Lingyuanfructus, A Unique Fossil Gymno-Angiosperm Catches the Long Sought Snapshot of Plant Evolution

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Article

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The Yixian Formation in northeast China is worldwide famous for its fossils of early angiosperms, which play a key role in the study of early evolution of angiosperms. Despite all efforts, the morphological gap between angiosperms and gymnosperms remain as conspicuous as ever, due to lack of a fossil plant intermediate between angiosperms and gymnosperms. It is well-known that angiosperms are distinguished from gymnosperms, which have naked ovules, by their enclosed ovules. A plant intermediate between angiosperms and gymnosperms should have both enclosed as well as naked ovules in the same plant. Although some extant angiosperms may have their ovules not fully enclosed and some extant gymnosperms have their seeds enclosed, none of fossil or living plants has its ovules naked and enclosed in the same plant hitherto. However, Darwinism does expect such a chimeric existence. Here I report such a long-expected plant, *Lingyuanfructus hibrida* gen. et sp. nov, from the Yixian Formation (Lower Cretaceous). The unique feature of *Lingyuanfructus* is that, in a single fossil, the ovules are both naked and enclosed, exactly the expected chimera filling the huge morphological gap between angiosperms and gymnosperms.

Key words: angiosperm, fossil, fruit, flower, evolution, Cretaceous, China.

The origin and early evolution of angiosperms have been foci of botanical debates [1-33] because the outcomes of such debates are the foundation for a natural angiosperm system. An angiosperm system sounds plausible when it can account for the origin and diversification of angiosperms that include more than 300,000 species (more than 90% species diversity of plants). Darwinism thinks that angiosperms are derived from their non-angiospermous ancestors with naked ovules. Theoretically, the ovules are exposed and naked in the supposed taxon transitional between angiosperms and gymnosperms. Unfortunately, such a theoretical expectation has never been honored by any fossil evidence hitherto, leaving the origin of angiosperms as mysterious as hundred years ago. This fact partially explains the frustration of botanists and palaeobotanists. Then a question is "As a scientific theory, if not testified, will Darwinism remain to be a part of science?" Regardless of the answer to this question, searching for more testing fossil evidence is always welcome. The Yixian Formation (Lower Cretaceous, Barremian-Aptian), which has yielded diverse angiosperms [1-5,8,17,24,28,30,31,34-37], is the most promising bonanza for such a search. Here I report a new angiosperm, *Lingyuanfructus hibrida* gen. et sp. nov, from the Yixian Formation of Lingyuan, Liaoning, China. Unique among all plants fossil and living, *Lingyuanfructus* demonstrates the above expected chimeric status: a plant with its ovules both exposed and enclosed in a single fossil plant. Such a discovery underscores the science affinity of Darwinism and, more importantly, provides a solution to the calcitrant problem of origin of angiosperms.

Lingyuanfructus gen. nov

Diagnosis: Distal portion of plant including branch, leaves and fruits/carpels. Branch slender and straight. Leaf strap-like, smooth-margined, parallel-veined, with rare mesh. Flower female, including paired fruits, without stamens and perianth. Ovules multiple per carpel, enclosed or rarely exposed.

Lingyuanfructus hibrida gen. et sp. nov.

(Figures 1-3)

Diagnosis: The same as the genus.

Description: The fossil is a compression, including two facing parts, embedded in yellowish siltstone of the Yixian Formation near Dawangzhangzi Village, Lingyuan, Liaoning, China. The fossil is 8.3 cm long, 3.7 cm wide, including a branch, leaves, and at least two pairs fruits (Figs. 1a, 3a). The branch includes at least three internodes, wide up to 1.7 mm in diameter basally, weakly tapering (Figs. 1a, 3a). An internode is up to 21 mm long and 1.5 mm wide (Fig. 1a). The leaves are strap-shaped, up to 20 (44?) mm long and 1.3 mm wide, smooth-margined, parallel-veined, with rare mesh (Figs. 1a-c). At the terminal of the branch, there is a 7 mm long shared stalk that bears a pair of approximately 7.5 mm long separate stalks (Fig. 1a). Each of the separate stalks bears a pair of fruits/carpels, smoothly transitional to the fruits, showing no trace or scars of perianth or other lateral appendages (Figs. 1a, d-e). There are at least five fruits, each 9-11 mm long and 2.8-3.7 mm wide (Figs. 1a, d-e, 2a). There are 10-15 ovules/seeds in each fruit/carpel (Figs. 1a, d-e, 2a). Each ovule is oval-shaped, 0.6-2.5 mm long and 0.6-1.4 mm wide (Figs. 1d-e, 2a). Although most ovules are enclosed in the carpels, one of the ovules is exposed and attached to the adaxial margin of the carpel/fruit (Figs. 1a, d-e, 2a). This ovule is 2 mm long, 1.26 mm in diameter, orthotropous, unitegmic, without obvious funiculus (Figs.

1d-e, 2b-d). The integument is 0.34 mm thick and 1.2 mm long, while the nucellus is 0.93 mm long and 0.65 mm in diameter, and free from the integument except at the base (Figs. 1d-e, 2b-d).

Remarks: The terms "carpel" and "fruit", "ovule" and "seed" are used interchangeably as the author cannot determine the maturity of *Lingyuanfructus hibrida* gen. et sp. nov.

Some of the leaves outlines in Fig. 3a may not physically connected to the main fossil, but these leaves are hard to distinguish morphologically from those physically connected and their orientation suggests possible connections.

Horizon: the Yixian Formation, Barremian-Aptian, Lower Cretaceous.

Holotype: PB328298.

Etymology: *Lingyuan-* for the fossil locality near Lingyuan, Liaoning, China (41°15'N, 119°15'E); *-fructus* for fruit; *hibrida* for chimeric morphology of the fruit.

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Literally, angiosperms are characterized by "angiospermy", which implies that the seeds are enclosed in fruits. In this way, the seeds of angiosperms are better protected and have more chances to give rise to next generation. However, as recent research suggests, protecting offsprings (including seeds) is not a patent of angiosperms [38] but is rather an implementation of ODC (Offspring Development Conditioning) that is ubiquitous in sexually reproduced organisms [39]. A more strict criterion that ensures an angiosperm affinity is angio-ovuly: ovule enclosed before pollination[8,38]. Since many of the ovules of *Lingyuanfructus* are enclosed in carpels (Figs. 1d-e, 2a), it is decent to interpret *Lingyuanfructus* as an angiosperm.

Contrary to the above discussed "enclosed ovules" that pins down its angiospermous affinity, the unique and intriguing feature of *Lingyuanfructus* is its exposed orthotropous unitegmic ovule on the adaxial margin of the carpel/fruit (Figs. 1a,d-e, 2b-d). The "exposedness" of this ovule implies either 1) that at least one ovule of *Lingyuanfructus* is exposed, implying that *Lingyuanfructus* is a gymnosperm, or 2) that *Lingyuanfructus*, if an angiosperm, has not fully completed its transition from gymnosperms to angiosperms, and plays a role of step stone between these two well-separated groups. *Lingyuanfructus*' ovules being orthotropous (Figs. 2b-d) implies that such a status of ovules is ancestral in angiosperms as it is also seen in the outgroup of angiosperms, gymnosperms. In contrast to bitegmic ovule frequently seen in angiosperms, ovules in gymnosperms are usually unitegmic. The occurrence of unitegmic ovule in *Lingyuanfructus* implies its resemblance to ovules of gymnosperms (outgroup of angiosperms) rather than those of typical and derived angiosperms. Taking all into consideration, it is decent to say that *Lingyuanfructus* is a gymno-angiosperm that alone convincingly bridges the formerly huge morphological gap between gymnosperms and angiosperms.

The adaxial position of the exposed ovule on the fruit/carpel in *Lingyuanfructus* is noteworthy. It is well known that the ovules and seeds in Magnoliales (previously assumed ancestral clade in angiosperms) and Amborellales are positioned on the adaxial of their fruits/carpels [40,41]. Such

positioning has been attributed to the provenance and nature of placenta in these plants: a placenta is an axillary ovule-bearing branch subtended by a foliar structure [8,25]. Although this generalization has been confirmed by a study of carpel variations in *Michelia* (Magnoliaceae) [42] and is compatible with the conclusions and implications given by gene function studies [43-46], favoring fossil evidence from early angiosperms is specious. For example, *Archaeanthus* and *Archaefructus* once were interpreted or implied as if having their ovules attached to the adaxial margins of the fruits/carpels [2,47]. But later studies proved that ovules in these taxa are either borne on the abaxial or both margins of fruits/carpels [34,37,48]. Now the adaxial position of the exposed ovule in *Lingyuanfructus* (Figs. 1d-e) indicates that a placenta in *Lingyuanfructus* is adaxial in the fruit/carpel, reinforcing the above generalization.

If the above generalization is correct, the search image of angiosperm ancestors should include some fossil taxa that have an ovule-bearing secondary branch in axil of a foliar structure. Such a configuration is not rare in fossil plants, for example, Cordaitales, Conifers and Glossopteridales are famously known possessing such a configuration. Long time careful studies of these three groups seemed to alienate them from angiosperms, partially because carpels of angiosperms were previously erroneously interpreted as equivalent to ovule-bearing leaves [49]. Now since a carpel in angiosperms is interpreted as composed of two parts, an axillary ovule-bearing branch and a subtending leaf [8,25], it is time to review previous works on these formerly disfavored groups and pay special attention to some poorly understood or controversial Mesozoic taxa. *Metridiostrobus*[50] and *Palissya*[51-53] are two fossil taxa that deserve special attention since they all have an axillary ovule-bearing structure subtended by a foliar structure.

It is noteworthy that the base and stalk of each fruit in *Lingyuanfructus* are smooth, showing no trace or scar of perianth or stamens. Such an observation indicates that *Lingyuanfructus* has no typical perianth, and is unisexual (male). The repeated lack of typical flowers in *Lingyuanfructus* and contemporary *Archaefructus*[2,3], *Sinocarpus*[4,5], *Baicarpus*[31], *Eofructus*[28], *Neofructus*[17] (all from the Yixian Formation) implies that flowers in the Early Cretaceous are routinely unisexual and perianthless, and may well represent one of ancestral statuses of flowers. Intriguingly, the insect damage on the fruit/carpel of *Lingyuanfructus* (Fig. 1e) indicates that the ecological tie between angiosperms and insects, the two groups of by far the greatest diversity in the current ecosystem, has started to emerge as early as 125 Ma ago.

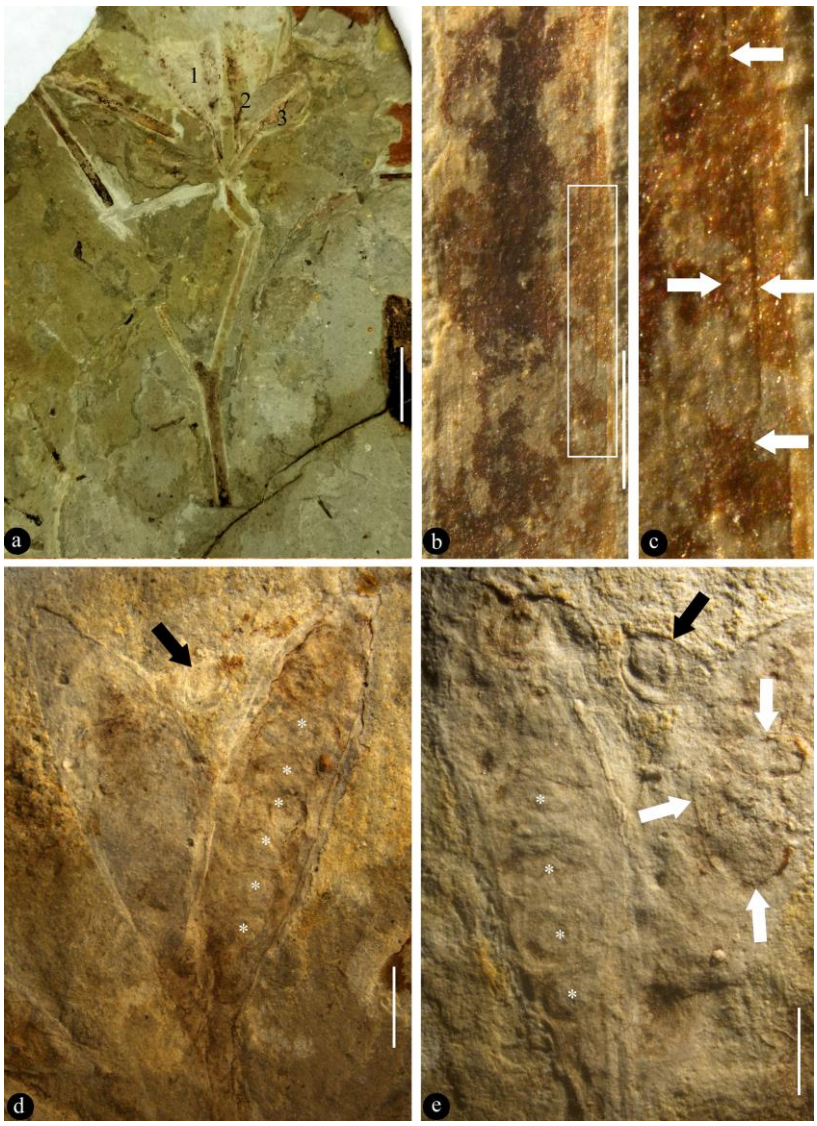

Figure 1 *Lingyuanfructus hibrida* gen. et sp. nov, and its details. b-e, stereomicroscopy.

A. General morphology of *Lingyuanfructus* on one of the two facing slabs, including physically connected branch, leaves, and two pairs of fruits (1, 2). Refer to Fig. 3a. Scale bar = 1 cm.

B. Strap-shaped leaf with smooth margins and parallel venation. Scale bar = 1 mm.

C. Parallel venation and a rare mesh (arrows), enlarged from the rectangle in Fig. 1b. Scale bar = 0.2 mm.

D. Counterpart of the paired fruits in Fig. 1e, with an ovule (arrow) outside and attached to the left fruit and ovules (asterisks) inside the right fruit. Scale bar = 2 mm.

E. The fruit pair labeled as 1 in Fig. 1a, showing an ovule (black arrow) outside and attached to the right fruit, ovules (asterisks) inside the left fruit, and possible insect damage on the fruit (white arrows). Scale bar = 2 mm.

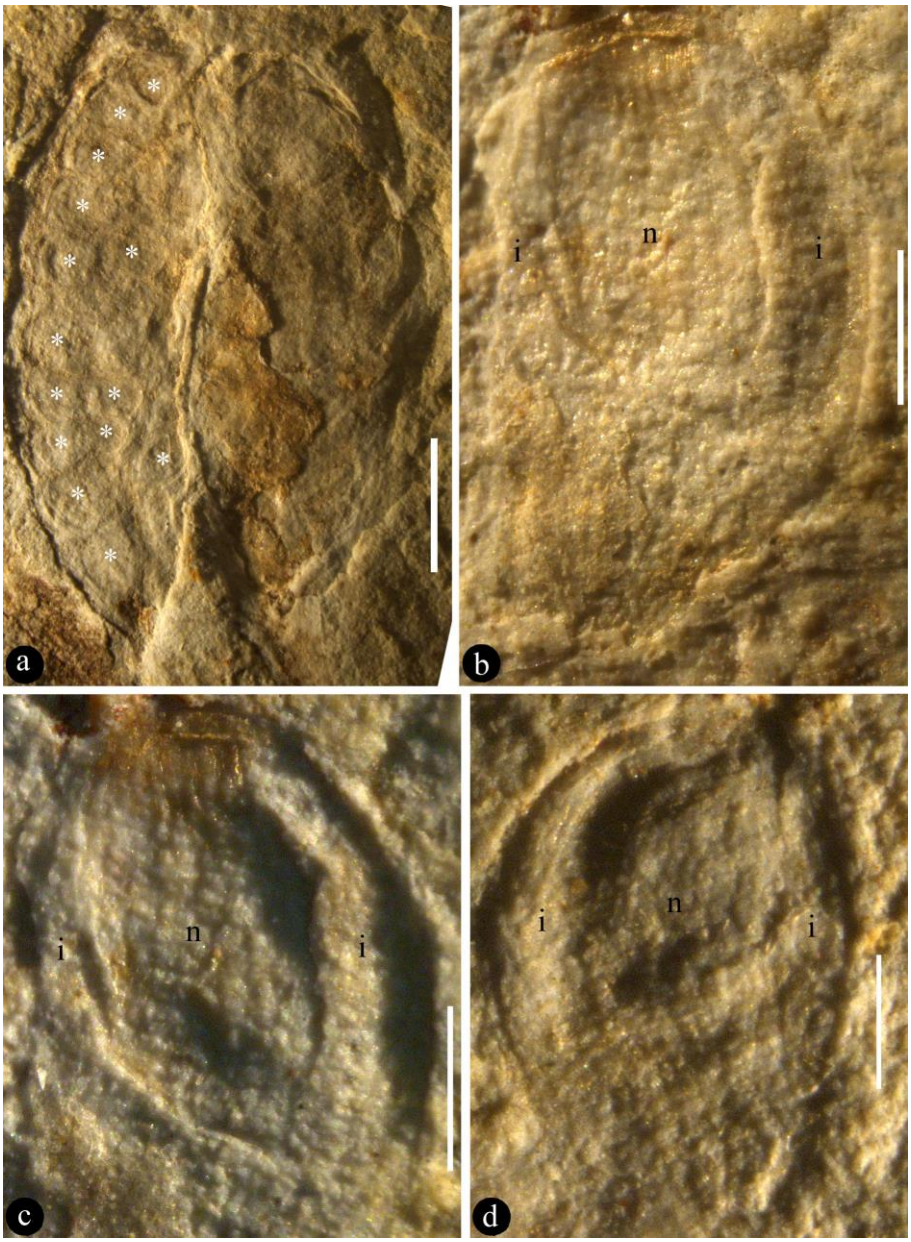

Figure 2 *Lingyuanfructus hibrida* gen. et sp. nov, and details of the exposed ovule. All light stereomicroscopy.

A. Two fruits labeled as 2 and 3 in Fig. 1a, with numerous oval ovules (asterisks) inside the left fruit. Scale bar = 2 mm.

B. Detailed view of the orthotropous unitegmic ovule outside carpel, enlarged from Fig. 1d, showing nucellus (n) and integument (i). Scale bar = 0.5 mm.

C. The same ovule as in Fig. 2b, with different lighting, showing nucellus (n) and integument (i). Scale bar = 0.5 mm.

D. Detailed view of the ovule outside carpel, enlarged from Fig. 1e, showing nucellus (n) and integument (i). Scale bar = 0.5 mm.

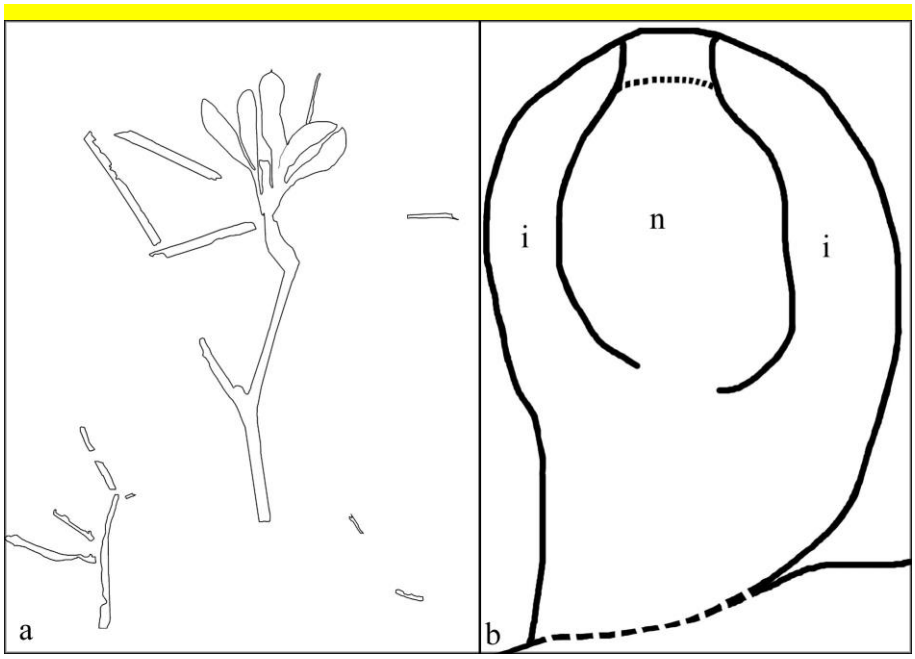

Figure 3 Sketches of *Lingyuanfructus* gen. et sp. nov.

A. Sketch of the specimen shown in Fig. 1a.
B. Sketch of the exposed orthotropous, unitegmic ovule shown in Fig. 2b that is attached to the fruit margin (bottom), showing nucellus (n) and integument (i).

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