Agora Paleobotanica

Zhangwuia: an enigmatic organ with a bennettitalean appearance and enclosed ovules

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ABSTRACT: The feature distinguishing typical angiosperms from gymnosperms is that their ovules are enclosed before pollination. Bennettitales were formerly related to angiosperms because of the flower-like organisation of the former’s reproductive organs. There is little information on how the naked ovules of Bennettitales became enclosed in angiosperms because fossil evidence for such a transition, if it exists, has not been described. Here, we report a reproductive organ, Zhangwuia gen. nov., from the Middle Jurassic of Inner Mongolia, China. Like many Bennettitales, the arrangement of the foliar parts around the female part in Zhangwuia demonstrates a resemblance to typical angiosperm flowers. It is noteworthy that the ovule is secluded from the exterior space in Zhangwuia, therefore implying the existence of angio-ovuly. Although Bennettitales have been related to angiosperms for more than a hundred years, their way of ovule-enclosing was not previously revealed. The discovery of Zhangwuia prompts a rethinking of the relationship between Bennettitales and angiosperms, as well as of the origin of angiosperms.

KEY WORDS: angiosperms, Bennettitales, China, Inner Mongolia, Middle Jurassic.

Angiosperms are unequivocally the most important plant group for human beings and current ecosystems. They are commonly characterised by their unique reproductive organs; i.e., flowers. In spite of all the effort invested in flowers, where they came from has long been a puzzle for botanists. Arber i.e., flowers. In spite of all the effort invested in flowers, where they came from has long been a puzzle for botanists. Arber & Parkin related the female part of Bennettitales with the gynoecium of Magnolia and declared the latter as the most primitive angiosperm (Arber & Parkin 1907). Almost all plant systematicists have been heavily influenced by this hypothesis. The morphology and anatomy of the female parts of Bennettitales, in which the ovules, with exerted micropylar tubes, are surrounded by interseminal scales, were well-documented in the last century (Wieland 1906; Seward 1919; Rothwell & Stockey 2002, 2010; Stockey & Rothwell 2003; Crane & Herendeen 2009). Ironically, the more that is learned of Bennettitales, the greater the gap between Bennettitales and angiosperms appears to be. A magnoliaceous carpel was thought to be derived from a foliar part bearing ovules along its margins (Eames 1961; Cronquist 1988; Dilcher 2010). However, relating the female part of Bennettitales to a duplicate magnoliaceous carpel is now problematic because evidence favouring this hypothesis has been lacking. Conversely, evidence negating this hypothesis is continuously emerging (Liu et al. 2014; Miao et al. 2017; Zhang et al. 2017).

Numerous plants and insects have been found in the Daohugou region (Zheng et al. 2003; Ji et al. 2004; Huang et al. 2006; Zhou et al. 2007; Ren et al. 2009, 2010; Wang et al. 2010b; Zheng & Wang 2010; Wang & Zhang 2011; Peng et al. 2012), and there is general consensus on the Middle Jurassic age of the Jiulongshan Formation (formerly Daohugou Formation) (Ren et al. 2002; Zhang 2002, 2006; Shen et al. 2003; Li et al. 2004; Liu et al. 2004; Ji et al. 2005; Huang et al. 2006, 2008a, b, 2009; 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, 2014; Liang et al. 2009; Shih et al. 2009; Wang et al. 2009a, b, c, 2010a; Wang & Ren 2009; Wang & Zhang 2009a, b). Ar40/Ar39 and SHRIMP U/Pb datings have been performed on the volcanic rocks in the overlying Tiaoshan Formation (Chen et al. 2004; Ji et al. 2004), suggesting an age of at least 164 Ma for the fossiliferous Jiulongshan Formation. In addition to various animal fossils (especially insects), abundant fossil plants have been reported from this region. According to current literature, the Daohugou flora includes algae of one species (within the Chlorophyceae), four genera and six species of bryophytes (Daohugoothallus, Metzgerites, Muscites, Ningchengia), two genera and two species of Lycopodaceae (Lycopodites, Selaginellites), two genera and two species of sphenophytes (Annularia, Equisetites), four genera and six species of Filicales (Coniopteris, Osmanda, Eboracia, Sphenopteris), seven genera and 12 species of cycads (Pierophyllum, Anomozamites, Nissoniaiopsis, Williamsonia, Welrichia, Cycadolepis, Tyrnia), four genera and four species of Czekanow skiales (Czekanowska, Solenites, Leptostrobus, Ixostrobus),
Figure 1 Geological information for the Jiulongshan Formation at Daohugou Village. Modified from Tan & Ren (2009): (a) geographical position of the fossil locality, Daohugou Village, Ningcheng, Inner Mongolia, China. The rectangular region is shown in detail in the inset, in which the black triangle represents Daohugou Village and the black dots represent cities in the region. (b) Geological section of the Jiulongshan Formation near Daohugou Village. Layer 3 is the major fossil-yielding layer: 1 = gneiss; 2 = tuffaceous conglomerate; 3 = tuffaceous conglomerate; 4 = tuffaceous siltstone; 5 = tuffaceous mudstone; 6 = tuffaceous shale; 7 = volcanic breccia; 8 = fossil locality. (c) Stratigraphic column of the Jiulongshan Formation near Daohugou Village. Layer 3 is the major fossil-yielding layer. (d) Geological map of Daohugou Village and adjacent region. Rectangle represents the fossil locality.
four genera and six species of Ginkgoales (Yimaia, Ginkgoites, Baiera, Sphenobaiera), 13 genera and 20 species of Coniferales (Pityocladus, Pityospermum, Schizolepis, Austrohamia (Yamiaoa), Brachyphyllum, Elatocladus, Amentotaxus, Taxus, Nageiopsis, Podocarpites, Cephalotaxopsis, ?Pseudofrenelopsis, Podozamites), two genera and two species of Caytoniales (Caytonia, Sagenopteris), three genera and three species of seeds/fruits with unknown affinities (Conites, Problematospermum, Carpolithus), and three genera and three species of angiosperms (Solaranthus, Juraherba, Yuhania) (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; Heinrichs et al. 2014; Dong et al. 2016; Han et al. 2016; Liu & Wang 2016b). As reported here, these works converge on a Middle Jurassic age for Zhangwuia.

Recently, a bennettitalean plant, Foxeoidea, was reported with its ovules surrounded by interseminal scales, although its ovules were not fully enclosed as they are in angiosperms (Rothwell & Stockey 2010). To help bridge this gap between Foxeoidea and typical angiosperms, we here report a fossil reproductive organ, Zhangwuia gen. nov., from the Jiulongshan Formation of the Middle Jurassic (>164 Ma) of Daohugou Village, Inner Mongolia, China [119°15'E, 41°19'N]. Zhangwuia demonstrates a great resemblance to angiosperm flowers, including its flower-like organisation, surrounding foliar parts, and, most importantly, angio-ovuly in the female part. Interestingly, the general morphology of Zhangwuia demonstrates a resemblance to Bennetitales. Such a mosaic combination of characters implies that at least some Bennettitales have...
the potential to reach angio-ovuly. In this way, \textit{Zhangwuia} could narrow the evolutionary gap between angiosperms and gymnosperms.

1. Material and methods

The fossil material was collected by a local fossil collector, Mr Hongtao Cai, from the outcrop of the Jilulongshan Formation near Daohugou Village, Ningcheng, Liaoning, China (119.236727°E, 41.315756°N; Fig. 1), and it was donated to the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences (CAS).

The general morphology and details of \textit{Zhangwuia} were observed and photographed using a Nikon SMZ1500 stereo-microscope with a digital camera. More details were further observed and recorded using a Leo 1530 VP scanning electron microscope (SEM) at the Nanjing Institute of Geology and Palaeontology (NIGPAS), Nanjing, China. Micro-computed tomography (CT) observation was performed using 225kv micro-CT (developed by the Institute of High Energy Physics, CAS) at the Key Laboratory of Vertebrate Evolution and Human Origin of CAS in the Institute of Vertebrate Palaeontology and Palaeoanthropology, scanning under a cone-beam energy of 130kV and a flux of 100μA with an 8.8μm slice distance. The transmission images of 1536 slices were reconstructed with a 2048 × 2048 matrix and 8.8μm pixel size through a 3D image processing software developed by the Institute of High Energy Physics, CAS. The images were processed using VGStudio Max2.2. The final results were saved as images or videos. All photographs were organised together for publication using Photoshop 7.0.

To make our description more neutral, we use the terms ‘female part’ and ‘female unit’, instead of ‘gynoecium’ and ‘carpel’ (which are restricted to angiosperms) to describe the morphology of \textit{Zhangwuia}.

2. Results

Order \textit{Incertae sedis}
Family \textit{Incertae sedis}
Genus \textit{Zhangwuia} gen. nov.

Generic diagnosis. Reproductive organ of radial symmetry. Outer foliar parts inflated, more or less rounded, probably

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Figure 3 Detailed views of the inner foliar parts of \textit{Zhangwuia mira} gen. et sp. nov. SEM: (a) an inner foliar part with a midrib (arrow) and an obtuse tip, the no. 1 arrowed part in Fig. 2a; (b) an inner foliar part with a bent tip (top) and no midrib, the no. 4 arrowed part in Fig. 2a; (c) detailed view of a bent tip of an inner foliar part, showing cellular details, from the no. 3 arrowed part in Fig. 2a; (d) cellular details on the margin of an inner foliar part, enlarged from the black rectangle in Fig. 3a; (e) detailed view of the middle portion of the inner foliar part (arrow in Fig. 3a), showing the midrib (arrow); (f) cellular details of the distal portion of the inner foliar part, enlarged from the white rectangle in Fig. 3a. Scale bars = 1 mm (a); 0.2 mm (b, e); 0.1 mm (c, d); 20 μm (f).
seven in number, radially arranged. Inner foliar parts above the outer foliar parts, radially arranged, in three cycles, approximately seven per cycle, alternate, tongue-shaped, obtuse-tipped, some with a weak midrib. Female part includes numerous spirally arranged female units. Female unit with secluded space, a blunt tip, and an ovule/seed inside.

Type species. *Zhangwuia mira* gen. et sp. nov.


Horizon. The Jiulongshan Formation, Middle Jurassic.

Age. The Callovian, Middle Jurassic (>164 Ma).

Locality. Daohugou Village, Ningcheng, Inner Mongolia, China [119°15′E, 41°19′N].

*Zhangwuia mira* gen. et sp. nov. (Figs 2–5)

Specific diagnosis. (In addition to that of the genus) Organ at least 12 mm in diameter. Outer foliar parts 4.3 mm long and 3.4 mm wide. Inner foliar parts approximately 4 mm long and 1.8 mm wide. Female part approximately 6 mm in diameter, conically formed, tapering distally, and bearing spirally arranged female units (Figs 2a–c, 4a, d). Each inner foliar part is approximately 4 mm long and 1.8 mm wide, with straight parallel entire margins and an obtuse tip, attached to the receptacle with its whole base, with a longitudinally oriented epidermal texture (Figs 2a, d, 3a, b, d–f). Some of the inner foliar parts may have weak midribs (Figs 2d, 3a, e) or tips bent adaxially (Figs 2a, d, 3b, c). The cells are approximately 45–50 μm long and 7–13 μm wide in the lateral regions of the inner foliar parts, and approximately 30–80 μm long and 19–24 μm wide in the midrib region of the inner foliar parts (Fig. 3d–f). The female part is approximately 6 mm in diameter, conically formed, tapering distally, and bearing spirally arranged female units (Figs 2a–c, 4d, 5e; supplementary videos V1–V2). The centre of the female part was replaced with sediment during the fossilisation (Fig. 2a, b). The peripheral tissue of the female part is broken, exposing the details of the female units (Figs 2e, 5a–c). The female unit is up to 1.9 mm long and 1.7 mm wide, and fused with neighbouring units basally (Figs 2c, e, 5e). The surface of the female units is integral, with epidermal cells 50–80 × 20–50 μm (Figs 2c, 5d, e). There is a secluded locule, separated from the exterior space by a 0.2-mm-thick wall, inside each female unit (Fig. 5a, d). An ovule isolated from the locule wall is seen inside the female unit (Fig. 5d).

Specimen number. PB21675.

Etymology. *mira* for *mirus*, meaning ‘wonderful’ in Latin.

Depository. The Nanjing Institute of Geology and Paleontology, Nanjing, China.

3. Discussion

‘Carpel’ is a frequently used term in angiosperm morphology. There are at least two usages of this term. First, carpel *sensu lato* designates any structure that encloses the ovules; namely, the basic unit of angiosperm gynoecium. Second, a carpel *sensu stricto* designates a foliar part enclosing ovules/seeds.
The carpel *sensu stricto* is hinged with the assumption that a carpel is derived from a megasporophyll, bearing ovules along its margins (Arber & Parkin 1907). This assumption has constituted the foundation for angiosperm systematics for more than a hundred years. However, a ‘sporophyll’ is purely an imaginary part that has never been seen in any fossil or extant plant (Wilson 1937; Melville 1963; Miao et al. 2017) because all ovules are borne on branches rather than on leaves (Herr 1995) and the only leaf-like ‘megasporophyll’ seen in *Cycas* is a result of mechanical pressure from the adjacent ovulate parts during the development (Wang & Luo 2013). Deciphering how the angiospermous carpel can be derived from the bennettitalean female part has been difficult for botanists. Until this question is answered satisfactorily, it is impossible to securely establish any of the hypotheses concerning the relationship between angiosperms and Bennettitales, as well as the systematics of angiosperm. Therefore, bridging the gap between angiosperms and Bennettitales using fossil evidence is of crucial importance for plant systematics.

The resemblance between *Zhangwuia* and Bennettitales is conspicuous. Bennettitales are a fossil group that have been well-documented by various authors in the past century (Wieland 1906; Seward 1919; Rothwell & Stockey 2002; Stockey & Rothwell 2003; Crane & Herendeen 2009; Rothwell & Stockey 2010). The inner foliar parts surrounding the female part in *Zhangwuia* are comparable to the foliar parts surrounding the female part in Bennettitales (Watson & Sincock 1992). The arrangement of the female units around the receptacle in *Zhangwuia* appears like that of the seeds and interseminal scales arranged around a receptacle in Bennettitales (e.g., Cycadeoidea, Williamsoniella, Williamso尼亚, and Buttercarpus (Watson & Sincock 1992; Rothwell & Stockey 2002; Stockey & Rothwell 2003; Crane & Herendeen 2009; Rothwell et al. 2009)). If this comparison is valid, there seems to be some phylogenetic relationship between *Zhangwuia* and Bennettitales. The bennettitalean female part would be identical to *Zhangwuia* if its ovules were completely covered by the adjacent interseminal scales (Fig. 6c, d). Such ovule-enclosure is almost achieved in another fossil taxon, *Foxeoidea* (Rothwell & Stockey 2010). The Middle Jurassic age and the morphology of *Zhangwuia* favour placing *Zhangwuia* in the Bennettitales.
It is worth emphasising that *Zhangwuia* demonstrates certain features unexpected for any Bennettitales; namely, the ovules in all Bennettitales (including the problematic Foxeoidea of Rothwell & Stockey 2010) are consistently, more or less, exposed to the exterior, while the ovules of *Zhangwuia* are inside the female units. An angiosperm flower is typically characterised by a perianth around a gynoecium and/or an androecium (Eames 1961). Similar organisation has been seen in both angiosperms and Bennettitales (Martens 1971; Watson & Sincock 1992; Biswas & Johri 1997). A female cone in Bennettitales has a heterogeneous surface comprising micropyle apices and polygonal interseminal scale heads (Watson & Sincock 1992; Crane & Herendeen 2009; Rothwell et al. 2009), while the surface of the female part of *Zhangwuia* is inside the female units. An angiosperm flower is typically characterised by a perianth around a gynoecium and/or an androecium (Eames 1961). Similar organisation has been seen in both angiosperms and Bennettitales (Martens 1971; Watson & Sincock 1992; Biswas & Johri 1997). A female cone in Bennettitales has a heterogeneous surface comprising micropyle apices and polygonal interseminal scale heads (Watson & Sincock 1992; Crane & Herendeen 2009; Rothwell et al. 2009), while the surface of the female part of *Zhangwuia* is inside the female units. An angiosperm flower is typically characterised by a perianth around a gynoecium and/or an androecium (Eames 1961). Similar organisation has been seen in both angiosperms and Bennettitales (Martens 1971; Watson & Sincock 1992; Biswas & Johri 1997). A female cone in Bennettitales has a heterogeneous surface comprising micropyle apices and polygonal interseminal scale heads (Watson & Sincock 1992; Crane & Herendeen 2009; Rothwell et al. 2009), while the surface of the female part of *Zhangwuia* is inside the female units. An angiosperm flower is typically characterised by a perianth around a gynoecium and/or an androecium (Eames 1961). Similar organisation has been seen in both angiosperms and Bennettitales (Martens 1971; Watson & Sincock 1992; Biswas & Johri 1997). A female cone in Bennettitales has a heterogeneous surface comprising micropyle apices and polygonal interseminal scale heads (Watson & Sincock 1992; Crane & Herendeen 2009; Rothwell et al. 2009), while the surface of the female part of *Zhangwuia* is inside the female units. 

**Figure 6** Diagrams showing the structure of *Zhangwuia mira* gen. et sp. nov. and its comparison with Bennettitales. (a) Vertical profile of the fossil organ, showing outer foliar parts (of), inner foliar parts (if), female units (fu) with internal space, and the receptacle. Note that the female units are missing in the distal portion. (b) Top view of the reconstructed organ, showing outer foliar parts (of), inner foliar parts (if) in three cycles, and female units around the receptacle. Note the presences of midribs and bent tips in some inner foliar parts. (c) Idealised longitudinal section of the female part in Bennettitales. The ovules (grey) have exerted micropylar tubes and are bracketed by interseminal scales (black). Both ovules and interseminal scales are attached to the receptacle. (d) Idealised longitudinal section of the female part in *Zhangwuia*. The ovules (grey) are separated from the exterior space by the surrounding tissues (black).

It is noteworthy that *Zhangwuia* bears a resemblance to angiosperm flowers. The arrangement of the female units in *Zhangwuia* may be compared to female flowers in the inflorescence of Araceae because they both have female units that are crowded on the surface of an axis (Barabé et al. 2003, 2004). Because of the breakage, the internal details of the female units of *Zhangwuia* are observable. As seen in Figs 2e, 5a–d, there are several locules exposed on the broken surface in the female part. These locules are isolated from the exterior space by a wall (Fig. 5a–e), suggesting that a female unit of *Zhangwuia* has a secluded internal space characteristic of angiosperms. The structure inside the female unit appears to be an ovule (Fig. 5d) as its large size is beyond the scope of microspores, implying the occurrence of angio-ovuly in *Zhangwuia*. Ovules enclosed before pollination are a feature guaranteeing an angiospermous affinity for the plant in question (Tomlinson & Takaso 2002; Wang 2010). Therefore, *Zhangwuia* may have a feature that was formerly only restricted to angiosperms. Such a mosaic combination of characters spanning angiosperms and Bennettitales makes *Zhangwuia* especially interesting in plant evolution. The enclosure of the ovule as seen in *Zhangwuia* is not a singular case. For example, Foxeoidea, an unusual element of Bennettitales, has been anatomically documented in the Cretaceous (Rothwell & Stockey 2010). According to Rothwell & Stockey (2010), ovules with micropylar tubes in Foxeoidea are almost completely enclosed by the adjacent interseminal scales that are histologically fused to...
Table 1  Comparison among Zhangwuia, some problematic Bennettitales and Gnetales, as well as angiosperms.

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<th>Cycadoideae</th>
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<th>Pseudoephedra</th>
<th>Zhangwuia</th>
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<td>Interseminal scales</td>
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each other and form a continuous layer around the ovules. The ovule-enclosing in Foxeidea is quite different from the imagined longitudinal folding of a ‘megasporophyll’ bearing ovules along its margins, as suggested by Arber & Parkin (1907) and their proponents (Crane 1985; Dilcher 2010). It should be noted that 1) the ovules in Foxeidea are not completely enclosed, so Foxeidea falls well within the scope of Bennettitales; and 2) it is still unclear which parts enclose the ovules in Foxeidea. According to Rothwell & Stockey (2010), the ovules with micropylar tubes in Foxeidea are surrounded by the adjacent interseminal scales. However, as the researchers admitted, histologically the ‘micropylar tube’ is indistinguishable from those of the adjacent interseminal scales because the outer surface of the ‘micropylar tube’ is never seen, despite its good anatomical preservation (Rothwell & Stockey 2010, fig. 4.3b, c). This observation makes an alternative interpretation more likely: namely, that their ‘micropylar tube’ is non-existent, and that the ovule-enclosure is completed by the adjacent interseminal scales. If this is the case, then the ovule-enclosing parts of Foxeidea will be very similar to Zhangwuia in nature. The near-complete enclosure in Foxeidea can be taken as a precursor to the complete ovule-enclosure of Zhangwuia. In both cases, the ovule-enclosure is completed by the same structure – the former interseminal scales. The anachronism created by Jurassic Zhangwuia and Cretaceous Foxeidea does not constitute a serious problem for this interpretation, as Zhangwuia and Foxeidea may belong to two different parallel lineages.

Parallel to Zhangwuia and Foxeidea, a possible Gnetales-related taxon with typical ephedroid morphology, Pseudoephedra (Liu & Wang 2016a), bears a solid style (a feature of angiosperms) instead of a micropylar tube as expected in Ephedra. According to molecular studies (Skinner et al. 2004), the placenta and ovarian wall correspond to an axillary branch and a leaf in gymnosperms, respectively. Foxeidea, Zhangwuia, and Pseudoephedra seem to suggest that there may be a novel evolutionary path for angio-ovuly (Wang et al. 2015): angio-ovuly may be reached by different plant groups in their own ways independently, as suggested by others previously (Krasilov 1977; Wu et al. 2002). The possibility of deriving conduplicate carpels from the assumed ‘megasporophylls’ which bear ovules along their margins, as assumed by Arber & Parkin (1907) and their proponents, is reduced to nil since the superficially leaf-like morphology of megasporophyll in Cycas has been experimentally proven to be an artefact due to mechanical pressure (Wang & Luo 2013). Given all the evidence, angio-ovuly seems to have been reached independently.

4. Conclusion

Zhangwuia is a reproductive organ showing a mosaic combination of bennettitalean and angiospermous features. While its lack of exserted micropylar tube makes it atypical in Bennettitales, its ovule enclosed inside the female unit makes Zhangwuia closer to angiosperms. Despite its enigmatic phylogenetic position, Zhangwuia appears to narrow the gap between Bennettitales and angiosperms in an unexpected way.

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6. Supplementary material

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7. References


