Xingxueanthus: An Enigmatic Jurassic Seed Plant and Its Implications for the Origin of Angiospermy

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Abstract: The origin of angiosperms has been tantalizing botanists for centuries. Despite the efforts of palaeobotanists, most of the pre-Cretaceous angiosperms are regarded either non-convincing or misdated. The applications of SEM and LM (light microscope) enable us to recognize a coalified fossil plant, Xingxueanthus sinensis gen. et sp. nov., from the Haifanggou Formation (Middle Jurassic, >160 Ma) in western Liaoning, China. Xingxueanthus is an "inflorescence" with more than 20 female units spirally arranged. Each female unit is situated in the axil of a bract. The female unit is composed of an ovule-container and a style-like projection at the top. There is a vertical column bearing several ovules in the ovule-container. The general morphology and the internal structure of Xingxueanthus distinguish itself from any known fossil and extant gymnosperms, and its structures are more comparable to those of angiosperms. Xingxueanthus, if taken as a gymnosperm, would represent a new class, demonstrate an evolutionarily advanced status of ovule-protection in gymnosperms never seen before, and provide new insights into the origin of angiospermy. Alternatively, if taken as an angiosperm, together with Schmeissneria, it would increase the diversity of Jurassic angiosperms, which has been underestimated for a long time, and suggest a much earlier origin of angiospermy than currently accepted.

Keywords: angiosperm, flower, origin, Liaoning, Jurassic

1 Introduction

Since the age of Darwin the origin of angiosperms has been a riveting topic for botanists (Cronquist, 1988; Sun et al., 1998; Friis et al., 2005; Frohlich and Chase, 2007). Palaeobotanists have claimed several pre-Cretaceous angiosperms, e.g., Cornet, Hochuli and other colleagues have provided much evidence of possible angiosperms in the Triassic and Jurassic (Cornet, 1986, 1989a, b, 1993; Cronquist, 1988; Cornet and Habib, 1992; Hochuli and Feist-Burkhardt, 2004), but their claims are not widely accepted yet (Cronquist, 1988; Friis et al., 2005, 2006). Northeastern China has been a focus of palaeobotanical research in the past decades (Pan, 1977, 1983; Duan 1998; Sun et al., 1998, 2002; Leng and Friis, 2003, 2006; Ji et al., 2004; Wang et al., 2007; Zheng et al., 2008; Quan and Sun, 2008, among many). Sun et al. (1998) claimed Archaefructus Sun et al. as a Jurassic angiosperm, but this claim raised much controversy on the age of the fossil (Ji et al., 2004; Friis et al., 2005). Since the controversy on the age of Archaefructus has been resolved as 125 Ma (Dilcher et al., 2007), Archaefructus is no longer a Jurassic angiosperm. Wang et al. (2007) reported a fossil inflorescence, Schmeissneria sinensis Wang, from the Haifanggou Formation (Middle Jurassic). While giving no reason or more decent treatment, Sun et al. (2008) cast doubt on the angiospermyous identity of Schmeissneria. In the mean time, Doyle (2008) put Schmeissneria as "closer stem relatives of the angiosperms" with uncertain morphology and relationships although he admitted that the ovules are enclosed, so the position of Schmeissneria appears to need more time to be widely recognized. Therefore, Darwin's "abominable mystery" is no less abominable now, and we are still in want of fossil evidence to solve the mystery. 2009 is the 200th anniversary of birthday of Charles Darwin, who raised this famous question 130 years ago. To make some contribution to the celebration, here we report an interesting seed plant, Xingxueanthus sinensis gen. et sp.
nov., from the Haifanggou Formation (>160 Ma, Middle Jurassic) in Liaoning, China. The “inflorescence” is composed of more than 20 female units spirally arranged. Each female unit is subtended by a bract. The female unit is composed of an ovule-container and a style-like projection at the top. The ovules are attached to a vertical column within the ovule-container. This kind of structure is never seen in gymnosperms but comparable to its counterpart in angiosperms. Whatever the final position it takes later, *Xingxueanthus* together with other fossil angiosperms from northeastern China (Wang et al., 2007a, b; Wang, 2009; Wang and Zheng, 2009) will play a key role in the systematics of seed plants and provides new insights into the origin of angiospermy.

2 Materials and Methods

al., 1997; Zheng et al., 2003). This floristic assemblage is typical for the Middle Jurassic (Kimura et al., 1994; Deng et al., 2003). The 160 Ma age of the overlying Tiaojishan Formation (Deng et al., 2003) suggests that the age of *Xingxueanthus* is more than 160 Ma old. The specimens included two counterparts of a coiled compression embedded in a dark gray silty mudstone (Figs. 2a, b). Initially, only the lower portion of the specimen was visible (Fig. 2b). The hidden portion of the specimen (upper portion in Fig. 2a) was uncovered by dégaging. Then the both parts were observed and photographed using a Leica MZ-16A stereomicroscope with a digital camera (Figs. 2a–j) and using a Leon 1530 VP SEM (scanning electron microscope) in VP mode (Figs. 3 and 4a–h) at Nanjing Institute of Geology and Palaeontology, Nanjing, China. Afterwards, one of the parts (8703b) was embedded in Epon 812, ground to expose the details embedded in the sediment, coated with gold and observed under SEM again (Figs. 4a–d). Epidermal details were observed under a SEM on some HF-cleaned detritus that was trimmed away during the dégaging (Fig. 4i). All information was used together to reconstruct the fossil.
Fig. 3. Female units with their ovule-bearing columns. Specimen number for a-d, and g is 8703a, for e and f is 8703b. All SEM photographs.

a. A detailed view of the female unit No. 4 shown in Fig. 2a. Note the column (double white arrows) connecting the base and top of the ovule-container, and bract (black arrow). Pieced from three photographs. Bar = 0.5 mm. b. A detailed view of the column shown in Fig. 3a. Note the funiculi (white arrows) around the column, and bottom (between black arrows) of the column. Bar = 0.2 mm. c. A detailed view of the female unit shown in Fig. 2b. Note the column (white arrows), funiculi (black arrows) attached to the column, bottom (between double black arrows) of the column, and bract (between double white arrow). Pieced from two photographs. Bar = 0.5 mm. d. A detailed view of the female unit No. 8 shown in Fig. 2a. Note the ovules (white arrows), the outline (white line) of the ovule, the top (double white arrow) of the ovule-container, and bract (black arrows). Bar = 0.2 mm. e. A detailed view of the column in the female unit shown in Fig. 2c. Note the funiculi (white arrows) around the column, and striations on the column converging to the funiculi. Bar = 0.1 mm. f. A detailed view of the column of the female unit No. 1 shown in Fig. 2b. Note the funiculi (white arrows) around the column, striations on the column converging to the funiculi, and bottom (black arrow) of the column. Bar = 0.2 mm. g. A detailed view of the ovule shown in Fig. 3d. Note the possible nucellus (white arrow), integument (double black arrows), column (black arrow). Bar = 0.1 mm.

(Fig. 5). All photographs were saved in TIFF format, and pieced together for publication using Photoshop 7.0.

3 Results

*Xingxeanthus* gen. nov.

**Diagnosis:** Numerous female units spirally arranged along an axis forming an “inflorescence”. Each female unit in axil of a bract, composed of an ovule-container and a style-like projection at the top. Ovules arranged spirally along a vertical column within the ovule-container.

**Etymology:** *Xingxe*-., dedicated to Dr. Xingxue Li, a leading Chinese palaeobotanist, for his contribution to palaeobotany; -*anthus* for flower in Latin.

*Xingxeanthus sinensis* gen. et sp. nov.

(Figs. 2–5)

**Diagnosis:** The “inflorescence” is slightly curved, over 23 mm long and 7.5 mm wide at the base, tapering distally, with over 21 female units attached. A female unit is composed of an ovule-container and a style-like projection at the top. The ovule-containers are up to 3 mm from the adaxial to abaxial side, up to 2 mm from side to side, up to 2.6 mm high. The column connects the base and the top of the ovule-container, 1.1–2.5 mm long, about 0.5 mm wide at the base and tapering to about 50 μm wide at the top. More than three ovules are spirally arranged along the column at an angle close to 90 degree. A style-like projection 130–190 μm wide and up to 0.9 mm long is inserted on the top of the ovule-container.

**Description:** The “inflorescence” is spicate, slightly curved, over 23 mm long and 7.5 mm wide at the base, tapering distally, with over 21 female units attached, maturing acropetally (Figs. 2a, b). “Inflorescence” axis is about 1 mm wide at the base, tapering distally, slightly twisted to accommodate the female units, with longitudinal striations (Figs. 2a, b, f). Female units and their subtending bracts are spirally arranged along the “inflorescence” axis (Figs. 2a, b). Bracts are about 3.5–5
mm long, diverging from the “inflorescence” axis at an angle slightly greater than 90 degrees, upturning at the both sides of the female units (Figs. 2f–h, 3a, c, d), with inward-curving tips of about 35 degrees (Figs. 2a, b, c, g, h, 3a, c, d), completely separated from the female units in their axis (Figs. 2c, d, f), with their distal ends not extended beyond the bottom extremities of the female units (Figs. 2c, d). The ovule-containers are in the axes of the corresponding bracts, up to 3 mm from the adaxial to abaxial side, up to 2 mm from side to side, up to 2.6 mm high (Figs. 2c, d, f–h; Fig. 3a, c, d). A female unit is composed of an ovule-container and a style-like projection

Fig. 4. Some morphological and anatomical details. All SEM photographs. Specimen number for c, h and i is 8703a, for a–d and f–g is 8703b.

a. An oblique section across an ovule. Note the cavity (white arrow) and cellular details in the ovule. Bar = 10 μm. b. A detailed view of the rectangular region in Fig. 4a. Note the cavity on top, cellular details and cell wall (arrows) between cells. Bar = 5 μm. c. An ovule embedded in the sediment. Note the ovular tissue and the sediment around (white arrow). Bar = 10 μm. d. A detailed view of the ovule tip shown in Fig. 4c. Note the radial cellular deployment reminiscent of a microple. Bar = 10 μm. e. A view of the bract and upper-left portion of female unit No. 7 shown in Fig. 2a. Note the bract (black arrow), ovule-container (O), and relics of unknown part (white arrows) between them. Bar = 0.1 mm. f. A pit on the cell wall of vascular tissue. Bar = 1 μm. g. Trichomes on the ovule-container surface of female unit shown in Fig. 2c. Note the trichomes (white arrows) single or in fascicules, and their relationship with ovule-container (O). Bar = 0.1 mm. h. A bract relic just below female unit No. 6 in Fig. 2a. Note the gland-like structure on the bract (white arrow), organic material block of the bract, and elongate outlines of the epidermal cells. Bar = 0.1 mm. i. A stomatal aperture, from a HF cleaned macerated tissue. Note the sunken stomatal pit and elongate aperture. Bar = 1 μm.

Fig. 5. Sketches of the reconstructed female unit. Labels: “inflorescence” axis = a, bract = b, ovule-container wall = c, column = d, ovule = e, trichomes = f, style-like projection = g, scars of the bract and the female unit = h, bract tip = i, and a portion of another female unit = j.

a. A longitudinal section from side to side of the female unit. Note the “inflorescence” axis, bract, ovule-container wall, column, ovule, trichomes, style-like projection, and scars of the bract and the female unit, bract tip. BB’ marks the position of the section that is shown in Fig. 5b. b. A longitudinal section from the “inflorescence” axis to the distal of the female unit. Note the slightly twisted “inflorescence” axis, bract, ovule-container wall, column, ovule, trichomes, style-like projection, bract tip, and a portion of another female unit. AA’ marks the position of the section that is shown in Fig. 5a. c. A sketch of the female unit in Figs. 3a and i. Note the style-like projection (gray). d. A sketch of the female unit in Fig. 2g. Note the style-like projection (gray).
at the top (Figs. 2c, d, g, i, j). The ovule-container has a slightly depressed top and a vertical column within (Fig. 2c, h; 3a-g). The column connects the base and the top of the ovule-container, almost parallel to the “inflorescence” axis, 1.1–2.5 mm long, about 0.5 mm wide at the base and tapering to about 50 μm wide at the top (Fig. 2h, 3a-g). When the organic material is preserved, the column and its attached ovules are visible as dark material (Fig. 2h, 3c); when the organic material falls off, the column and its attached ovules are suggested by their imprints left on sediment (Figs. 3a, b, c, f). Striations on the column converge where funiculi are attached (Figs. 3b, e, f). More than three ovules are spirally arranged along the column at an angle close to 90 degree (Figs. 3a, b, d, f). Funiculi range from 100 to 320 μm in diameter (Figs. 3b, c, e, g). Ovules are 100–380 μm in diameter (Figs. 3d, g, 4a-d). A style-like projection 130–190 μm wide and up to 0.9 mm long is inserted on the top of the ovule-container (Figs. 2c, d, g, i, j). The epidermal cells are elongate subrectangular (Fig. 4h). There are trichomes on the surface of the ovule-container (Figs. 2c, j, 4g). Trichomes are about 1-2 cells and 40–50 μm in diameter, up to 328 μm long, single or in fascicles (Figs. 2c, j, 4g). Stomatal aperture is about 6–7 μm long and 2–3 μm wide, slightly sunken (Figs. 4i).

**Holotype:** 8703a.

**Paratype:** 8703b.

**Etymology:** *sin.:* *lot sino,* referring to China, where the specimens were found in China; *-ensis,* Latin suffix.

**Type locality:** Sanjiaochengcun, Jixi, western Liaoning, China (120°21’E, 40°58’N).

**Stratigraphic horizon:** the Haifanggou Formation, Middle Jurassic (>160 Ma).

**Depository:** the Department of Palaeobotany, Chinese National Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing, China.

**Remarks:** Since the inherent cavity in the ovulate tissue (Figs. 4a-b) is much deeper than any stomata or gland-like structure in *Xingxueanthus,* and no canal or cavity is expected in any other part of an ovule, therefore the cavity may stand for a micropylar canal formed by an integument. In addition, the radial deployment of cells in Figs. 4c–d is reminiscent of the cellular arrangement near the micropyte of an ovule (Endress and Igersheim, 2000; Igersheim et al., 2001).

The possibility of missing trichome for style-like projection is slim since two of them are distinct in length (0.3 mm vs 0.9 mm) and width (40–50 μm vs 130–190 μm) (Figs. 2c, d, g, i, j), and only one style-like projection is found single and only at the top of the ovule-container (Figs. 2c, d, g, i, j) while the trichomes are frequently in fascicles on the ovule-container (Figs. 2i–j, 4g).

Gland-like structures are found on the epidermis of bract (Fig. 4h), column (Fig. 3g) and “inflorescence” axis. Simple pits are found on the cell wall of a vascular element (Fig. 4f).

Figs. 4a–d and f are taken after the female units of specimen 8703b, which were originally covered in the sediment, are exposed by grinding away the covering sediment. Therefore they cannot be correlated with the female units visible on the slab surface, and no number is labeled on them. Fig. 4i is taken on the cleaned macerate of the dégaged detritus, therefore the exact source is hard to specify.

### 4 Discussions

The faithful preservation of *Xingxueanthus* is undeniable: the coalified fossil material make its morphology obvious under light microscope (Figs. 2a–j) and SEM even without gold coating (Figs. 3a–g, 4e, b); the cellular details have been faithfully preserved (Figs. 4a–b). Therefore any morphological and anatomical observation above cell level should be reliable. All these constitute a solid foundation for the following interpretation.

Apparently, *Xingxueanthus* belongs to a vascular plant, and it does not look like a vegetative part of any known plant. Among the reproductive organs, the possibility of fern’s sori and pollen organs of higher plants can be excluded easily since 1) no trace of spores or pollen (which are more liable to preservation) has been detected even after long-time intensive search in more than twenty female units of various maturity using the SEM (total seven times, 19 hours, 226 pictures), and 2) to the best of our knowledge, no pollen organ like *Xingxueanthus* has been documented in extant or fossil plants yet. Therefore the most plausible possibility left for *Xingxueanthus* is a female organ of a seed plant.

Among the known Mesozoic and extant seed plants, an ovulate part in the axil of a bract compares well with those in conifers (Chamberlain, 1957), but the ovules are situated on the adaxial surface of the scale in conifers (probably with exceptions of Taxaceae and Podocarpaceae, which are apparently out of the question here) (Chamberlain, 1957), while the ovules are spirally arranged around a column in *Xingxueanthus.* Some early conifers and cordaites may have megasporophylls spirally arranged, but they are short of an ovule-enclosing structure and a style-like projection (Taylor, 1981), as in *Xingxueanthus.* Bennettitales have ovules spirally arranged on a dome-shaped receptacle, but their numerous and unique interseminal scales (Taylor, 1981; Delevoryas, 1982, 1991; Crane, 1986) are totally absent in *Xingxueanthus* and their ovulate organs are in the center of
the "flower" (Taylor, 1981; Delevoryas, 1982, 1991; Crane, 1986), not in the axils of bracts as in *Xingxueanthus*. The bract and the arrangement of the ovules around a column in *Xingxueanthus* exclude the possibility for Ginkgoales (Taylor, 1981; Zhou, 2003; Zhou and Zheng, 2003). Similarly, the spiral arrangement of ovules around a column in an ovule-container excludes the possibility of Cycadales, Caytoniales, Glossopteridales, Czekanowskiales, Pentaxycales and Gnetales (Berridge, 1911; Thoday and Berridge, 1912; Chamberlain, 1919, 1920, 1957; Thomas, 1925; Harris, 1940, 1941, 1961, 1964, 1969; Harris and Miller, 1974; Harris and Millington, 1974; Retallack and Dilcher, 1981; Taylor, 1981; Delevoryas, 1982, 1991, 1993; Yang, 2001, 2004; Yang et al., 2005). Furthermore, the ovule-container wall and the style-like projection at the top together distinguish *Xingxueanthus* from all above taxa. Therefore the only possibility in seed plants remaining for *Xingxueanthus* is either an angiosperm or a new class of gymnosperms.

When compared with angiosperms, the fossil demonstrates certain surprisingly similar features. The general morphology of this "inflorescence" compares well with catkins (Heywood, 1979). Ovules attached to a column in their container compare with those of a free central placentaion in an ovary (Heywood, 1979), the latter is only found in angiosperms to date. A style-like projection at the top of the ovule-container is a character seen only in angiosperms, Gnetales, Bennettitales and Erdmanthecales. The latter three groups are distinct from *Xingxueanthus* in general organization (Friis et al., 2009; Crane and Herendeen, 2009; Rothwell et al., 2009).

Gynoeicum alone in the axil of a bract appears strange in angiosperms, but the pistillate inflorescences of *Cercidiphyllum* do display such an arrangement (Eames, 1961). Angio-ovuly is the only consistent difference that separates angiosperms from gymnosperms, and ovule enclosure before fertilization is a character sufficient to identify an angiosperm (Tomlinson and Takaso, 2002). Apparently, ovule enclosed in the container in *Xingxueanthus* satisfying this criterion for angiosperms. If accepted as a Jurassic angiosperm, *Xingxueanthus*, together with *Schmeissneria* (from the same locality), would lend a strong support to the hypotheses on pre-Cretaceous origin of angiosperms, enrich the diversity of angiosperms in the Jurassic, suggest the existence of several Jurassic lines of angiosperm evolution, and help to reconcile the discrepancy between molecular clock (Chase, 2004; Sanderson et al., 2004; De Bodt et al., 2005) and the fossil record (Friis et al., 1987, 2005, 2006; Cronquist, 1988; Hughes, 1994). This is in agreement with the hard-to-explain high diversity of angiosperms in the Early Cretaceous, including *Chaoyangia*, *Archaeoarcturus* and *Sinocarpus* and *Callianthus* from the Yixian Formation in western Liaoning (Duan, 1998; Sun et al., 1998, 2002; Leng and Friis, 2003, 2006; Dilcher et al., 2007; Wang, 2009; Wang and Zheng, 2009). Characters such as free central placentaion and evident style were thought to be derived based on data of extant plants (Puri, 1952; Eames, 1961; Cronquist, 1988; Doyle and Endress, 2000), but their presences in this Jurassic angiosperm would require a reconciling with existing theories on angiosperm evolution including evolutionary trends and polyphyley or monophyly of angiosperms (Fig. 6). These conflicts imply either that the existing theories on angiosperm origin are flawed, or that angiosperms have a much longer history than currently recognized, or both.

Alternatively, if *Xingxueanthus* were recognized as a new class in seed plants, it would suggest that angiospermy is not unique for angiosperms. Some other seed plants may have achieved such an advanced protection for their ovules far before the well-accepted angiosperms did. If this were the case, then much effort would be needed to draw a line between angiosperms and gymnosperms. The greatest challenge among all is making this line acceptable, at least for most botanists.

Being angiosperms or gymnosperms, *Xingxueanthus* and *Schmeissneria* demonstrate certain resemblance to the angiosperms in a key aspect. Their angiospermy suggest that this feature may well be a common convergence for many seed plants during the Jurassic, therefore the occurrence and success of later full-fledged angiosperms is something within expectation. If they are accepted as

![Fig. 6. Possible relationship among Xingxueanthus and other early angiosperms.](image-url)
angiosperms, it implies either that angiospermy may have been achieved independently in several groups of seed plants, or that their angiospermy is derived from a common ancestor, which is much older than the Cretaceous, probably in the Triassic or older period (Fig. 6).

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