

An Era of Errors

Unveiling the Truth of *Archaeanthus* and Its Implications for Angiosperm Systematics

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Abstract *Archaeanthus* is a famous Cretaceous angiosperm from the Albian-Cenomanian of Kansas, USA documented by Dilcher and Crane in 1984. Its seeds/ovules were interpreted as arranged along the adaxial (ventral) suture of the fruits. This interpretation used to be plausible, especially under the light of then-dominating doctrine of angiosperm evolution. However, Dilcher and Crane's interpretation of ovule insertion was not fully supported even by their own evidence. Considering the early age, importance and influence of *Archaeanthus* in palaeobotany and angiosperm systematics, it is necessary to double check the ovule insertion in *Archaeanthus* and its implications for homology of carpel as well as origin of angiosperms. New observation on the type materials of *Archaeanthus* indicates that, besides adaxial(ventral) arrangement of ovule/seed as assumed formerly, at least some ovules/seeds in *Archaeanthus* are attached to the abaxial(dorsal) margin of the fruit. This information undermines the former assumed Magnoliaceous affinity of *Archaeanthus*, and falsifies its support to the influencing speculation of carpel homology and origin of angiosperms. Analysis of the common reason underlying the misinterpretations of early fossil angiosperms (including *Archaeanthus*, *Archaeofructus*, and others) indicates that the speculation of Arber and Parkin is groundless and the major culprit in flouting botany in the past century.

Keywords: carpel, homology, origin, fossil, angiosperms.

Angiosperms are the most important group of plants in the current earth ecosystem. However, little is known about the origin of angiosperms, which has been a headache for many botanists. The core question in the origin of angiosperms is the homology of carpels. Formerly, Arber and Parkin¹ speculated that the carpels in angiosperms are derived from the former megasporophylls bearing ovules along their margins. Consequently, conduplicate carpels bearing ovules on its adaxial(ventral) margins (as in Magnoliaceae) were taken as the most ancestral among angiosperms^{2,3}. This hypothesis remained unsupported by fossil evidence until the famous fossil plant *Archaeanthus*⁴ was published in 1984. Such a support was later reinforced by the so-called "first flower" *Archaeofructus*^{5,6}, which was assumed to have "conduplicate" carpels. However, more careful research indicates that *Archaeofructus* has no "conduplicate" carpels (namely, its ovules are inserted along the dorsal side of the fruits)^{7,8}, greatly reduces the credibility of Arber and Parkin's hypothesis¹, especially when the basalmost angiosperm *Amborella* with ascidiate carpels does not fit in the Arber and Parkin's image of ancestral angiosperms. The situation becomes more suspicious when it is found that Dilcher and Crane's evidence did not fully support their own interpretation of ovule insertion in *Archaeanthus*. Therefore the ovule insertion in *Archaeanthus* being adaxial or abaxial becomes a crucial question in botany, as the answer to which may decide the ultimate fate of hypothesis of Arber and Parkin¹ that has been the foundation for many botanical progresses. To ascertain the ovule insertion in *Archaeanthus*, I re-examined the type materials of *Archaeanthus* described by Dilcher and Crane⁴ and report my observation here.

My observation focuses on only one feature of *Archaeanthus*, namely, the ovule insertion in the fruits, therefore other aspects of *Archaeanthus* will be ignored and not be discussed here, since Dilcher and Crane⁴ have documented them well before. To demonstrate the ovule insertion in the fossil clearly, two infructescences of *Archaeanthus* are shown in Figs. 1a-b, with their apices pointing to the top. Enlarging from the organ in Fig. 1a, I show one of the fruits in Fig. 1c. The adaxial side of the fruit is oriented to the upper, and abaxial side to the lower. There are several seeds inside this fruit, some in the proximal portion and some in the distal portion (Fig. 1c). The proximal seeds are clearly inserted along the abaxial side (Figs. 1c-d), while the two distal seeds/ovules are apparently inserted along the adaxial side (Figs. 1c, e). So the ovules are inserted along both adaxial and abaxial sides in this single fruit of *Archaeanthus* (Figs. 1c-e). In the meantime, ovules/seeds in some fruits of *Archaeanthus* are indeed inserted along the adaxial margin (Figs. 1b, f). This result is apparently at odds with interpretation of Dilcher and Crane⁴, in which the ovules were interpreted as inserted along the "adaxial suture" (page 351, 363, 364, 371).

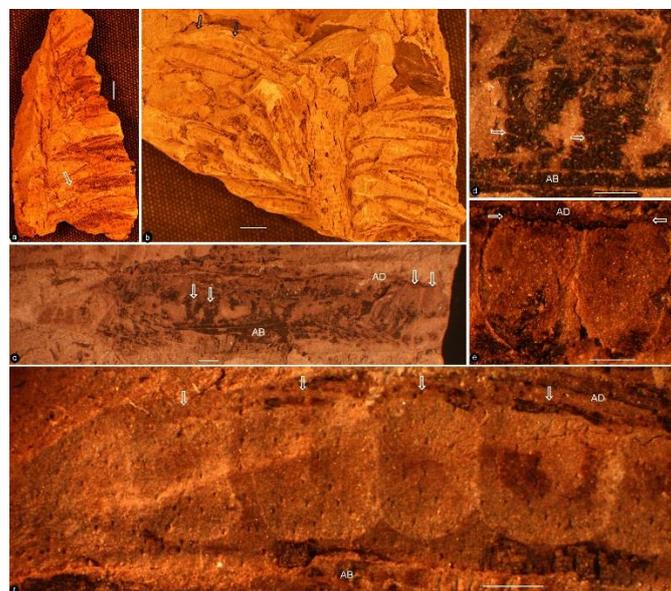


Figure 1 Infructescences, fruits, and *in situ* seeds of *Archaeanthus linnenbergeri*. **A.** An infructescence. IU15703-2300'. Bar = 5 mm. **B.** Another infructescence. IU15703-2300''. Bar = 5 mm. **C.** Detailed view of the fruit arrowed in Fig. 1a. Note the positions of four seeds (arrows) and their spatial relationship relative to the adaxial (AD) and abaxial (AB) margins of the fruit. Bar = 1 mm. **D.** Detailed view of the two proximal seeds (marked by two left arrows in Fig. 1c). Note the attachment of seeds (arrows) to the abaxial margin (AB) of the fruit. Bar = 0.5 mm. **E.** Detailed view of the two distal seeds (marked by two right arrows in Fig. 1c). Note their attachment (arrows) to the adaxial margin (AD) of the fruit. Bar = 0.5 mm. **F.** Detailed view of a row of seeds (arrows) inside the fruit marked by the arrows in Fig. 1b. Note the attachment of seeds to the adaxial margin (AD) of the fruit. Bar = 1 mm.

Can this difference between my observation and that of Dilcher and Crane⁴ be due to observing different fruits of *Archaeanthus linnenbergeri*? Such a possibility can be ruled out completely, as what I observed is exactly the same fruit in the same specimen (IU15703-2300') as shown in Fig. 24 of Dilcher and Crane⁴. Examining Fig. 24 of Dilcher and Crane⁴, one can easily find that the ovules are apparently indeed inserted along the "abaxial" margin of the fruit. But Dilcher and Crane⁴ interpreted the ovules/seeds of *Archaeanthus* as inserted along the "adaxial" margin inside the fruit. How could this happen? What was wrong then?

There are two possible scenarios to account for the above difference in observation. 1) Dilcher and Crane did not note the abaxial ovule insertion in *Archaeanthus*, due to carelessness or whatever reason. They took it for granted and subconsciously documented *Archaeanthus* in such a way, compatible with the expectation of majority botanists (the then-dominating botanical doctrine), and making their fossil flower more comparable to the assumed ancestral angiosperms (Magnoliaceae) and thus more attractive and more important in botany. 2) Dilcher and Crane were aware of the abaxial ovule insertion in *Archaeanthus*, but after long-time balancing and calculating they managed to make a decision to ignore this fact because they could afford to tell the truth since such a truth would topple their long-adopted botanical doctrine advanced by Arber and Parkin¹, incur criticisms from peers who are loyal to the doctrine and thus feel offended by their telling the truth, and, unacceptably, probably kill their paper. Which scenario was the case? After 34 years, only Dilcher and Crane can tell.

No matter which scenario is the case, it is apparent that Dilcher and Crane were victims of the then-overwhelming botanical doctrine, which is the major culprit underlying many mistakes in botany. Now it is clear that the ovules are not inserted ONLY along the adaxial suture in *Archaeanthus*. Instead the ovules in *Archaeanthus* may be inserted either along the abaxial, or adaxial, or both sides of fruits. This information rules out any magnoliaceous affinity for *Archaeanthus* since in Magnoliaceae the ovules are not inserted along the abaxial in the fruits³. Interestingly, *Neofructus*, a fossil recently found from the Early Cretaceous Yixian Formation, demonstrates clearly that, at least in some fruits, the ovules are inserted along both the adaxial and abaxial margins in the same fruit⁹. The carpels in *Archaeanthus* and *Neofructus* may be derived from formerly two facing ovule-bearing branches (placentas) and two facing foliar parts (ovarian walls), and ovule insertion on only one margin of the carpel/fruit (as in *Archaeofructus*^{7,8}, *Nothodichocarpum*¹⁰, and some *Archaeanthus*) may be derived from those with ovules along both margins by loss of one placenta. The chimerical occurrence of both abaxial + adaxial as well as adaxial only ovule insertions in *Archaeanthus* appears to be an ideal intermediate status between those in *Neofructus* and *Magnolia*.

It is noteworthy that, like in *Archaeanthus*⁴, the carpels in *Archaeofructus liaoningensis*⁵ used to be similarly misinterpreted as "conduplicate", implying adaxial ovule insertion in the fruits. A recent study¹¹ indicates that a typical carpel in Magnoliaceae actually is a composite organ derived from a former ovule-bearing branch plus a subtending foliar part, rather than be a "megasporephyll", which has been proven non-existing among seed plants^{12,13}. Therefore the assumed support for the doctrine advocated by Arber and Parkin¹ from *Archaeanthus*, *Archaeofructus* and Magnoliaceae has gone vaporized, leaving all conclusions in angiosperm systematics hinged with such a doctrine in the past century shaky and suspicious. The situation becomes more embarrassing when the readers realize that, as early as 1925, Parkin had admitted that their 1907 speculation had no fossil support¹⁴. It appears that the speculation of Arber and Parkin (1907) was groundless since the very beginning! Apparently, ensuing botanists (especially the fanatic proponents of Arber and Parkin's speculation) lack the capability of critical thinking, and they appeared to have formed a faction that is characterized by their naivety and loyalty. Although great palaeobotanists, Dilcher and Crane were unexceptionally not immune to the then-influencing, illusive, distorted perspective of plant evolution. Their misinterpretations about ovule insertion in *Archaeanthus* and

Archaeofructus more or less reflect their overawing authority and their preference of conformity (political correctness) in botany. Similarly, the claims of non-existing ovule insertion in Magnoliaceae³, bitegmic ovules in *Monetianthus*¹⁵, and free carpels in *Kajanthus*¹⁶ are very likely the products of knowingly data-processing more or less related to the "assumedly correct" classical theory of angiosperm evolution. Such treatments are the routine and hallmark of the age rather than a personal character or weakness. The current deadlock in origin of angiosperms is a direct consequence of Arber and Parkin's speculation. Any essential progress in angiosperm systematics and origin of angiosperms will not be possible before the influence of Arber and Parkin (1907) is purged thoroughly throughout botany.

Methods Specimens were photographed with a Sony ILCE-1 digital camera. Details of the specimens were observed and photographed under a Nikon SMZ-10 stereomicroscope equipped with a Canon EOS Rebel XSi digital camera. All photographs were saved in JPEG format and organized for publication using Photoshop 7.0.

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