

3D MODELS OF TWO SPECIES OF *ARCHAEFRUCTUS*, ONE OF THE EARLIEST ANGIOSPERMS, RECONSTRUCTED TAKING ACCOUNT OF THEIR ECOLOGICAL STRATEGIES

Kazuo TERADA¹, Ge SUN² and Harufumi NISHIDA³

¹Fukui Prefectural Dinosaur Museum, 51-11, Terao, Muroko, Katsuyama, Fukui 911-8601, Japan

²Research Center of Palaeontology and Stratigraphy, Jilin University, 6 Ximinzhu Street, Changchun 130026, China

³Faculty of Science and Engineering, Chuo University, 1-13-27 Kasuga, Bunkyo, Tokyo 112-8551, Japan

ABSTRACT

Archaeofructus is one of the earliest known angiosperms discovered from the Upper Jurassic/Lower Cretaceous Yixian Formation in Liaoning, China. We created 3D reconstruction models of two of the three known species of *Archaeofructus*, namely, *A. liaoningensis* and *A. sinensis*. During the course of modeling, we noticed some species-specific features. *A. liaoningensis* differs from *A. sinensis* in having fluted structure as longitudinal ridges on the stem surface. The flowering in *A. liaoningensis* initiates basipetally from the main shoot to the lateral shoots, while that in *A. sinensis* initiates acropetally from basal lateral shoots to the main shoot. If both species are aquatic herbs, these differences in morphological features and flowering order may reflect adaptive or ecological strategies. Because *A. liaoningensis* was a small plant growing in shallow water, its stem ridges, which were an adaptation to unpredictable changes in the water level, provided mechanical strength to the stem when the water level dropped. Moreover, the basipetal flowering in *A. liaoningensis* enhances rapid seed propagation during the plant's short lifespan before the onset of unpredictable dry periods, which is a r-selection strategic phenomenon. In the case of the considerably large *A. sinensis* that might have inhabited deeper water, acropetal flowering slowly and continuously produced lateral shoots during a longer lifespan under minor water stress, which is a K-selection strategic phenomenon. Different adaptive strategies in these two earliest angiosperm species of the same genus suggest the possibility of physiological modifications during their developmental stages.

Key words: *Archaeofructus*, basal angiosperm, plant evolution, r-K selection strategy, 3D model

寺田和雄・孫 革・西田治文 最初期の被子植物 *Archaeofructus* 2種の生態的戦略を考慮した3次元復元模型. 福井県恐竜博物館紀要 4: 35–44.

Archaeofructus は中国遼寧省の義縣累層（ジュラ紀後期～白亜紀前期）から発見された最初期の被子植物の一つである。今までに記載されている3種のうち、2種 *A. liaoningensis* と *A. sinensis* の精巧な復元模型を製作した。その復元過程で、両種の形態的差異をいくつか見出した。*A. liaoningensis* は、茎の表面に縦に走る溝をもつが、*A. sinensis* には見られない。両種の開花から結実までの過程を個体ごとに比較すると、*A. liaoningensis* では、中央の主軸の花がまず成熟し、ついで求基的に側枝の花が開花するが、*A. sinensis* では、最下部の側枝から順に求頂的に開花結実し、主軸が最後に成熟する。両種が水生草本だとすると、この違いは次のように説明できる。*A. liaoningensis* は小さく、湖岸など浅い、水位の変動を受けやすい環境で生育していたので、茎を條溝のような構造で補強し、低水位時に体を物理的に支える必要があった。また、水が干上がる前に果実を成熟させる必要があり、変動を受けやすい環境に対応して r 選択戦略的に、短い生活史のあいだに主軸がまず先に成熟し、素早く種子生産を行うことができる開花様式をとった。一方、比較的大きい *A. sinensis* は、水深があり、水が干上がることの少ない安定した環境に生育していたと考えられるため、K 選択戦略的に長い生活史のもとで、多くの側枝を成長させて、主軸は最後に成熟する開花様式をとった。*Archaeofructus* の2種は、すでに生態的には異なる特性を進化させており、また、花の形成順序に関わる生理的な分化も確立していた可能性がある。

Corresponding author — Kazuo TERADA

Phone: +81-779-88-0001, Fax: +81-779-88-8710

E-mail: k-terada@dinosaur.pref.fukui.jp (*を半角@に変えてご入力ください)

INTRODUCTION

The origin and early evolution of flowering plants (angiosperms), which Charles Darwin referred to as an "abominable mystery," have not yet been elucidated by biologists. In 1998, *Archaeofructus liaoningensis* Sun, Dilcher, Zheng & Zhou, one of the oldest angiosperm megafossils (Fig. 1), was discovered from the lower part of the Upper Jurassic/Lower Cretaceous Yixian Formation in Beipiao, western Liaoning, China (Sun, Dilcher et al., 1998). In 2002, an additional species *A. sinensis* Sun, Dilcher, Ji & Nixon (Fig. 2) was described from the same formation exposed at Lingyuan in western Liaoning (Sun, Ji et al., 2002). Based on these fossil species, a new family Archaeofructaceae was established by Sun,

Ji et al. (2002). They also proposed a cladogram in which the family was placed at the basal-most position as a sister to the clade that included all other living angiosperms. Subsequently, a third species *A. eoiflora* Ji, Li, Bowe, Liu & Taylor was added to the family by Ji et al. in 2004.

Archaeofructus Sun, Dilcher, Zheng & Zhou has been reconstructed as a branching aquatic herb. Each vegetative shoot terminates into a reproductive organ that is typically interpreted as a single flower bearing a basal microsporangiate organ and a distal megasporangiate organ, but lacking petals and sepals. The microsporangiate organ has stamens that are attached to an elongated floral axis. The megasporangiate organ is composed of conduplicate carpels containing several obliquely oriented ovules (2–5 in *A. liaoningensis*, 8–12 in *A.*



FIGURE 1. Fossils of *Archaeofructus liaoningensis*. **A** and **B**, The holotype specimen. **A**, Whole specimen showing that the main shoot matured before the lateral shoot. M: Main shoot, L: Lateral shoot. Boxed area is magnified in **B**; **B**, Reproductive part of the main shoot showing completely matured carpels and fluted structure on the shoot surface. Scale bar: 1 cm; **C**, Another specimen deposited in the Jilin University, showing that the main shoot matured before the lateral shoot. M: Main shoot, L: Lateral shoot. Scale bar: 2 cm.

sinensis; Figs. 1, 2). The flower was probably raised above the water level during anthesis, and it might have remained in this position until seed dispersal. The leaves are alternate and the fronds are dissected. The roots are poorly developed (Sun, Dilcher et al., 1998; Sun, Zheng et al., 2001; Sun, Ji et al., 2002).

At the Fukui Prefectural Dinosaur Museum, we had an opportunity to reconstruct three-dimensional (3D) models of the

previously described two species of *Archaeofructus*, *A. liaoningensis* and *A. sinensis*, for an exhibition. During the reconstruction work, we noticed some morphological features for the first time; these characteristic features pertain to the ecological adaptations of the two species. Here, we briefly report the model reconstruction procedures; further, we note the adaptive segregations inferred for these two closely related early angiosperm species.

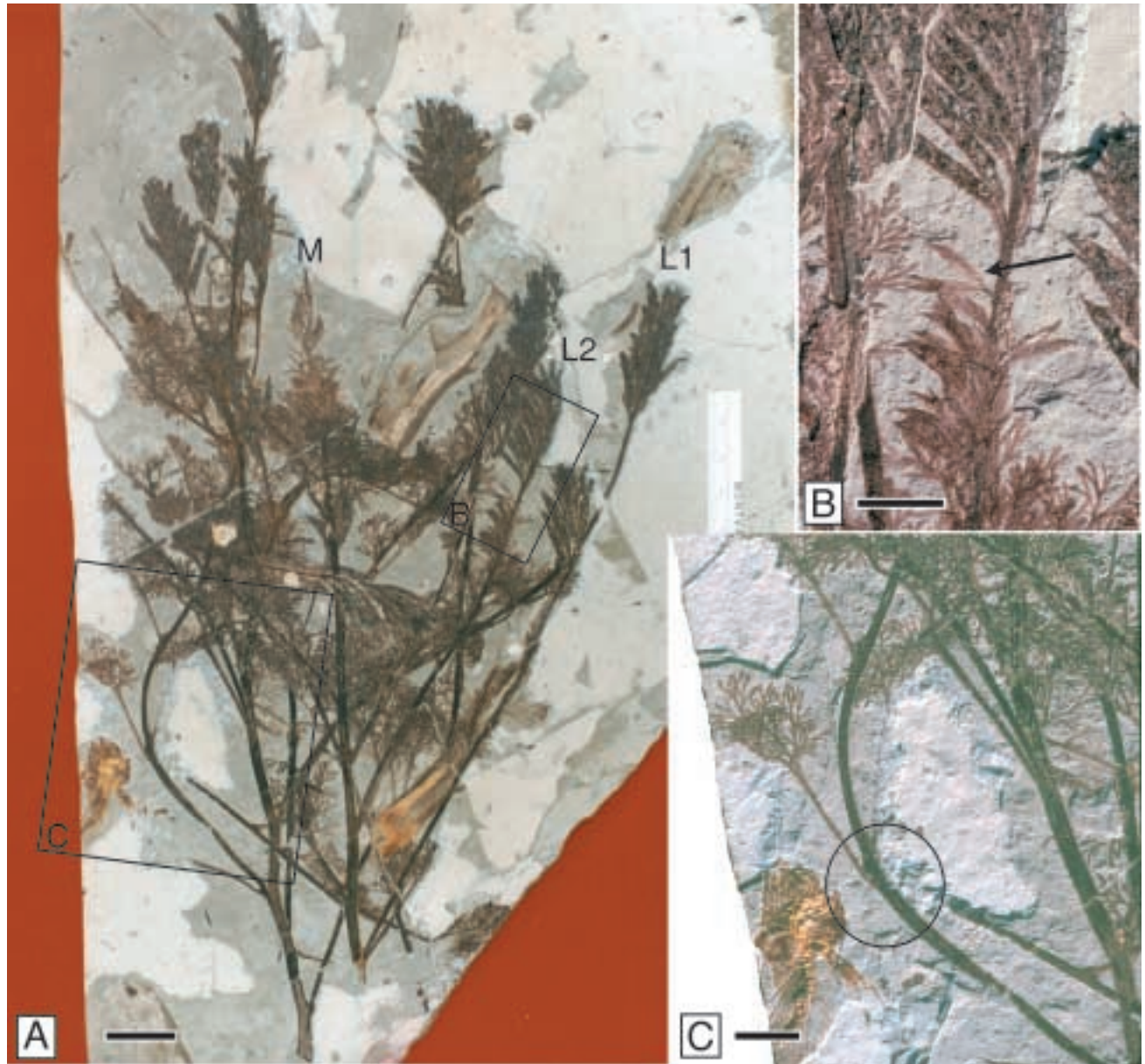


FIGURE 2. Fossils of *Archaeofructus sinensis*. **A** to **C**, The holotype specimen. **A**, Whole specimen, showing that the main shoot is least matured compared to the lateral shoots. M: Main shoot, L1 and L2: Lateral shoots. Scale bar: 5 cm. Boxed areas are magnified in **B** and **C**; **B**, Reproductive part of the lateral shoot (L2) showing the completely matured carpels along with basifixed paired stamens and smooth shoot surface. Arrow indicates basifixed paired stamens. Scale bar: 1 cm; **C**, Vegetative part of the shoot showing dissected leaves in detail and a long petiole. Circle indicates a petiole base lacking a swollen feature. Scale bar: 1 cm.

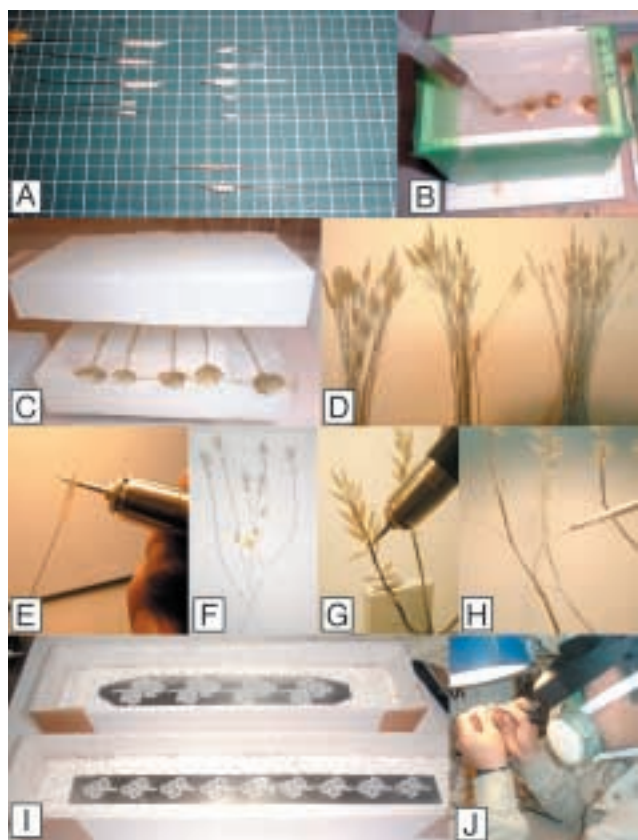


FIGURE 3. Making process of 3D models. **A**, Master casts of carpels (follicles) and stamens made of epoxy resin showing carpels (follicles) of different sizes that correspond to the stages of maturity; **B**, Polyester resins being poured into silicon-rubber molds, which were made using the master casts; **C**, Isolation of solid polyester resin casts attached to steel wires; **D**, Casts of reproductive organs; **E**, Cast being carved by hand-made chisel; **F**, Arranged casts of reproductive organs; **G**, Bundled steel wires attached to the reproductive organs; **H**, Coating the body with a polyester resin; **I**, Stainless-steel panels that have been transcribed with illustrations of leaves before acid etching; **J**, Hand-made 3D models being made.

RECONSTRUCTION OF THE MODELS

Since the reconstruction concepts and procedures differ between organs among plants, we now describe processes featured by each organ separately (Fig. 3).

Carpels (Fruits) and Stamens

1. Master casts were made of epoxy resin (Fig. 3A). Carpels or follicles enclosing ovules or seeds were reconstructed in order to clearly show their conduplicate nature. Small grains (ovules and seeds) were wrapped one by one like a Chinese chaozu (gyouza). The size variations of carpels (follicles) reflect different stages of maturity (Fig. 3A).

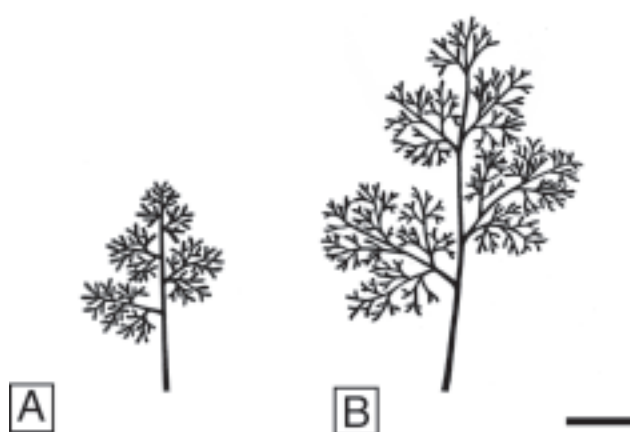


FIGURE 4. Illustrations of leaves drawn from *Archaeofructus* fossils. **A**, *Archaeofructus liaoningensis*; **B**, *Archaeofructus sinensis*. Scale bar: 1 cm.

2. Silicon-rubber negative molds were made using the master casts. The molds were cut into halves to isolate the original casts.

3. In order to form each organ part, polyester resins were poured into the molds (Fig. 3B) and a flexible steel wire of 0.03 mm in diameter was put into the resins. Solid casts are formed after the polyester resins hardened (Fig. 3C).

4. Cast details were carved on each resin cast with hand-made chisels (Fig. 3E).

Leaves

1. Master illustrations were prepared by using 1:1 magnification photographs of the fossil leaves of *Archaeofructus* (Fig. 4).

2. These illustrations were transcribed onto 0.5 mm thick stainless-steel panels (Fig. 3I).

3. Each leaf was reconstructed by deforming the steel panel by acid etching.

Stems and attached organs

1. Thin steel wires were bundled to create a general configuration of the stem (Fig. 3F).

2. The bundled wires were twisted, if necessary, to allow the insertion of helically attached organs such as stamens and carpels in the same orthostichy (Fig. 3G). Leaves were alternately inserted by cutting the corresponding part of the stem wires.

3. Lateral shoots were attached in the axils of the corresponding axillary leaves.

4. Finally, the body was coated with a polyester resin (Fig. 3H) and finished by coloring the surface with acrylic resin paint.

MAIN CONCEPT UNDERLYING THE CREATION OF MODELS

Archaefructus liaoningensis

The reconstruction was made based on the original and emended descriptions of the species (Sun, Dilcher et al., 1998; Sun, Ji et al., 2002) and by referring to the type specimen and some photographs of the fossils (Fig. 1; see Sun, Dilcher et al., 1998: fig. 2A, B; Sun, Ji et al., 2002: fig. 2E, J to L; Leng et al., 2003: fig. 252).

Model features.— The entire body was reconstructed as a relatively small herbaceous plant that is 16 cm tall and 10 cm wide. It has a rooted main shoot that monopodially branches twice giving rise to lateral shoots at its base (Fig. 5A). Each shoot terminates into an achlamydeous bisexual flower that is composed of basal stamens and distal monocarpic carpels, both of which are helically arranged on the floral axis (Fig. 5A, B). The flower is protandrous. The length ratio of gynoecium (carpelate axis) and androecium (staminate axis) corresponds to that in the fossil specimens (see Leng et al., 2003: fig. 252). Roots were reconstructed as a poorly developed, sparsely branched subterranean organ (Fig. 5A).

The carpels develop into follicles on the post-anthetic floral axis. The main shoot is 12 cm long, it is approximately 3 mm in diameter at the base and tapers to a diameter of 1 mm at the distal end (Fig. 5A, B). The lateral shoots emerge from the axil of each subtending leaf on the main shoot (Fig. 5A, B) and are up to 11 cm in length with diameters of 2 mm at the base and 1 mm at the distal end.

The carpel was reconstructed as a conduplicate organ. It is 7 to 10 mm long and 2 to 3 mm wide, and has a pedicle of 1 to 2 mm and a finger-like terminal projection with an approximate length of 1 mm (Fig. 5A, D, E, F). The carpels are helically arranged on the stem axis and crowded near the shoot apex (Fig. 5A, D, E, F). The main axis has 16 carpels, and the two lateral axes have 18 or 16 carpels each (Fig. 5A, D, E, F). The carpel (follicle) casts were prepared by individually placing two to four grains that resembled ovules or seeds in a conduplicate envelope, and then agglutinating the envelope along its adaxial stigmatic crest (Fig. 5D, E, F). The seeds were obliquely oriented in the follicle. The young carpel walls were reconstructed to have a thickness of 1–1.2 mm, whereas the follicle walls were reconstructed to have a thickness of 1.4–1.6 mm (Fig. 5D, E, F). The young carpels were inserted into the floral axis at acute angles (Fig. 5D, by referring to Leng et al., 2003: fig. 252); however, the carpels of later developmental stages or the follicles were inserted at wider angles (Fig. 5F, by referring to Fig. 1A).

The main shoot has six stamens and eight filamentous remains of fallen stamen bases. The two lateral shoots have 13 stamens each. The stamens occur approximately 15 mm below the gynoecium. The stamen consists of a short bifurcating

filament approximately 0.5 mm long; each filament terminates into an anther. The anther is 3 to 5 mm long and 1.2 mm wide, and has an extended narrow tip that is 0.5 mm long; it is basifixed and four-loculed with two distinct thecae in parallel arrangement and dehices longitudinally (Fig. 5D, E, F).

The leaves are arranged alternately. The lamina is pinnate and dissected three to four times. The opposite to alternate pinna or pinnules are further dissected into rounded ultimate segments that are 0.5 to 1 mm wide (Fig. 5C). The petiole is approximately 10 mm long. The original leaf form (Fig. 4A) for reconstruction was taken from a fossil photograph of Leng et al. (2003: fig. 252). Although Sun, Ji et al. (2002) first described the petiole base to be slightly swollen, this feature was not confirmed in the other specimens (Fig. 1A, C). Therefore, our model lacks such a swollen petiole base (Fig. 5C). The presence of fossil samples of nearly complete isolated leaves suggests that the leaves were deciduous.

Archaefructus sinensis

The reconstruction was based on the original description and figures (Sun, Ji et al., 2002), and some photographs of the fossils (Fig. 2; see Sun, Ji et al., 2002: fig. 2 A to D, H, I and supplementary material on the web fig. S1; Leng et al., 2003: fig. 253; Friis et al., 2003: fig. 2).

Model features.— The entire plant consists of roots and a main shoot bearing five lateral shoots (Fig. 6A). The model is 35 cm tall and 17 cm wide (Fig. 6A). The diameter of the main shoot is 3 mm at the base and narrows gradually to 1 mm at the top. The roots are poorly developed, consisting of a primary root with a few short lateral roots (Fig. 6C). The leaves are pinnately dissected two to five times (Fig. 6B). Ultimate leaf segments have rounded tips. For reconstruction, the original leaf form was taken from the holotype specimen (Fig. 2) and from the study of Sun, Ji et al. (2002: fig. 3)(Fig. 4B). The petiole length varies from 0.5 to 4.0 cm and shortens in the more distal leaves (Fig. 6A). Although Sun, Ji et al. (2002) illustrated the petiole with a pulvini-like swollen base (see Sun, Ji et al., 2002: fig. 3), such a feature was not confirmed in the course of this study (Fig. 2C). Our reconstructed model, therefore, lacks the swollen petiole base (Fig. 6A, B).

The lateral shoots emerge from the axils of each subtending leaf on the main stem at angles of 30 to 35 degrees and are 1 to 2 mm in diameter at the base (Fig. 6A). Although Sun, Ji et al. (2002) illustrated as three times branching (see Sun, Ji et al., 2002: fig. 3), the branching of the model was reconstructed five times (Fig. 6A). The branching is monopodial. Each lateral shoot terminates into an achlamydeous bisexual flower. The flower is an elongated reproductive axis consisting of a proximal androecium and a distal gynoecium. The gynoecium is composed of a cluster of numerous carpels (12 to 20) that are small (10 to 18 mm long, 1.5 to 2.0 mm wide) and monocarpic (Fig. 7A–F). The carpels are arranged on the elongated



FIGURE 5. 3D model of *Archaeofructus liaoningensis*. **A**, Whole 3D model. M: Main shoot, L1 and L2: Lateral shoots. Scale bar: 2 cm; **B**, Close-up of the main shoot, showing fluted structure on the surface. Scale bar: 0.5 cm; **C**, Close-up of a leaf blade that is pinnately dissected two to five times. Scale bar: 0.5 cm; **D–F**, Close-up of reproductive organs. Scale bar: 1 cm.



FIGURE 6. 3D model of *Archaeofructus sinensis*. **A**, Whole 3D model, M: Main shoot, L1 to L5: Relative developmental stages of the lateral shoots. Scale bar: 5 cm; **B**, Close-up of a leaf blade that is pinnately dissected two to five times. Scale bar: 1 cm; **C**, Close-up of root system, showing the primary and a few short lateral roots. Scale bar: 1 cm; **D–F**, Close-up of reproductive organs showing their relative developmental stages.



FIGURE 7. Details of the reproductive organs located on the 3D model of *A. sinensis*, **A**, Main shoot, M of Fig. 6; **B–F**, Lateral shoots, B: L5, C: L4, D: L3, E: L2, F: L1 of Fig. 6. Flowers of developmental series (A to F): the immature carpels and stamens (A), the mature follicles and stamens (F). Scale bar: 1 cm.

gynoecial receptacle in helical or sometimes whorled or opposite arrangement. In the post-anthetic stage, the carpel matures into a follicle containing 8 to 12 seeds (Fig. 7E, F). As described by Sun, Ji et al. (2002), immature follicles are inserted into the gynoecial axis at acute angles (Fig. 7A, B), while the mature ones diverge from the axis at wider angles (Fig. 7E, F).

The stamens (8 to 18) are helically arranged on the androecial axis (Fig. 7A–F). Each stamen consists of a short thin filament with an approximate length of 1 mm, which terminates into a pair of anthers after bifurcation (Fig. 7A–F). The anthers are 4 to 5 mm long, 0.5 to 0.8 mm wide, and have a prominent narrow tip that is 0.5 to 1 mm long (Fig. 7A–F). Each anther is basifixed on a short stalk that is 0.25 to 0.5 mm long, is four-loculed with two distinct thecae in parallel arrangement, and dehisces longitudinally (Fig. 7A–F). The stamens fall off in old flowers (Fig. 7F). In order to clearly show the distinct pair of thecae, the details of stamen replicas were finished by carving each cast model with hand-made chisels.

Coloring the models

Although color reconstruction of fossils is based on imagination, the colors should be inferred from botanical bases. In our case, the color of the *Archaeofructus* model was based on the color of extant aquatic plants. In the case of *A. sinensis*, we referred to the plants of genus *Cabomba* of the Cabombaceae, because this family belongs to Nymphaeales that neighbors the most primitive extant angiosperm *Amborella* in the angiosperm clade of a recent phylogenetic analysis (Judd et al., 2002; APGII, 2003). Nymphaeales also comprises aquatic plants. *Cabomba* has totally submerged, dissected leaves resembling those of *Archaeofructus*; further, it has aerial flowers, and its habitat is likely to resemble that of the fossils (Friis et al. 2003). As *A. sinensis* is regarded as a totally submerged plant, we decided to color *A. sinensis* in pale yellowish green with a little transparency (Fig. 6A).

On the contrary, *A. liaoningensis* might have been a small plant that probably grew in shallower environments such as lakefront where unpredictable dry conditions endangered the plant frequently. The model of *A. liaoningensis* was, therefore, painted in darker colors to clearly reflect its dry-resistant, thicker tissues (Fig. 5A).

NOVEL FEATURES NOTICED IN THE PROCESS OF MODEL MAKING AND THEIR BIOLOGICAL INTERPRETATION

In the course of the reconstruction work, we noticed some morphological peculiarities in *A. liaoningensis* and *A. sinensis*, particularly in shoot morphology and flowering sequences.

The fluted stem surface of *A. liaoningensis* was observed to have many longitudinal parallel ridges or grooves (Fig. 1A, B).

This structure is considered to be an adaptive measure and provides mechanical support to the stem against possible gravity stress in shallow water. Such a structure is absent in *A. sinensis* (Fig. 2A, C); the plant probably inhabited deeper water that was safe from sudden dry stress.

The two species also differed in their branching morphology and flowering sequences. *A. liaoningensis* was reconstructed as a small plant that monopodially branched only twice at the base of the main stem (Fig. 5A). Flowering initiates from the main axis and shifts to the laterals basipetally. This was confirmed by examining the original specimens (Fig. 1). The branching architecture of the plant was drawn based on the relative location of the shoots and the subtending leaves. In the type specimen (Fig. 1A), a lateral shoot (L1) has follicles that are less matured than those on the main shoot (M). The same sequence was observed in other specimens (Fig. 1C); the stamens have fallen in M, but are still attached in L1.

On the other hand, the frequency of branching in *A. sinensis* was more; the branching occurred five times in the reconstructed model (Fig. 6A). Although the branching is monopodial, the complete branching architecture of the plant changes from monopodial to sympodial. This is due to the rapid growth of the earlier-branched laterals that precede the growth of the main shoot and other successive laterals. Flowering initiates from the basal-most lateral shoot and acropetally continues to the distal shoots. The follicles of one of the basal lateral shoots (L1) of the type specimen are large and likely to be the most developed (Fig. 2A). Stamens of L1 are lost. The follicles of a subsequent lateral shoot (L2) are younger and accompany the stamens (Fig. 2B). The probable main shoot (M) has relatively the youngest flower components. Although the hypothetical reconstruction of *A. sinensis* in Sun, Ji et al. (2002: fig. 3) illustrated the main shoot as the most developed and the laterals as maturing basipetally, we conclude that the plant flowered acropetally, as has been presented in the model.

The architectural differences between the two species can also be explained from an ecological viewpoint. The basipetal flowering of *A. liaoningensis* probably countered the unstable habitat of the plant and had the advantage of rapid seed propagation. When unpredictable changes occur in the water level, rapid maturity of the flower on the main shoot is advantageous. This is crucial because the lateral flowers occur at a lower position and are subjected to more risk of being submerged in water. In addition, the plant needs to have a longer lifespan in order to allow the laterals to mature; this in turn increases the risks while facing unpredictable dry conditions. The reproductive strategy of *A. liaoningensis*, therefore, seems to be rather a r-selection strategic phenomenon, producing as many seeds as possible at the shortest intervals in its limited lifespan.

The acropetal flowering of the much larger plant *A. sinensis* that might have grown in deeper water would be more a K-selection strategic phenomenon. This plant produced seeds very

slowly and continuously in its relatively stable habitat which allowed a longer lifespan for the plant under minor water stress. The growth of this plant is rather unlimited in contrast to that of *A. liaoningensis*, which is limited.

The different adaptive features inferred for the two species of *Archaeofructus* suggest that physiological modifications such as gibberellins transport and expression in response to the changing environment had already been established in the developmental process of some of the earliest angiosperms.

ACKNOWLEDGMENTS

We wish to thank Mr. Norio Iijima (DEF Co., Ltd.) for his elaborated and exquisite workmanship and Mr. Yoshito Inoue (Nomura Co., Ltd.) for his help in making the models. Many thanks would be extended to Prof. D. L. Dilcher (Florida Museum of Natural History, USA) for his kind support and viewing the reconstruction illustrations in Jilin University. We also thank Mr. Fumio Harada (DEF Co., Ltd.) for his photographing the models and Mr. Shigeo Hayashi for his comments on modeling terms. Special thanks to two reviewers: Dr. Masahiro Kato (National Science Museum, Tokyo) and a reviewer, for their critical comments and useful suggestions on our manuscript.

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