A Jurassic flower bud from China

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Abstract: Angiosperms may be distinguished from their gymnosperm peers by their flowers. However, flowers and their parts are usually too frail to be preserved in the fossil record. This makes the origin of angiosperms and their flowers the foci of controversy in botany. Eliminating such botanical controversies can only be achieved by studying related plant fossils. Applying routine scanning electron microscopy, light microscopy and micro-computed tomography (micro-CT) technologies, we document a fossil flower bud, Florigerminis jurassica gen. et sp. nov., from the Jurassic of Inner Mongolia, China. This fossil includes not only a leafy branch but also physically connected fruit and flower bud. The developmentally interpolated existence of a blooming flower between the flower bud and mature fruit in Florigerminis suggests that angiosperm flowers were present in the Jurassic, in agreement with recent botanical progress. Florigerminis jurassica underscores the presence of angiosperms in the Jurassic and demands a rethinking of angiosperm evolution.

As the most diversified plant group in the world, angiosperms provide most of the materials necessary for the well-being of human beings. However, when and how this important group came into existence are still unanswered questions (Arber and Parkin 1907; Hagerup 1936; Crane 1985; Hickey and Taylor 1996; Sun et al. 1998, 2002; Frohlich 2003; Doyle 2008; Doyle et al. 2008; Friis et al. 2010; Wang 2010a, 2017, 2020, 2021). Angiosperms are characterized by their flowers; therefore, a fossil flower is a good proxy of early angiosperms (Thomas 1936). However, searching for such fossils is far from easy, and the related efforts were termed as an ‘unbroken record of failure’ by Harris (Beck 1976). The 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. 2004b; Wang 2010a, 2015, 2018; Liu et al. 2021) implies a cryptic prior history for angiosperms, and there is increasing evidence of pre-Cretaceous angiosperms (Cornet 1989a, b, 1993; Hochuli and Feist-Burkhardt 2004, 2013; Wang et al. 2007; Wang 2010a, b, 2015; Wang and Wang 2010; Liu and Wang 2016; Fu et al. 2018, 2020; Li et al. 2019; Silvestro et al. 2021). Although over 100 blooming flowers of Nanjinganthus exemplify the truthful existence of angiosperms in the Jurassic (Fu et al. 2018, 2020), our current knowledge of early angiosperms is still sparse. Here we report Florigerminis jurassica gen. et sp. nov, a fossil plant including physically connected flower bud, fruit and leafy branch, from the Jiulongshan Formation (the Middle–Late Jurassic: >164 Ma) of Inner Mongolia, China. The flower bud is characterized by several tightly enwrapping tepals, while the mature fruit is of distinct morphology. Its Jurassic age makes Florigerminis jurassica the currently earliest typical flower bud. This discovery reinforces the previous reports of Jurassic angiosperms, extends the fossil-evidenced history of angiosperms to the pre-Cretaceous age and sheds new light on the evolution of early angiosperms.

Materials and methods

The fossil was collected from an outcrop of the Jiulongshan Formation near Daohugou Village (41° 18’
39.60° N, 119° 13′ 29.14° E) located at the SE corner of Inner Mongolia, China, close to the boundaries with the Liaoning and Hebei provinces (Fig. 1a, b).

Various fossils uncovered in the Daohugou region have been intensively studied over decades. Abundant animal fossils, especially insects, have been reported from the Daohugou region (D.-Y. Huang et al. 2006, 2008, 2009; J. Huang et al. 2008; J. Zhang 2006; D.-Y. Huang and Nel 2007, 2008; Petrulevicius et al. 2007; Lin et al. 2008; Liu and Ren 2008; Selden et al. 2008; X.-W. Zhang et al. 2008; K. Zhang et al. 2009; Fang et al. 2009; Liang et al. 2009; Shih et al. 2009; Y. Wang and Ren 2009; B. Wang and Zhang 2009a, b; B. Wang et al. 2009a, b, c), among them are some potentially related to flowering plants (Yao et al. 2006; Wang and Zhang 2011). In the meantime, various fossil plants from this region have been reported, including Daohugouthallus ciliiferus, Selaginellites chaoyangensis, Coniopiteris burejensis, Cycadolepis spp., Tyrnia taiichishanensis, Yimaia capituliformis, Ginkgoites sp., Zamites gigas, Anomozaemites villosus, A. angulatus, A. sinensis, A. haifanggouensis, Pterophyllum spp., Williamsonia sp., Welrichtia daohugouensis, Yanhaoa sinensis, Pityocladus sp., Problematospermum ovale, Solaranthus daohugouensis, Jurherra bodaie, Yuhania daohugouensis and Jurafructus daohugouensis (Zheng et al. 2003; Li et al. 2004; Zhou et al. 2007; Wang et al. 2010a, b; Zheng and Wang 2010; Pott et al. 2012; Han et al. 2016; Liu and Wang 2017; Chen et al. 2020).

There is a general consensus regarding the Middle–Late Jurassic age of the Jiuulongshan Formation (also previously called the Daohugou Formation) (Ren et al. 2002; Zhang 2002; Shen et al. 2003; Chen et al. 2004; Li et al. 2004; Liu et al. 2004; Ji et al. 2005). However, Wang et al. (2005) challenged the dating and claimed that the Daohugou Formation was of Early Cretaceous age. This conclusion by Wang et al. (2005) was later refuted and disputed by more stratigraphic and palaeobiological works (Gao and Ren 2006; D.-Y. Huang et al. 2006, 2008, 2009; J. Zhang 2006; D.-Y. Huang and Nel 2007, 2008; Petrulevicius et al. 2007; Sha 2007; Zhou et al. 2007; J. Huang et al. 2008; Lin et al. 2008; Liu and Ren 2008; Selden et al. 2008; X.-W. Zhang et al. 2008; Chang et al. 2009; Fang et al. 2009; Liang et al. 2009; Shih et al. 2009; B. Wang et al. 2009a, b, c; X. Wang et al. 2010b; B. Wang and Zhang 2009a, b; Y. Wang and Ren 2009; K. Zhang et al. 2009; J. Zhang et al. 2011; Chang et al. 2014). $^{40}$Ar/$^{39}$Ar and SHRIMP U/Pb dating of the volcanic rocks overlying the fossiliferous layer performed by Chen et al. (2004) and Ji et al. (2004a) suggest that the Jiuulongshan Formation is at least 164 myr old. Therefore, the authors adopt a Middle–Late Jurassic age for Florigerminis jurassica.

The specimen was preserved as a compression with some coalified residue. The specimen was observed and photographed using a Nikon SMZ1500 stereomicroscope with a digital camera. Degauging some sediment was necessary before the whole flower bud, which was formerly covered in sediments (Fig. 2a), could be observed (Fig. 2b). Later, a replica of nitric cellulose was made of the leafy branch and its lateral appendages. The replica was cleaned with HCl and HF before SEM observation was performed using a Leo 1530 VP scanning electron microscope (SEM) at the Nanjing Institute of Geology and Palaeontology, Nanjing, China. The specimen was scanned using a GE vtomelx M300&180 micro-computed tomography (micro-CT) scanner (GE Measurement & Control, Wunstorf, Germany), housed at the Key Laboratory of

![Fig. 1. The fossil locality of Florigerminis jurassica gen. et sp. nov. (a) Map of NE China. The arrow points to the junction region between Liaoning, Inner Mongolia and Hebei, which is enlarged in (b). (b) Detailed map showing Daohugou Village, Ningcheng, Inner Mongolia, China (41° 18′ 39.60° N, 119° 13′ 29.14° E) (arrow) very close to the junction of Inner Mongolia, Hebei and Liaoning.](http://sp.lyellcollection.org/Downloaded from)
Vertebrate Evolution and Human Origin of Chinese Academy of Sciences. The dataset has a resolution of 8.912 µm, and the scan was carried out at 100 kV and 90 µA. One frame per projection was acquired by a timing of 2000 ms for a total of 2500 projections. All images were recorded in TIFF or JPEG format, and organized for publication with Photoshop 7.0.

Results

**Florigerminis gen. nov.**

*Type species.* Florigerminis jurassica gen. et sp. nov.

**Genetic diagnosis.** Woody branch with nodes, leaf scars, physically connected fruit and flower bud. Leaves abscised, helically arranged, with decurrent petioles. Flower–fruit pairs helically clustered on the distal portion of the branch. Flower bud terminated on the branch, paired, with a straight pedicel, oval-shaped, with several tepals suggested by their sculpture. Multiple tepals smooth-margined, tightly enwrapping the centre. Fruit borne on a slender curving pedicel, oval-shaped, with four persistent decussately arranged foliar parts and an apical invagination. Endocarp elongated oval, with a pointed tip.

**Locality.** Daohugou Village, Ningcheng, Inner Mongolia, China (41° 18′ 39.60″ N, 119° 13′ 29.14″ E).

**Horizon.** The Jiulongshan Formation.

**Florigerminis jurassica** gen. et sp. nov.

**Etymology.** jurassica for the Jurassic, the age of the fossil plant (Figs 2 & 3).

**Species diagnosis.** In addition to the genetic diagnosis, branch 21 mm long and 2.6 mm wide, slightly tapering distally, internode 2.9–5.1 mm long. Leaf scars 0.4–0.6 mm wide and 0.23 mm thick. Flower bud pedicel straight, 4.6 mm long and 1 mm wide. Flower bud 3.8 mm long and 3.3 mm wide. Lower tepals 1.2 mm long and >0.8 mm wide. Upper tepals 1.8–3.8 mm long and 1.5–2.6 mm wide. Fruit approximately 11.5 mm long and 7.7 mm wide, on a pedicel 22 mm long and only 0.65 mm wide, subtended by four (only three visible in the fossil) foliar parts approximately 2.4 mm long and 1.4 mm wide. Endocarp approximately 9 mm long and 6 mm wide.

**Holotype.** PB21737.

**Description.** The holotype specimen is 42 mm long and 20 mm wide, preserved as a compression with some coalified residue and an impression (Fig. 2a). The plant tissues are embedded in yellowish volcanic tuff (Fig. 2a–c). When the coalified residue falls off, an exquisite morphological impression is left on the fine sediment matrix (Figs 2d–i & 3a–g). The preserved part of the fossil includes a leafy branch that is physically connected to a fruit and a flower bud (Fig. 2a). The branch is elongated, approximately 21 mm long and 2.6 mm wide, with longitudinal fine striations on its surface and at least five nodes, tapering distally (Figs 2a, d, h & 3b, d, e). The nodes are marked by several transversal wrinkles (Figs 2h & 3b). The lengths of the internodes increase from 2.9 mm at the proximal to 5.1 mm at the distal (Fig. 2a, h). Leaves with decurrent bases are helically arranged along the branch, more concentrated to the distal portion of each internode (Figs 2h & 3d). All of the leaves have been abscised and only have their scars left on the branch (Figs 2a, h & 3d). The leaf scars are 0.4–0.6 mm wide and 0.23 mm thick, with terminal abscission zones (Fig. 3b, d & e). Close to the terminal of the branch, fruit pedicel scars are subtended by bracts (Fig. 3a–c). The fruit pedicel with longitudinal fine striations is rounded in cross-view, branching into a pair (Figs 2a–c, i, j & 3h–i). The fruits are inserted subapically (Figs 2a, b & 3a). The flower bud (only one visible in full) is in pairs, on a straight pedicel approximately 4.6 mm long and 1 mm wide, oval in shape, approximately 3.8 mm long and 3.3 mm wide (Fig. 2a, b, e–g, i, j). Several layers of upper tepals enwrap the central part (Figs 2e–g, 3g–i, 4 & 5a). Micro-CT sections indicate that the tepals surround the bud centre (gynoecium?) (Fig. 3h, i). Upper tepals vary from 1.8 to 3.8 mm in length and from 1.5 to 2.6 mm in width (Figs 2e–g, 3g & 5a), distinguishing from each other by differently orientated sculpture (Figs 2e–g, 3g, 4 & 5a). The fruit is approximately 11.5 mm long and 7.7 mm wide, on a pedicel 22 mm long and only 0.65 mm wide, subtended by four (only three visible in the fossil) foliar parts approximately 2.4 mm long and 1.4 mm wide, with an apical invagination approximately 0.5 mm deep (Figs 2a, c, k, l & 3j). Only the mesocarp and endocarp of the fruits are visible, while the exocarp (epidermis) is too thin to see (Figs 2a, c, k & 5b). The mesocarp is approximately 0.34–1.1 mm thick, much thinner near the fruit tip (Figs 2a, c, k & 5b). The endocarp is approximately 9 mm long and 6 mm wide, with a pointed tip (Figs 2a, c & 5b).

**Repository.** The Nanjing Institute of Geology and Palaeontology, Nanjing, China.

**Remarks.** Only one flower bud and one fruit are preserved in entirety in this fossil. However, there is one extra slender pedicel that is identical to that of the preserved fruit (Fig. 2a, b, i), and there seems to be another pedicel of a flower bud embedded in the sediments (Fig. 2i, j). Considering the morphology of the fruit pedicel, we assume that it is another fruit, which, unfortunately, is not visible in this specimen. Furthermore, several fruit pedicel scars (Fig. 3a–c) strongly imply the existence of fallen fruits in *Florigerminis*. Therefore, we assume that this fossil originally bore two fruits and two flower buds.

**Discussions**

One merit of the specimen of *Florigerminis* (PB21737) is that its various parts, including branch, leaf scars, flower bud and fruit, are all physically connected. This feature is the basis of our following interpretation.
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Fig. 3. SEM and micro-CT details of *Florigerminis jurassica* gen. et sp. nov. (a) Detailed view of the fruit/flower pedicels and leaf scar near the branch apex. Note the fruit pedicels (1 and 2), flower bud pedicel (3), two additional fruit pedicel scars (black arrows) and a leaf scar (white arrow). Labelled as in Figure 2b. The scale bar is 1 mm. (b) Details near a node, showing a leaf scar (white arrow), transversal wrinkles (black arrow) at the node and two possible fruit pedicel scars (outlined) subtended by scales. The scale bar is 0.2 mm. (c) Elliptical fruit pedicel scar enlarged from (a), subtended by a scale (arrows). The scale bar is 0.1 mm. (d) Branch with helically arranged decurrent leaf scars (arrows). The scale bar is 1 mm. (e) Decurrent leaf base (arrow) with abscission zone at the tip. The scale bar is 0.1 mm. (f) Subtending scale (below the line) and an axillary primordium (arrow), enlarged from the rectangle in (a). The scale bar is 0.1 mm. (g) Fragments of three overlapping tepals (1–3) with differently orientated surface textures. The scale bar is 0.1 mm. (h) Longitudinal micro-CT view of the flower bud with tepals (white arrow) surrounding gynoecium (?) (right arrow) in the centre. The fruit pedicel has obvious longitudinal fine striations (lower arrow). The scale bar is 1 mm. (i) Longitudinal micro-CT view of the flower bud with gynoecium (?) (arrow) in the centre and tips of the tepals at the top. The scale bar is 1 mm. (j) Longitudinal micro-CT view of the fruit with an apical invagination (arrow). The scale bar is 2 mm.
Interpreting the structure

The structure of crucial importance in *Florigerminis* is its fruit. This structure might be alternatively interpreted as a seed due to its Mesozoic age, an age of gymnosperms. If taken as a seed, the structure in Figure 2c may be interpreted as a sclerotesta surrounding a nucellus (sarcotesta and endotesta might be too thin to see). However, this interpretation faces the following challenges: (1) a sclerotesta is supposed to be more labile to be preserved than a nucellus, and the preservation is reversed in *Florigerminis*: the assumed nucellus has more organic material preserved, while the assumed sclerotesta has little organic material preserved. (2) A seed usually has an even surface or a protruding terminus in known gymnosperms (Chamberlain 1957; Biswas and Johri 1997; Zhang 2013), in strong contrast to the apical invagination seen in the fruit of *Florigerminis* (Figs 2c, k & 3j). However, this invagination could be rationally interpreted as a consequence due to a lack of style, as frequently seen in basal angiosperms. (3) Developmental changes in *Florigerminis* are hard to reconcile with this seed alternative. Ovules and seeds are usually naked and without additional surrounding layers in gymnosperms, except in some Mesozoic seed plants (such as *Caytonia*: Harris 1933; Nixon *et al.* 1994; and *Petriellaea*: Taylor *et al.* 1994), of which seeds/ovules may be partially or completely surrounded by a layer of tissue (cupule wall) throughout its life cycle. However, in these gymnospermous plants, there are usually more than one seed in each cupule and there is no report of seeds persisting on pedicel but without a cupule wall. In contrast, in *Florigerminis*, the gynoe- cium (developmental precursor of the fruit) is covered by several layers of tepals before maturity.

![Fig. 4. SEM view of the flower bud of *Florigerminis jurassica* gen. et sp. nov., showing tepals with sculptures.](image)

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![Fig. 5. Details of *Florigerminis jurassica* gen. et sp. nov. (a) Sketch showing the arrangement of patches of overlapping tepals. There are at least four layers of tepals (1–4), one over the other. The scale bar is 1 mm. (b) Sketch showing the organization of the fruit, showing the endocarp (black) inside the mesocarp (yellow) supported by a carpopodium (grey) subtended by foliar parts (blue). Refer to Figure 2c, g and h. The scale bar is 2 mm.](image)
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(Figs 2e–g, 3g–i & 5a) (as in angiosperms), and it grows into a naked fruit (without any additional enwrapping layers) on a long pedicel (Fig. 2a, c).

(4) Although some gymnosperms (Ginkgo) may have a seed subtended by a collar, a morphology more or less similar to the fruit in Florigerminis, the collar in Ginkgo is integral and so far has never been seen lobed, quite different from the foliar parts at the bottom of the fruit in Florigerminis (Fig. 2a, c, l). (5) Even if the fruit of Florigerminis was taken as a seed similar to that of Ginkgo, it is well known that the ovules or immature seeds of Ginkgo are naked, never enwrapped by any foliar structures, a situation quite different from the foliar parts at the bottom of the fruit in Florigerminis (Fig. 2a, c, l). Given these discrepancies, we interpret the structure in Figure 2c as a fruit.

Affinity

Although fruits usually have less taxonomic value compared to flowers, here the fruit plays an important role in determining the affinity of Florigerminis. (1) The slender, long, curving fruit pedicel seen in Florigerminis (Fig. 2a, b) is never seen in any fructifications of Mesozoic gymnosperms including Cycadales, Gnetales, Coniferales, Pentaxylales, Bennettitales, Corystospermales and Peltaspermales (Bierhorst 1971; Stockey and Rothwell 2003; Zhou et al. 2007; Taylor et al. 2009), and is only seen in some Taxales, Ginkgoales, some early Cordaitales and angiosperms among seed plants. However, careful comparison finds that the two pairs of opposite persistent foliar parts at the fruit bottom of Florigerminis (Fig. 2c, l) are never seen in Cordaitales and are distinct from the collar subtending seeds in Ginkgo. Some conifers (e.g. Abies in Pinaceae) do have scales with longitudinal striations overlapping each other and surrounding the centre, just like our flower bud, but mature cones in these plants are cones quite distinct from the fruit of Florigerminis in morphology. Although the seeds of some Taxaceae (Torreyana and Amentotaxus) may be subtended by one or more whorls of scales, their tips are convex rather than invaginated (Academia Sinica Silviculture et al. 1978; Yin 2013), and thus differ from the fruit of Florigerminis. Gnetales (especially Ephedraceae) are frequently considered to be closely related to angiosperms, and thus deserves special attention. Florigerminis shares distinct nodes with Ephedraceae and Gnetaceae. However, other than this, there are few features shared between them. The most characteristic features of all gnetalean members include strict decussately arranged lateral appendages attached to the nodes and elongated micropylar tubes. These characters are completely absent in Florigerminis: the leaves are helically (not oppositely or decussately) arranged between (not on) the nodes (Figs 2h & 3e) and the fruit has a distal invagination (not protruding micropylar tube) (Figs 2k & 5b). Although seeds are reported on the terminals of long stalks in some Early Cretaceous ephedraceous fossil (figs 1 & 16 in Yang et al. 2005), more or less similar to the fruit seen in Florigerminis, differences in branching pattern, phyllotaxy and apical invagination on the fruit tip in strong contrast to micropylar tube in Ephedra (Yang et al. 2005) are obvious enough to distinguish these two taxa. In addition, the straight stem of Ephedra (Yang et al. 2005) is quite distinct from the curving fruit pedicel of Florigerminis (Fig. 2a). All these distinctions extinguish any possible relationship between Florigerminis and Gnetales. The above comparison leaves only one alternative for Florigerminis among known seed plants: angiosperms. (2) This conclusion is strengthened by the morphology of the physically connected flower bud (Figs 2c, f, 3g & 5a). Currently, no known (fossil or extant) gymnospermous bud is comparable to Florigerminis, the resemblance of which to an angiosperm flower bud is obvious: several tepals tightly enwrap and protect central parts in the bud. (3) Among angiosperms, Prunus (Rosaceae) demonstrates a great resemblance to Florigerminis, with a long fruit pedicel, paired fruits and drupaceous fruit (Sterling 1953). Although this resemblance does not necessarily imply a close phylogenetic relationship between Florigerminis and Prunus, it underscores a potential relationship between Florigerminis and angiosperms.

Interpolated blooming flower

The physical connection between fruit and flower bud is of vital importance in confirming the angiosperm identity of Florigerminis. The fruit of Florigerminis is oval in shape, with an apical invagination and surrounded by a fleshy mesocarp (Fig. 2a, c, g, h). These features are distinct from the composition and configuration of its flower bud, which is oval in shape but with a convex apex and enwrapped by layers of tepals (Figs 2a, e–g, 3g & 4). If these two parts were preserved as isolated parts, it would be hard to imagine that they were from the same plant. However, the physical connection between these parts expels all doubts. It is apparent that the fruit must have undergone a blooming flower stage before reaching its current stage (Fig. 2c). This inferred blooming flower of Florigerminis, although, unfortunately, not preserved in this fossil, provides additional support for the angiospermous affinity of Florigerminis. We expect future studies may confirm the existence of a blooming flower in Florigerminis in the Jurassic.
Development

Developmental changes can be inferred by comparing the fruit and flower bud of *Florigerminis*. The flower bud occupies a more distal position than the fruit in *Florigerminis* (Figs 2a, i & 3a), indicating that the plant matures acropetally. The apical invagination on the fruit (Fig. 2c, k) forms a drastic contrast to the convex apex of the flower bud (Fig. 2e, g), suggesting that the fruit is derived from a gynoecium that is eclipsed by the tepals in the flower bud before the fruit is developed. The pedicle of the flower bud is relatively shorter than its counterpart in the fruit (Fig. 2a, b, i), implying that the pedicle increases greatly in length during maturation. The foliar parts (Fig. 2e) at the bottom of the fruit (Fig. 2c, l) imply that the flower is hypogynous and foliar parts are persistent in *Florigerminis*. Most tepals, in patches and layers, in the flower bud (Figs 2e–g, 3g & 5a) are absent in the fruit (Figs 2c, k, 1 & 5b), implying that they have fallen off the flower after fulfilling their functions, as in extant flowers, a phenomenon never seen in any known gymnosperms. Dimension measurement suggests that the gynoecium has at least tripled its size during its development from a flower bud to a fruit (Fig. 2a–c). Such a great increase in volume after pollination is more characteristic of angiosperms than of gymnosperms (Leslie and Boyce 2012). The organic connection of a fruit and a flower bud in a single shoot indicates a long anthesis for *Florigerminis* if both are of the same year, as the development from a flower bud to a fruit definitely takes some time. However, it should be borne in mind that if the flower bud and the fruit were of two different years in *Florigerminis*, it would mean that the fruit takes more than 1 year to mature.

Habit

The presence of five nodes and the arrangement of leaves along the branch (Figs 2a, h & 3a, b, d) imply a perennial woody habit for *Florigerminis*. The internode length increases distally from 2.9 to 5.1 mm (Fig. 2a, h). The distalmost internode bears flowers/fruit (Fig. 2a, b), which only leave scars on the proximal portion of internodes (Fig. 3b), implying fruiting in the preceding years. The rigid configuration of the branch implies that the mother plant is woody (Figs 2a, h & 3d). The abscission of leaves (Figs 2a, b & 3b, d) implied by the leaf scars suggests that *Florigerminis* is deciduous and inhabits in a region with seasonality. Although the organic connection of mature fruit and flower bud is surprising, a similar situation does exist in extant angiosperms (e.g. Rosaceae, Theaceae and Tapisciaceae) (Liu et al. 2008). In short, *Florigerminis* is a perennial, deciduous, woody plant living in a region with seasonality.

Confirming Jurassic angiosperms

Hitherto, we have had very limited knowledge about early flowers in the pre-Cretaceous. The most convincing record of flowers is *Nanjinganthus* from the Early Jurassic of Jiangsu, China (Fu et al. 2018, 2020). However, *Nanjinganthus* is isolated from other parts, and its flower bud morphology is not clearly known. Various independent data suggest that angiosperms may have a history longer than currently accepted; the great diversity of early angiosperms (Duan 1998; Sun et al. 1998, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009; Wang 2010; Fu et al. 2018, 2020) and derived status of *Archaefructus* from the Early Cretaceous (Friis et al. 2003), independently claimed trace of early angiosperms (Schweitzer 1977; Cornet 1989a, b, 1993; Chaw et al. 2004; Hochuli and Feist-Burkhardt 2004, 2013; Soltis et al. 2008; Prasad et al. 2011), and insects closely related to angiosperms or flowers reported from the Daohugou area (Wang and Zhang 2011; Hou et al. 2012), as well as other analyses (Li et al. 2019; Silvestro et al. 2021) all point to the pre-Cretaceous origin of angiosperms. However, quite a few palaeobotanists are still reluctant to accept this fact (Herendeen et al. 2017). We hope that the discovery of *Florigerminis*, with its branch, leaf scars, flower bud and physically connected fruit, may help to ease the pain of accepting pre-Cretaceous angiosperms.

According to Darwinism and outgroup comparison, well-differentiated perianth is thought to be derived and not expected for pioneer angiosperms (Doyle and Endress 2000; Doyle 2008; Friis et al. 2010), but this thinking is now challenged by the presence of well-differentiated perianth in Jurassic *Euanthus* (Liu and Wang 2016) and *Nanjinganthus* (Fu et al. 2018, 2020). *Florigerminis* constitutes a drastic contrast against the lack of a perianth in Cretaceous *Archaefructus* (Sun et al. 1998, 2002; Sun and Dilcher 2002; Ji et al. 2004; Wang 2010; Wang and Zheng 2012). Such an anachronism may be reconciled by the possibility that they are independently evolved, and/or that *Archaefructus* is a rather specialized derived taxon. Because differentiated perianth is lacking in all gymnosperms, it is unlikely for perianth as differentiated as in *Euanthus* (Liu and Wang 2016) and *Nanjinganthus* (Fu et al. 2018, 2020) to represent a plesiomorphy in angiosperms; thus, the Jurassic age of these fossils implies a cryptic prior history of angiosperms. This is in line with Jurassic fossil insects whose extant relatives are closely tied to flowers (Wang and Zhang 2011; Hou et al. 2012), as well as with recent analysis
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(Li *et al.* 2019; Silvestro *et al.* 2021). It is noteworthy that *Florigerminis* demonstrates little resemblance to both *Magnolia* and *Amborella*, which are thought by various authors to be basal-most among extant angiosperms (Angiosperm Phylogeny Group 2009). Such a discrepancy between fossils and theoretical expectation implies that the currently accepted theory of angiosperm evolution needs to be revised.

Conclusions

The organic connection of fruit and flower bud in a Middle–Late Jurassic fossil plant recovered from Inner Mongolia, China indicates that *Florigerminis*, a Jurassic angiosperm, marks an early record of a flower bud. The unexpected occurrence of flowers such as *Florigerminis, Euanthus* and *Nanjinganthus*, all from the Jurassic, implies that the related theories of angiosperm evolution lack the predictability required for a scientific theory.

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Data availability All data generated or analysed during this study are included in this published article. The specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Nanjing, China, and is publicly available.

References


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