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Yuhania: a unique angiosperm from the Middle Jurassic of Inner Mongolia, China

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ABSTRACT

Despite increasing claims of pre-Cretaceous angiosperms, whether there really are angiosperms in the Jurassic is apparently still an open question for many people before further evidence is available. This question can only be answered by studying more Jurassic plant fossils. Here we report a fossil angiosperm, *Yuhania daohugouensis* gen. et sp. nov, from the Middle Jurassic of Inner Mongolia, China. The plant includes connected stem, leaves, flowers, aggregate fruits, fruitlets, and seeds within fruitlets. The leaves are helically arranged along the curving stem, linear in shape, with 5–6 parallel veins. The aggregate fruit is pedicellate, composed of over 20 carpels/fruitlets helically arranged. Each fruitlet encloses a seed. The reproductive organs in various stages are found in the same plant, allowing us to understand the development of *Yuhania*. The occurrence of *Yuhania* in the Middle Jurassic re-confirms the Jurassic history for angiosperms that has been suggested by other independent research and adds to the on-going study on the early evolution of angiosperms.

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KEYWORDS
Angiosperm; fossil; origin; evolution; Jurassic; China; *Yuhania*

Introduction

The origin and early evolution of angiosperms have riveted botanists for long time (Arber & Parkin 1907; Hagerup 1936; Crane 1985; Hickey & Taylor 1996; Sun et al. 1998; Frohlich 2003; Doyle et al. 2008; Friis et al. 2010; Wang 2010b). An earlier origin time has been repeatedly suggested for angiosperms (Wu et al. 2003; Lu & Tang 2005; Soltis et al. 2008; Hilu 2010; Smith et al. 2010; Prasad et al. 2011; Magallón 2014), but many palaeobotanists adhere to the 'No Angiosperms Until the Cretaceous' misconception (Duan 1998; Gandolfo et al. 1998; Sun et al. 1998, 2002; Leng & Friis 2003; Ji et al. 2004b; Doyle et al. 2008). This discrepancy between groups can only be resolved by studying early fossil angiosperms. There are increasing number of reports (or at least claims) of pre-Cretaceous angiosperms, including possible Triassic angiosperm pollen (Hochuli & Feist-Burkhardt 2004, 2013) and Jurassic megafossil angiosperms (*Schmeissneria* (Wang et al. 2007; Wang 2010b, 2010c), *Xingxueanthus* (Wang & Wang 2010; Wang 2010b), *Euanthus* (Liu & Wang 2016b), and *Juraherba* (Han et al. 2016). But many palaeobotanists remain silent and still insist on ignoring these evidences. Fossil plants with various parts connected are most wanted in palaeobotanical studies because reconstructions based on isolated parts frequently introduce artifacts and errors (Crane et al. 2004; Rothwell et al. 2009; Tekleva & Krassilov 2009). Here we report an angiosperm, *Yuhania daohugouensis* gen. et sp. nov, from the Jiulongshan Formation (the Middle Jurassic > 164 Ma) of Inner Mongolia, China. The plant includes connected stem, leaves, flowers, aggregate fruits, fruitlets, and seeds within fruitlets. The leaves are helically arranged, linear, with 5–6 parallel veins. The aggregate fruit is pedicellate, including over 20 fruitlets. Each fruitlet encloses a seed. The ovulate organs in various developmental stages make it possible to reconstruct the development of the female organ of *Yuhania*, which confirms the fossil-evidenced history of angiosperms back to the Middle Jurassic. This is in agreement with previous reports of possible angiosperms in the Jurassic and Triassic (Cornet 1986, 1989a, 1989b; Cornet & Habib 1992; Cornet 1993; Hochuli & Feist-Burkhardt 2004, 2013; Wang et al. 2007; Zheng & Wang 2010; Wang 2010b, 2010c) and molecular clock studies (Chaw et al. 2004; Soltis et al. 2008; Prasad et al. 2011). These all reduce the credibility of the above misconception about the history of angiosperms.

Materials and methods

The fossil was collected from an outcrop of the Jiulongshan Formation near Daohugou Village. Daohugou Village of Ningcheng City (119°14′40″E, 41°19′25″N) is located at southeast corner of Inner Mongolia, China, close to its boundaries with Liaoning and Hebei Provinces (Figures 1(a), (b), and S1(a)–(c)). Abundant animal fossils, especially those of insects, have been reported from the Daohugou region (Huang et al. 2006, 2008a, 2008b, 2009; Zhang 2006; Huang & Nel 2007, 2008; Petrulevicius

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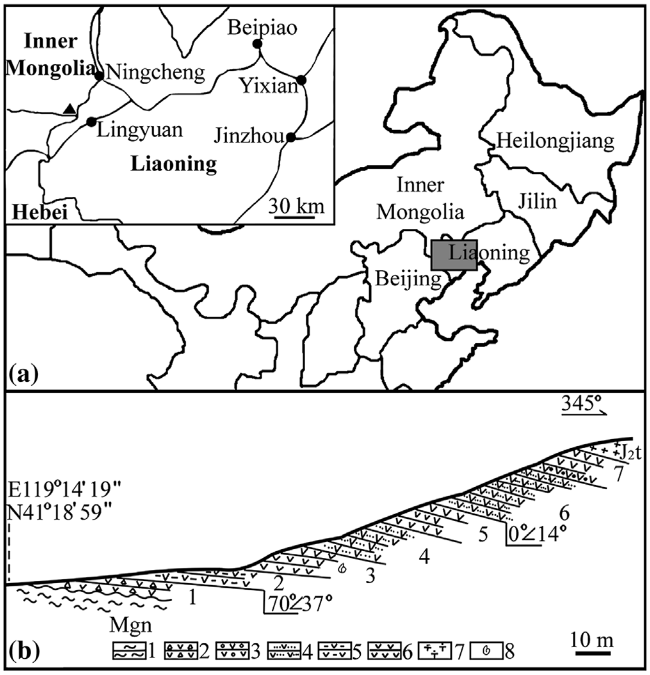

Figure 1. Geological information of the fossil locality at Daohugou Village. Reproduced from Han et al. (2016). (a) Geographical position of Daohugou Village, Ningcheng, Inner Mongolia in China (119°14′40″E, 41°19′25″N). The rectangular region in the main map is shown in detail in the inset, in which the black triangle represents Daohugou Village and the black dots represent local cities, and (b) geological section of the Jiulongshan Formation near Daohugou Village. Layer 3 is the major fossil yielding layer. (1) gneiss; (2) tuffaceous grand conglomerate; (3) tuffaceous conglomerate; (4) tuffaceous siltstone; (5) tuffaceous mudstone; (6) tuffaceous shale; (7) volcanic breccia; and (8) fossil locality.

et al. 2007; Lin et al. 2008; Liu & Ren 2008; Selden et al. 2008; Zhang et al. 2008, 2009; Fang et al. 2009; Liang et al. 2009; Shih et al. 2009; Wang & Ren 2009; Wang & Zhang 2009a, 2009b; Wang et al. 2009a, 2009b, 2009c). In the meantime, various fossil plants have been reported from this region. According to the previous reports and recent survey in press, the Daohugou flora includes Algae 1 genus/species (Chlorophyceae), Bryophytes 4 genera, 6 species (*Daohugouthallus*, *Metzgerites*, *Muscites*, *Ningchengia*), Lycopodaceae 2 genera, 2 species (*Lycopodites*, *Selaginellites*), Sphenophytes 2 genera, 2 species (*Annularia*, *Equisetites*), Filicales 4 genera, 6 species (*Coniopteris*, *Osmunda*, *Eboracia*, *Sphenopteris*), Cycads 7 genera, 12 species (*Pterophyllum*, *Anomozamites*, *Nissoniopteris*, *Williamsonia*, *Weltrichia*, *Cycadolepis*, *Tyrmia*), Czekanowskiales 4 gnerea, 4 species (*Czekanowskia*, *Solenites*, *Leptostrobus*, *Ixostrobus*), Ginkgoales 4 genera, 6 species (*Yimaia*, *Ginkgoites*, *Baiera*, *Sphenobaiera*), Coniferales 13 genera, 20 species (*Pityocladus*, *Pityospermum*, *Schizolepis*, *Austrohamia* (*Yanliaoa*), *Brachyphyllum*, *Elatocladus*, *Amentotaxus*, *Taxus*, *Nageiopsis*, *Podocarpites*, *Cephalotaxopsis*, ?*Pseudofrenelopsis*, *Podozamites*), Caytoniales 2 genera, 2 species (*Caytonia*, *Sagenopteris*), Seeds/fruits with unknown affinities 3 genera, 3 species (*Conites*, *Problematospermum*, *Carpolithus*). Angiosperms 2 genera, 2 species (*Solaranthus*, *Juraherba*) (Zheng et al. 2003; Li et al. 2004; Zhou et al. 2007; Zheng & Wang 2010; Wang et al. 2010a, 2010b; Pott et al. 2012; Heinrichs et al. 2014; Han et al. 2016; Dong et al. in press).

The Daohugou region has been intensively studied by various geologists (most stratigraphers and palaeontologists). Among these them, there is a general consensus on the Middle Jurassic age of the Jiulongshan Formation (formerly Daohugou Formation). Wang et al. was the only group who challenged this consensus on the age of Jiulongshan Formation in Daohugou region and they interpreted the strata as of the Early Cretaceous (Wang et al. 2005). Later it has been proven that Wang et al. (2005) was careless in fossil collecting, mixing fossils of the Yixian Formation in near region into the Daohugou biota, and this mistake resulted in their erroneous age interpretation. Their conclusion (Wang et al. 2005) was later overwhelmed and disputed by more stratigraphic and palaeobiological works on insects, conchostracans, vertebrates, and plants (Gao & Ren 2006; Huang et al. 2006, 2008a, 2008b, 2009; Zhang 2006; Huang & Nel 2007, 2008; Petrulevicius et al. 2007; Sha 2007; Zhou et al. 2007; Lin et al. 2008; Liu & Ren 2008; Selden et al. 2008; Zhang et al. 2008, 2009, 2011; Chang et al. 2009; Fang et al. 2009; Liang et al. 2009; Shih et al. 2009; Wang & Ren 2009; Wang & Zhang 2009a, 2009b; Wang et al. 2009a, 2009b, 2009c, 2010b; Chang et al. 2014). In addition to biostratigraphy, isotopic dating including Ar^{40}/Ar^{39} and SHRIMP U/Pb datings of the volcanic rocks overlying the fossiliferous layers (Chen et al. 2004; Ji et al. 2004a) suggest that the absolute age of Jiulongshan Formation is at least 164 Ma years old, namely, the Middle Jurassic in age. Taking all into consideration, it appears that the present authors have no alternative but to adopt a Middle Jurassic age for our fossil plant here reported.

The specimen was photographed using a Panasonic DMC-LX5 digital camera. Details of the fossil were observed and photographed using a Leica MZ-16A stereomicroscope with a digital camera. Afterward nitro cellulose replicas were made on the specimen, and the replicas were cleaned with HCl and HF, coated with gold, and observed using a Leo 1530 VP SEM (scanning electron microscope) at the Nanjing Institute of Geology and Palaeontology (NIGPAS), Nanjing, China. All photographs were saved in TIFF format and organized together for publication using Photoshop 7.0.

The holotype (PB21544) of *Yuhania* was kept at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China, and the isotype (NOCC20130506018) was kept at the Orchid Conservation & Research Center of Shenzhen, Shenzhen, China.

Results

Genus *Yuhania* gen. nov.

Generic diagnosis

Plant including connected stem, leaves, flowers, aggregate fruits, fruitlets, and seeds in fruitlets. Stem curving, with longitudinal ridges and hairs. Leaves linear, probably spirally arranged, clasping the stem, entire margined, with an acute tip and five to six (rarely seven) parallel veins. Flowers unisexual, female, axillary, including carpels helically arranged along an axis. The carpels rhomboidal-shaped in early stages. Aggregate fruit pedicellate, with helically arranged fruitlets and bracts.

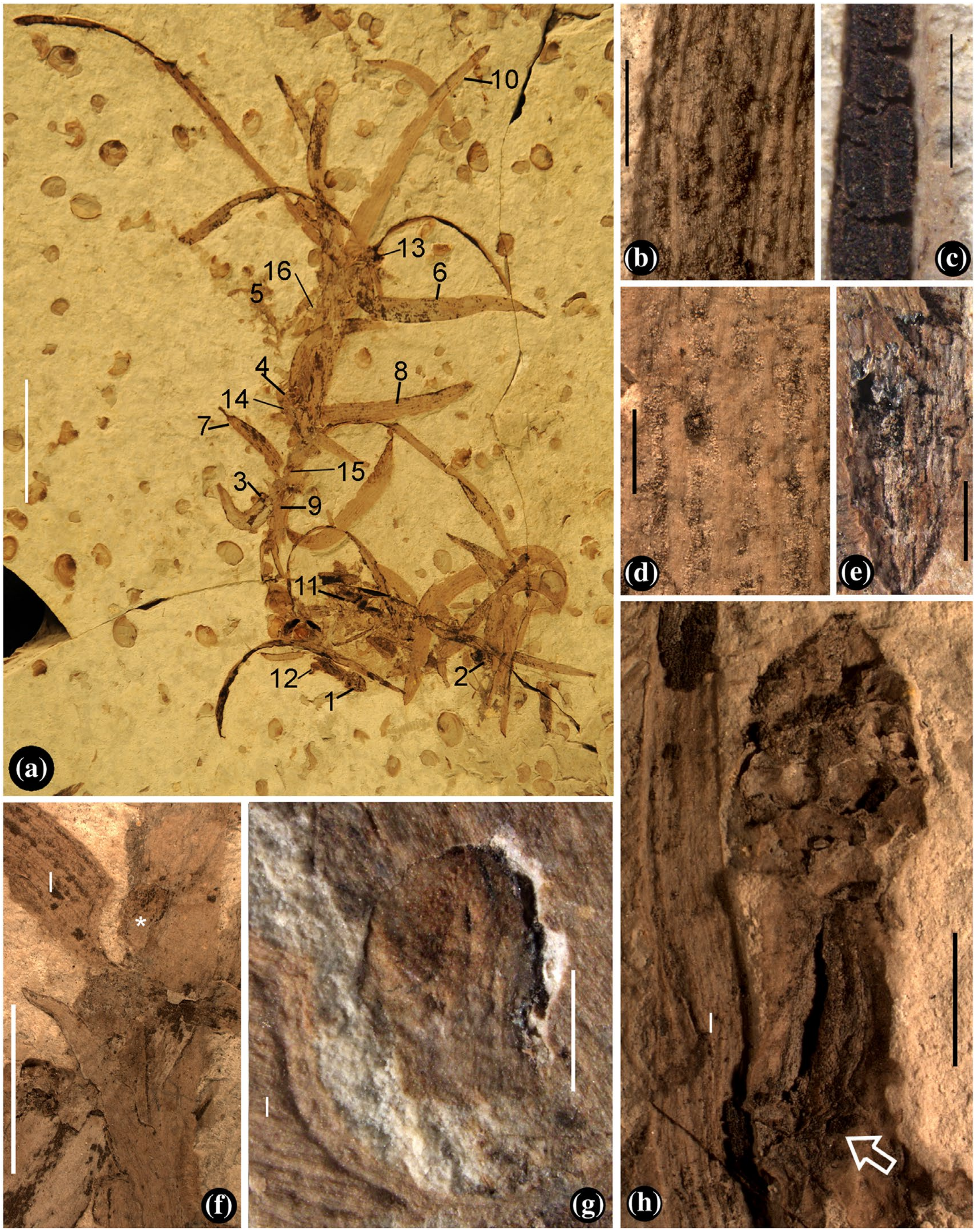

Figure 2. *Yuhania daohugouensis* gen. et sp. nov, and its details. Light microscopy. (a) The fossil embedded in yellowish tuffaceous siltstone. Some of the labeled regions are shown in later Figures. 1–4 and 12–13 are six aggregate fruits, 14–15 are immature flowers, 5 is an associated lichen (*Daohugouthallus ciliiferus* (Wang et al. 2010a)), 6–10 are leaves, and 16 is a lateral bud. Bar = 2 cm, (b) details of the leaf marked as 7 in Figure 2(a), with parallel veins and entire margin. Bar = 1 mm, (c) a leaf preserved as compression to the left and as impression to the right. Bar = 1 mm, (d) detailed view of the leaf marked as 8 in Figure 2(a), with entire margin, alternating veins and stomata zones. Bar = 1 mm, (e) stem with longitudinal ridges, partially embedded in the sediments. Bar = 1 mm, (f) detailed view of the region as 15 in Figure 2(a), showing an immature flower (asterisk) in leaf (l) axil. Bar = 5 mm, (g) detailed view of the immature flower in leaf (l) axil in Figure 2(f). Bar = 1 mm, and (h) the aggregate fruit marked as 1 and 12 in Figure 2(a). Note the pedicel connected (arrow) to the stem. Bar = 2 mm.

Each fruitlet with a cuspidate or rounded tip, enclosing a seed. Seed inserted on the floral axis, on the abaxial of the enclosing foliar part.

Type species

Yuhania daohugouensis gen. et sp. nov.

Etymology

Yuhania for Ms. Yuhan Cai, the daughter of Mr. Hongtao Cai who helped collecting the specimen for this study.

Type locality

The Daohugou Village, Ningcheng, Inner Mongolia, China (Figure 1(a) and (b)).

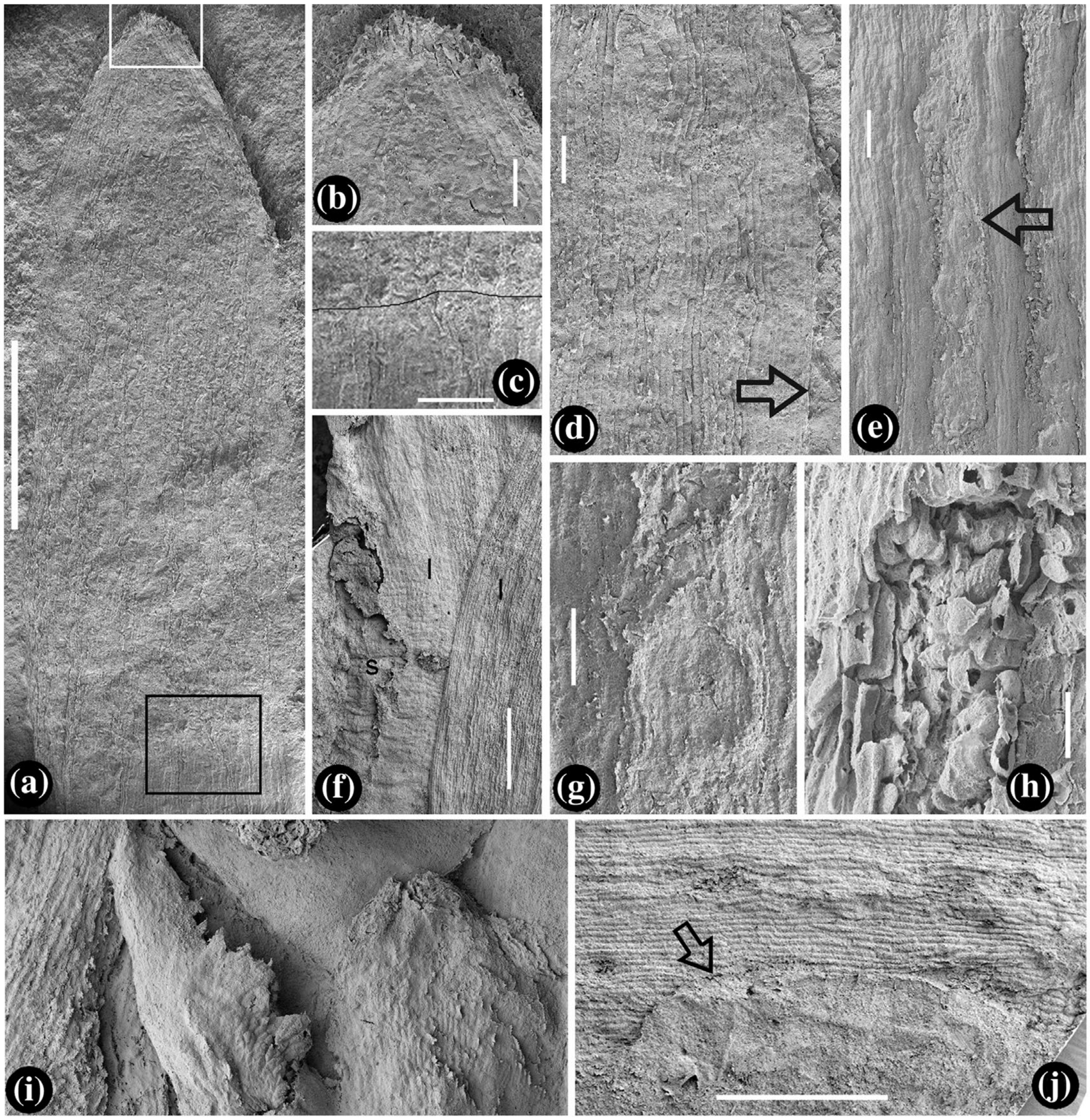

Figure 3. Leaves and their details. SEM. (a) Abaxial view of leaf tip marked as 10 in Figure 2(a), showing the entire leaf margin and parallel veins. Bar = 1 mm, (b) leaf tip with papillae, enlarged from the white rectangle region in Figure 3(a). Bar = 0.1 mm, (c) leaf texture transitional from regular (below the line) to chaotic (above the line), enlarged from the black rectangle in Figure 3(a). Bar = 0.2 mm, (d) an adaxial view of a leaf, showing longitudinal epidermal cells and entire leaf margin (arrow). Bar = 0.1 mm, (e) an abaxial view of the leaf in Figure 2(d), showing well-defined alternating vein and intervein (stomata, arrow) zones. Bar = 0.2 mm, (f) leaf (l) clasping and diverging from the stem (s) with horizontal wrinkles. Note the leaf texture changes from the horizontal to longitudinal from the bottom up. Bar = 0.2 mm, (g) detailed view of the stomata arrowed in Figure 3(e). Bar = 0.1 mm, (h) a leaf with elongate epidermal cells (upper-left) and mesophyll aerenchyma. Bar = 50 μm, (i) a leaf in its earliest developmental stage, fringed with dentate protrusions. Bar = 0. 1 mm, and (j) leaf probably damaged by insect (arrow). Bar = 0.5 mm.

Horizon

The Jiulongshan Formation, Callovian, Middle Jurassic (>164 Ma).

Species *Yuhania daohugouensis* gen. et sp. nov.
(Figures 2–4 and S1–5)

Specific diagnosis

The same as the genus for the time being.

Description

The fossil is preserved as compression and impression, including part and counterpart, with some coalified materials embedded in yellowish tuffaceous siltstone, associated with many conchostracans that are characteristic of some strata of the Jiulongshan Formation near Daohugou Village (Figures 1(a), (b), 2(a)–(c), S1(a)–(c), S2(a), (b), and S3(d)). The fossil is 12 cm long, 10 cm wide, including physically connected stem, buds, leaves, flowers, aggregate fruits, fruitlets, and seeds in fruitlets (Figures 2(a)–(h), 3(d), (f), (i), 4(a), (d)–(g), 5(a), S1(c), S2(a), (b), and S3(a)). The stem is about 2.5 mm in diameter, curving, bearing leaves probably helically (Figures 2(a), 3(f), S4(a)–(c), and S5(b), (c)). The stem bears longitudinal ridges and hairs when there is no leaf attached (Figures 2(e), and S4(a), (c)), bears transverse wrinkles when there are leaves or scales attached (Figures 3(f), S3(a), S4(b), and S5(b), (c)). Lateral bud includes helically arranged scales, is about 3.3 mm long and 2.3 mm wide at the base, tapering distally (Figure S3(a)). The smallest leaf observed so far is only 0.68 mm long, fringed with dentate

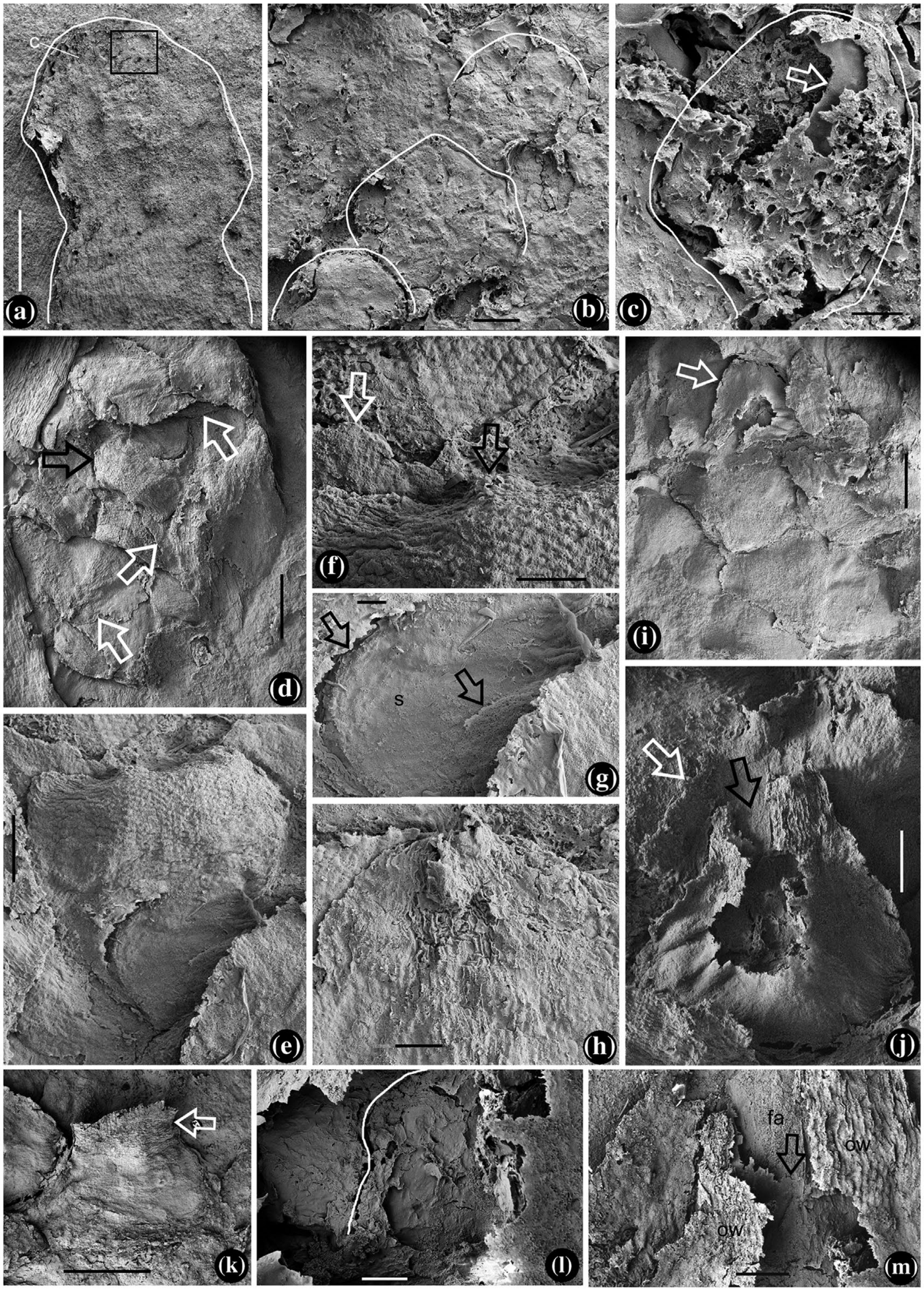

Figure 4. Flower and aggregate fruits of *Yuhania*. SEM. (a) The immature flower in Figure 2(g), with a stout pedicel and spherical receptacle. Bar = 0.5 mm, (b) detailed view of the rectangle in Figure 4(a), showing outlines of the carpels helically arranged. Bar = 20 μm, (c) the sac-like carpel marked as C in Figure 4(a). Bar = 10 μm, (d) SEM view of the aggregate fruit in Figure 2(h), with helically arranged fruitlets. Bar = 0.5 mm, (e) one of the fruitlets from the aggregate fruit in Figure 4(d), with its seed exposed. Bar = 0.2 mm, (f) detailed view of the distal portion of the fruitlet in Figure 4(e). Note the cuspidate tip (black arrow), the greatest width near the distal of the fruitlet, and a bract (white arrow). Bar = 0.1 mm, (g) detailed view of the proximal part of the fruitlet in Figure 4(e), showing the broken fruitlet wall (arrows) and exposed seed (s) in the fruitlet. Bar = 50 μm, (h) rounded tip of a bract, note the longitudinal texture in the middle. Bar = 0.1 mm, (i) SEM view of the aggregate fruit marked as 2 in Figure 2(a) and shown in Figure S4(e) and (f). Bar = 0.5 mm, (j) a young 'carpel' with a broken tip (black arrow), wide base, and a bract in the background (white arrow). Note the empty space in the 'carpel.' Bar = 0.2 mm, (k) a young fruitlet with an extended terminus (arrow). Bar = 0.5 mm, (l) detailed view of young fruitlet shown in Figure 4(j), showing outline of a possible ovule (white line). Bar = 50 μm, and (m) detailed view of young fruitlet shown in Figure 4(j), showing ovarian wall (ow) fused (arrow) to the floral axis (fa). Bar = 0.1 mm.

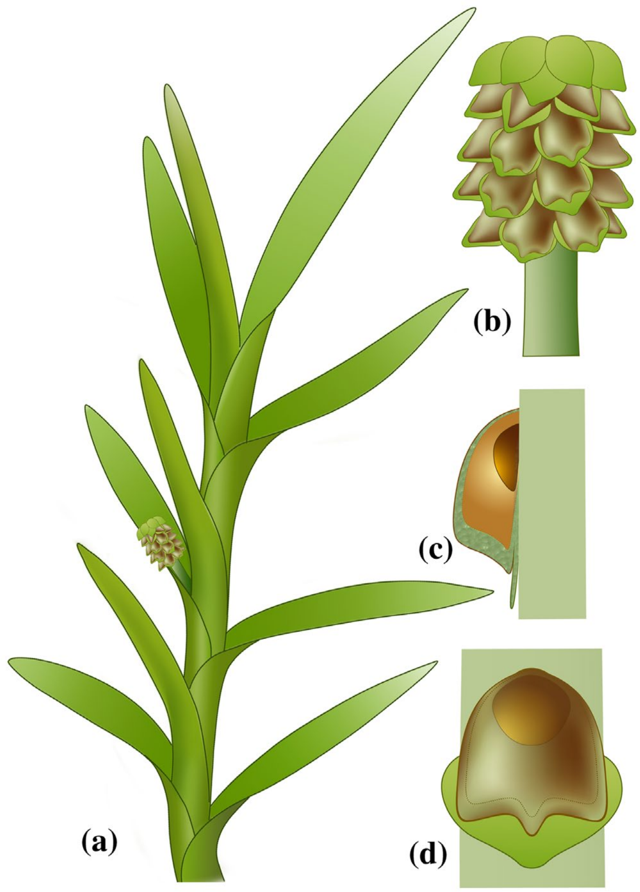

Figure 5. Reconstruction of *Yuhania*. (a) Shoot with leaves and aggregate fruit, (b) pedicellate aggregate fruit, (c) longitudinal section of a carpel/fruitlet, showing an ovule/seed inserted on floral axis and enclosed in ovary, and (d) surface view of a carpel/fruitlet, showing an ovule/seed inserted on floral axis and enclosed in ovary.

protrusions (Figure 3(i)). The other leaves are simple, 9–70 mm long, 1.2–4 mm wide, clasping the stem, linear, entire-margined, curving or almost straight (Figures 2(a)–(d), (f), 3(a)–(f), (j), and S2(a), (b)). Each of them has an acute tip, five to six (rarely seven) parallel veins, lacking midvein (Figures 2(a)–(d), (f), 3(a)–(f), (j), and S2(a), (b)). The veins are 0.1–0.23 mm wide, with interveins about 0.13–0.34 mm wide in between, bifurcating only in the basal part of the leaf (Figures 2(b)–(d), 3(a), (d)–(f), (j), S3(b)–(d), S4(e), and S5(d), (e), (i)). The veins are obviously parallel in the middle portion of the leaves (Figures 2(a), (b), (d), (f), 3(a), (d)–(f), (j), S3(b), (c), S4(e), and S5(d), (e), (i)), but the vein pattern becomes similar to the transverse wrinkles on the stem in the basal portion of leaves (Figures 3(f), and S5(b), (c)). The regular vein pattern is suddenly lost in the apical portion of the leaves, probably due to the leaf apical meristematic activity (Figure 3(a)–(c)). The adaxial surface of the leaves has longitudinally oriented epidermal cells, stomata-free (Figures 2(b), 3(d), and S5(d), (e), (i)). The abaxial surface of the leaves has alternating vein and intervein zones (Figures 2(d), 3(e), S3(c), and S5(g), (h), (j)). Stomata are on the abaxial surface of the leaves, arranged in files between the veins, close to round in shape, about 156–180 μm long and 211–264 μm wide, with pit naked or covered by protrusions (Figures 2(d), 3(e), (g), and S5(g), (h), (j)). Mesophyll includes two-cell-layered longitudinally oriented adaxial parenchyma and spongy parenchyma above the abaxial epidermis (Figures 3(h), and S5(e), (f)). Possible insect damage is seen on some leaves (Figure 3(j)). At least six aggregate fruits and two flowers have been seen physically connected with the fossil (Figures 2(a), (f)–(h), 4(a), (d), (i), S4(c)–(j), and S5(a)). The pistillate flower are spherical, 1.3–1.46 mm wide and 1.3–1.39 mm long, attached to a stout pedicel, with helically arranged rhomboidal immature carpels (Figures 2(f)–(h), 4(a)–(c), S4(d), and S5(a)). The flower pedicel is 0.6–1 mm wide and 0.5–0.7 mm long (Figures 2(g), 4(a), S4(d), and S5(a)). The aggregate fruit pedicel is up to 4.3 mm long and 2.1 mm wide (Figures 2(a), (h), and 5(b)). A flower is 4–4.5 mm long and 2.6–3.1 mm wide, attached to the stem, with more than twenty fruitlets helically arranged (Figures 2(a), (h), 4(d), (i), and S4(c), (e)–(j)). Each fruitlet is subtended by a bract (Figure 4(f) and (j)). Each bract has a midrib and a rounded tip, at least 0.9 mm long and 0.9 mm wide (Figure 4(h)). The bracts and fruitlets point to the proximal of the aggregate fruit (Figure 4(d), (i)). Young or aborted fruitlet appears triangular in shape, about 0.9 mm long and 0.9 mm wide, widest near the proximal, constricting rapidly to the distal, sometimes broken near the tip (Figure 4(i), (j)). Mature fruitlets are up to 0.9 mm long and 0.7–1.1 mm wide, widest near the distal part, converging rapidly to a cuspidate or rounded tip (Figures 4(e), (f), and 5(c), (d)). A seed with a smooth surface and round shape is inserted on the floral axis, covered by the foliar part bending to the proximal, and becomes visible only when the fruitlet wall is broken (Figure 4(e), (g)).

Holotype

PB21544, deposited in the Nanjing Institute of Geology and Palaeontology, Nanjing, China.

Isotype

NOCC20130506018, deposited in the Orchid Conservation & Research Center of Shenzhen, Shenzhen, China.

Etymology

daohugouensis for Daohugou Village, Ningcheng, Inner Mongolia, China, where the specimen was collected.

Discussion

Good preservation is the foundation for a robust interpretation on any aspect of a fossil plant. Normally, parenchyma is the tissue most labile to decay in plants and is rarely seen in fossil plants, and tender young leaves tend to be destroyed during fossilization because of lack of hard parts. The preservation of mesophyll parenchyma and tender young leaf in *Yuhania* (Figure 3(h) and (i)) strongly suggests that preservation of *Yuhania* is good enough to justify reliable morphological interpretations. Furthermore, connection among various parts (including leaves, branches, and fructifications) in the same specimen (rather than isolated plant fragments) makes the reconstruction of *Yuhania* free of imagination and artifacts, and thus more believable. These constitute the solid foundation for our following interpretation and conclusion.

Usage of 'carpel'

'Carpel' is a term frequently used in angiosperm morphology (Eames 1961; Cronquist 1988). It appears more applicable in Magnoliales that are apocarpous, and more compatible with the previously prevailing theories of angiosperm evolution, in which carpels are thought derived from the assumed 'megasporophylls' that bear ovules along their margins (Eames 1961; Cronquist 1988; Dilcher 2010). The most embarrassing thing for the proponents of this theory is that the assumed 'megasporophyll' is never seen in any living or fossil plant yet despite long time painstaking searching. On the contrary, only leaf-like female parts among living plants that are seen in *Cycas* have been recently proven being branches metamorphosed to leaf-like form due to mechanical pressure (Wang & Luo 2013). The term 'carpel' in traditional sense faces challenge in other groups, for example, Basellaceae (Sattler & Lacroix 1988) and Piperaceae (Tucker 1982), in which and other syncarpous taxa the leaf-derived 'carpels' are hard to seek. However, if 'carpel' is taken as any structure that encloses ovules, as Rothwell and Stockey (2010) used for problematic Bennettitales, then the origin of carpels (also of angiosperms) will become much easy and may be derived in multiple ways. These ways may be exemplified at least by *Foxeoidea* (Rothwell & Stockey 2010), *Pseudoephedra* (Liu & Wang 2016a), as well as *Yuhania* reported here. Considering that ambiguity around the 'carpel,' we will minimize our usage of this term. If used, it will be *sensu lato* as Rothwell and Stockey (2010) used.

Consistent criterion for angiosperm recognition

There are multiples characters that can be used to identify angiosperms, including reticulate leaf venation, double fertilization, vessel element, and enclosed seed/ovule (Wang 2010b; Friis et al. 2011). The multitude of criteria explains the messy situation in palaeobotanical study of early angiosperms. The eagerness to champion the research makes the situation worse. For example, Friis et al. (2001) claimed that their late Aptian – early Albian (Friis et al. 2009) fossil represented the earliest unequivocal angiosperm, completely ignoring the late Barremian - early Aptian (~125 Ma old) *Archaefructus* (Friis et al. 2003) documented by another group (Sun et al. 1998). Therefore, to make claims about early angiosperms more believable, a consistent criterion and equanimity of the researchers are necessary. For each of the characters proposed as criteria identifying an angiosperm in fossils, there are exceptions. This situation makes many confused in choosing a decent criterion in their palaeobotanical practice. Angio-ovuly before pollination is proposed as a strict criterion for angiosperms (Tomlinson & Takaso 2002; Wang 2010b) as this criterion can guarantee an angiospermous affinity for a fossil of question. The exception to this criterion is that a few of angiosperms may be 'wronged' as gymnosperms. Fortunately, as long as we only apply this criterion to determine that a fossil IS an angiosperm (not that a fossil plant IS NOT an angiosperm), this criterion works perfectly. For example, the problematic fossil taxon, *Caytonia*, was initially thought an angiosperm (Thomas 1925) but was later proven to be gymnospermous due to the pollen grains found inside its so-called cupules (Harris 1933, 1940). This example implies that angiospermy (present in *Caytonia*) cannot ensure an angiospermous affinity. Therefore demonstrating the existence of angio-ovuly in a fossil is more reliable than any other characters (including angiospermy and double fertilization) in pinning down angiospermous affinity for a fossil plant, which may be seen in both angiosperms and gymnosperms. Although not always declared explicitly, this criterion has been applied on various fossils to justify their angiospermous affinity, e.g. *Archaefructus lianoningensis* (Sun et al. 1998), *Monetianthus mirus* (Friis et al. 2009), *Schmeissneria sinensis* (Wang et al. 2007), *S. microstachys* (Wang 2010c), *Xingxueanthus sinensis* (Wang & Wang 2010), *Baicarpus huangbanjigouensis* (Han et al. 2013), and *Liaoningfructus ascidiatus* (Wang & Han 2011). In all of these cases, there is no or little helpful information of male parts, leaves, or other defining characters of angiosperms, the judgment is reached solely or at least mainly on enclosed ovules/seeds. This is also the criterion we adopt here.

Female parts and implications

Each aggregate fruit of *Yuhania* includes multiple fruitlets (Figures 2(h), 4(d), (i), and S4(c), (e)–(j)). Although these fruitlets could be alternatively interpreted as seeds aggregated around an axis, the space inside the assumed seed is a challenge for this interpretation (Figure 4(e)–(g), (j)). Furthermore the assumed seed coat normally is of relatively uniform thickness with neat organization of sclerenchymatous tissue, and would not break in a way seen in Figure 4(e) and (g). These expectations are in contrary to the observation in Figure 4(d)–(f). According to our interpretation, the assumed seed with empty space and internal body can be more rationally interpreted as a fruitlet enclosing a seed in its locule. It is noteworthy that this conclusion is further supported by analyzes of other features of *Yuhania*.

For most of *Yuhania* fruitlets, their tips are complete and closed, and their seeds are not visible from outside (Figure 4(d) and (i)), indicating the occurrence of angiospermy in *Yuhania*. Exposing seeds after fruitlet maturation is a frequently seen way of seed dispersal in angiosperms (e.g. *Magnolia*) (Romanov & Dilcher 2013), thus the fruitlet with an exposed seed in *Yuhania* (Figure 4(e) and (g)) implies that the fruitlet of *Yuhania* is mature rather than that the ovule is exposed. As seen above, so far there is no exception to the rule that enclosed ovules before pollination are restricted to angiosperms. Each young/aborted fruitlets of *Yuhania* has an extended tip (Figure 4(j) and (k)), and the breaking of one of these tips (Figure 4(j)), probably due to the lack of well-developed cuticle as expected for an immature carpel, allows us to see the details in a secluded cavity within the 'carpel.' The scar of a possible ovule and adnation of the 'carpel' wall to the axis can be seen in this 'carpel' (Figure 4(l) and (m)), an arrangement expected for angiosperms but never seen in gymnosperms yet. The drastic contrast in form between this young carpel and mature fruitlets (Figure 4(b), (c), (e), and (j)) suggests that *Yuhania* must have undergone a great developmental change after pollination, which is also helpful to distinguish angiosperms from gymnosperms (Leslie & Boyce 2012). All these features point to an angiospermous affinity for *Yuhania* although angio-ovuly in young 'carpel' of *Yuhania* still requires confirmation.

Position of ovule

Compared with all known angiosperms, *Yuhania* is unique in its abaxial ovule position related to the ovarian wall. This feature alone distinguishes *Yuhania* from most Coniferales and Cordaitales, in which the ovules are borne on secondary axillary shoot in the axil of a bract. In at least most angiosperms, the ovules are positioned adaxially relative to the foliar parts that enclose them: namely, either the ovules are borne on the shoot apices and enclosed by the subapical foliar parts, or the ovules are in the axils of the subtending foliar parts, as generalized in the Unifying Theory (Wang 2010b). In the fossil world, the ovules in Caytoniales and Petriellales are also on the adaxial side of the covering parts (Thomas 1925; Harris 1933, 1940, 1951; Reymanowna 1970; Krassilov 1977; Taylor et al. 1994, 2006; Wang 2010a). This spatial relationship between ovules and enclosing parts are conceivable and easy to understand considering that, among seed plants, axillary branching is almost ubiquitous and all ovules are borne on branches. But, in *Yuhania,* the ovule is enclosed by a foliar part bending back to the proximal of the reproductive organ, namely, the ovule is on the abaxial side of the enclosing part (Figure 4(e)–(g), (l), and (m)). In the fossil world, some Corystospermales (*Umkomasia*) have demonstrated similar relationship between the ovules and their covering parts (Klavins et al. 2002; Zan et al. 2008; Shi et al. 2016). Apparently, *Yuhania* and Corystospermales fall out of the expectation of the Unifying Theory, implying that the Theory still needs some modification and improvement to address all variations and evolutionary scenarios in seed plants.

Jurassic monocot

Features including parallel venation with files of stomata, longitudinally oriented epidermal cells, alternating leaf zones with and without stomata, linear leaf shape, entire leaf margin, and leaf base clasping stem in *Yuhania* are frequently seen in monocots (Fahn 1982; Stevens 2008). Although it is true that some of these features are also in some conifers, the morphological assemblage of the above reproductive features have eliminated conifers from our consideration. Among these six features, the first four have been considered as basic features or synapomorphies of monocots (Doyle et al. 2008). The presence of fruitlets in *Yuhania* indicates that the plant was already mature when fossilized. Little or no secondary growth in this mature plant suggests that *Yuhania* is not woody but herbaceous. This is not surprising as an herbaceous angiosperm *Juraherba bodae* has been reported recently from the same locality (Han et al. 2016), in addition to reports of early herbaceous angiosperms from the Early Cretaceous (Taylor & Hickey 1990; Sun et al. 1998, 2002; Leng & Friis, 2003; Jud 2015). Monocots have been assumed as a monophyletic taxon derived from the basal clades in angiosperms (APG 2009). If Middle Jurassic *Yuhania* were related to monocots, then it would be implied either that monocots are more plesiomorphic than previously assumed, or that angiosperms must have originated much earlier before the Middle Jurassic, or both. However, the unique organization of female parts in *Yuhania* prevents us from relating it to monocots, therefore we leave the systematic position of *Yuhania* open for the time being.

Leaf structure and habitat

The good preservation of *Yuhania* is partially reflected in the preservation of delicate aerenchyma in mesophyll of its leaves. This allows us to reveal more secrets of this ancient plant which are otherwise unavailable. Lack of well-developed palisade in the leaves of *Yuhania* (Figure 3(h)) is of taxonomic and ecological interest. Well-developed palisade is present under both leaf epidermis in xeromorphic plants (Fahn 1982). Lack of palisade is frequently seen in plants living in wet shady habitat (Feild et al. 2003; Feild & Arens 2007) and many monocots (Fahn 1982; Gu et al. 1993). This is in good agreement with the presence of proxy for humid habitat, lichen in the Daohugou flora (Wang et al. 2010a), which also associates *Yuhania* here (5 in Figure 2(a)). All these suggest that the niche of *Yuhania* is relatively humid and shady, and *Yuhania* is not the dominating elements exposed to strong sunshine in the ecosystem then.

Origin of angiosperms

Although a Jurassic age for angiosperms appears surprising to many, our result is compatible with independent research and is expected by many. Earlier origin time for angiosperms have been repeatedly proposed based on molecular clock studies (Wu et al. 2003; Lu & Tang 2005; Soltis et al. 2008; Hilu 2010; Smith et al. 2010; Prasad et al. 2011; Magallón 2014). The previous fossil record of possible early angiosperms (Cornet 1986, 1989a, 1989b, 1993; Axsmith et al. 2013), especially the recently discovered angiosperm-like pollen in the Triassic (Hochuli & Feist-Burkhardt 2013), *Schmeissneria microstachys* with various parts connected from the Early Jurassic (Wang 2010c), perfect flower (*Euanthus panii*) from the Middle Jurassic (Liu & Wang 2016b), rice tribe (*Changii indicum*) in the latest Cretaceous (Prasad et al. 2011), and herbaceous angiosperm (*Juraherba bodae)* from the Middle Jurassic, all push the origin of angiosperms to an earlier time. According to the BEAST analysis (Prasad et al. 2011), the age of angiosperms should be pushed back to 202–235 Ma (the Triassic), and monocots back to the Middle Jurassic (145–161 Ma). The 164+ Ma age of *Yuhania* falls well within the expectations of this independent study. Ecologically, the occurrence of flower-visiting insects (Tenebrionoidea) in Daohugou area (Ren et al. 2009; Wang & Zhang 2011) makes the existence of angiosperms in the Middle Jurassic both plausible and expected. These independent research converge to that angiosperms are truthful existence in the Jurassic. The former conception 'No Angiosperms Until the Cretaceous' now appears simply to be a function of multiple parameters including former lack of fossil evidence, irrational presumption of ancestral angiosperms, and loyalty to unfounded theories.

These earlier occurrences of angiosperms seem to suggest that, although not frequently seen and not dominating in the floras, angiosperms must have existed in the Jurassic. However, angiosperms did not gain much advantage in their competition against gymnosperm peers until much later. The distinction in Bau-plans of the reproductive organs among these pioneer angiosperms implies that there appears to be little phylogenetic or evolutionary relationship among them, based on current understanding. So, if angiosperms are monophyletic, the diversification of these groups must have occurred much long before. However, if such diversity of angiosperms have originated polyphyletically, then the origin time does not have to be too early, the so-called synapomorphy of angiosperms (angio-ovuly) may be a result of convergence that simply symbolizes the evolutionary grade in parallel developed lineages. The diversification of angiosperms in the Early Cretaceous may be a flourishing of the lucky relics of long-existing Jurassic angiosperms, which have undergone long silent evolution and did not flourish until coupled with suitable Cretaceous environment. Whether there is a pre-Cretaceous radiation for angiosperms is a question deserving further investigation. Whether *Yuhania* stands for a precursor of some unknown angiosperms or simply a dead-end of plant evolution is also an open question. Apparently, increased number of early angiosperms bring up more questions rather than answers.

Conclusion

As a fossil plant with various parts physically connected, well-preserved *Yuhania* sheds unique light on the early angiosperms. Although not directly related to any extant groups, *Yuhania* and other pioneer angiosperms suggest that angio-ovuly appears to be an evolutionary grade for plants, which can be reached by various groups independently at different times and before the Cretaceous. The formerly assumed one-episode radiation of angiosperms in the Early Cretaceous may be over-simplified story of angiosperms, the truthful version of which could be revealed only by deepened careful investigation on early angiosperm fossils.

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