Androecium of *Archaefructus*, the Late Jurassic Angiosperms from Western Liaoning, China

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Abstract Androecium of the earliest known flowering plant *Archaefructus liaoningensis* was found from the Upper Jurassic Jianshangou Formation of western Liaoning, China. The androecium consists of numerous stamens bearing in pair on the reproductive axes below conduplicate carpels. The stamens are composed of a short filament and basifixed anther for each. Monosulcate pollen *in situ* are found from the anthers. The characters of the androecium reveals that *Archaefructus* are probably protandrous, and the paired stamens and monosulcate pollen appear to indicate that *Archaefructus*, as primitive angiosperms, might be derived from extinct seed - ferns during the Older Mesozoic. *Archaefructus* is considered Late Jurassic in age.

Key words Androecium, *Archaefructus*, Early angiosperm, Late Jurassic, Western Liaoning of China

Introduction

Archaefructus, the oldest known angiosperms, were found from the Upper Jurassic Jianshangou Formation (i. e. the former lower part of Yixian Formation) of Beipiao in western Liaoning, China (Sun et al. ,1998; Sun et al. ,2001) (Text - Fig. 1). However, the type - specimen of *Archaefructus liaoningensis* only shows the main and lateral fertile shoots which bear follicles (conduplicate carpels) enclosing seeds (ovules) and arranged above some "peg - like" projections remaining on the axes (Pl. 1, Fig. 8). The main fertile shoot is up to 85 mm long and 3 mm wide basally tapering to 1 mm distally. The lateral fertile shoot is thinner, about 86 mm long and tapering upwards also. Both the shoots have numerous fruits (18 ~ 30 observed) which are follicles derived from conduplicate carpels. The carpels contain 2 ~ 5 seeds (ovules) which fill fruits in an oblique orientation. Cuticle of the seed coats are thin, epidermal cells are rectangular - polygonal in shape, anticlinal cell walls are sinuous and cutinized, and periclinal cell walls are somewhat unevenly cutinized. The flowering plants are less specialized in floral morphology, particularly lack petals and sepals.

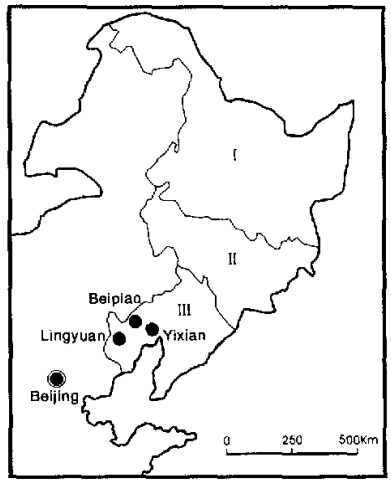

Fig. 1 Geographic positions of the Localities of *Archaefructus*

I-Heilongjiang; II-Jilin; III-Liaoning

Since 1999, some unique fossils of *Archaefructus*

with androecium and leaves were found by the authors (Sun et al., 2001). The androecium consists of the stamens bearing in pairs on the axes below the carpels, which has reveals that the "peg - like" projections previously seen on the axes were actually the remains of *Archaefructus* stamens abscised leaving the mature shoots. The leaves are small, thin, pinnately dissected 3 ~ 4 times and subtending a fertile shoot in its axis. The leafy and fertile stems are slender, extending for some distance. Numerous fish (*Peipiaosteus* and *Lycoptera*) are associated with the fossil plants. All the characters suggest an aquatic habitat and herbaceous nature for *Archaefructus* (Sun et al., 2001). *Archaefructus* probably was exposed above the water during pollination and may have remained for seed dispersal (Pl. 1, Fig. 6).

1 Androecium

Several specimens of the fertile shoots bearing stamens and carpels have been found and studied by the authors for the recent years. The androcium consists of 15 ~ 26 stamens usually in pairs attached to those projections. The stamens are about 3.5 ~ 4.5mm long by 1 ~ 1.2mm wide for each, consisting of a short filament (0.25 ~ 0.5mm long) basifixed to an anther (2 ~ 3mm long by 1 ~ 1.2mm wide) and usually with an extended tip about 0.5 to 1mm long. The narrow tip of the anther extends past the thecae and may be a narrow attenuate connective tip or an extension of the filament. The anthers appear to have two distinct thecae parallel in arrangement and perhaps each containing two longitudinal pollen sacs. Pollen are found from the anthers *in situ*, nearly elliptic in form and about 17 ~ 36μm × 15 ~ 20μm in size. They are monosulcate in aperture, with sulcus extending along the long axis of grains on distal surface and reaching the equator, and exine reticulated by subcircular lumina about 0.3 ~ 0.5μm in size with muri about 0.5 ~ 1.0μm wide. Under epifluorescent microscopy the authors observed some isolated pollen on the stigmatic crests of the carpels, particularly on the extended tips of the young carpels.

The new material of the female and male reproductive organs of *Archaefructus* shows various stages of their reproductive maturity. The carpels appear to mature last, after the pollen has been dispersed and anthers lost on the same axis. The stamens were produced in pairs and attached on the stalks only while the carpels were very young, as suggested by their small size and close spacing. As the carpels matured, the stamens abscised leaving the short stalks that remain on the mature shoots.

Although the stamens and carpels of *Archaefructus* superficially more or less resemble those of *Caytonia*, a similar age plant, they are very different when examined closely. The carpels of *Archaefructus* are closed along an adaxial stigmatic crest, and the stamen symmetry is bilateral with monosulcate pollen. In *Caytonia* the "fruit" is not completely closed, and in *Caytonanthus* the stamen symmetry is radial and the pollen is bisaccate (Harris, 1964).

2 Phylogenetic Significance

The stamen record provides useful information for phylogenetic analysis of angiosperm characters. The stamens of *Archaefructus* described demonstrate a distinct differentiation between the short filament and the anthers that are not laminar. This supports the hypothesis that there is no homologous relationship between the stamen and the carpel. The presence of non - laminar stamens extremely early in angiosperm history supports the view that stalked anthers are primitive. Stamen bundles are formed in a variety of living angiosperms when there is a secondary subdivision of the androecial primordium (Endress, 1994). As a result of this secondary primordial activity a single primordium may produce several stamens. The stamens produced this way are basally fused. The stalks found in *Archaefructus* may represent the remains of stamen filaments that are fused together. The paired stamens

of Archaefructus may be collateral pairs of stamens that result in doubling of organs as has been observed in the Magnoliidae and in the Alismatidae (Endress, 1994). Such stamen pairs resulting from paired initial primordia might reflect an ancient history of this character found in the stamen bundles of *Archaefructus*. This type of primordia in the androecium has been presented as a possible primitive character.

The stamens matured while the carpels were very young, which implies that *Archaefructus* might be protandrous. The functional nature of the pollen and stigmas cannot be determined from the fossils, but the potential for pollen to mature and be dispersed before the carpels associated on the same axis were receptive, is certainly possible. This type of dichogamy would increase fitness by establishing a self – isolating mechanism to insure outbreeding. The small size of the immature carpels and the ovules contained in them suggests that unless pollination and fertilization occurred they would never have developed into mature fruits and seeds. Early in angiosperm history, fruit development was probably closely tied to successful pollination. In this way, the angiosperms can avoid investing energy in the production of sterile fruit and seed tissue.

There are no petals, sepals or bracts to help define the floristic nature of these reproductive organs, but simply a leaf basal to each complete set of male and female reproductive organs in *Archaefructus liaoningensis*. If we consider that the term "flower" is related to an organizational plan, then it is reasonable to consider that each set of multiple carpels and stamens helically arranged along individual elongated shoots and subtended by leaves could be considered a flower. The "flower" of *Archaefructus* may represent a stage in evolution in which its reproduction is angiospermous (ovules enclosed in carpels) while the organization of the traditional floral unit(s) is still poorly defined. Perhaps as the evolutionary history of the modern ovulate pine cone can be understood only by knowing its complex branching ancestors, the evolutionary history of the flower may also involve complex branched ancestral axes.

Morphological characters, especially those of the reproductive (flower) organs have been the traditional basis for organizing the phylogeny of the angiosperms (Cronquist, 1981). Because patterns of reproductive organs have been the traditional basis for establishing a natural system of flowering plant classification, it is important to study reproductive organs from the fossil record. *Archaefructus liaoningensis* is much more completely known and they become the most complete earliest flower and flowering plants known. The origin of the organization of reproductive organs seen in *Archaefructus* has a bearing upon how we view the potential ancestor of flowering plants. Many theories or hypotheses of angiosperm origin have been proposed in the past century. Among these are the euanthium (Arber & Parkin, 1908) and the pseudanthium (Wettstein, 1907; Krassilov, 1997) theories. The euanthium theory interpreted the angiosperm flower organization as evolving from a bisexual strobilus with numerous, helically arranged ovules and pollen bearing organs as found in *Cycadoidea* or other Mesozoic bennettialean plants. The ovule and pollen bearing organs were already differentiated and associated with perianth organs that were suggested to be attractive to insect pollinators. The pseudanthium theory proposed that the ancestral plants of angiosperms had separate branching systems containing ovules and pollen organs. As the hypothetical floral units that formed these branching systems were clustered together, they eventually condensed and modified into a shoot with terminal carpels subtended by stamens. Petals and sepals evolved and became part of the whole unit subtending these newly organized reproductive shoots. Ancestors with male and female organs on separate branches are found in the Mesozoic seed ferns such as *Caytonia*. *Archaefructus* appears to support the pseudanthium theory with the stalks bearing paired

stamens perhaps being remnants of an earlier branching system while the petals and sepals have not yet evolved from subtending leaves.

3 Geological Age

The geological age of the Yixian Formation of western Liaoning, China has been in controversy, which is concerned in the age of *Archaefructus*. The authors have still considered the age as ca. 143Ma (Wang, 1983) to 147Ma (Lo et al., 1999). It has been suggested that the lower part of the Yixian Formation is Late Jurassic age, while the upper part of the formation is the latest Jurassic to Early Cretaceous (Sun et al., 2001). In a comprehensive survey of the flora, of which *Archaefructus* is a part, the authors found that it consists of at least 88 species belonging to 56 genera (Sun et al., 2001). Among them the taxa *Coniopteris angustiloba* Brick, *Xiajiajienia mirabila* Sun et Zheng, *Solenites murrayana* L. et H. and *Problematospermum ovale* Tur. - Ket., have only been recorded in the Middle - Upper Jurassic floras from the Karatau of Kazakhstan (Doludenko et al., 1976), the United Kingdom (Harris et al., 1974) and Jilin of China (Sun et al., 1992). The occurrence of Gnetales (e. g. *Ephedrites*, *Gurvanella*), Bennettitales (*Otozamites*) and cheirolepidiaceous Conifers (e. g. *Brachyphyllum*, *Pagiophyllum*) associated with *Archaefructus* implies an arid or semiarid climate in western Liaoning, and possible eastern Asia. This is consistent with observations by Vakhrameev for cheirolepidiaceous pollen *Classopollis* that indicates a time of Late Jurassic (Vakhrameev, 1988). Paleontologists have considered the animal fossils found in the lower part of the Yixian Formation characteristic of the Late Jurassic, such as the "feathered" dinosaurs *Sinosauropteryx* that is comparable to the theropod dinosaur Compsognathoid from the Upper Jurassic (lower Tithonian) of Solnhofen, Germany (Chenet al., 1998); the pterosaur *Dendrorhynchushas* has not been recorded younger than the Late Jurassic (Ji et al., 1999), the insect *Aeschnidium heishankowense* from the same beds bears a close resemblance to *Aeschnidium densum* from the lower Tithonian of Germany (Zhang, 1999). Some isotopic dating of the lower part of Yixian Formation has supported the age of Late Jurassic as 142.5Ma (Wang, 1983) and 147.1 ± 1.8Ma(Lo et al., 1999). But, there have been some differences in opinion on the age. Recent radiometric dates published indicate an age about 122.9 Ma (Smith et al., 1995) and 124.6Ma (Swisher et al., 1999). But, it should be mentioned that there are several volcanic intrusive between the fossil - rich beds in this area that might affect the isotopic dating results. A cautious range of ages Upper Jurassic (ca. 145Ma) is given as the age in this paper in order to present the fossil. The age range given still makes this the oldest, most complete angiosperm reproductive fossil known as far as we can determine.

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Explanation of the Plate

The specimens shown in the plate are hosted in the following places: PB18938, PB18944, PB18948 in the Nanjing Institute of Geology and Palaeontology, CAS in Nanjing; B - 2000 and RCPS - A0001 in the Research Center of Paleontology & Stratigraphy, Jilin University in Changchun, China.

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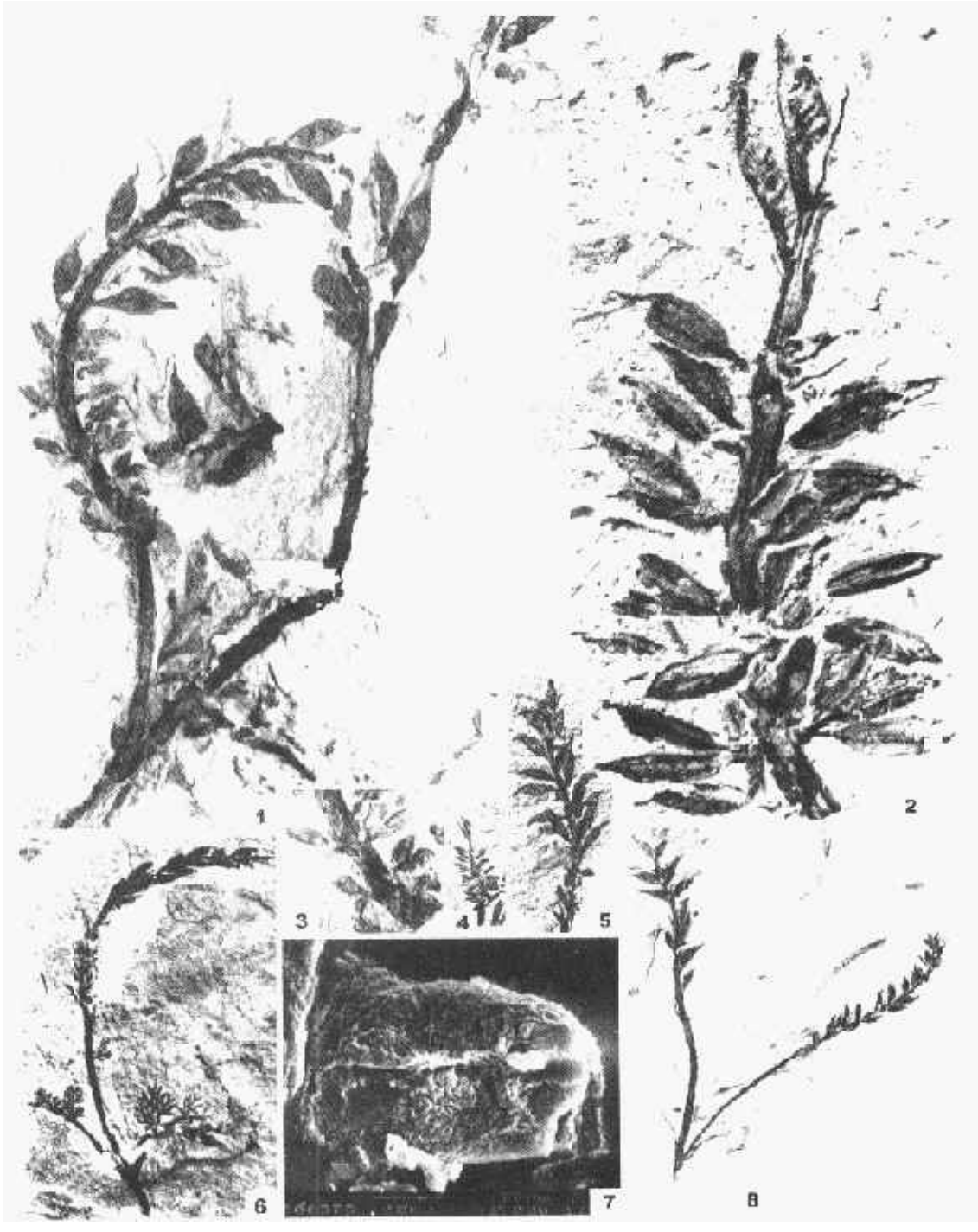
Plate 1 ***Archaefructus liaoningensis*** **Sun, Dilcher, Zheng et Zhou**

1, 3-Paratype (B - 2000): 1-showing mature fruits and peg - like projections on the main shoot while to the left side there is a lateral shoot with stamens and young fruits; and a leaf base extended across the lateral shoot with the distal portion of the dissected leaf preserved; ×2. 5; 3-showing the paired stamens, ×3. 5; 2, 4-Two young fruits with stamens below, 2 is enlargement of 4, ×7, PB18948; 5-A reproductive shoot with younger carpels and stamens, ×2, PB18944; 6-A complete shoot with leaves subtending the main reproductive axis, ×0. 8, RCPS - A0001; 7-Pollen grains showing monosulcate aperture (SEM200575), the pollen from the specimen PB18943; 8-The type - specimen, ×0. 67, PB18938.



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