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A perfect flower from the Jurassic of China

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Flower, enclosed ovule and tetrasporangiate anther are three major characters distinguishing angiosperms from other seed plants. Morphologically, typical flowers are characterised by an organisation with gynoecium and androecium surrounded by corolla and calyx. Theoretically, flowers are derived from their counterparts in ancient ancestral gymnosperms. However, as for when, how and from which groups, there is no consensus among botanists yet. Although angiosperm-like pollen and angiosperms have been claimed in the Triassic and Jurassic, typical flowers with the aforesaid three key characters are still missing in the pre-Cretaceous age, making many interpretations of flower evolution tentative. Thus searching for flower in the pre-Cretaceous has been a tantalising task for palaeobotanists for a long time. Here, we report a typical flower, *Euanthus panii* **gen. et sp. nov.**, from the Middle–Late Jurassic of Liaoning, China. *Euanthus* has sepals, petals, androecium with tetrasporangiate dithecate anthers and gynoecium with enclosed ovules, organised just like in perfect flowers of extant angiosperms. The discovery of *Euanthus* implies that typical angiosperm flowers have already been in place in the Jurassic, and provides a new insight unavailable otherwise for the evolution of flowers.

Keywords: flower; angiosperm; Jurassic; China; Liaoning

1. Introduction

Despite angiosperms are the most diversified and important plant group in the current ecosystem and they make the well-being of human beings possible, the origin of angiosperms and their flowers remains a tantalising question for botanists (Arber and Parkin 1907; Hagerup 1936; Crane 1985; Hickey and Taylor 1996; Sun et al. 1998; Frohlich 2003; Doyle et al. 2008; Friis et al. 2010; Wang 2010a), and is one of the top science questions for human beings (Kennedy and Norman 2005). Before the 1960s, many believed that angiosperms had an ancient history much older than the Cretaceous, but later studies found that many of the pre-Cretaceous records were not as reliable as claimed (Doyle 1978; Friis et al. 2011). Later, numerous proposals of early angiosperms from the pre-Cretaceous age (Cornet 1989a, 1989b, 1993; Hochuli and Feist-Burkhardt 2004; Wang et al. 2007; Wang 2010b, 2010a; Wang and Wang 2010; Hochuli and Feist-Burkhardt 2013), although in agreement with molecular clock and morphological analyses (Wu et al. 2003;Lu and Tang 2005; Soltis et al. 2008; Hilu 2010; Smith et al. 2010; Prasad et al. 2011), are not widely accepted by many palaeobotanists (Doyle 2008; Friis et al. 2011). Angiosperms are characterised by their flowers, enclosed ovules and tetrasporangiate dithecate anthers (Friis et al. 2011). It is logical and widely believed that angiosperms are derived from their ancient gymnospermous ancestors and there should be a series of transitional stages in between (Beck 1976). Searching for such intermediate entities is so challenging that Tom Harris characterised the history of this research as an ‘unbroken record of failure’ (Beck 1976). The earliest records of well-accepted megafossil angiosperms (Duan 1998; Sun et al. 1998, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009; Wang 2010a) and typical flower (Wang and Zheng 2009) are all from the Early Cretaceous Yixian Formation. However, such an unexpectedly great diversity of angiosperms in the Yixian Formation (Duan 1998; Sun et al. 1998, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009) implies that the origin of angiosperms should be older, at least older than the Barremian, namely, flowers, the most reliable evidence for an angiosperm (Thomas 1936), should be in place in the pre-Barremian age. In favour of this inference, here in we report *Euanthus panii* **gen. et sp. nov.**, a fossil flower, from the Jiulongshan Formation (the Middle–Late Jurassic, 162–167 Ma) of Liaoning, China. *Euanthus* demonstrates a typical flower organisation, including sepals, petals, androecium of tetrasporangiate dithecate anthers and gynoecium with enclosed ovules, implying that flowers are already in place in the Jurassic. Since enclosed ovules, tetrasporangiate dithecate anther and flower-like organisation are all seen in *Euanthus*, we place *Euanthus* in angiosperms with

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decent confidence. The Middle–Late Jurassic age of *Euanthus*, in supplement to and in agreement with the previous fossil reports (Cornet 1986, 1989a, 1989b, 1993; Cornet and Habib 1992; Hochuli and Feist-Burkhardt 2004; Wang et al. 2007; Wang 2010b, 2010a; Zheng and Wang 2010; Han et al. 2013; Hochuli and Feist-Burkhardt 2013) and molecular clock (Chaw et al. 2004; Soltis et al. 2008; Prasad et al. 2011), underscores the existence of flowers in the Jurassic and prompts a rethinking on flower evolution.

2. Materials and methods

2.1 Geological background

Jurassic strata are widely distributed in western Liaoning, China. In this region, they are divided into the Xinglonggou Formation, Beipiao Formation, Jiulongshan Formation, Tiaojishan Formation and Tuchengzi Formation, in ascending order (Figure 1(b)). The first two formations belong to the Lower Jurassic, the ensuing two the Middle Jurassic, and the last one the Upper Jurassic

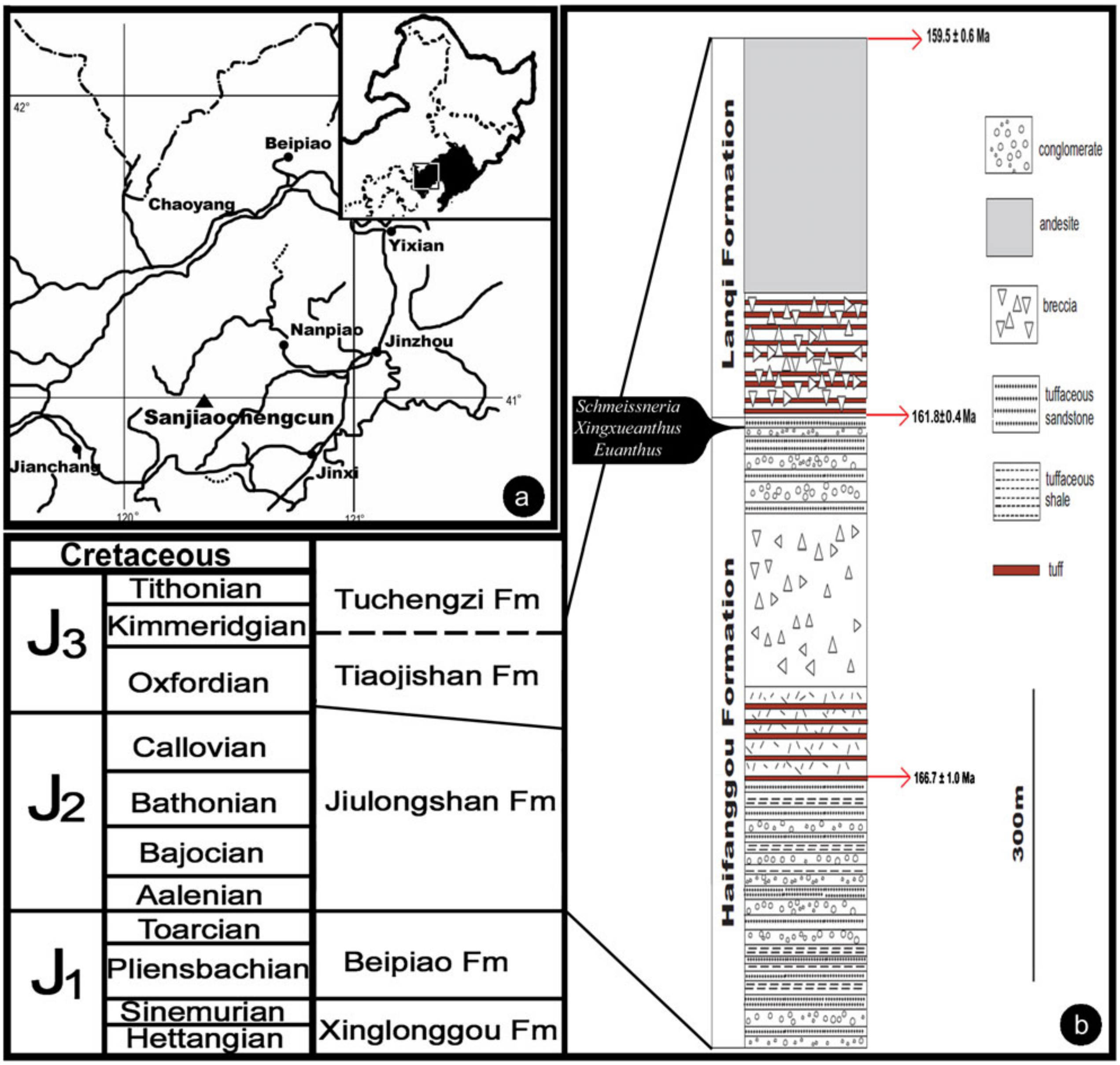

Figure 1. (Colour online) Geographical and stratigraphical information of *Euanthus*. (a) The inset map shows Liaoning (black region) in northeast China, and the rectangular region in it is enlarged in the main map. The round dots show the major cities in western Liaoning. The triangle marks the position of the holotype locality at Sanjiaocheng Village, Huludao, Liaoning, China (120°22′5.75″E, 40°58′7.25″N). Reproduced from Wang et al. (2007) and Wang and Wang (2010), courtesy of BMC Evolutionary Biology and Acta Geological Sinica (English version). (b) Stratigraphical information of the Jurassic and the fossiliferous layer in western Liaoning. Note that *Schmeissneria*, *Xingxueanthus* and *Euanthus* are from the topmost layer of the Jiulongshan Formation, which is at least 161 Ma old. Modified from Chang et al. (2014).

(Figure 1(b); Deng et al. 2003). To make the nomenclature and stratigraphical correlation uniform in northeastern China, the former Haifanggou Formation and Lanqi Formation are now correlated to and called the Jiulongshan Formation and Tiaojishan Formation, respectively, in western Liaoning and adjacent regions. The specimen of *Euanthus*, together with those of *Schmeissneria* (Wang et al. 2007) and *Xingxueanthus* (Wang and Wang 2010), was collected from the same outcrop of the Jiulongshan Formation at Sanjiaocheng Village, Huludao, Liaoning, China (120°22′5.75″E, 40°58′7.25″N; Figures 1 (a) and 2(a)–(c)). The fossiliferous layer is about 1–2 m below the boundary between the underlying Jiulongshan Formation and the overlying Tiaojishan Formation (Figure 1(b)). The repeated Ar^{39}/Ar^{40} datings of the bottom layer of the overlying Tiaojishan Formation give an age of 161.8 Ma (Chang et al. 2009, 2014), implying that *Euanthus* is at least 161.8 Ma old (Figure 1(b)). Because the boundary age between the Callovian and Oxfordian and Middle/Late Jurassic was adjusted to 164 Ma recently (Walker et al. 2012), we accept the age of *Euanthus* as the Callovian–Oxfordian (Middle–Late Jurassic).

Mr Kwang Pan (also known as Guang Pan, Figure 3 (a)) collected numerous fossil plant specimens from the outcrop at Sanjiaocheng Village in the 1970s (Figures 1(a), (b), 2(a)–(c) and 3(b)–(d)) and claimed several angiosperms (Pan 1983), although many of such claims were declined by others (Xu 1987). The Jiulongshan Formation is widely distributed in western Liaoning (Figure 2(a)–(b)). Many palaeobotanical works have been carried out on the palaeoflora of the formation. The flora of the Jiulongshan Formation is very diversified, at least including bryophytes (*Hepaticites* and *Thallites*), lycophytes (*Selaginellites* and *Lycopodites*), equisettitales (*Equisetum* and *Neocalamites*), ferns (*Marattia*, *Todites*, *Clathropteris*, *Hausmannia*, *Coniopteris*, *Dicksonia*, *Eboracia*, *Pteridiopsis*, *Cladophlebis* and *Raphaelia*), bennettitales (*Ptilophyllum*, *Pterophyllum*, *Tyrmia*, *Jacutiella*, *Cycadolepis*, *Cycadocites* and *Anomozamites*), cycadales (*Nilssonia*, *Beania*, *Ctenis* and *Pseudoctenis*), ginkgoales (*Ginkgo*, *Baiera*, *Sphenobaiera*, *Czekanowskia*, *Solenites*, *Phoenicopsis*, *Leptostrobus*, *Ixostrobus* and *Antholithus*), coniferales (*Pityocladus*, *Pityophyllum*, *Pityospermum*, *Podozamites*, cf. *Aethophyllum*, *Yanliaoa*, *Schizolepis* and *Elatocladus* (*Cephalotaxopsis*?)), caytoniales (*Sagenopteris*), angiosperms (*Schmeissneria* and *Xingxueanthus*) and plants with unknown affinity (*Nanpiaophyllum*, *Desmiophyllum* and *Problematicum*) (Pan 1983, 1997; Zhang and Zheng 1987; Wang et al. 1997, 2007; Zheng et al. 2003; Wang and Wang 2010) (For detailed taxon list, see supplemental data). The *Coniopteris simplex–Eboracia lobifolia* assemblage recovered in the formation is typical for the Middle Jurassic (Zhang and Zheng 1987; Kimura et al. 1994; Wang et al. 1997; Deng et al. 2003). The palynoflora of the formation is characterised by the *Cyathidites–Asseretospora–Pseudopicea* assemblage, which is dominated by fern spores (55%) and gymnosperm pollen (45%) (Xu et al. 2003). The fern spores mainly include *Cyathidites* and *Deltoidospora* (25–45.9%), while the gymnosperm pollen is mainly of *Cycadopites* (21.4%) and bisaccate pollen grains (Xu et al. 2003). The biostratigraphical implication of such flora and palynoflora compositions is in agreement with other independent biostratigraphical works. For example, the *Euestheria haifanggouensis–Euestheria ziliujingensis* estherian assemblage, *Darwinula sarytirmenensis–Darwinula magna–Darwinula stenimpudica* ostracode assemblage, *Samarura gigantea–Mesobaetis sibirica–Mesoneta antiqua* entomofauna assemblage and *Ferganoconcha haifanggouensis–Yananoconcha triangulata* bivalve assemblage recovered from the formation all are comparable to their counterparts of the Middle Jurassic (Pan 1983, 1997; Zhang and Zheng 1987; Kimura et al. 1994; Wang et al. 1997, 2007; Deng et al. 2003; Xu et al. 2003; Zheng et al. 2003; Wang and Wang 2010). This consensus on age is further strengthened by repeated isotopic datings aimed at early angiosperm fossils (Figure 1 (b); Chang et al. 2009, 2014).

2.2 Methods

The specimen of *Euanthus* **gen. nov.** included two facing parts. It was preserved as compression with flecks of coalified residue. The specimen was observed and photographed using a Nikon SMZ1500 stereomicroscope with a digital camera. One of the two facing parts was observed using a Leo 1530 VP scanning electron microscope (SEM) at the Nanjing Institute of Geology and Palaeontology, Nanjing, China (NIGPAS). A replica of nitro cellulose was made for one of the parts, cleaned with HF and HCl, coated with gold and observed using the Leo 1530 VP SEM and a Benchtop SEM TM3030 at NIGPAS. All images were recorded in TIFF or JPEG format, organised together using Photoshop 7.0 for publication.

3. Results

Euanthus **gen. nov.**

Generic diagnosis: Flower perigynous, with half-inferior ovary, of pentamerous symmetry, with connected calyx, corolla and gynoecium. Sepals short, stout, with a round distal concave portion and a stout base, attached by its whole base. Petals long, alternate to the sepals, with a round concave limb and a slender claw, and attached by the claw. Androecium with tetrasporangiate dithecate anthers and *in situ* pollen grains. Gynoecium including a long, slender hairy style and an unilocular ovary enclosing unitegmic ovules inserted on the ovarian wall.

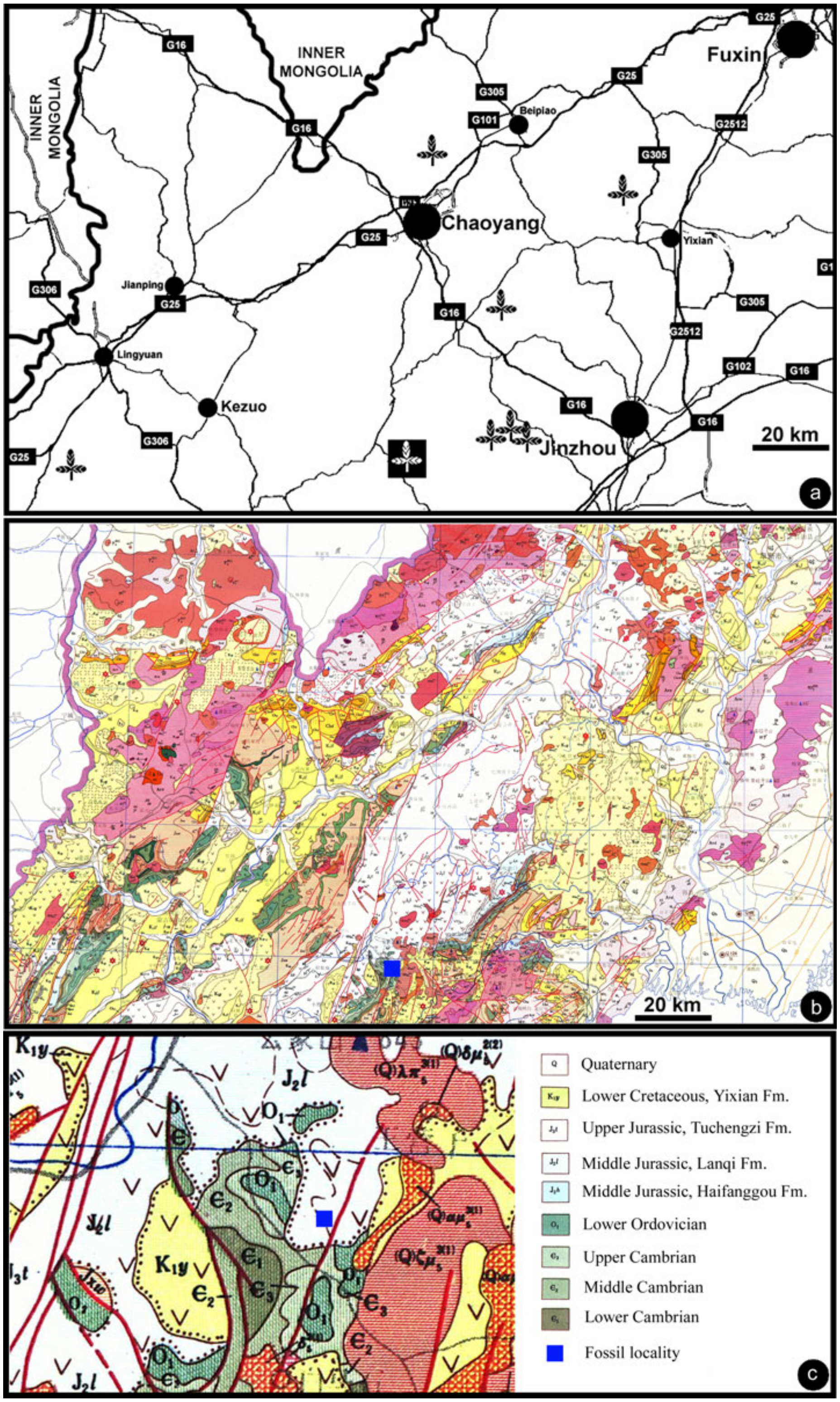

Figure 2. (Colour online) Geological background of the holotype locality of *Euanthus*. (a) Several localities of the Jiulongshan Formation in the western Liaoning. The bottom central one is the holotype locality of *Euanthus*. (b) Geological map of the region shown in panel (a). Note the position of the fossil locality (blue square). Reproduced and modified from attached map 1 of Liaoning Provincial Agency of Geology and Mineral Resources (1989). (c) Geological map of the region near the fossil locality (blue square). Note the position of the fossil locality (blue square). Enlarged from (b).

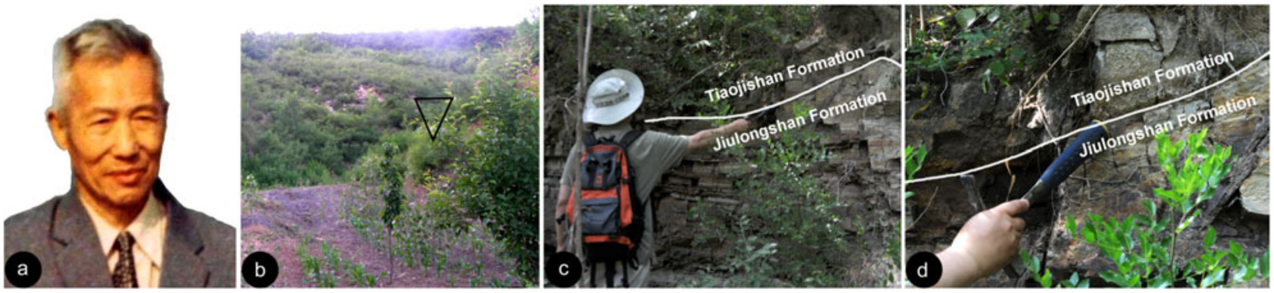

Figure 3. (Colour online) The holotype collector and donor of *Euanthus* specimen and the holotype outcrop of the Jiulongshan Formation near Sanjiaocheng Village. (a) Mr Kwang Pan, the holotype collector and donor of *Euanthus*. (b) The outcrop at the holotype locality of *Euanthus*, north of Sanjiaocheng Village in Huludao, Liaoning. The triangle points to the fossil locality. (c) The spatial relationship of the Jiulongshan Formation and its overlying Tiaojishan Formation near the fossil locality. Note the boundary between the two formations. The fossiliferous stratum is about 1–2 m below this boundary. (d) Detailed view of the boundary between the Jiulongshan Formation and Tiaojishan Formation.

Type species: *Euanthus panii* **gen. et sp. nov.**
Etymology: *Euanthus*, for real flower in Latin.
Horizon: the Jiulongshan Formation.
Locality: Sanjiaocheng Village, Huloudao City, Liaoning, China (120°22′5.75″E, 40°58′7.25″N).

Euanthus panii **gen. et sp. nov.**

(Figures 3–7)

Specific diagnosis: In addition to generic diagnosis, flower about 12 mm long and 12.7 mm wide. Receptacle about 2.3 mm in diameter, pentagonal in cross view. Sepals 3.6–3.85 mm long, 3.6 mm wide, with a round tip and a 1.9 mm-wide base. Petals 5–5.75 mm long and 3.8–4.2 mm wide. Stamen preserved only as anthers. Anther tetrasporangiate, dithecate, about 370 μm wide and 218 μm high, lacking of obvious connective, with *in situ* pollen grain about 12.6–16.2 μm in diameter. Style 8.5 mm long, 1.4 mm wide, elongate, tapering distally, covered with hairs, of cells with straight wall. Ovary pentermaous, about 2.2 mm in diameter, enclosing unitegmic ovules, with papilae on its inner wall.

Description: The fossil is preserved as a compression, with some coalified residue, split as part and counterpart (Figure 4(a),(b)). This part-and-counterpart preservation allows both the adaxial and abaxial surfaces is of the same part to be observed (Figure 5(a),(b)). The flower is about 12 mm long, 12.7 mm wide, including sepals, petals, possible androecium and gynoecium (Figures 4(a),(b) and 8(a)). The receptacle is about 2.3 mm in diameter, pentagonal in shape, with sides 1.55 mm long, and the angle between adjacent sides is about 110° (Figure 4(c)–(e)). Only two of the sepals are visible, 3.6–3.85 mm long, 3.6 mm wide, each opposite to a side of the receptacle pentagon and attached with its full base (Figure 4(a),(c)). Each sepal has two portions, namely a 3.6-mm-wide, elliptical distal portion and a stout, 1.9-mm-wide, parallel-sided base (Figure 4(a)–(c)). The distal portion is concave when viewed adaxially, and has an abaxial keel (Figure 5(c)). Only three of the petals are visible, alternate with the sepals, 5–5.75 mm long, 3.8–4.2 mm wide, each opposite to a corner of the receptacle pentagon (Figures 4(a),(c) and 5(a),(b)). Each petal has two portions, a round distal limb and an ob-triangular basal claw (Figures 4(a),(b) and 5(a),(b)). The limb is 3.2 mm long, 4.2 mm wide, concave when viewed adaxially, with concentric wrinkles at the margin and a round tip and lacking of an obvious keel (Figure 5(a),(b)). The claw is ob-triangular in shape, narrowing to the base, with obvious transverse wrinkles on its distal abaxial (Figure 5(a),(b),(d)). The stamens are inserted between the petals and gynoecium, not physically connected with any parts, with only two partially preserved anthers (Figures 4(e), 6(d)–(h) and 7(f)). The filament is slender, about 32 μm wide, not preserved in whole, inferred to be 3.1–3.8 mm long (Figure 6(a)–(c)). The anther lacks obvious connective, is tetrasporangiate, dithecate, constricted between the left and right halves, with two adjacent pollen sacs on one side confluent forming an eight-shaped configuration (Figure 6(d),(f),(h)). Pollen sac wall is about 23 μm thick, including epidermis and tapetum (Figure 6(d),(h)). Possible pollen grains 12.6–16.2 μm in diameter are found *in situ* in one of the anthers (Figure 6(f),(i)). The gynoecium is preserved in the centre of the flower, including an ovary and a style, with some coalified residues (Figures 4(a)–(e) and 7(a)–(k)). The total length of the style is about 10 mm long (Figures 4(a),(b) and 7(a),(b)). The style is visible as two separated segments, eclipsed by a sepal in between (Figures 4(a),(b),(e) and 7(a),(b),(f)). The basal segment is physically connected with the ovary, about 1.3 mm wide, elongate, tapering distally, with longitudinal hairs on its surface (Figures 4(e), 6(g) and 7(f)). The distal segment is 5.8 mm long, 0.7 mm wide, tapering distally, with possible secretory structures (Figures 4(a),(b) and 7(a)–(d)). A hair is about 29 × 33 μm in cross view (Figure 7(a)–(e)). The ovary is pentamerous, about 2.3 mm in diameter (Figures 4(c),(d)

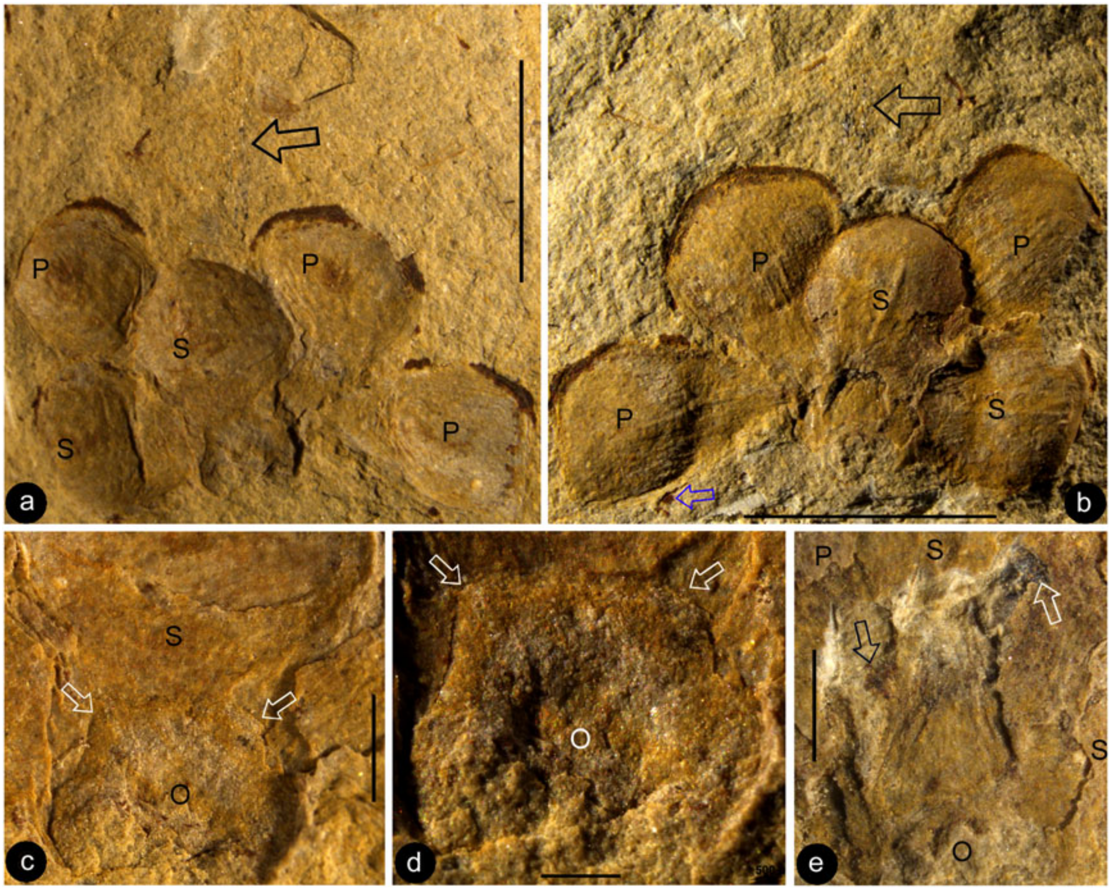

Figure 4. (Colour online) *Euanthus panii* **gen. et sp. nov** and its details. Stereomicroscopy. (a, b) The flower in two facing parts, with sepals (S) and petals (P) radiating from the receptacle. The black arrows mark the distal of the style, and the blue arrow in (b) marks the stamen shown in Figure 6(d),(e),(h). Holotype: PB21685, PB21684. Bar = 5 mm. (c) A sepal (S) is almost structureless between the two arrows, implying that it is attached to the receptacle (O) with its whole base. Enlarged from (a). Bar = 1 mm. (d) Pentamerous receptacle with ovarian cavity (O) in its centre. Note the corners (arrows) of about 110°. Bar = 0.5 mm. (e) Basal portion of the flower after degagement. Note spatial relationship among the ovary (O), style base, a possible filament stub (arrow), sepals (S) and petal (P). Refer to Figure 7(f). Bar = 1 mm.

and 7(f)–(h)). On the side wall of the ovary are several protrusions, and at least one of them can be interpreted as an ovule due to its micropyle-like structure (Figure 7(f)–(j)). The ovule is 0.2–0.4 mm long, with a pointed micropyle (Figures 7(h)–(j) and 8(b)). Only one layer of integument is seen, 5–8.8 μm thick, separated from and covering the nucellus (Figures 7(i),(j) and 8(b)). Papilae are seen on the inner wall of the ovary (Figure 7(k)). Pits are seen on the side wall of a vascular element (Figure 6(j),(k)). The whole flower is sketched in Figure 8(a) and reconstructed in Figure 8(c).

Etymology: *panii* for Mr Kwang Pan (1920–2014), the collector and donor of the specimen.

Holotype: PB21685 (Figure 4(a)), PB21684 (Figure 4(b)).

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Remark: All the parts of the flower *Euanthus* are physically connected each other, except the male parts shown in Figure 6(a)–(f),(h). The two anthers are not fused with either of the petals (Figures 4(b) and 6(a)–(c)). Although no filaments are seen connecting the anthers and receptalce, a stub of possible filament is seen between the gynoecium and petal (Figures 4(e), 6(g) and 7(f)). A slender filament (Figure 6(a)–(c)) close to the margin of a petal and position of the anther (Figures 4(b) and 6(a),(e)) suggest a position alternate the petals for the stamens.

4. Discussions

There used to be some controversy over the age of some Chinese angiosperm fossils (Sun et al. 1998; Swisher et al. 1998; Friis et al. 2003). Although this controversy has been resolved (Dilcher et al. 2007; Sha 2007), it warns us against potential errors about the age of our fossil, *Euanthus*. The Callovian–Oxfordian (Middle–Late Jurassic) age of *Euanthus* is not claimed by us or any single group alone, but is agreed on by various authors working in different fields using different techniques and based on various types

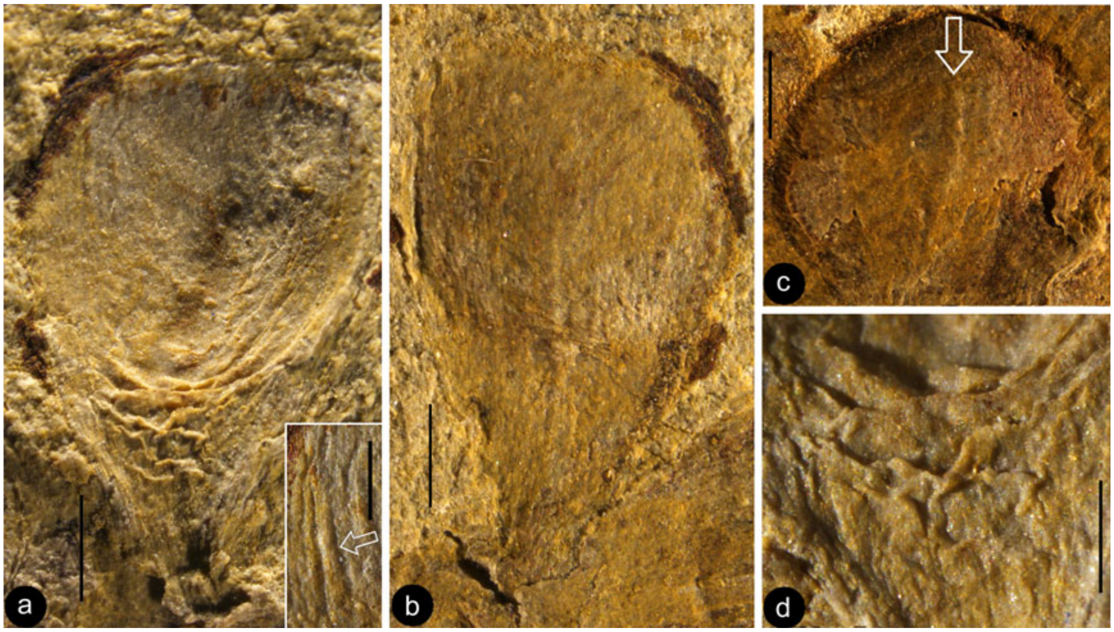

Figure 5. (Colour online) Details of the sepals and petals. Stereomicroscopy. (a) Adaxial view of a complete petal, from the lower-right of Figure 4(a), showing a round concave limb and a claw with transverse wrinkles. Bar = 1 mm. The inset shows the parallel concentric wrinkles along the limb margin. Inset bar = 0.5 mm. (b) Abaxial view of the petal in (a), from the lower-left in Figure 4(b), showing the round convex limb and the claw with no obvious wrinkles. Bar = 1 mm. (c) Detailed view of the sepal pointing to the upper right in Figure 4(b) with an abaxial keel (arrow). Bar = 1 mm. (d) Transverse wrinkles on the abaxial surface on the distal of the claw in (a). Bar = 0.5 mm.

of evidence including biostratigraphical as well as isotopic data (Pan 1983, 1997; Zhang and Zheng 1987; Kimura et al. 1994; Wang et al. 1997, 2007; Deng et al. 2003; Zheng et al. 2003; Chang et al. 2009, 2014; Wang and Wang 2010; Walker et al. 2012). It is noteworthy that two of the isotopic datings have been performed specially to determine the age of the strata yielding early angiosperms, including *Euanthus*, *Schmeissneria* and *Xingxueanthus* (Figure 1(b); Chang et al. 2009, 2014). These Ar^{39}/Ar^{40} datings indicate that these early angiosperm fossils are at least 161.8 Ma old (Chang et al. 2009, 2014). At least for the time being, we cannot imagine that there could be more direct or better dating for *Euanthus*. Therefore, we have to adopt the concurring conclusion reached by previous independent authors. Namely, *Euanthus* is of the Callovian–Oxfordian (161.8–166.7 Ma, Middle–Late Jurassic) in age.

Angiosperms are the most important plant group that provides most of the materials necessary for sustaining development of human beings. Angiosperms are characterised by various features, including vessel elements, reticulate venation, tetrasporangiate anthers, enclosed ovules and flowers (Wang 2010a). Among them, flowers are by far the most well-known and reliable criterion identifying an angiosperm (Thomas 1936), and enclosed ovules are a defining character to pin down angiospermous affinity. A typical angiosperm perfect flower includes four whorls of parts, namely, calyx, corolla, androecium and gynoecium (Judd et al. 1999). Flower organisation is characterised by the perianth (foliar parts) arranged around the gynoecium/androecium (Bateman et al. 2006). As seen above and below, *Euanthus* has most, if not all, of the characteristics of typical flowers of angiosperms.

Various flower features distinguish *Euanthus* from the reproductive organs of gymnosperms. The perianth of *Euanthus* and angiosperms is morphologically differentiated into calyx and corolla that are distinguished by their shape and size (Figures 4(a),(b) and 5(a)–(c)), while, in Bennettitales/Gnetales, foliar parts surrounding female and/or male parts are always isomorphic, scale-like and barely differentiated (Watson and Sincock 1992; Rothwell and Stockey 2002; Stockey and Rothwell 2003; Bateman et al. 2006; Crane and Herendeen 2009). The well-differentiated sepals and petals, transverse wrinkles on the abaxial of its petals, pentagonal receptacle, slender hairy style and lack of interseminal scales (Figures 4(a),(d), 5(a)–(c), 6(d),(h) and 7(a)–(c)) make *Euanthus* an angiosperm and less-likely a bennettitalean element, and considering the 'receptacle' is round in cross view, numerous seeds are tightly surrounded by interseminal scales on the periphery of the gynoecium in the Bennettitales (Table 1; Watson and Sincock 1992; Crane and Herendeen 2009; Friis et al. 2009; Rothwell et al. 2009). Decussate arrangement of scales/bracts, characteristic of Gnetales, is hard to reconcile with the pentamerism of *Euanthus* (Figure 4(d)). Finally, micropylar tube, characteristic of both Bennettitales and Gnetales, is smooth, free of hairs and completely absent in *Euanthus* (Figure 7(a)–(c); Table 1). Most importantly, ovules with micropyle and integument enclosed inside the ovary (Figures 7(h)–(j) and 8(b)) support the placement of *Euanthus* in angiosperms. This is further strengthened by the presence of tetrasporangiate dithecate anther in *Euanthus* (Figure 6(d),(h)), which is never seen in any gymnosperms. Interestingly, the pitting pattern seen on the side wall of vascular element of *Euanthus* (Figure 6(k)) is very similar to the one on the intervessel wall of a Miocene angiosperm fossil wood (*Ruprechtioxylon multiseptatus*, Polygonaceae, Figure 2(h)–(i) of Cevallos-Ferriz et al. 2014), although the validity of the last comparison requires more investigation to confirm.

Various studies indicate that angiosperms may have a history longer than currently accepted. Hitherto, we have very limited knowledge on the origin and early evolution of flowers in the pre-Cretaceous. However, the unexpectedly great diversity of angiosperms in the Early Cretaceous Yixian Formation (Duan 1998; Sun et al. 1998, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009; Wang 2010a) implies a prior crypt history of angiosperms; palaeobotanists have demonstrated the existence of angios-

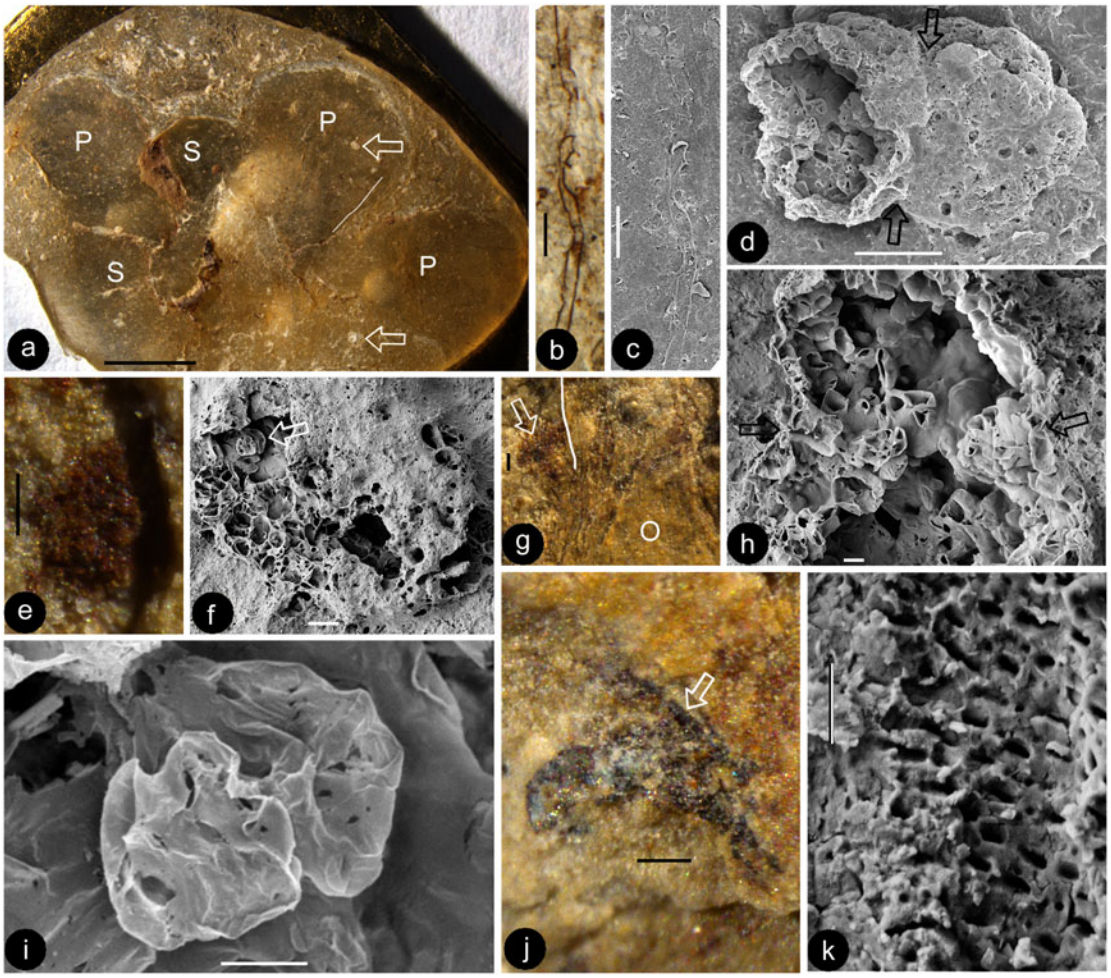

Figure 6. (Colour online) Stamens of *Euanthus panii* **gen. et sp. nov.** Stereomicroscopy and SEM. (a) Nitro cellulose replica of the specimen in Figure 4(b), showing the positions of two anthers (white arrows) relative to the sepals (S) and petals (P). The white line marks the position of the possible filament shown in (b) and (c). Bar = 2 mm. (b, c) A possible filament on the replica, marked with a white line in (a). Stereomicroscopy (b) and SEM (c). Bar = 0.1 mm. (d) The anther marked by a lower arrow in (a) shows the constriction (arrows) between the left and right halves of the anther. The left half is broken, and its internal details are visible. Bar = 0.1 mm. (e) Dark organic material of the anther, marked by a blue arrow in Figure 4(b) and a lower white arrow in (a). Bar = 0.1 mm. (f) The anther marked by the upper arrow in (a), showing a broken anther with possible *in situ* pollen grains (arrow). Bar = 20 μm. (g) Details of the portion marked by the black arrow in Figure 4(e), showing a possible filament stub (arrow) beside the hairy style (to the right of white line) and the ovarian cavity (O). Bar = 0.1 mm. (h) Details of (d), showing two confluent pollen sacs in the anther (arrows) and its cellular details. Bar = 10 μm. (i) Detailed view of the possible *in situ* pollen grains in the anther shown in (f). Bar = 5 μm. (j) Organic material preserved in the flower, enlarged from the region marked by the white arrow in Figure 4(e). Bar = 0.1 mm. (k) Pitting on a vascular element, enlarged from the arrowed region in (j). Bar = 2 μm.

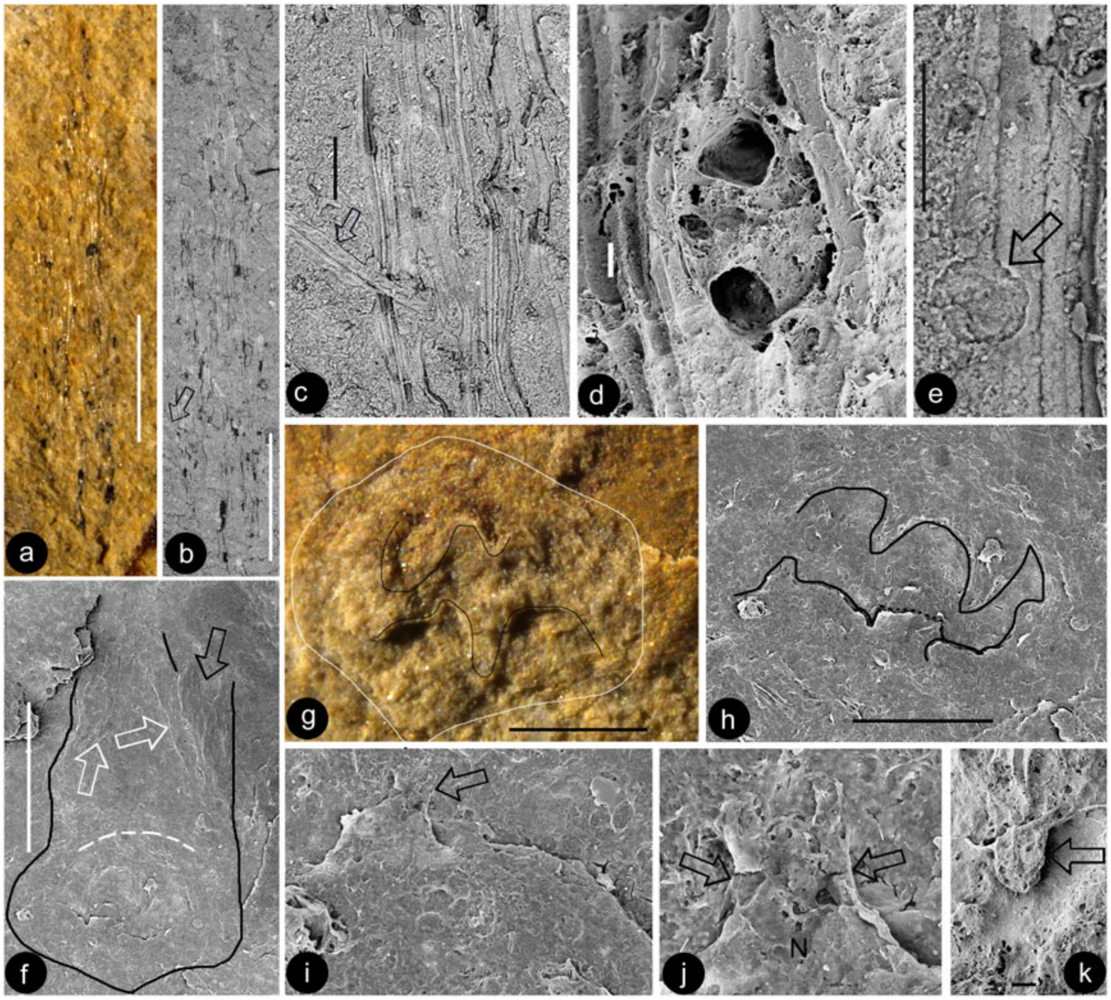

Figure 7. (Colour online) Gynoecium of *Euanthus panii* **gen. et sp. nov.** Stereomicroscopy and SEM. (a, b) The distal style with hairs, viewed under SEM (a) and stereomicroscope (b). Bar = 1 mm. (c). A hair (arrow) branching off from the style, enlarged from the arrowed region in (b). Bar = 0.1 mm. (d) A possible secretory structure in the style. Bar = 10 μm. (e) Cells in the style with straight cell walls. Note a scar (arrow) left by a fallen-off hair. Bar = 50 μm. (f) The basal portion style and ovary (outlined). Note the branching-off possible filament stub (black arrow) and inner wall (white arrows) of the ovary. Refer to Figure 4(e). Bar = 1 mm. (g, h) Detailed view of the same receptacle and ovary, under stereomicroscope and SEM. Note the pentamerous outline of the receptacle (white line) and protrusions (black lines) on the inner wall of the ovary. Bar = 0.5 mm. (i) The ovule enlarged from (h), with a micropyle (arrow). Bar = 50 μm. (j) Details of the micropyle in (i). Note that there is only one layer of integument (arrows) covering the nucellus (n). Refer to Figure 8(b). Bar = 20 μm. (k) One of the papillae on the inner ovarian wall. Bar = 10 μm.

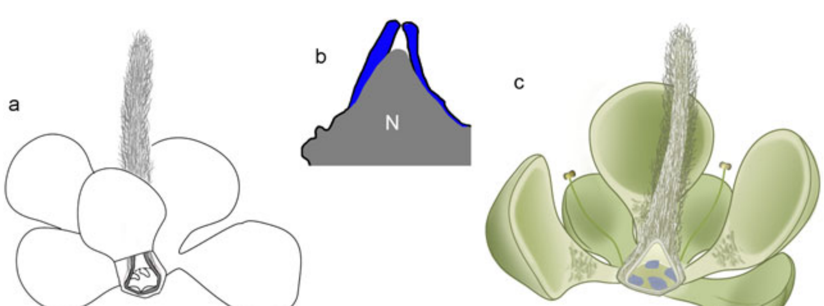

Figure 8. (Colour online) Sketch, details of micropyle and reconstruction of *Euanthus panii* **gen. et sp. nov**. (a) Sketch of the specimen shown in Figure 4(a). (b) Sketch of the micropyle, nucellus (N), and integument (blue) shown in Figure 7(j). (c) Reconstruction of *Euanthus panii* **gen. et sp. nov.**

permy in fossil plants from the Jurassic (Wang et al. 2007; Wang 2010a, 2010b; Wang and Wang 2010); pollen grains indistinguishable from angiosperms have been seen in the Triassic (Hochuli and Feist-Burkhardt 2004, 2013) and independent studies have also converged to the same conclusion (Schweitzer 1977; Cornet 1989a, 1989b, 1993; Chang et al. 2004; Soltis et al. 2008; Prasad et al. 2011). Interestingly, insects closely related to angiosperms or flowers have been reported from the Middle Jurassic in northeast China (Wang and Zhang 2011; Hou et al. 2012). In spite of all these, most palaeobotanists appear hesitant to accept before a fossil flower typical of angiosperms is seen in the pre-Cretaceous. Satisfying 13 different definitions of flower advanced by various authors (Bateman et al., 2006) makes *Euanthus* the first unequivocal Jurassic flower. The discovery of *Euanthus* indicates clearly that flowers have been in place in the Jurassic, pushing the origin of flowers further back to more ancient times.

Like in all flowers, all of the parts of *Euanthus* are inserted onto the same receptacle. Although obliquely compressed, the pentagonal outline of the receptacle is still discernible in *Euanthus* (Figure 4(c),(d)), just as in typical eudicots (Judd et al. 1999). Opposite to the sides of the receptacle pentagon and alternate to the petals are the sepals of *Euanthus*. They are relatively smaller and stouter than the petals, and attached to the receptacle sides with their whole bases, while the petals are bigger and slightly slender, and inserted onto the receptacle corners with a slender claw. A well-differentiated perianth is thought derived and not expected for pioneer angiosperms (Doyle and Endress 2000; Doyle 2008; Friis et al. 2010), their unexpected presence in Jurassic *Euanthus* is not only surprising but also constitutes a drastic contrast against the lack of a perianth in *Archaefructus* and the lack of a well-differentiated perianth in *Callianthus* from the Early Cretaceous (Sun et al. 1998; Sun and Dilcher 2002; Ji et al. 2004; Wang and Zheng 2009, 2012; Wang 2010a), creating an anachronism in term of perianth evolution. This anachronism defies an explanation. A plausible explanation is either that they are independently evolved and phylogenetically unrelated, or the status seen in these Cretaceous angiosperms is secondarily derived, as suggested by others (Friis et al. 2003). If undifferentiated perianth must occur before differentiated ones, then the well-differentiated perianth of Jurassic *Euanthus* implies that there must be a crypt history prior to *Euanthus*. According to Endress and Doyle (2009), the presence of a perianth is a feature for the most recent common ancestor of all angiosperms. If truly phylogenetically related to later angiosperms, *Euanthus*'s perianth (sepals and petals) appears favouring Endress and Doyle's conclusion. However, the situation would be much more complicated if perianth or flowers originated multiple times independently and the above anachronism is taken into consideration. The present authors would like to leave this question open and wait for further fossil evidence to shed more light on this issue.

The style of *Euanthus* is similar to those of angiosperms. Surrounded by the sepals and petals of *Euanthus* is its gynoecium with a hairy style. The orientations and surface hairs of its both segments of the style (Figures 4(a),(b),(e), 6(g) and 7(a)–(c),(f)) suggest that both segments are of the same style. This hairy style is comparable to those in some angiosperms (especially Poales and Asterales; Maout 1846; Judd et al. 1999), while something with similar surface feature and morphology is never seen in male parts of any seed plants (Maout 1846; Melville 1963; Friis and Pedersen 1996). These hairs may have performed the function of pollen collecting in *Euanthus*, as in some extant angiosperms (Maout 1846; Judd et al. 1999). This is in line with the possible secretory structure seen in the style (Figure 7(d)).

The aforesaid implication on earlier age and origin of angiosperms given by *Euanthus* is in agreement with other contemporary Jurassic angiosperms, including *Schmeissneria* (Wang et al. 2007; Wang 2010b) and *Xingxueanthus* (Wang and Wang 2010), found from exactly the same locality of the Middle–Late Jurassic. These three genera of angiosperms together imply that there must be a prior crypt history. Among them, *Schmeissneria* appears more controversial because it has been studied not only in China but also in Europe, and the conclusions reached on the same materials of *Schmeissneria* by Chinese and European colleagues are completely contradictory, and van Konijnenburg–van Cittert's conclusion on its ginkgoalean affinity appears of more influence (Doyle 2008; Zhou 2009). The early age and controversial phylogenetic position of *Schmeiss-*

Table 1. Comparison among *Euanthus*, angiosperms and some gymnosperms.

	Micropylar tube	Interseminal scales	Distal–basal differentiation of subtending foliar parts	Differentiation among subtending foliar parts	Hairy projection	Pentagonal receptacle	Ovule enclosed	Tetrasporangiate dithecate anther
Euanthus	–	–	+	+	+	+	+	+
Angiosperms	–	–	+/–	+/–	+	+/–	+	+
Bennettitales	+	+	–	–	–	–	–	–
Gnetales	+	–	–	–	–	–	–	–
Coniferales	–	–	–	N/A	N/A	–	–	–

neria make it necessary to elucidate briefly here. *Schmeissneria* is a genus established in 1994 (Kirchner and van Konijnenburg–van Cittert 1994). The authors did not critically revaluate the affinity of the plant although their major discovery is that *Schmeissneria* is connected to 'wrong' leaves (*Glossophyllum*?), not *Baiera* as assumed formerly (Schenk 1890). In 1890, Schenk put the reproductive organ later called *Schmeissneria* into Ginkgoales based on his erroneously assumed relationship with associated leaves (*Baiera*) (Schenk 1890). The authors of *Schmeissneria* ignored the presence of more than 45 infructescences of *Schmeissneria* on a single specimen (BSPG4713 in München collection) although they did selectively show a short shoot surrounded by these infructescences on this specimen in their Plate III, Figure 2 (Kirchner and van Konijnenburg-van Cittert 1994). It remains unknown why they did so, but it is obvious that the information of these infructescences could topple their cherished ginkgoalean affinity, as seen later in more detailed study on the infructescence, fruits and seeds of *Schmeissneria* (Wang 2010b). Ignoring the works with contradicting conclusions (Wang et al. 2007; Wang 2010b), van Konijnenburg-van Cittert insisted on the ginkgoalean affinity of *Schmeissneria*, based on her assumed male part of *Schmeissneria* (van Konijnenburg-van Cittert 2010). Her conclusion could be plausible only if both of the following two assumptions are true, namely, that monosulcate pollen are only seen in Cycadales and Ginkgoales, and that the male part she studied (*Stachyopitys*) is physically connected to *Schmeissneria* (van Konijnenburg-van Cittert 2010). Unfortunately, both these assumptions are actually false. First, besides Cycadales and Ginkgoales, monosulcate pollen at least have been seen also in Bennettitales, many Magnoliales, many monocots and some early angiosperms (Doyle and Hickey 1976; Zavada and Dilcher 1988; Zavada 2003; Doyle et al. 2008; Zavialova et al. 2009; Doyle and Le Thomas 2012). It is noteworthy that van Konijnenburg-van Cittert co-authored one of these papers on Bennettitales that was published in 2009 (Zavialova et al. 2009), and she ignored her own publication only 1 year later in 2010 (van Konijnenburg-van Cittert 2010). Such a wide distribution of monosulcate pollen among groups other than Cycadales and Ginkgoales and the inconsistency of van Konijnenburg-van Cittert herself not only nullify the aforesaid first assumption for van Konijnenburg-van Cittert but also reduce the credibility of her conclusion (van Konijnenburg-van Cittert 2010). Second, the male part van Konijnenburg-van Cittert studied is never connected with *Schmeissneria*, although it was claimed as 'always found associated' with *Schmeissneria* (van Konijnenburg-van Cittert 2010). Instead there is evidence showing that *Stachyopitys* is physically connected with another different leaf, *Sphenobaiera*, which is physically connected with a completely different female organ, *Hamshawvia* (Anderson and Anderson 2003). van Konijnenburg-van Cittert was apparently aware of this fact in 2010 and somehow ignored it completely (van Konijnenburg-van Cittert 2010). Therefore, even if van Konijnenburg-van Cittert could prove that the monosulcates she studied did belong to Ginkgoales, it would be very likely what she proved is only that some non-*Schmeissneria* plant (*Hamshawvia*) belonged to Ginkgoales. Thus, van Konijnenburg-van Cittert's conclusion on the ginkgoalean affinity of *Schmeisseria* requires extreme imagination or devotion to believe. Taken together, the claim of a ginkgoalean affinity for *Schmeisseria* is untenable, and *Schmeisseria* is a *bona fide* angiosperm having gynoecium with enclosed ovules/seeds from the Early–Middle Jurassic, according to more detailed studies (Wang et al. 2007; Wang 2010b).

Eudicots are characterised by floral pentamerism and tricolpate pollen grains (Doyle 2012). If the pentamerism of *Euanthus* were phylogenetically related to that of eudicots, then either the currently well-accepted derived status of eudicots in the tree of angiosperms (APG 2009) will be challenged, or it simply implies that basal angiosperm clades must have an undetected prior history, a conclusion repeatedly converged to as seen above.

5. Conclusion

Euanthus from the Middle–Late Jurassic of Liaoning, China is a perfect flower typical of angiosperms, prompting a rethinking on the origin and history of flowers and angiosperms. If *Euanthus* were really related to eudicots, it would be intriguing to search for typical eudicot leaves in the Jurassic strata. The presence of a full-fledged flower such as *Euanthus* in the Jurassic is apparently out of the expectations of any currently accepted evolutionary theories, implying either that these theories are flawed, and/or the history of angiosperms is much longer than previously assumed.

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Disclosure statement

The authors declare no conflict of interest.

Supplemental data

The supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/08912963.2015.1020423>, in which the taxon list for the Haifanggou Formation can be found.

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Note

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