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A perfect flower typical of angiosperms, including androecium, gynoecium and tepals,  
from western Liaoning, China marks the earliest record of undoubted flowers in the  
early Cretaceous (>125 Ma).

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## **The Earliest Perfect Flower**

Despite of angiosperms in the Yixian Formation (>125 Ma, early Cretaceous), there is no perfect flower typical of angiosperms to date. Here we report *Euanthus dilaensis* gen. et sp. nov as the earliest perfect flower known to date. The flower includes tepals, androecium and gynoecium. The anthers are globose in form, with bristles atop and *in situ* round-triangular pollen grains. The gynoecium is  
5 composed of probably two carpels with plumose stigmas and a carpel-enclosing receptacle. The discovery of *Euanthus* increases the diversity of early angiosperms, and indicates that perfect flowers occurred as early as 125 Ma ago.

Since the publishing of *Archaeofructus*<sup>1-3</sup>, the Yixian Formation (>125 Ma ago) has become famous worldwide. Later another angiosperm, *Sinocarpus*<sup>4</sup>, and well-preserved vertebrates<sup>5</sup> are reported from the formation. However, there have always been controversies over these early angiosperms. The age and nature of the reproductive organ (being an inflorescence or a flower) of *Archaeofructus* are highly debated<sup>2,6</sup>. According to Dilcher et al., whether the genus *Sinocarpus* is a valid one also appears to be an open question now<sup>7</sup>. However, it appears to be widely acknowledged that there is no unambiguously accepted perfect flower from the Yixian Formation yet since *Sinocarpus* is a fruit associated with leaves and *Archaeofructus* has no generally accepted flower<sup>6</sup>. Here we report a perfect flower from the Yixian Formation. The flower has the organization typical of angiosperms, including tepals, androecium and gynoecium. The tepals are spatulate, with a long claw and a round tip. The anthers are globose in form, with bristles atop and round-triangular shaped pollen grains *in situ*. The carpels are enclosed by a receptacle except their plumose stigmas protrude through a floral pore. As the earliest perfect flower known to date, *Euanthus* increases the diversity of angiosperms in the early Cretaceous, and helps to decipher the early evolution of angiosperms.

The specimens included two slabs, part and counterpart, of the same flower embedded in grayish yellow thick muddy siltstones. The specimens were collected from Huangbanjigou Village, Shangyuan Town, Beipiao City, western Liaoning, China, the same locality as *Archaeofructus liaoningensis*<sup>1</sup>. The specimens were observed and photographed under a Leica MZ-16A stereomicroscope with a digital camera (Figs. 1a-h) and under a Leon 1530 VP SEM (scanning electron microscope) in VP mode (Fig. 2a) at Nanjing Institute of Geology and Palaeontology, Nanjing, China. Parts of the specimen PB21047b were degaged under the stereomicroscope to expose the details of the flower covered by the sediments. The removed parts of the flower were coated with gold and observed under the SEM (Figs.

2b, 3a-e). Cellulose transfers were made on the specimen PB21047b. The transfers were cleaned with HF, coated with gold and then observed under the SEM (Figs. 2b-e). All related information was used in whole to reconstruct the flower. All photographs were saved in TIFF format and put together for publication using Photoshop 7.0.

5 *Euanthus* gen. nov.

**Type species:** *Euanthus dilaensis* gen. and sp. nov.

**Diagnosis:** Flower small, with a slender pedicel. Flower perfect, hypogynous. Tepals, androecium, gynoecium attached to the pedicel at the same point. Tepals spatulate, with a long claw and a round tip.

Anther globose in form, with a filament at the base and numerous bristles atop, bearing *in situ*

10 round-triangular pollen grains with rugulate and/or verrucate sculpture. Gynoecium attached to the pedicel with a stipe, with carpels enclosed by a receptacle except the stigmas protruding through the central floral pore at the top. Carpels urceolus, with plumose stigmas.

**Etymology:** *Eu-* for true in Greek, *-anthus* for flower in Latin.

**Type locality:** Huangbanjigou, Shangyuan, Beipiao, Liaoning, China.

15 **Stratigraphic horizon:** the Yixian Formation (Barremian or lower, lower Cretaceous, >125 Ma).

*Euanthus dilaensis* gen. et sp. nov.

(Figures 1-4)

**Diagnosis:** Currently, the same as that of the genus.

**Description:** The flower is small, perfect, hypogynous and with superior ovary, 6.9 mm high, 7.3  
20 mm wide (Figs. 1a-b). The pedicel is up to 1.8 mm long and 0.35 mm in diameter (Figs. 1a-b). Four tepals and two stamens are attached to the pedicel almost at one point (Figs. 1a-b,h). Tepals are spatulate, free, with two nerves in the distal portion, spatulate with a long claw and a round tip, up to

6.5 mm long and 0.9 mm wide in the distal portion (Figs. 1a-d). Anthers are attached to the pedicel by a filament about 1.2 mm long and 0.15 mm in diameter (Figs. 1a-b,e). Anthers are globose in form, about 0.5 mm in diameter, with numerous up to 1 mm long and 60-65  $\mu\text{m}$  wide bristles atop (Figs. 1a-b,e-f). Pollen grains *in situ* are round-triangular in shape, 28-30  $\mu\text{m}$  in diameter, with rugulate or verrucate sculpture (Figs. 3a-e). Gynoecium has a superior ovary, attached to the pedicel by a stipe, surrounded by a receptacle (Figs. 1a-b,h). The receptacle has a nearly flat top, with a central floral pore for the stigmas to protrude through, and with a rough surface (Figs. 1a-b,g, 2d). The receptacle is widest at the middle portion (about 4.2 mm in diameter) and about 3.75 mm in diameter at the top, 0.6-1.6 mm thick, with the projections about 0.4 mm high at the margin (Figs. 3a-b). The carpels are urceolus, stipitate, and with stigmas atop (Figs. 1a-b,g). The stipe is about 0.8 mm long and 180  $\mu\text{m}$  in diameter (Figs. 1a-b,h). The ovary is globose, about 3.1 mm high and 2.6 mm in diameter, completely enclosed by the receptacle except for the floral pore (Figs. 1a-b). Stigma is at the top of the ovary, probably plumose, up to 1 mm long and about 0.2 mm wide (Figs. 1a-b,g, 2a,c). Stoma is seen on the tepals, with stomatal aperture 1-2 $\times$ 7-8  $\mu\text{m}$ , guard cell about 2-3  $\mu\text{m}$  wide and 15  $\mu\text{m}$  long (Figs. 2b,e).

**Holotype:** PB21047a.

**Paratype:** PB21047b.

**Etymology:** *dila-* for the collector of the fossil, Mr. Dila Chen; *-ensis*, Latin suffix.

**Type locality:** Huangbanjigou, Shangyuan, Beipiao, Liaoning, China (41°12'N, 119°22'E).

**Stratigraphic horizon:** the Yixian Formation, lower Cretaceous (>125 Ma).

**Depository:** The specimens are deposited in the Palaeobotanical Collection, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

**Remarks:**

The word “tepal” is preferred because we have not seen any significant differentiation in the perianth. However, the tepals look more like typical petals rather than sepals. Although only four tepals are visible in the specimens (Figs. 1a-b), the total number of tepals may be more than eight, if a radial symmetry (a frequently seen one for Cretaceous flowers<sup>8</sup>) is assumed for the flower. The number of  
5 stamens should be more than two, but the exact number cannot be determined now.

The central dark structure is interpreted as a carpel because of 1) the presence of plumose stigma, 2) the urceolus shape and central position of the structure, 3) absence of coat seed, which, if present, would be more liable to preservation than the stigma is, 4) its direct physical connection with the pedicel, 5) also the presence of stamens, which would be more likely to abscise when seeds mature as  
10 in Zhang’s specimen<sup>9</sup>.

Bristles on the top of the stamens are rare in angiosperms. Although there are some reports of anther appendages in Melastomaceae<sup>10</sup>, they can be distinguished from the bristles in *Euanthus* in morphology, number, and spatial relationship relative to the pollen chamber.

A typical carpel has three parts: an ovary (ovule-bearing part), a stigma (distal pollen receiving  
15 part), and a style (median sterile part)<sup>10</sup>. A stigma is characteristically papillose and often secretory<sup>10,11</sup>. Since the two projections at the distal of the gynoecium are plumose (probably papillose, Figs. 2a,c) and there is no evident differentiation along their whole length (Figs. 1a-b,g, 2a,c), we interpret them as two stigmas. Therefore the carpel of *Euanthus* may be astylous.

The number of the carpels in *Euanthus* is probably two, considering the two stigmas atop, the  
20 separation extended to the basal portion between two carpels, and the usual one-to-one correlation between stigmas and carpels in living plants. However, this correlation is not always constant in living plants<sup>10</sup>, therefore the exact number of carpels in *Euanthus* needs more evidence to ascertain. Degaging

failed to reveal the existence of the third stigma.

The round-triangular pollen grain in Fig. 3e is probably triporate and angulaperturate. However, this needs further evidence to confirm.

*Erenia stenoptera* Krassilov is a winged fruit with a “persistent, funnel-shaped, sessile” stigma  
5 from the Cretaceous of Mongolia<sup>12</sup>. It has a smooth membranous wing “avoiding the stalk” and  
elliptical endocarp<sup>12</sup>. Compared with *Erenia stenoptera*, *Euanthus* is distinct in having projections  
along the upper rim, two distinct hairy stigmas, stamens and tepals. However, *Erenia stenoptera*  
Zhang<sup>9</sup> from western Liaoning is apparently different from the holotype of *Erenia stenoptera* Krassilov  
and should be assigned to *Euanthus dilaensis* even though it is short of stamens and tepals. The  
10 absences of stamens and tepals in *Erenia stenoptera* Zhang<sup>9</sup> (*Euanthus dilaensis*) suggests that the fruit  
of *Euanthus dilaensis* may fall off when mature and its fleshy receptacle may function in attracting  
animals for seed dispersal.

### General Discussion

The Yixian Formation, famous for its early angiosperms including *Archaeofructus* and  
15 *Sinocarpus*, is widely distributed in Hebei, Liaoning and Inner Mongolia, China<sup>7,13</sup>. It is rich in fossils  
of bivalves, gastropods, conchostracans, ostracods, insects, vertebrates, and plants<sup>4,13-15</sup>. Among the  
plants, there are Lycopods, Equisetales, Filicales, Pteridospermae, Cycadales, Bennettiales, Ginkgoales,  
Czekanowskiales, Coniferales and Angiospermales<sup>13,16</sup>. There was once a controversy over the age of  
the Yixian Formation<sup>1-4,6,17</sup>. Now the controversy seems to be resolved since there is an increasing  
20 consensus on the early Cretaceous age (125 Ma) of the Yixian Formation<sup>7</sup>. However, there are still  
unresolved controversies over *Archaeofructus* and *Sinocarpus*. Whether the reproductive organ of  
*Archaeofructus* is an inflorescence or a flower is still an open question<sup>2,6</sup>. The question whether



*Sinocarpus* is a validly published genus also emerged recently<sup>7</sup>. However, one thing clear now is that there is no unanimous perfect flower from the Yixian Formation yet since *Sinocarpus* is a fruit associated with leaves<sup>4</sup> and *Archaeofructus* has no accepted flower<sup>6</sup>.

*Euanthus* can be put in angiosperms because 1) its bisexuality distinguishes it from all known gymnosperms except some Bennettitales and Gnetales; 2) the absence of interseminal scale, dome-shaped receptacle and fleshy pollen organs, and the presence of stigma distinguish *Euanthus* from Bennettitales; 3) the absence of micropyle tube and presence of stigma, plus pedicellate solitary flower, distinguish *Euanthus* from Gnetales; 4) the flower organization typical of angiosperms is present in *Euanthus*. Thus *Euanthus* can be safely assigned to angiosperms and thus become the oldest known perfect flower (>125 Ma).

As an element of early angiosperms, the status of *Euanthus* in the following characters is more or less concordant with the conclusion based on the analysis of living angiosperms: bisexuality, small size, no style, undifferentiated perianth, superior ovary, free tepals, moderate or low number of floral parts, free stamens, medium-sized pollen grains, possible wet stigma of the flower<sup>18,19</sup>. However, there are several features unexpected, including those of floral receptacle and stamen, in *Euanthus*.

An interesting character of *Euanthus* is the structure surrounding the carpels. Rarely in angiosperms are the carpels enclosed almost completely by a structure, such as floral roof (velum) in *Siparuna* and *Glossocalyx* (Siparunaceae)<sup>20</sup>, *Daphnandra* (Atherospermataceae)<sup>20</sup>, perigynium in *Carex* (Cyperaceae)<sup>21</sup>, and receptacle in *Nelumbo* (Nelumbaceae)<sup>11</sup>. Similar to *Euanthus*, both *Siparuna* and *Daphnandra* have a fleshy floral roof enclosing the carpels except where the styles/stigmas protrude through the floral pore. However, their tepals and/or stamens are inserted on the outer surface of the floral roof<sup>20</sup>, unlike the situation in *Euanthus*, where the stamens and tepals are completely separated

from the floral receptacle (Figs. 1a-b,e-f,h). *Carex* is also similar to *Euanthus* in general organization of the perigynium (receptacle), the carpels, and the protruding styles/stigmas<sup>22</sup>. But the perigynium in *Carex* is apparently not so fleshy and usually separated from the carpels, while the receptacle in *Euanthus* is fleshy and tightly enclosing the carpels. The receptacles in *Nelumbo* and *Euanthus* are similar to each other in the fleshy nature, enclosing carpels, separation from the stamens and tepals. But *Nelumbo* has many apocarpous carpels rather than a couple of closely packed carpels. In terms of the independence from the stamens and tepals, perigynium in *Carex* and receptacle in *Nelumbo* are more similar to receptacle in *Euanthus*. The fleshiness of the receptacle further makes homology between the receptacles in *Nelumbo* and *Euanthus* more plausible. Since there is no receptacle enclosing carpels found in the previous Cretaceous fossil record<sup>8</sup>, *Euanthus* appears strange even from the perspective of fossils. Whether there is any phylogenetic significance for this character apparently is still an open question.

Several characters of *Euanthus* are not well understood yet. These include nature of bristles at the top of the anthers, number of sporangia per anther, and nature of the pollen grain. Bristles at the top of the anther appear strange in angiosperms. Normally, a connective rather than bristles is expected here. The function of the bristles is currently an open question. Number of the sporangia per anther is hard to determine. The globose form of the anther and its relationship with the filament makes it unlikely that there are more than one sporangia in the anther. If this were the case, this anther would be quite unique in angiosperms. Apparently, the pollen grains *in situ* are not monosulcate, as expected for early angiosperms<sup>19</sup>. The pollen grains appear to rather look like triporate, even though not confirmed yet. This would suggest either that the triporate pollen grains may be rather primitive, or that there may be a cryptic history of angiosperms before *Euanthus*. The former alternative requires a revision of theory on

angiosperm evolution in terms of pollen. The latter alternative is supported by recent reports of Jurassic angiosperm, *e.g.* *Schmeissneria*, as well as the diversified microfossil and macrofossil angiosperms in the Yixian Formation<sup>1-4,15</sup>.

Sun et al.<sup>1,23</sup>, Leng and Friis<sup>4</sup> have independently reported megafossils of angiosperms from the Yixian Formation. Wang et al. have found early angiosperm pollen grains from the formation<sup>15</sup>. Ren et al. also discussed the presence of angiosperms based on the flower-loving insects in the formation<sup>24</sup>. Therefore all information from microfossils as well as macrofossils confirms the unambiguous presence of angiosperms in the Yixian Formation. It is therefore non-surprising to find one more angiosperm, *Euanthus*, from the Yixian Formation. The round-triangular shaped pollen grains (probably related to eudicots) found in *Euanthus* are non-typical in early angiosperms and only abundant in post-Aptian age<sup>25</sup>. Therefore, if isolated from the mother plant, no one dares to claim them as angiosperms in strata as early as the early Cretaceous. This partially explains why they escaped from the pollen list given by Wang et al.<sup>15</sup>. Therefore the abundance of angiosperms in the Yixian Formation may have been under-represented by the palynological evidence. The current picture of angiosperm radiation based on palynological record and leaves in the Potomac Group demonstrates a gradual increase of angiosperm diversity in the early Cretaceous<sup>26</sup>, just as many people expect and believe. However, this picture may be biased since a palaeobotanist might be blind to the non-typical angiosperm pollen grains in *Euanthus* and non-typical angiosperm leaf in *Archaeofructus*, especially when they are from early Cretaceous or older strata. Few people would hesitate excluding them from angiosperms. Palaeobotanists appear to need to be more cautious to apply regularity of extant angiosperms onto their ancestors. The “abominable mystery” may be due to the unrecognizability of the relics of early angiosperms.

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## Figure Legends

*Figure 1 - The flower and some of the details. The specimen is deposited in the Palaeobotanical Collection, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. All Stereomicroscope photograph.*

5 Fig. 1a. A general view of the flower. Note the tepals (black arrows) and stamens (white arrows).  
Specimen number PB21047a. Bar = 2 mm.

Fig. 1b. A view of the flower, counterpart of that in Fig. 1a. Note the stigmas (black arrows), outline of the carpel (white double arrow), separation between the two carpels in the center, and receptacle (white arrow). Specimen number PB21047b. Bar = 2 mm.

10 Fig. 1c. A detailed view of one of the tepals. Note the two veins (white arrows). Specimen number PB21047a. Bar = 1 mm.

Fig. 1d. A view of a complete tepal exposed after degaging. Note the spatulate shape, long claw (white arrow) and the round tip. Specimen number PB21047b. Bar = 1 mm.

15 Fig. 1e. A view of one of the anthers, enlarged from Fig. 1a (left white arrow). Note the filament at the base (white double arrow), globose anther (white arrow) and the bristles atop (black arrows).  
Specimen number PB21047a. Bar = 0.5 mm.

Fig. 1f. A view of the counterpart of the anther shown in Fig. 1e, enlarged from Fig. 1b. Note globose anther (white arrow) and the bristles atop (black arrows). Specimen number PB21047b. Bar = 0.5 mm.

20 Fig. 1g. A detailed view of the stigmas. Note the deployment of the stigma, the relationship between the receptacle (black arrow) and the carpel (white arrow). Specimen number PB21047b. Bar = 1 mm.

Fig. 1h. The arrangement of the floral parts. Note the spatial relationship between the pedicel

(central bottom) and tepals (black arrows), stamens (white arrows) as well as gynoecium (black double arrows). Specimen number PB21047b. Bar = 1 mm.

**Figure 2 - Some details of the flower. All SEM photographs. Specimen number PB21047b except in Fig. 2a.**

5 Fig. 2a. A view of the right stigma in Fig. 1a (black triangle). Note hair-like structures (black arrows) on its surface. Pieced from two original images. Specimen number PB21047a. Bar = 0.2 mm.

Fig. 2b. A detailed view of the cuticle of the tepal. Note the possible stomatal aperture (white arrow). Bar = 5  $\mu$ m.

10 Fig. 2c. Some details on the surface of the stigma in Fig. 2a, but on a broken cellulose transfer made from the counterpart (PB21047b). Note the hairs (black arrow) and the scars of hairs on the stigma (white arrow). Bar = 10  $\mu$ m.

Fig. 2d. Clusters of trichomes on the surface of the receptacle (white arrow). The outside of the receptacle is on the top. Bar = 10  $\mu$ m.

15 Fig. 2e. A view of a stomatal aperture on one of the tepals. The black triangle in Fig. 1b indicates the approximate position of the stomata in the tepal. Note the aperture, guard cells, and angular crystals not completely dissolved by HF on the transfer. Bar = 5  $\mu$ m.

**Figure 3 - In situ pollen grains of the flower. All SEM photograph. Specimen number PB21047b.**

20 Fig. 3a. A piece of the sediment removed from the anther area. Note that a couple of clusters of pollen grains (black arrows) are visible on the surface of the sediment even without any chemical processing. Bar = 50  $\mu$ m.

Fig. 3b. A detailed view of the pollen cluster pointed by the lower black arrow in Fig. 3a. Bar = 10  $\mu\text{m}$ .

Fig. 3c. A detailed view of the pollen grain pointed by the black arrow in Fig. 3b. Bar = 10  $\mu\text{m}$ .

Fig. 3d. The rugulate sculpture on the surface of the pollen, enlarged from the rectangular region  
5 in Fig. 3c. Bar = 1  $\mu\text{m}$ .

Fig. 3e. A detailed view of the pollen grain pointed by the white arrow in Fig. 3b. Note the  
round-triangular shape of the pollen grain, possible pores at the angles (white arrows) and verrucate  
sculpture on the surface of the pollen grain. Bar = 10  $\mu\text{m}$ .

**Figure 4 - The reconstruction of the flower. Note the central carpels, receptacle around the  
10 carpels, globose anther with bristles atop, and tepals.**









