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Qiang Fu , Jie Sun , Shaolin Zheng , Xin Wang *

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Article

Unique Jurassic Fruits Shed a New Light on the Nature of Carpels

Qiang Fu [1], Jie Sun [2], Shaolin Zheng [3] and Xin Wang [1,*]

[1] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and CAS Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China
[2] Shaanxi Key Laboratory of Early Life and Environments, State Key Laboratory of Continental Dynamics, Department of Geology, Northwest University, Xi'an 710069, China
[3] The Shenyang Center of Geological Survey and Institute of Geology and Mineral Resources, Ministry of National Land and Resources, Shenyang 110034, China
* Correspondence: xinwang@nigpas.ac.cn; Tel.: +86-25-8328-2266

Abstract: Carpels are a reproductive feature restricted to angiosperms, therefore they are a focus of many botanical studies. However, there are controversies over the nature of carpels. A reason underlying these controversies is mixing implications given by conflicting interpretations on fossil carpels in early fossil angiosperms from the Cretaceous. These controversies hinder a clear understanding of angiosperm evolution and systematics. A key to these questions is older fossil fruits bearing concerned information. Here we report a new fossil fruit, *Xenofructus dabuensis* gen. et sp. nov, from the Middle Jurassic of Liaoning, China. Unlike previously reported fruits of early angiosperms that were interpreted as bearing seeds either on adaxial or abaxial margin by various authors, our fossil demonstrates clearly that the seeds in *Xenofructus* are neither borne on the adaxial nor abaxial margin of the fruit, instead the seeds of *Xenofructus* are borne on an axis positioned between two margins. This new feature implies that a placenta in carpels is an ovule/seed-bearing axis, a carpel is a composite organ comprising an enclosing leaf (fruit wall) and an axis (placenta). The adaxial or abaxial position of ovules/seeds frequently seen in fossil and extant angiosperms is a consequence derived through long time evolution (coalescence of placenta with either margin of fruits). Carpels can be taken as foliar structures enclosing their associated ovulate branches.

Keywords: *Xenofructus*; fruits; carpels; evolution; angiosperms; Jurassic; China

1. Introduction

Angiosperms are the most diversified plant group that is closely related with the well-being of the humans. Carpels are a feature idiosyncratic to angiosperms, and thus a focus of studies and debates. Formerly, a carpel was taken as an equivalent of a leaf [1]. However, this ancient saying dated back to the Goethe age has never been honored by any fossil evidence [2] despite palaeobotanists have been painstakingly searching for related evidence. A recently raised hypothesis stated that a carpel is a composite organ derived from an ovule-bearing axis and a subtending and enclosing leaf [3–5]. The latest progresses include 1) recognizing the branch-terminal position of seeds in gymnosperms [6,7], 2) treating ovule and carpel (wall) separately, which become tightly synorganized, in extant angiosperms [8]. Although these moves are in the right direction, the controversy over nature of carpels continues, partially due to on-going debates on ovule/seed position in fruits of early angiosperms, including famous *Archaefructus* [9–12] and *Archaeanthus* [13,14] (Figure 3). In these debates, the seeds were interpreted as borne either on the adaxial or the abaxial margin (two opposite positions) of the fruits, and neither of the confronting schools could convince the other. How to reconcile these conflicting parties? The stalemate between these two conflicting parties cannot be broken until independent informative fossil occurs. Here we report a new fruit, *Xenofructus dabuensis* gen. et sp. nov, from the Middle Jurassic of Liaoning, China. It appears that this new fossil provides a new insight on nature of carpels.

2. Materials and Methods

The specimen was collected from an outcrop of the upper member of the Dabu Formation in the Tianshifu Coal Mine (N41°14′58″, E124°23′03″) in 1978 by Dr. Shaolin Zheng and Dr. Wu Zhang. The specimen bearing the fossil plants is dark-colored siltstone, lacking good lamination. There are two similar fruits preserved on the surface of the same block. Previously reported fossil plants from the upper member of the Dabu Formation include *Equisetum beani, E. laterale, Neocalamites hoerensis, Todites williamsoni, Dicksonia concinna, Eboracia lobifolia, Clathropteris pekingensis, Cladophlebis asiatica, C.* sp., *Coniopteris simplex, Pterophyllum propinquum, P. angustum, P.* sp., *Ctenis kaneharai, Williamsoniella buracovae, W. minima,* ***W. dabuensis****, Nilssonia tenuinervis, Ginkgo concinna, G.* sp., *Czekanowskia* sp., *Baiera gracilis, B. furcata, Sphenobaiera gyron, Phoenicopsis augustifolia, Sphenarion latifolia, "Elatidies" chinensis, Storgaardia mentoukouensis, Lindleycladus lanceolatus, Carpolithus* sp., *Raticites* sp.. Other than these taxa, the fossil plants from the Dabu Formation include *Lycopodites falcatus, Neocalamites carrerei, Annulariopsis* sp., *A.* sp., *Marattiopsis hoerensis, M. muensteri, Coniopteris hymenophylloides, C. kuandianensis, C. karatiubensis, Kuandiania crassicaulis, Clathropteris meniscioides, Hausmannia* cf. *dentata, Todites denticulata, Dicksonia kendalli, Cladophlebis raciborskii, C. argutula, C. shansiensis, C. fukiensis, C. haiburnensis, C. nebbensis, Pterophyllum issykkulense, Nilsonia mosserai, N.* aff. *acuminata, N.* cf. *compta, N. orientalis, N. mosserayi, Anomozamites* cf. *major, A. inconstans, A.* spp., *Pterophyllum aequale, P. ctenoites, P. nathorsti, Ctenis lingyuanensis, Pityophyllum nordenskioldi, P. longifolium, Tyrmia grandifolia, Baiera asadai, B.* cf. *lindleyana, Ginkgo beijingensis, G. obrutschewi, G. manchurica, G. sibirica, Sphenobaiera huangi, Czekanowskia rigida, Phoenicopsis* aff. *speciosa, Elatidies ovalis, Elatocladus* (*Cephalotaxopsis*?) *angustifolius, E. lindongensis, Ferganiella* cf. *podozamioides, Solenites vimineus, Leptostrobus laxifolia, Isostrobus heeri* [15,16]. The fossil flora is comparable to the *Coniopteris-Phoenicopsis* flora, and the fossiliferous strata are thought belonging to the early Middle Jurassic as it shares 17 species with the typical Middle Jurassic Yorkshire Flora [15,16].

The whole specimen was photographed using a Huawei digital camera, and details of the fossil were photographed using a Nikon SMZ1500 stereomicroscope at the Nanjing Institute of Geology and Palaeontology, Nanjing, China. The specimen was investigated on a Phoenix v|tome|x m scanner using a voltage of 190 Kv and a current of 140 μA at the State Key Laboratory of Continental Dynamics (Northwest University), Xi'an, Shaanxi Province, China. The specimen was mounted on the stage using self-adhesive tape. In total, 2000 projections were obtained. The dataset had a resolution of 74.56 μm. Three-dimensional reconstructions were generated using VG Studio 3.2. All images were saved in TIFF or JPEG format. The brightness and contrast of images were adjusted in whole. All figures were organized for publishing using a Photoshop 7.0.

3. Results

Angiosperms

***Xenofructus* gen. nov**

Synonym: *Williamsoniella* Zheng and Zhang 1990

Type species: *Xenofructus dabuensis* gen. et sp. nov

Etymology: *Xeno–* for unexpected morphology and occurrence of the fossil, *–fructus* Latin word for fruit.

Generic diagnosis: Fruit with a short stalk, straight on abaxial, convex on adaxial. Abaxial ridge robust. Placenta positioned between abaxial and adaxial margins of fruit. Seeds enclosed in fruit, in cluster, sickle-shaped.

Remarks:

The specimens studied here were previously identified as *Williamsoniella dabuensis* Zheng and Zhang in 1990 [15], which was placed in Bennettitales. Indeed, the general morphology did resemble what shown in Text-Figure 3 of Harris [17]. However, the features of our specimen appear to fall out of the morphological scope of Bennettitales, which are expected to have conic receptacle bearing numerous seeds and interseminal scales or pollen sacs on the adaxial surface of microsporophylls [17,18]. Forms and variations of seeds in our specimen suggest that they are not pollen sacs, as suggested by Zheng and Zhang (1990), which are expected to be more uniform in morphology. Therefore, we re-studied the specimen and revealed some new features.

The fruit of *Xenofructus dabuensis* gen. et sp. nov is unique in its placenta position (internal in the fruit, positioned between the adaxial and abaxial margins of the fruit) and sickle-shaped seeds borne in cluster on a branch. The combination of both features has never been seen in previously reported in any fossil taxa, thus justifying a new genus.

***Xenofructus dabuensis* gen. et sp. nov**

(Figures 1, 2 and S1)

Synonym: *Williamsoniella dabuensis* Zheng and Zhang 1990, Plate V, Figure 7A, page 220 [15]

Diagnosis: The same as that of the genus.

Description: The specimens studied here include two isolated fruit parallel oriented on surface of the same block (Figures 1, 2 and S1). Both fruits are preserved as coalified compressions (Figures 1a,b and S1a). The general morphology of these two fruits agrees each other, although there is slight difference in dimension (Figure 1a,b,g). One of the fruit (Fruit A) measures 19 mm long and 8.4 mm wide (Figure 1a), while the other (Fruit B) measures 21 mm long and 6.9 mm wide (Figure 1b). Fruit A has a stalk 4.7 mm long and 2.5 mm wide, gradually transitional to the base of the fruit (Figures 1a and 2a). Fruit B has a stalk 5.6 mm long and 1.8 mm wide, gradually transitional to the base of the fruit (Figures 1b and 2b). Due to difference in breaking, different features are shown separately in these two fruits (Figures 1a–f, 2a,b and S1a–d). The foreground part of Fruit A is almost fully removed, exposing the internal cluster of seeds and robust abaxial ridge (Figures 1a,g,h, 2a and S1a–c), while the foreground part of Fruit B is partially removed, with the clustered seeds (placenta) are partially covered by the fruit wall (Figures 1b,c,e, 2b and S1a,c). The internal position of placenta (cluster of seeds) within the fruit is suggested by the presence of the stubs of the fruit wall (Figures 1b,c,e). The placenta is a central axis bearing several seeds (Figures 1a–c, 2a,b and S1a,c). The seeds are sessile, have variable orientations and morphologies, depending on their positions on the placenta (Figures 1a–c,f, 2a,b and S1a,c,d). The basal seeds tend to be corpulent and round in shape, up to 1.9 mm long and 0.95 mm thick (Figures 1c and S1c,d), while the distal ones tend to more slender and sickle-shaped, up to 2.5 mm long and 1.1 mm thick (Figure 1c,f). There appears to be some trace of micropyle at the distal of a seed, suggestive of orthotropous ovules (Figure 1c,f).

Holotype specimen: KP10-18A.

Etymology: *dabuensis*–, species epithet conserved from *Williamsoniella dabuensis* Zheng and Zhang, former name of the specimen.

Type locality: Tianshifu Coal Mine, Liaoning, China.

Stratigraphic horizon: The Dabu Formation (the Middle Jurassic, >164 Ma).

Depository: The Shenyang Center of Geological Survey and Institute of Geology and Mineral Resources, Ministry of National Land and Resources, Shenyang, China.

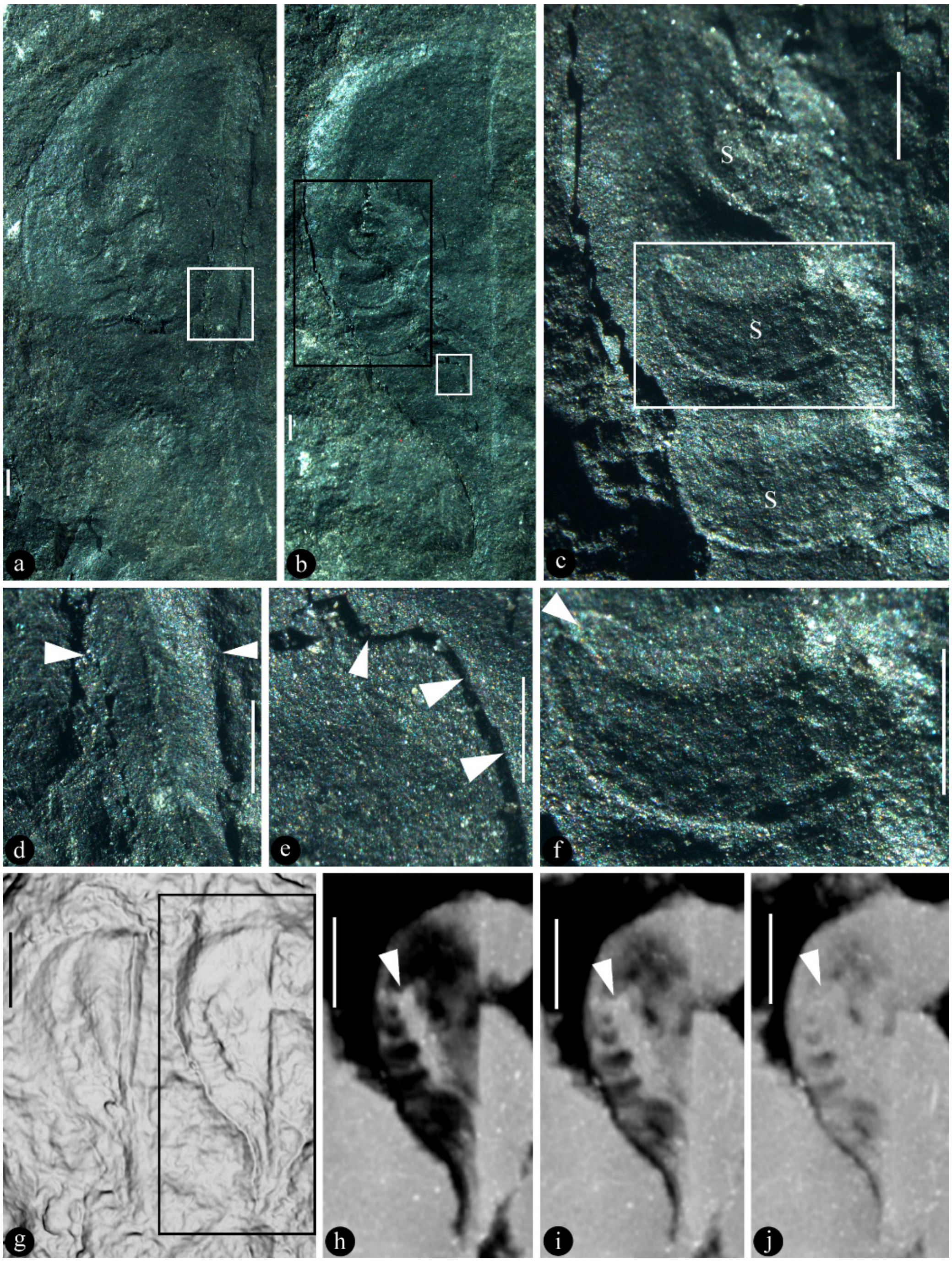

Figure 1. ***Xenofructus dabuensis*** **gen. et sp. nov and its details.** Specimen number KP10-18A. **a**. Holotype, showing profile of Fruit A and its seeds exposed. Scale bar = 1 mm. **b**. Fruit B and its internal seeds partially exposed and partially covered by the broken fruit wall. Scale bar = 1 mm. **c**. Detailed view of the black rectangle in Figure 1b, showing three seeds (s) of variable shapes and fruit wall (upper right) covering other seeds. Scale bar = 1 mm. **d**. Detailed view of the rectangle in Figure 1a, showing robust abaxial margin (between the triangles) of the fruit. Scale bar = 1 mm. **e**. Broken fruit wall (upper right) and exposed internal of the fruit (lower left), and the boundary in between (triangles), enlarged from the white rectangle in Figure 1b. Scale bar = 0.5 mm. **f**. A sickle-shaped seed with a distal invagination (possible micropyle, triangle), enlarged from the rectangle in Figure 1c. Scale bar = 1 mm. **g**. A Micro-CT rendering of the specimen showing two fruits parallel deployed on the surface of the specimen. **h-j**. Serial sections of Fruit B, showing the seed-bearing placenta (triangles) independent from both margins of the fruit. Scale bar = 2 mm.

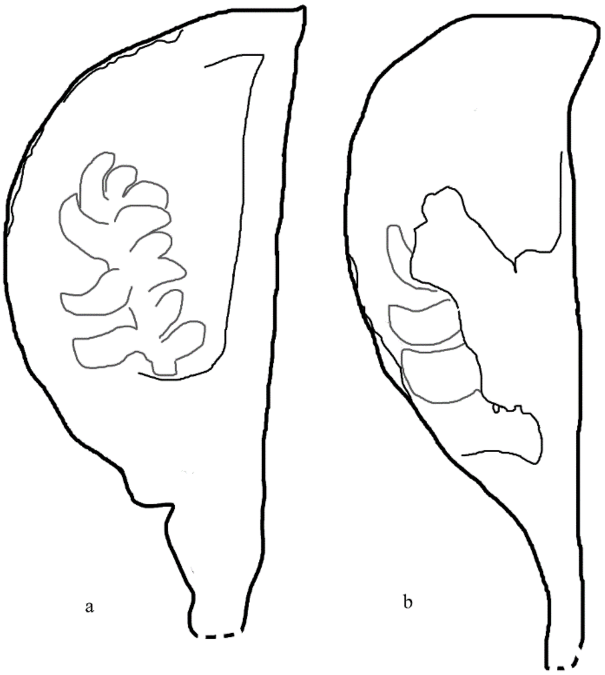

Figure 2. Sketches of two *Xenofructus* fruits. Fruit outline is in black, while seed outline is in gray. a. The fruit in Figure 1a. b. The fruit in Figure 1b.

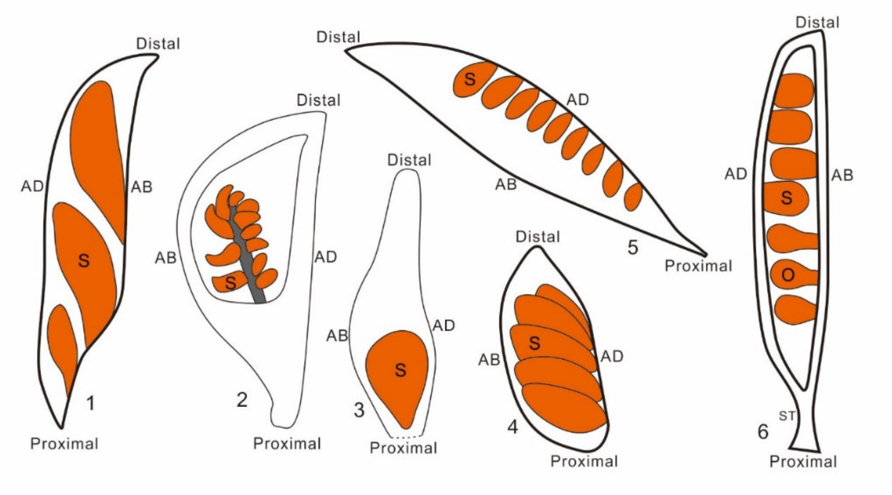

Figure 3. Several representatives of early angiosperms, showing variable seed arrangement in the fruit. Seed (S)/ovule(O) are inserted either along the adaxial (AD), abaxial (AB), or both margins of a fruit, or is basally fixed in a fruit. 1. *Archaefructus*, according to Wang and Zheng [12]; 2. *Xenofructus*; 3. *Qingganninginfructus*, according to Han et.al. [19]; 4.*Gansufructus*, according to Du et al. [20]; 5. *Sinocarpus*, according to Leng and Friis [21]; 6. *Archaeanthus*, according to Wang [13].

4. Discussion

The term “angiosperms” was coined by German botanist Paul Hermann (1646-1695) in 1690. He combined two Greek words, *angeion* (vessel) and *spermos* (seed), into a new word “angiosperm” designating “plant with seeds contained in a protective vessel” (www.etymonline.com). This definition has been accepted widely by many leading botanists [22]. For example, the so-called “First Flower” *Archafructus liaoningensis* was recognized following this definition. Wang [3,23–35] has been applying this criterion identifying various early angiosperms. Thus here we adopt this criterion for angiosperms to identify our fossil plant, *Xenofructus* gen. nov.

As seeds are supposed to be enclosed in angiosperm fruits, so angiosperm seeds are not to be visible to naked eyes unless the enclosing fruit wall is broken. This makes proving enclosed seeds in a fossil plant a great challenge for palaeobotanists, especially when there is only one specimen of fossil fruit available for observation. We are lucky in that there are two fruits preserved side by side in the same specimen, AND these two fruits are preserved in slightly different statuses (Figures 1a,b and S1a). Fruit A in Figure 1a is a broken fruit, namely, the foreground fruit wall is almost fully removed (Figures 1a,g,h and S1c), exposing the seeds formerly enclosed in the fruit, and allows us to view all clustered seeds. These seeds are clustered along an axis, forming an equivalent of placenta. The counterpart of this placenta is only partially seen in Fruit B (Figure 1b,c), as the placenta in this fruit is partially covered and eclipsed by the fruit wall (Figure 1b,c). Comparing these two fruits suggests that the placentae (including the seeds on them) of *Xenofructus* are sandwiched between to fruit walls and thus fully enclosed in the formerly integral fruits, satisfying the criterion of angiosperms.

The presence of fruit wall in *Xenofructus* is suggested by the partially preserved placenta in Fruit B. Comparing Figure 1a–c, it is easy to see that there are less seeds in Figure 1b,c than in Figure 1a, and that the deployment of seeds in both fruits differ. These differences are due to the partial removal and partial preservation of fruit wall in Figure 1b,c. The presence of fruit wall is further suggested by Figure 1e, which shows a detailed view of the basal portion of Fruit B in Figure 1b, in which the fallen off fruit wall left a clear stub. Both Figure 1e and Figure 1b,c indicate that the fruit wall covers both basal and upper parts of the fruit. Actually, the presence of fruit wall is obvious on the adaxial and abaxial margins if a careful observation is paid: in Figure 1b,c, the dark shadow of the fruit wall, although thin, on the left is clearly shown for Fruit B. Similar residue of fruit wall or epidermis is also visible in Fruit A in Figure S1b: a robust straight ridge (abaxial margin) of Fruit A (Figures 1a,d,g,h and S1a,b) is covered by an additional thin layer. It is not a pure imagination that the fruit wall was integral and covered the whole fruit, although the current preservation cannot demonstrate this.

Seeds of *Xenofructus* vary in their morphology, even in the same fruit (Figures 1a–c,f and S1a–d). Such a variation is rather expected, as ovules borne on the same placenta may be in their different developmental stages, as seen in extant *Nymphaea* [36]. For example, three adjacent seeds of Fruit B are of different shapes (Figure 1c). The lowermost one is more corpulent and round in shape, the uppermost one is apparently more slender and smaller, sickle-shaped, while the middle one is intermediate between these two. Such variation suggests an acropetal development of the ovules in *Xenofructus*. It is noteworthy that all seeds are consistently sickle-shaped. Not alone, a similar variation of ovules can be seen in Fruit A (Figures 1a and S1a,c,d). It is important that there seems to be an invagination at the tip of seed/ovule (Figure 1f). This conjures to micropyle, a feature frequently seen at the tip of an ovule, rejecting former interpretation of these seeds as pollen sacs. We attribute the above differences in seed morphology to the various developmental stages of the ovules in *Xenofructus*.

The most intriguing feature of *Xenofructus* may be its placenta positioning. Unlike previously reported fossil plants including *Archaefructus* [9–12], *Sinocarpus* [21,37], *Archaeanthus* [13,14], in which the seeds/ovules were interpreted as borne either on adaxial or abaxial margin of fruits, the seeds in *Xenofructus* are clustered around an axis independent of both adaxial and abaxial margins. This phenomenon is so far never seen in extant angiosperms. Therefore its occurrence in a Jurassic pioneer angiosperm *Xenofructus* is of significance, as it potentially represents an ancestral status of placenta. The placenta intermediately positioned between the adaxial and abaxial margins in fruit of *Xenofructus* indicates that previously seen adaxial or abaxial position of seeds in a (fossil or extant) fruit may represent a derived feature of carpels, and placenta originally is an ovule-bearing branch that is independent of either carpel margin. This conclusion is in agreement with result of studies on *Michelia* [5] and *Illicium* [4], and with the generalization given by Wang [3]. Most importantly, studies on gene function have long given a similar implications [38–41], which, unfortunately, have been largely ignored by many botanists. Such a consensus among palaeobotany, plant morphology, and molecular studies seems to indicate that we are approaching the truth.

There are increasing independent molecular datings suggesting a Jurassic or even Triassic origin of angiosperms [42–47]. A recent study using numerous genes of most taxa in angiosperms and 62 fossil calibrations [46,48] suggested that there is a "Jurassic Gap" for angiosperms. This conclusion is further strengthened by the latest phylogenomic study on 353 gene sets in almost 800 genera of angiosperms carried out by 279 scientists from 138 institutions in 27 countries [47]. Now our *Xenofructus* represents a Middle Jurassic (>164 Ma) angiosperm, filling the so-called "Jurassic Gap". It appears that the impression of "Jurassic Gap" is either due to our lack of knowledge on Jurassic angiosperms, or due to intentional turning back to Jurassic angiosperms, just as Herendeen et al. [49] did. We cannot know the truth until we calm down and study fossils carefully. Actually, there have been enough studies suggestive of pre-Cretaceous angiosperms [3,19,26–28,33,34,50–57].

We still do not know anything about the whole plant of *Xenofructus* yet. The occurrence of two *Xenofructus* fruits on the surface of the same specimen seems to suggest that *Xenofructus* was not rare or proliferated in the flora. These fruits are parallel in orientation, suggesting either that they belonged to the same plant and were connected each other by an unpreserved part, or that they represented two of many fruits in the fossil flora, implying many unseen fruits awaiting further digging in the fossil flora. We expect future studies will shed more light on *Xenofructus* and other angiosperms that lived in the Jurassic of Liaoning, China.

Previous studies on megafossils and palynology of the Dabu Formation showed that the fossil flora bearing *Xenofrucuts* was dominated by Cycadales (28.57%), ferns (27.27%) and Ginkgoales (24.68%), followed by Coniferales (11.69%), Equisetales (6.49%), and Lycopodiales (1.3%) [16]. These plants constitute a forest dominated by trees of Ginkgoales, Czekanowskiales, and Coniferales, with flourished bushes of Cycadales and Bennettitales, and under store of ferns [16]. We hope this information can be helpful for future studies on the ecological background of angiosperm evolution. It is rather expected that some other primitive angiosperms may still survive in a more or less similar extant environment.

5. Conclusions

Xenofructus represents a new taxon of Jurassic angiosperms. Its early age and unique morphology not only confirm the truthful occurrence of angiosperms in the pre-Cretaceous age, but also shed a new light on the homology of carpels and on the origin of angiosperms.

Author Contributions: S. Z. collected the specimen; X.W. and Q.F. carried out the observation and photography; J.S. carried out the Micro-CT observation and rendering. X.W. and Q.F. drafted the manuscript. Q.F., J.S., S.Z. and X.W. modified and finalized the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: Q.F. and X.W. contributed to the study conception and design. S.Z. collected the material for study. J.S. carried out the Micro-CT observations and figure processing. All authors analyzed the data. The first draft of the manuscript was written by X. W. and all authors commented on versions of the manuscript. All authors read and approved the final manuscript.

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