a). This hypothesis is favored by increasing fossil evidence (Wang Xin and Wang Shijun, 2010; Han Gang et al., 2017; Liu Zhongjian and Wang Xin, 2017) and studies of living Magnoliaceae (Liu et al., 2014; Zhang et al., 2017) as well as developmental genetics of *Arabidopsis* (Rounsley et al., 1995; Roe et al., 1997; Skinner et al., 2004; Mathews and Kramer, 2012). The different (ventral or dorsal) ovule insertions in *Archaefructus* and *Sinocarpus* (Fig. 3f) suggest that a placenta is independent of the enclosing foliar part (ovarian wall or carpel wall), and may be fused to either the margins or midvein of the enclosing foliar part. Here *Neofructus* constitutes a new test for these two competing hypotheses. Unlike situation in *Archaefructus* and *Sinocarpus*, the ovules in *Neofructus* are found inserted along both the ventral and dorsal sides of the fruits, and such an arrangement can be seen within in a single fruit (Fig. 2c–d, 3a–e). Such a unique ovule deployment not only confirms that the placentae are independent of the foliar parts, but also justifies *Neofructus* as a new angiosperm in the Yixian Formation, as two placentae and two carpel walls suggested by such an ovule insertion (Fig. 2c–d, 3a, d–e) have not been seen in the Yixian Formation before. Similar gynoecium is not seen in the assumed basal angiosperms (*sensu* classical theories (Cronquist, 1988) or APG system (APG, 2016)), but frequently seen in more derived eudicots, *e.g. Arabidopsis* (Brassicaceae) and *Corydalis, Glaucium, Chelidonium* (Papaveraceae)(APG, 2016), in which two carpel walls and two alternate placentae together form a unilocular ovary. However, the proximal occurrence of stamens in these living plants prevent us from further comparison. It is noteworthy that the famous *Archaeanthus* (Wang 2018b) may share similar Bau-plan with *Neofructus*, although the original authors interpreted the gynoecium of *Archaeanthus* as if similar to that of Magnoliaceae (Dilcher and Crane, 1984). Apparently, *Archaeanthus* deserves a further serious re-examination. Unlike the carpels in *Archaefructus* and *Sinocarpus*, in which a single placenta is enclosed by a single foliar part (carpel wall or ovarian wall) (Fig. 3f), the gynoecium of *Neofructus* is formed by two facing placentae (ovule-bearing branches) and two facing foliar parts (ovarian walls or carpel walls) (Fig. 3e). Similar arrangement of placentae and carpel walls has been well-studied and well-characterized genetically in *Arabidopsis* (Rounsley et al., 1995 ; Roe et al., 1997; Skinner et al., 2004; Mathews and Kramer, 2012). The discrepancy between fossil finds and expectations of classical theories suggests that the well-accepted theories are not favored by fossils of early angiosperms. The diversity of angiosperm gynoecia in the Yixian Formation suggests that angiosperms have a cryptic history before the age of the Yixian Formation (Barremain-Aptian, Early Cretaceous). This is in line with the trace of pre-Cretaceous angiosperms (Hochuli and Feist-Burkhardt, 2004, 2013; Wang et al., 2007; Wang Xin and Wang Shijun, 2010; Liu and Wang, 2017; Wang Xin, 2018a). Herendeen et al. (2017) insisted on an Early Cretaceous origin of angiosperms. But their conclusion is shaky, as their interpretations of raw data were highly

Table 1 Comparison between *Neofructus* and other angiosperms from the Yixian Formation

	sexuality	#seed/fruit	seed insertion	carpel arrangement	stamen	perianth	reference
Neofructus	female	10–12	ventral, dorsal	helical	unknown	none	this study
Archaefructus	bisexual	2–12	dorsal	whorled, opposite	present	none	Sun et al., 1998, 2002; Ji Qiang et al., 2004; Wang Xin and Zheng Xiaoting, 2012
Sinocarpus	female?	~10	ventral	decussate	?	?	Leng and Friis, 2003, 2006
Nothodichocarpum	bisexual	7–8	dorsal	paired	present	?	Han Gang et al., 2017

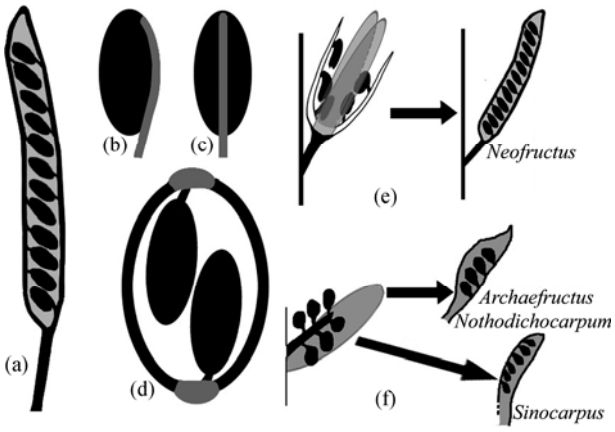

Fig. 3. *Neofructus* (a-d) and its derivation from presumed counterparts in gymnospermous ancestor (e) as well as comparison with other Early Cretaceous angiosperms (f).
(a), A fruit with elongated pedicel and seeds inserted on both ventral and dorsal fruit margins. (b), Side view of a seed derived from an anatropous ovule. Note the funiculus/raphe (gray) to the right side. (c), A view of the seed in Fig. 3b, rotated 90 degrees around its vertical axis, showing the raphe (gray) in the foreground. (d), Cross view of a fruit, showing seeds/ovules attached to the ventral (top) and dorsal (bottom) placentae (gray). (e), Deriving the fruit of *Neofructus* from former two facing ovule-bearing branches and two facing foliar parts. (f), Deriving the fruits of *Archaefructus, Nothodichocarpum* and *Sinocarpus* from a former axillary ovule-bearing branch and a subtending foliar part. Note the ovule-bearing branch fuses with different parts of the foliar part and thus gives rise to different fruits.

problematic and self-conflicting. For example, the original descriptions of Herendeen et al.'s No.1 exemplar angiosperm *Monetianthus* by Friis et al. (2001, 2009, 2011) were whimsical and inconsistent and did not meet the criterion for angiosperms set up by Herendeen et al. (Wang, 2017). Lacking solid interpretation of fossils makes all their conclusions dubious. The discovery of *Neofructus* calls for a theory innovation and re-thinking on angiosperm evolution in the coming years.

6 Conclusions

Neofructus is characterized by its ovules inserted along both the dorsal and ventral sides of the fruits, a new way to derive carpels in the fossil world. Together with previous fossil angiosperms, *Neofructus* indicates that the carpel deriving in early angiosperms occurred parallel and independently in the Early Cretaceous, implying a history of angiosperms unexpectedly longer than currently accepted by most palaeobotanists, refuting the Early Cretaceous origin of angiosperms.

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