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Research paper

# Reconsiderations on two characters of early angiosperm *Archaefructus*

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**Abstract**

*Archaefructus* is a genus of considerable interest and importance in the study of early angiosperms. Three previously documented species have provided important information about early angiosperms, although some of their characters have been interpreted in various ways. Additional new materials presented in this paper along with the holotype of *Archaefructus liaoningensis* illustrate branching pattern, fruit arrangement, and seed attachment in *Archaefructus*. New observations indicate that *Archaefructus* has ovules/seeds attached to the midrib on the abaxial side of the fruits and a whorled/opposite arrangement for the fruits on the axis. New fossil material of *Archaefructus sinensis* demonstrates that fruit pairs are inserted on the infructescence axis oppositely. The diagnoses of *Archaefructus* and Archaefructaceae are emended, and their significance on early angiosperm evolution is discussed.


*Keywords:* *Archaefructus*; Reinterpretation; Flower; Inflorescence; Carpel; Fruit

## 1. Introduction

*Archaefructus* has been recognized as an important fossil angiosperm for more than a decade (Sun et al., 1998), and Archaefructaceae is a family established based on two species described in *Archaefructus* (Sun et al., 2002). Later one more species was added to the family by Ji et al. (2004). These fossil plants have provided important information about early angiosperms although some characters have been interpreted in significantly different ways (Sun et al., 1998, 2001, 2002; Friis et al., 2003, 2006; Ji et al., 2004). For example, Ji et al. (2004) reported that the seeds are attached to the midrib on the abaxial side of the fruits, and a fertile axis bearing two carpels and one stamen is positioned between carpellate and staminate sections of *Archaefructus eoflora*. This is apparently different from the description by Sun et al. (1998, 2002), in which the seeds are attached to the adaxial margins of the carpels, just as in the marginal placentation of conduplicate carpels. These differences imply that either some concerned details of *Archaefructus* were overlooked, or *Archaefructus* has a wider spectrum of variations than previously assumed. To clarify these differences, the holotype of *Archaefructus* is re-examined and compared with newly found materials. The new data and observations provide the opportunity to emend the diagnosis for *Archaefructus* and Archaefructaceae. The new information will enhance the understanding of the character variation of Archaefructaceae and their significance in early angiosperm evolution.

## 2. Materials and methods

The specimens reported here were collected at the outcrops of the Yixian Formation near Dawangzhangzi, Lingyuan and Huangbanjigou, Shangyuan, Beipiao, both in Liaoning Province, China (Sun et al., 1998, 2002; Leng et al., 2003). The specimens were preserved as compressions embedded in grey or yellowish siltstones. They were photographed using an Olympus C765 Ultra Zoom digital camera first. Then they were observed and photographed using a Leica MZ-16A stereomicroscope with a digital camera. Afterward replicas were made for parts of interest, using the method described by Zhu (1983). The replicas were cleaned with HCl and HF, coated with gold, and then observed using a Leo 1530 VP SEM (scanning electron microscope) at the Nanjing Institute of Geology and Palaeontology, Nanjing, China. The figures were organized into five plates using Photoshop 7.0.

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All specimens except STM47-952 are deposited in the Nanjing Institute of Geology and Palaeontology, Nanjing, China. STM47-952 is deposited in the Tianyu Natural History Museum of Shandong, Pingyi, Shandong, China.

## 3. Results

Family Archaefructaceae

Genus *Archaefructus* Sun, Dilcher, Zheng and Zhou, emended

*Emended generic diagnosis*: Herbaceous, aquatic plants with branching stems. Main axis often bearing axillary infructescence axes terminating in fruits, and infructescence axes organized alternately. Poorly developed sparsely branched roots. Leaves helically arranged, petiole bases slightly enlarged, petioles of various lengths. Blades pinnately dissected two to six times into linear to slightly spatulate lobes, stipules absent. Reproductive axes forming a lateral branching system or a pseudo-indeterminate system associated with a main inflorescent axis in a cymose pattern. Infructescence axis long, unisexual/bisexual, occasionally branching, bearing stamens at the proximal and fruits at the distal. Stamens 2–3 per cluster, linear, with connectives. Pollen monosulcate, exine reticulate to verriform. Carpel and stamen rarely in the same cluster. Two or more fruits in groups or pairs, oppositely or whorled arranged along the infructescence axis. Fruit with a pedicel, 3–26 mm long, with 1–12 seeds per fruit. Ovules/seeds inserted on the midrib on the abaxial side

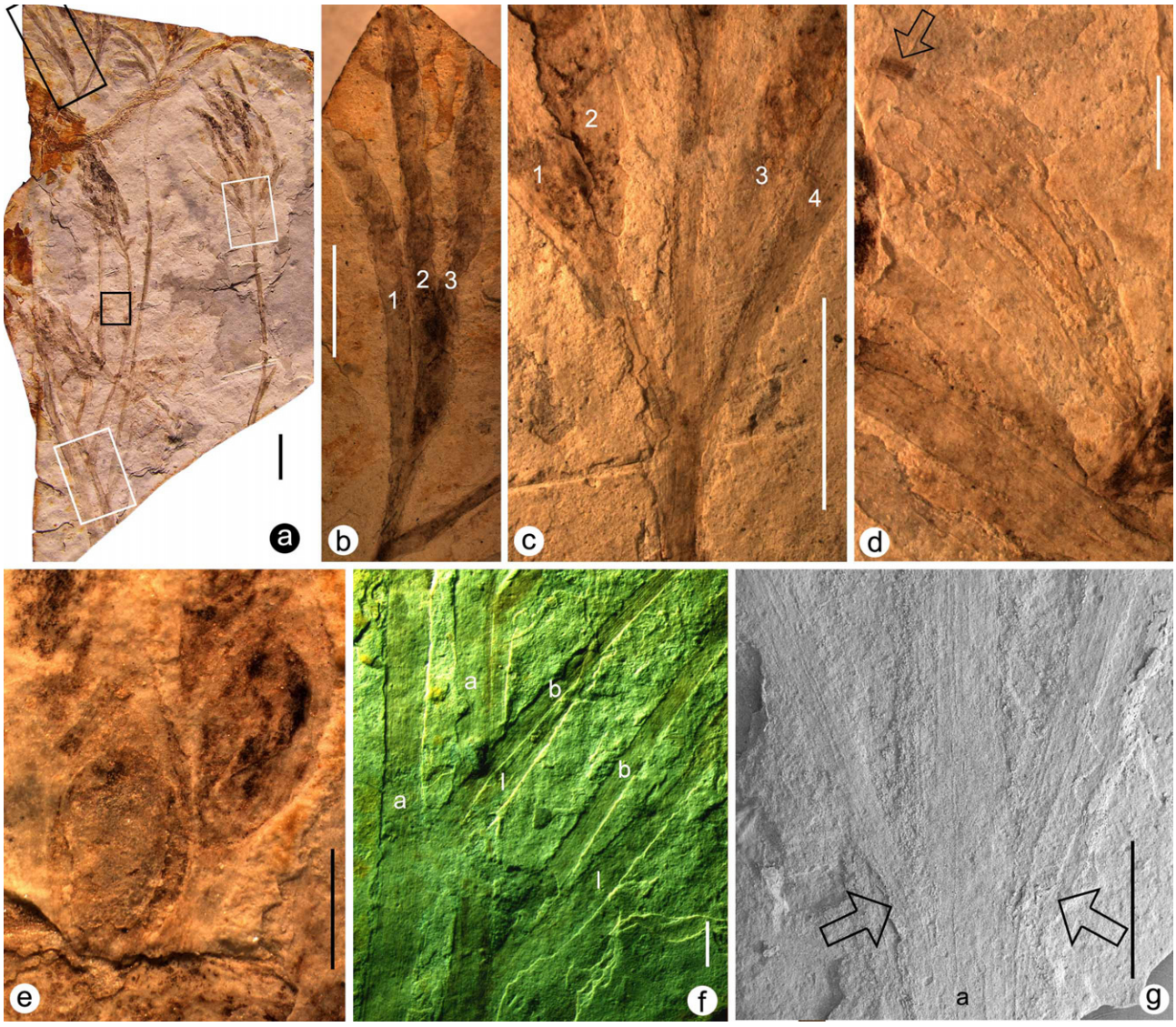


Fig. 1. Infructescences, fruits, and seeds of *Archaefructus sinensis*. All except (a) and (g) are light microscopy. PB21535. (a) The general morphology of the fertile parts, showing the relationship among the axes and fruits. Camera picture. Scale bar = 10 mm. (b) A cluster of fruits (1–3) on a shared fruit pedicel, long fruit with numerous seeds, and another infructescence axis (bottom right). Scale bar = 5 mm. (c) Opposite arrangement of fruit pairs along the vertical axis (central). Scale bar = 5 mm. (d) Clusters of stamens. Note 2–3 stamens in a cluster and a connective (arrow). Scale bar = 1 mm. (e) Two oval seeds in two separate and parallel fruits. Scale bar = 1 mm. (f) Branching pattern of the axes. Note that two of the infructescence axes (b) are attached on the main axes (a) in the axils of leaves (l). Scale bar = 2 mm. (g) Opposite branching pattern of the axes, detailed view of branches in (c). Note the longitudinal vascular bundles in the main axis (a) and two oppositely arranged shared fruit pedicel (arrows). SEM. Scale bar = 1 mm.