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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 and 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 exserted 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 conduplicate magnoliaceous carpels 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). Ar^{40}/Ar^{39} and SHRIMP U/Pb datings have been performed on the volcanic rocks in the overlying Tiaojishan 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 (*Daohugouthallus*, *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*, *Osmunda*, *Eboracia*, *Sphenopteris*), seven genera and 12 species of cycads (*Pterophyllum*, *Anomozamites*, *Nissoniopteris*, *Williamsonia*, *Weltrichia*, *Cycadolepis, Tyrmia*), four genera and four species of Czekanowskiales (*Czekanowskia*, *Solenites*, *Leptostrobus*, *Ixostrobus*),

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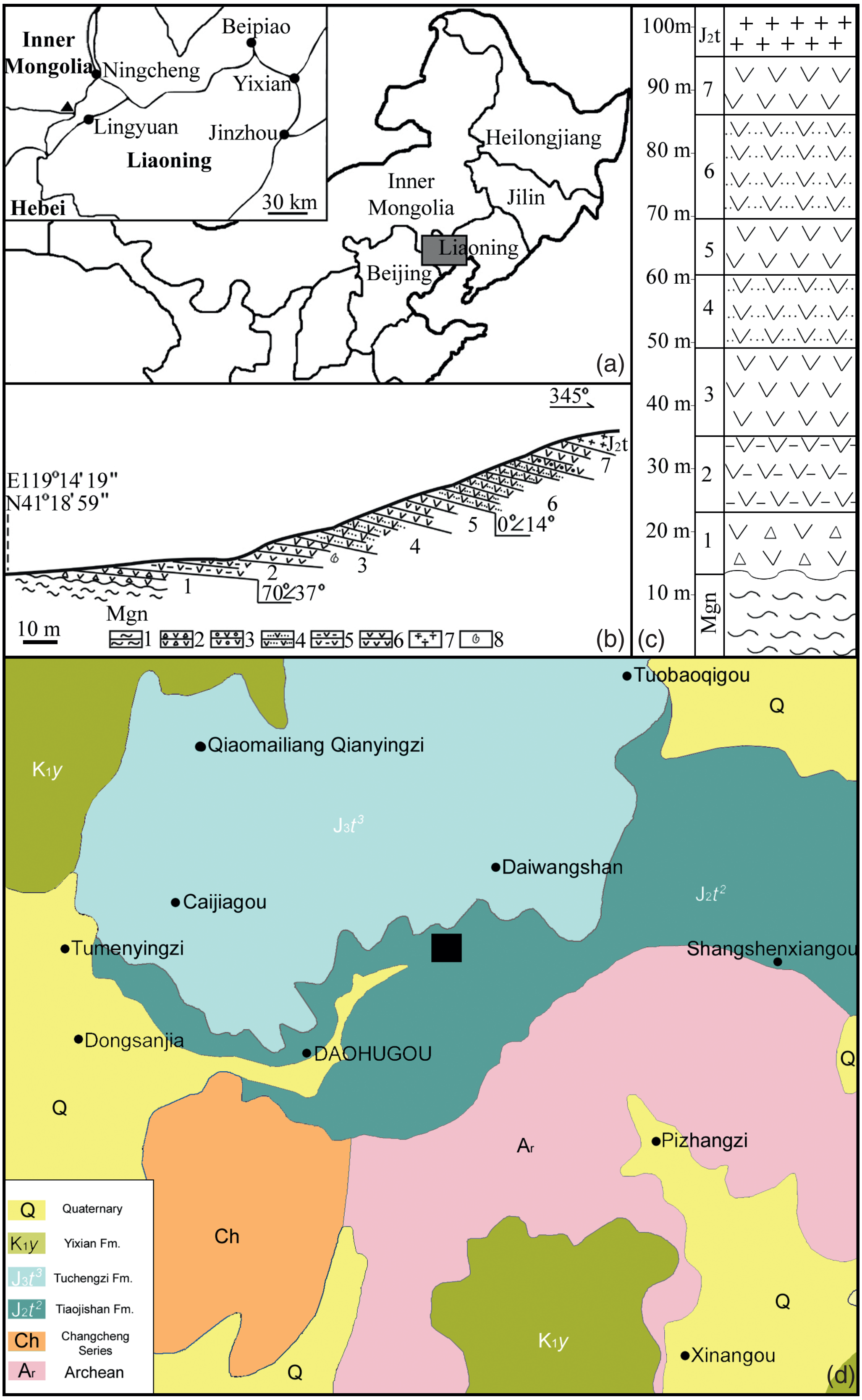

Figure 1 Geological information for the Jiulongshan Formation at Daohugou Village. Modified from Tan & Ren (2009): (a) geographical position of the fossil locality, Daohugou Village, Ningcheng, Inner Mongolia, China. The rectangular region is shown in detail in the inset, in which the black triangle 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 grand 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.

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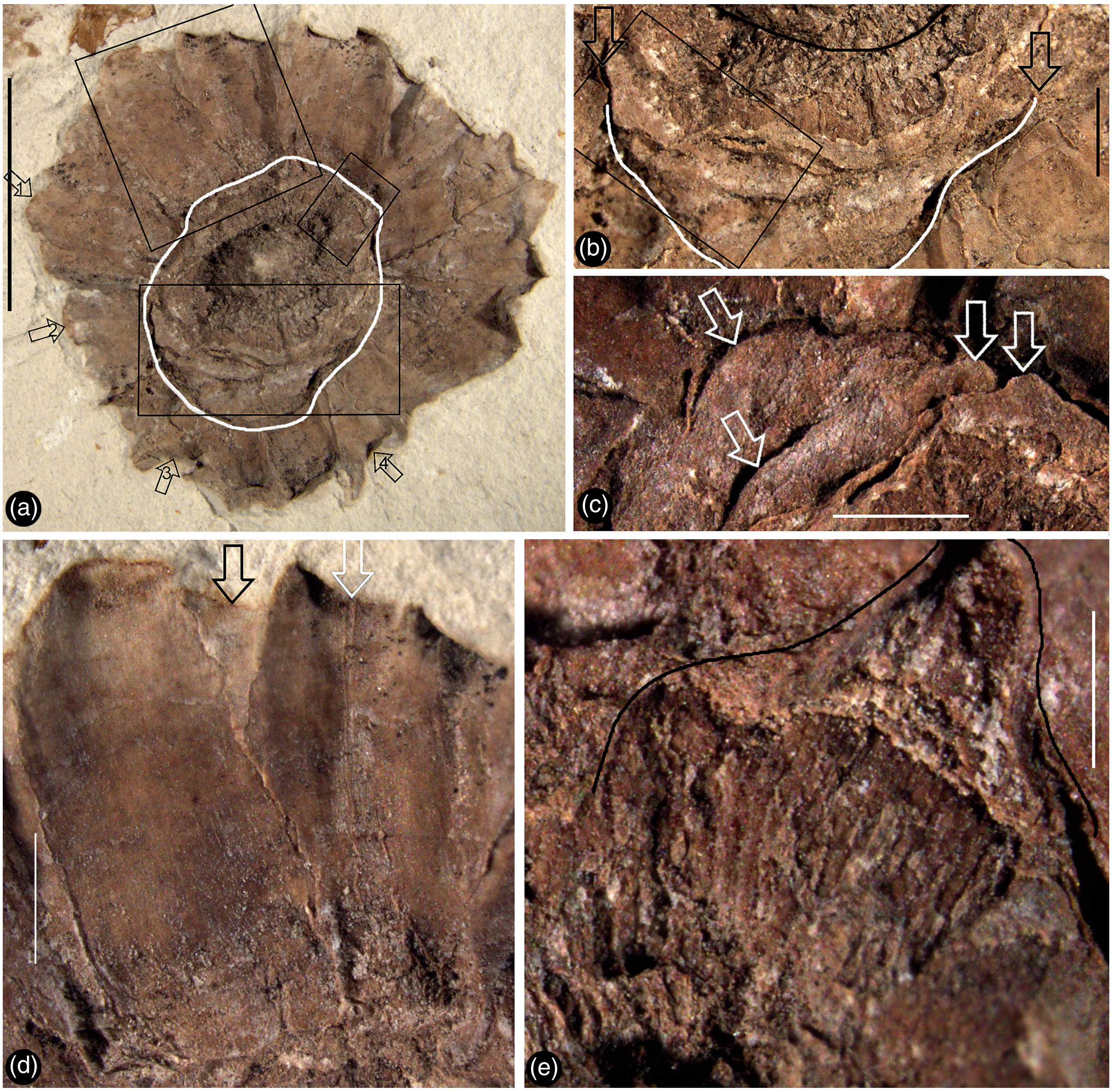

Figure 2 *Zhangwuia mira* gen. et sp. nov. and its details. Stereomicroscopy. Holotype, PB21675: (a) the organ with radially arranged inner foliar parts surrounding the central female part (white outline). Rectangles show position of enlargements (b–e); (b) partial view of the organ, enlarged from the lower rectangle in (a), showing the border (white line and arrows) between the inner foliar parts and female part, as well as the border (black line) between receptacle and the female units; (c) detailed view of the female part, enlarged from the rectangle in (b), showing several tips (arrows) of spirally arranged female units; (d) three partially overlapping inner foliar parts, enlarged from the upper rectangle in (a) – the left one has an obtuse tip and no midrib, while the right one has a bent tip and a midrib (white arrow), and note a third inner foliar part (black arrow) in the background; (e) a broken female unit (outline) exposing its internal details, enlarged from the small rectangle (a) (see Fig. 5b, c). Scale bars = 5 mm (a); 1 mm (b–c); 0.5 mm (e).

four genera and six species of Ginkgoales (*Yimaia*, *Ginkgoites*, *Baiera, Sphenobaiera*), 13 genera and 20 species of Coniferales (*Pityocladus*, *Pityospermum*, *Schizolepis*, *Austrohamia* (*Yanliaoa*), *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 Bennettitales. Such a mosaic combination of characters implies that at least some Bennettitales have

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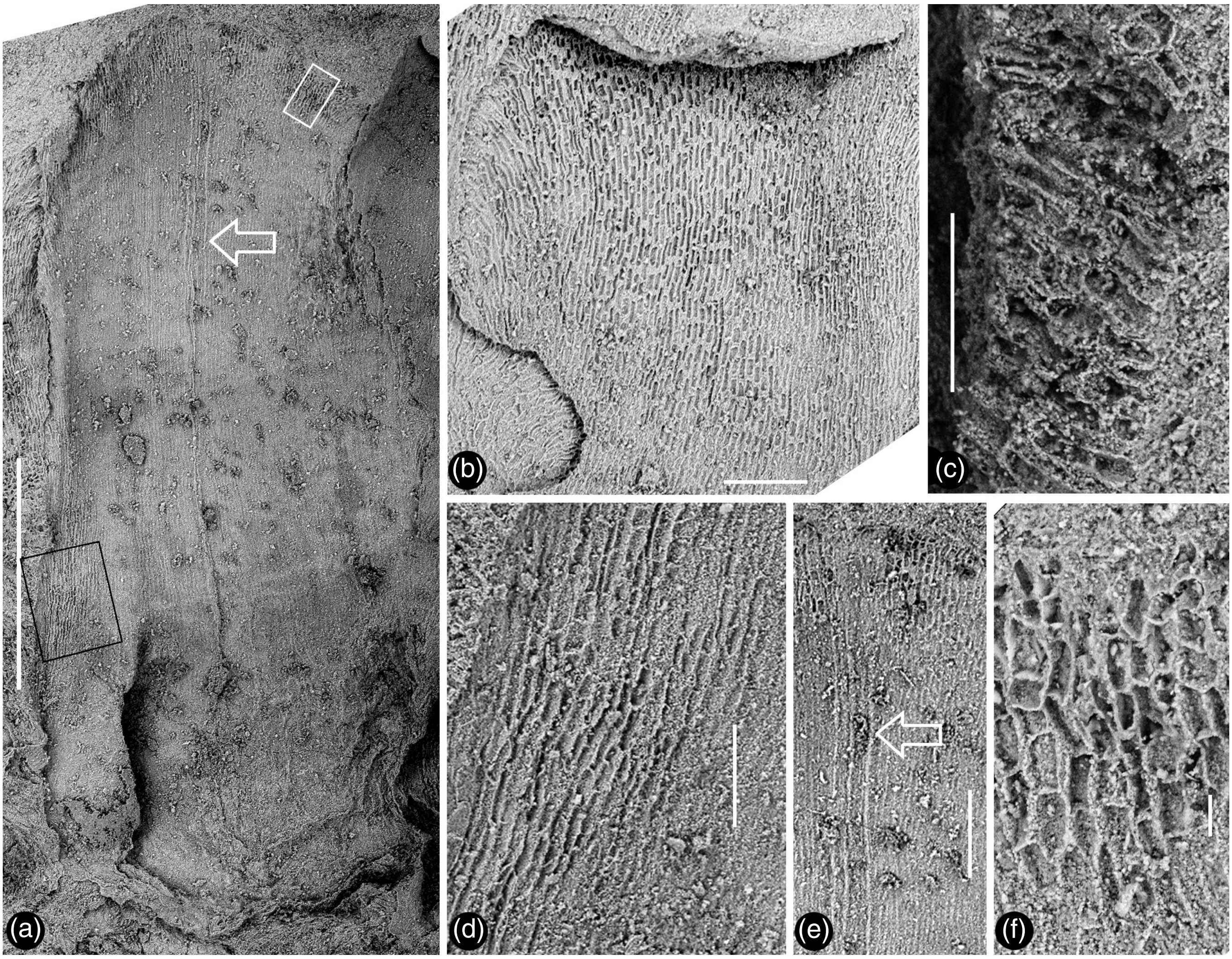

Figure 3 Detailed views of the inner foliar parts of *Zhangwuia mira* gen. et sp. nov. SEM: (a) an inner foliar part with a midrib (arrow) and an obtuse tip, the no. 1 arrowed part in Fig. 2a; (b) an inner foliar part with a bent tip (top) and no midrib, the no. 4 arrowed part in Fig. 2a; (c) detailed 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).

the potential to reach angio-ovuly. In this way, *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 Jiulongshan 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 *Zhangwuia* were observed and photographed using a Nikon SMZ1500 stereomicroscope 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 225 kv 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 130 kV and a flux of 100 μA with an 8.8 μm slice distance. The transmission images of 1536 slices were reconstructed with a 2048 × 2048 matrix and 8.8 μm 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 *Zhangwuia*.

2. Results

Order *Incertae sedis*
Family *Incertae sedis*
Genus *Zhangwuia* gen. nov.

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

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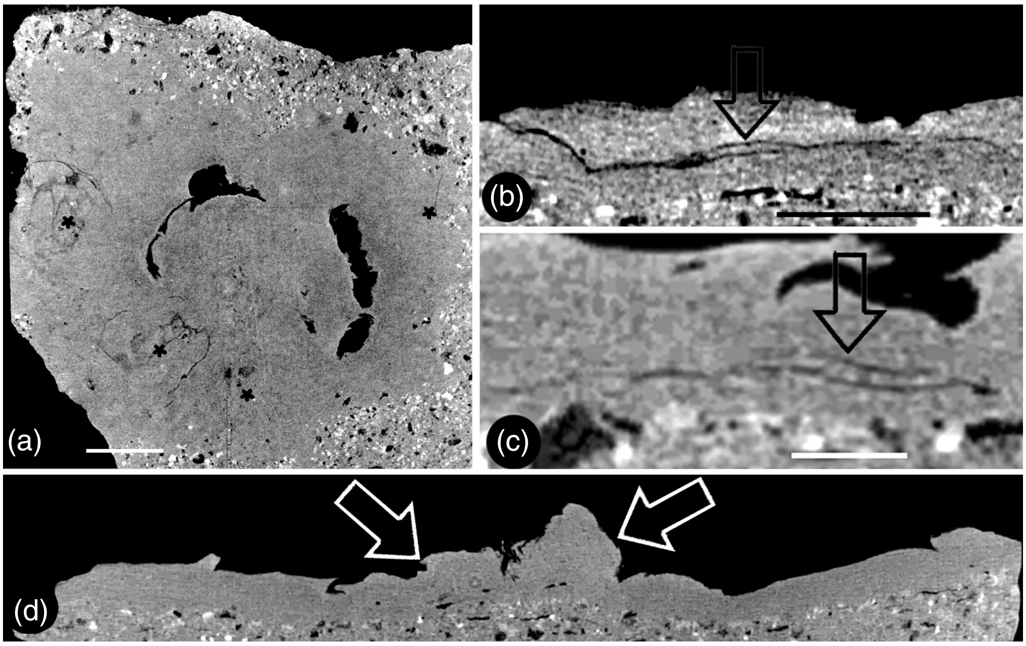

Figure 4 Micro CT virtual sections of *Zhangwuia mira* gen. et sp. nov.: (a) snapshot of the video showing the organ in cross section. Two of the outer foliar parts are visible in this view. The positions of the outer foliar parts are marked with asterisks. For more information, see supplementary materials, available at https://doi.org/10.1017/S1755691018000257. (b) Tangential section of the organ showing the cross view of an outer foliar part with an inflated portion (arrow) in the middle bottom. (c) Radial section of the organ showing a longitudinal view of the outer foliar part shown in Fig. 4b, with an inflated portion (arrow) near its base. The organ centre is to the right. (d) Longitudinal central section of the organ showing the female unit (left arrow) and the central protruding receptacle (right arrow). Scale bars = 2 mm (a); 1 mm (b, c).

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.

Etymology. *Zhangwu* – for the senior Chinese palaeobotanist, Professor Wu Zhang (8 August 1937–27 June 2016).

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 at the base. Female unit approximately 1.2 mm long, fused basally with adjacent units.

Description. The fossil is brown in colour, embedded in yellowish tuff, preserved in three dimensions, and the exposed part is approximately 12 mm in diameter (Figs 2a, 4a, d; supplementary video V1). The organ includes outer and inner foliar parts and female part (Fig. 2a, b). The outer foliar parts are not visible to the naked eye but can be visualised through the application of micro-CT (Fig. 4a; supplementary video V1). The positions of the individual outer foliar parts imply that there may be seven outer foliar parts (Fig. 4a; supplementary video V1). Each outer foliar part is approximately 4.3 mm long and 3.4 mm wide, more or less rounded, with an inflated portion in the middle base (Figs 4a–c; supplementary videos V1–V3). The inner foliar parts include approximately 23 members preserved alternately in three cycles (Fig. 2a, 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 Palaeontology, 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.

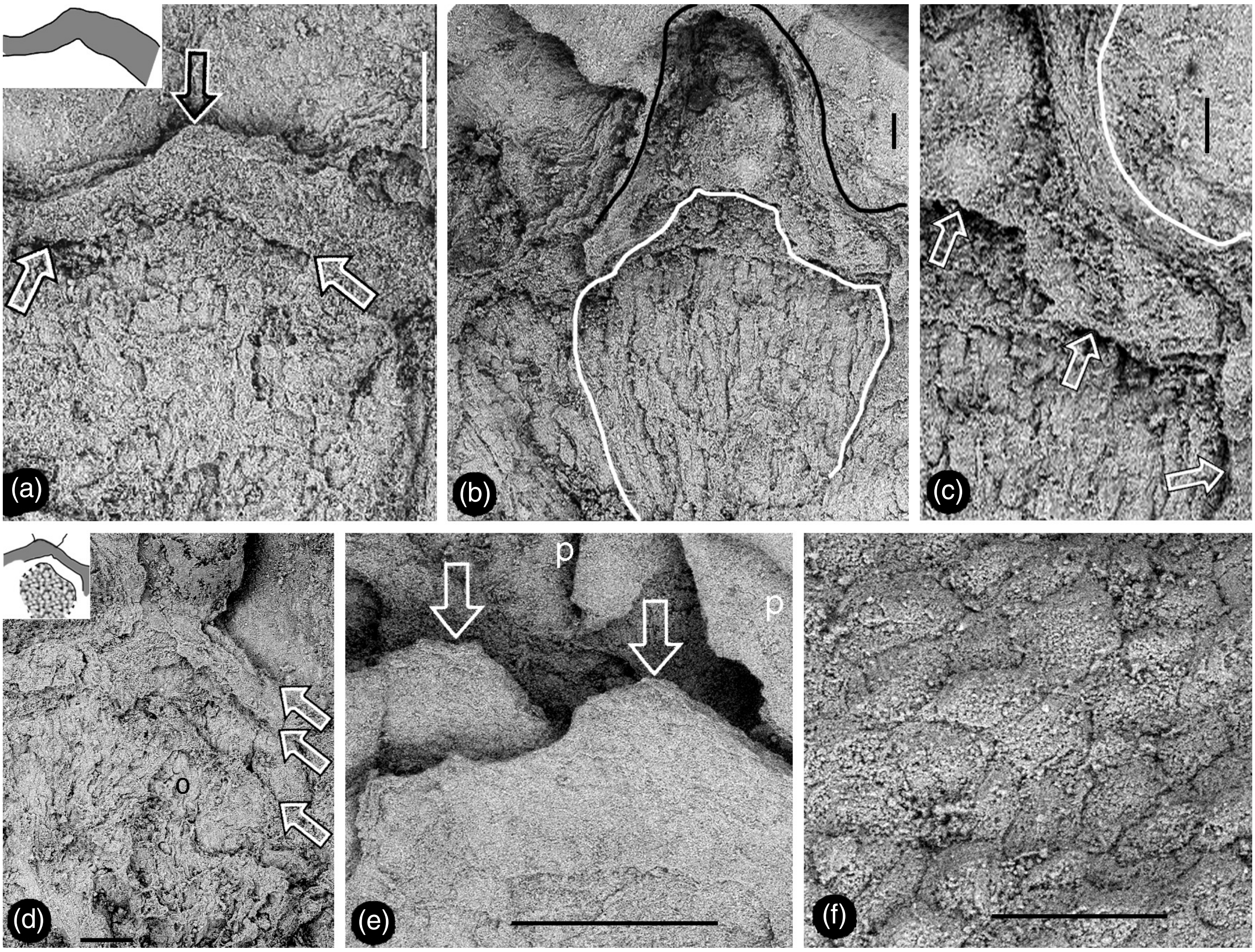

Figure 5 Details of female part of *Zhangwuia mira* gen. et sp. nov. SEM. (a) Tip (top arrow) of female unit and the margin (lower arrows) of its locule. Inset shows the outline of the locule wall. (b) Details of the female unit shown in Fig. 2e. Note the outline of the female unit (black line) and margin (white line) of the locule. (c) Surface (white line) of the female unit and margin (arrows) of the locule, enlarged from Fig. 5b. (d) An ovule (o) partially covered by other tissue, and a locule wall (between two upper arrows). Note the gap between the ovule and locule wall (between two lower arrows). Refer to the inset. (e) Tips (arrows) of two spirally arranged female units with integral surface. Refer to Fig. 2c. (f) Epidermal cellular details on the tip of a female unit. Scale bars = 0.2 mm (a, d); 0.1 mm (b, c, f); 0.5 mm (e).

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 ovulates 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 receptacle of some Bennettitales is also conical in form and may become filled with sediment (Watson & Sincock 1992), which is very similar to *Zhangwuia*. 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*, *Williamsonia*, 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.

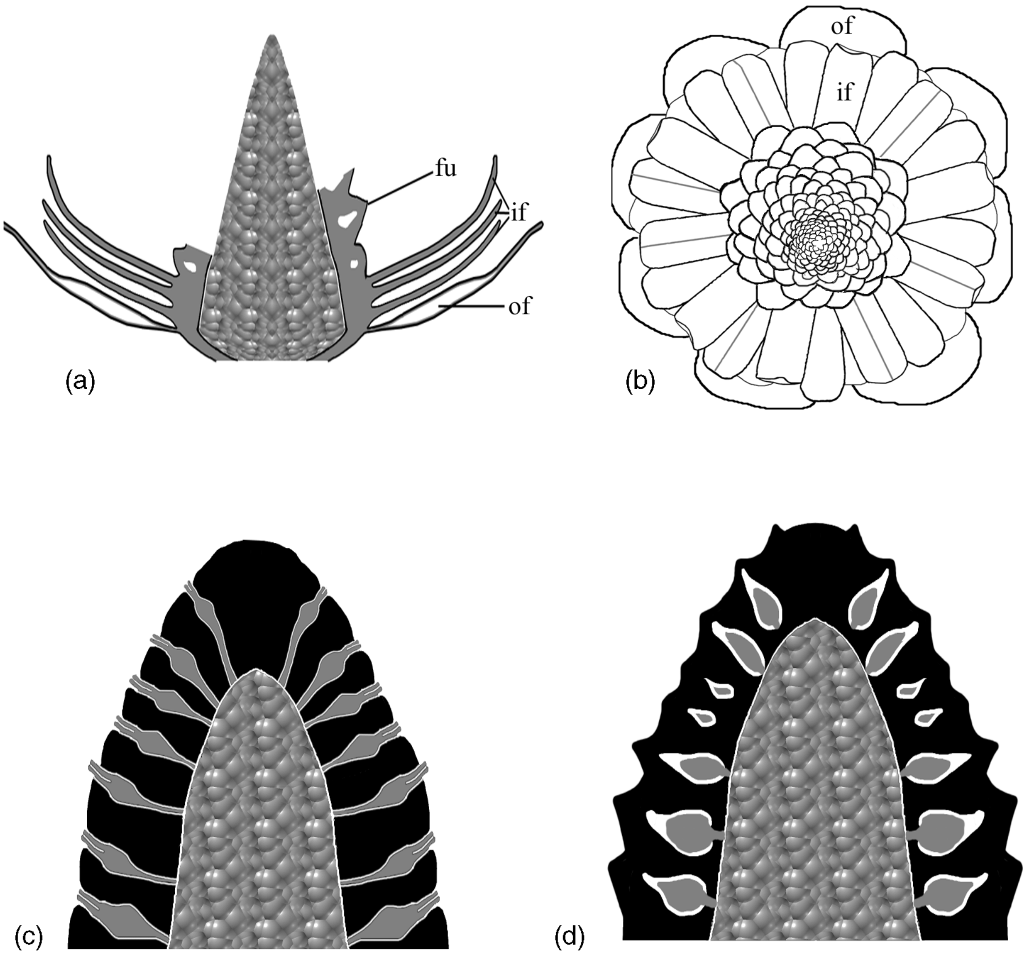

Figure 6 Diagrams showing the structure of *Zhangwuia mira* gen. et sp. nov. and its comparison with Bennettitales. (a) Vertical profile of the fossil organ, showing outer foliar parts (of), inner foliar parts (if), female units (fu) with internal space, and the receptacle. Note that the female units 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 exserted 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 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 homogeneous, smooth, and integral (Figs 2c, 5e, f) with no trace of a micropylar tube. Furthermore, the locule within the female unit and the ovules inside the locule of *Zhangwuia* (Fig. 5d) are never seen in other Bennettitales (Rothwell *et al*. 2009; Table 1), in which the ovules have exserted micropyles and are tightly surrounded by the interseminal scales. Therefore, if *Zhangwuia* were put into Bennettitales, it would appear that at least some Bennettitales have achieved angio-ovuly through the connation of interseminal scales.

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

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Table 1 Comparison among *Zhangwuia*, some problematic Bennettitales and Gnetales, as well as angiosperms.

	Cycadeoidea	*Foxeoidea*	*Pseudoephedra*	*Zhangwuia*	Typical angiosperms
Ovule	Exposed	Almost enclosed	Nucellus enclosed	Enclosed	Enclosed
Ovule surrounded by	Interseminal scales	'Interseminal scales'	Integument	'Interseminal scales'	Ovarian wall
Interseminal scale tip	Peltate	Peltate?	Not applicable	Not applicable	Not applicable
Interseminal scales	Isolated	Connate	Not applicable	Not applicable	Not applicable
Micropyle	Exserted	Not exserted	Exserted	Not exserted	Not exserted
Internal space	None	None?	?	Ovarian locule?	Ovarian locule
Peripheral foliar parts	Not differentiated	None	Not differentiated	Differentiated	Differentiated or not
Female part position	Central	?	Central	Central	Central

each other and form a continuous layer around the ovules. The ovule-enclosing in *Foxeoidea* 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 *Foxeoidea* are not completely enclosed, so *Foxeoidea* falls well within the scope of Bennettitales; and 2) it is still unclear which parts enclose the ovules in *Foxeoidea*. According to Rothwell & Stockey (2010), the ovules with micropylar tubes in *Foxeoidea* 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 *Foxeoidea* will be very similar to *Zhangwuia* in nature. The near-complete enclosure in *Foxeoidea* 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 *Foxeoidea* does not constitute a serious problem for this interpretation, as *Zhangwuia* and *Foxeoidea* may belong to two different parallel lineages.

Parallel to *Zhangwuia* and *Foxeoidea*, 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. *Foxeoidea*, *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 (Krassilov 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.

5. Acknowledgements

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6. Supplementary material

Supplementary material is available online at https://doi.org/10.1017/S1755691018000257

7. References

Arber, E. A. N. & Parkin, J. 1907. On the origin of angiosperms. *Journal of the Linnean Society of London, Botany* **38**, 29–80.
Barabé, D., Lacroix, C. & Gibernau, M. 2003. Development of the flower and inflorescence of *Arum italicum* (Araceae). *Canadian Journal of Botany* **81**, 622–32.
Barabé, D., Lacroix, C., Bruneau, A., Archambault, A. & Gibernau, M. 2004. Floral development and phylogenetic position of *Schismatoglottis* (Araceae). *International Journal of Plant Sciences* **165**, 173–89.
Biswas, C. & Johri, B. M. 1997. *The Gymnosperms*, **494**. Berlin: Springer-Verlag.
Chang, S.-C., Zhang, H., Renne, P. R. & Fang, Y. 2009. High-precision $^{40}Ar/^{39}Ar$ age constraints on the basal Lanqi formation and its implications for the origin of angiosperm plants. *Earth and Planetary Science Letters* **279**, 212–21.
Chang, S.-C., Zhang, H., Hemming, S. R., Mesko, G. T. & Fang, Y. 2014. $^{40}Ar/^{39}Ar$ age constraints on the Haifanggou and Lanqi formations: when did the first flowers bloom? *Geological Society, London, Special Publications* **378**, 277–84.
Chen, W., Ji, Q., Liu, D. Y., Zhang, Y., Song, B. & Liu, X. Y. 2004. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* **23**, 1165–69.
Crane, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals Missouri Botanical Garden* **72**, 716–93.
Crane, P. R. & Herendeen, P. S. 2009. Bennettitales from the Grisethrope Bed (Middle Jurassic) at Cayton Bay, Yorkshire, UK. *American Journal of Botany* **96**, 284–95.
Cronquist, A. 1988. *The evolution and classification of flowering plants*, **555**. Bronx: New York Botanical Garden.

https://doi.org/10.1017/S1755691018000257 Published online by Cambridge University Press

Dilcher, D. L. 2010. Major innovations in angiosperm evolution. *In* Gee, C. T. (ed.). *Plants in the Mesozoic time: innovations, phylogeny, ecosystems*, 97–116. Bloomington and Indianapolis: Indiana University Press.

Dong, C., Yang, X. & Zhou, Z. 2016. Fossil plants. *In* Huang, D. (ed.). *Daohugou biota*, 252–302. Shanghai: Shanghai Science and Technology.

Eames, A. J. 1961. *Morphology of the angiosperms*, **518**. New York: McGraw-Hill Book Company, Inc.

Han, G., Liu, Z.-J., Liu, X., Mao, L., Jacques, F. M. B. & Wang, X. 2016. A whole plant herbaceous angiosperm from the Middle Jurassic of China. *Acta Geologica Sinica* **90**, 19–29.

Heinrichs, J., Wang, X., Ignatov, M. S. & Krings, M. 2014. A Jurassic moss from Northeast China with preserved sporophytes. *Review of Palaeobotany and Palynology* **204**, 50–55.

Herr, J. M. J. 1995. The origin of the ovule. *American Journal of Botany* **82**, 547–64.

Huang, D., Selden, P. S. & Dunlop, J. A. 2009. Harvestmen (Arachnida: Opiliones) from the Middle Jurassic of China. *Naturwissenschaften* **96**, 955–62.

Huang, D.-Y, Nel, A., Shen, Y., Selden, P. A. & Lin, Q. 2006. Discussions on the age of the Daohugou fauna – evidence from invertebrates. *Progress in Natural Science* **16**, 308–12.

Huang, D.-Y., Zompro, O. & Waller, A. 2008a. Mantophasmatodea now in the Jurassic. *Naturwissenschaften* **95**, 947–52.

Huang, D.-Y. & Nel, A. 2007. A new Middle Jurassic "grylloblattodean" family from China (Insecta: Juraperlidae fam. n.). *European Journal of Entomology* **104**, 837–40.

Huang, D.-Y. & Nel, A. 2008. New 'Grylloblattida' related to the genus *Prosepididontus* Handlirsch, 1920 in the Middle Jurassic of China (Insecta: Geinitziidae). *Alcheringa* **32**, 395–403.

Huang, J., Ren, D., Sinitshenkova, N. D. & Shih, C. 2008b. New fossil mayflies (Insecta: Ephemeroptera) from the Middle Jurassic of Daohugou, Inner Mongolia, China. *Insect Science* **15**, 193–98.

Ji, Q., Chen, W., Wang, W., Jin, X., Zhang, J. P., Liu, Y. Q., Zhang, H., Yao, P. Y., Ji, S. A., Yuan, C. X., Zhang, Y. & You, H. 2004. *Mesozoic Jehol Biota of western Liaoning, China*, **375**. Beijing: Geological Publishing House.

Ji, Q., Liu, Y., Chen, W., Ji, S. A., Lu, J., You, H. & Yuan, C. 2005. On the geological age of Daohugou biota. *Geological Review* **51**, 609–12.

Krassilov, V. A. 1977. The origin of angiosperms. *Botanical Review* **43**, 143–76.

Li, N., Li, Y., Wang, L.-X., Zheng, S.-L. & Zhang, W. 2004. A new *Weltrichia* braun in north China with a special bennettitalean male reproductive organ. *Acta Botanica Sinica* **46**, 1269–75.

Liang, J.-H., Vrsansky, P., Ren, D. & Shih, C. 2009. A new Jurassic carnivorous cockroach (Insecta, Blattaria, Raphidiomimidae) from the Inner Mongolia in China. *Zootaxa* **1974**, 17–30.

Lin, Q.-B., Huang, D.-Y. & Nel, A. 2008. A new genus of Chifengiinae (Orthoptera: Ensifera: Prophalangopsidae) from the Middle Jurassic (Jiulongshan Formation) of Inner Mongolia, China. *Comptes Rendus Palevol* **7**, 205–09.

Liu, W.-Z., Hilu, K. & Wang, Y.-L. 2014. From leaf and branch into a flower: *Magnolia* tells the story. *Botanical Studies* **55**, 28.

Liu, Y., Liu, Y., Li, P., Zhang, H., Zhang, L., Li, Y. & Xia, H. 2004. Daohugou biota-bearing lithostratigraphic succession on the southeastern margin of the Ningcheng basin, Inner Mongolia, and its geochronology. *Regional Geology of China* **23**, 1180–87.

Liu, Y. & Ren, D. 2008. Two new Jurassic stoneflies (Insecta: Plecoptera) from Daohugou, Inner Mongolia,China. *Progress in Natural Science* **18**, 1039–42.

Liu, Z.-J. & Wang, X. 2016a. An enigmatic *Ephedra*-like fossil lacking micropylar tube from the Lower Cretaceous Yixian formation of Liaoning, China. *Palaeoworld* **25**, 67–75.

Liu, Z.-J. & Wang, X. 2016b. *Yuhania*: a unique angiosperm from the Middle Jurassic of Inner Mongolia, China. *Historical Biology* **29**, 431–41.

Martens, P. 1971. *Les Gnetophytes*. Berlin: Gebrueder Borntraeger.

Melville, R. 1963. A new theory of the angiosperm flower: II. The androecium. *Kew Bulletin* **17**, 1–63.

Miao, Y., Liu, Z.-J., Wang, M. & Wang, X. 2017. Fossil and living cycads say "No more megasporophylls". *Journal of Morphology and Anatomy* **1**, 107.

Peng, N., Liu, Y., Kuang, H., Jiang, X. & Xu, H. 2012. Stratigraphy and geochronology of vertebrate fossil-bearing Jurassic strata from Linglongta, Jianchang County, Western Liaoning, Northeastern China. *Acta Geologica Sinica* **86**, 1326–39.

Petrulevicius, J., Huang, D.-Y. & Ren, D. 2007. A new hangingfly (Insecta: Mecoptera: Bittacidae) from the Middle Jurassic of Inner Mongolia, China. *African Invertebrates* **48**, 145–52.

Pott, C., McLoughlin, S., Wu, S. & Friis, E. M. 2012. Trichomes on the leaves of *Anomozamites villosus* sp. nov. (Bennettitales) from the Daohugou beds (Middle Jurassic), Inner Mongolia, China: mechanical defence against herbivorous arthropods. *Review of Paleobotany and Palynology* **169**, 48–60.

Ren, D., Gao, K., Guo, Z., Ji, S., Tan, J. & Song, Z. 2002. Stratigraphic division of the Jurassic in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* **21**, 584–91.

Ren, D., Labandeira, C. C., Santiago-Blay, J. A., Rasnitsyn, A., Shih, C., Bashkuev, A., Logan, M. A. V., Hotton, C. L. & Dilcher, D. 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. *Science* **326**, 840–47.

Ren, D., Shih, C., Gao, T., Yao, Y. & Zhao, Y. 2010. *Silent stories, insect fossil treasures from dinosaur era of the Northeastern China*, **322**. Beijing: Science Press.

Rothwell, G. W., Crepet, W. L. & Stockey, R. A. 2009. Is the anthophyte hypothesis alive and well? New evidence from the reproductive structures of Bennettitales. *American Journal of Botany* **96**, 296–322.

Rothwell, G. W. & Stockey, R. A. 2002. Anatomically preserved *Cycadeoidea* (cycadeoidaceae), with a reevaluation of systematic characters for the seed cones of Bennettitales. *American Journal of Botany* **89**, 1447–58.

Rothwell, G. W. & Stockey, R. A. 2010. Independent evolution of seed enclosure in the Bennettitales: evidence from the anatomically preserved cone *Foxeoidea connatum* gen. et sp. nov. *In* Gee, C. T. (ed.). *Plants in the Mesozoic time: innovations, phylogeny, ecosystems*, 51–64. Bloomington and Indianapolis: Indiana University Press.

Selden, P. A., Huang, D.-Y. & Ren, D. 2008. Palpimanoid spiders from the Jurassic of China. *The Journal of Arachnology* **36**, 306–21.

Seward, A. C. 1919. *Fossil plants, a text-book for students of botany and geology*, **4**, 543. Cambridge: The Cambridge University Press.

Sha, J. 2007. Current research on Cretaceous lake systems in northeast China. *Cretaceous Research* **28**, 143–45.

Shen, Y.-B., Chen, P.-J. & Huang, D.-Y. 2003. Age of the fossil conchostracans from Daohugou of Ningcheng, Inner Mongolia. *Journal of Stratigraphy* **27**, 311–13.

Shih, C., Liu, C. & Ren, D. 2009. The earliest fossil record of pelecinid wasps (Inseta: Hymenoptera: Proctotrupoidea: Pelecinidae) from Inner Mongolia, China. *Annals of the Entomological Society of America* **102**, 20–38.

Skinner, D. J., Hill, T. A. & Gasser, C. S. 2004. Regulation of ovule development. *Plant Cell* **16**, S32–45.

Stockey, R. A. & Rothwell, G. W. 2003. Anatomically preserved *Williamsonia* (williamsoniaceae): evidence for Bennettitalean reproduction in the Late Cretaceous of western North America. *International Journal of Plant Sciences* **164**, 251–62.

Tan, J. & Ren, D. 2009. *Mesozoic archostematan fauna from China*. Beijing: Science Press.

Tomlinson, P. B. & Takaso, T. 2002. Seed cone structure in conifers in relation to development and pollination: a biological approach. *Canadian Journal of Botany* **80**, 1250–73.

Wang, B., Li, J., Fang, Y. & Zhang, H. 2009a. Preliminary elemental analysis of fossil insects from the Middle Jurassic of Daohugou, Inner Mongolia and its taphonomic implications. *Chinese Science Bulletin* **54**, 783–87.

Wang, B., Ponomarenko, A. G. & Zhang, H. 2009b. A new coptoclavid larva (Coleoptera: Adephaga: Dytiscoidea) from the Middle Jurassic of China, and its phylogenetic implication. *Paleontological Journal* **43**, 652–59.

Wang, B., Zhang, H. & Szwedo, J. 2009c. Jurassic Palaeontinidae from China and the higher systematics of Palaeontinoidea (Insecta: Hemiptera: Cicadomorpha). *Palaeontology* **52**, 53–64.

Wang, B. & Zhang, H. 2009a. A remarkable new genus of Procercopidae (Hemiptera: Cercopoidea) from the Middle Jurassic of China. *Comptes Rendus Palevol* **8**, 389–94.

Wang, B. & Zhang, H. 2009b. Tettigarctidae (Insecta: Hemiptera: Cicadoidea) from the Middle Jurassic of Inner Mongolia, China. *Geobios* **42**, 243–53.

Wang, B. & Zhang, H. 2011. The oldest Tenebrionoidea (Coleoptera) from the Middle Jurassic of China. *Journal of Paleontology* **85**, 266–70.

Wang, X. 2010. *The dawn angiosperms*. Heidelberg: Springer.

Wang, X., Krings, M. & Taylor, T. N. 2010a. A thalloid organism with possible lichen affinity from the Jurassic of northeastern China. *Review of Palaeobotany and Palynology* **162**, 567–74.

Wang, X., Zheng, S. L. & Jin, J. H. 2010b. Structure and relationships of *Problematospermum*, an enigmatic seed from the Jurassic of China. *International Journal of Plant Sciences* **171**, 447–56.

Wang, X., Liu, Z.-J., Liu, W., Zhang, X., Guo, X., Hu, G., Zhang, S., Wang, Y. & Liao, W. 2015. Breaking the stasis of current plant systematics. *Science & Technology Review* **33**, 97–105.

https://doi.org/10.1017/S1755691018000257 Published online by Cambridge University Press

Wang, X. & Luo, B. 2013. Mechanical pressure, not genes, makes ovulate parts leaf-like in *Cycas*. *American Journal of Plant Sciences* **4**, 53–57.
Wang, Y. & Ren, D. 2009. New fossil palaeontinids from the middle Jurassic of Daohugou, Inner Mongolia, China (Insecta, Hemiptera). *Acta Geologica Sinica* **83**, 33–38.
Watson, J. & Sincock, C. A. 1992. Bennettitales of the English Wealden. *Monograph of Palaeontographical Society* **145**, 1–228.
Wieland, G. R. 1906. *American fossil cycads*, **34**, 295. Washington, DC: The Wilkens Sheiry Printing Co.
Wilson, C. L. 1937. The phylogeny of the stamen. *American Journal of Botany* **24**, 686–99.
Wu, Z.-Y., Lu, A.-M., Tang, Y.-C., Chen, Z.-D. & Li, D.-Z. 2002. Synopsis of a new "polyphyletic-polychronic-polytopic" system of the angiosperms. *Acta Phytotaxonomica Sinica* **40**, 289–322.
Zhang, J. 2006. New winter crane flies (Insecta: Diptera: Trichoceridae) from the Jurassic Daohugou formation (Inner Mongolia, China) and their associated biota. *Canadian Journal of Earth Science* **43**, 9–22.
Zhang, J., D'Rozario, A., Yao, J., Wu, Z. & Wang, L. 2011. A new species of the extinct genus *Schizolepis* from the Jurassic Daohugou Flora, Inner Mongolia, China with special reference to the fossil diversity and evolutionary implications. *Acta Geologica Sinica* **85**, 471–81.
Zhang, J. F. 2002. Discovery of Daohugou Biota (pre-Jehol Biota) with a discussion on its geological age. *Journal of Stratigraphy* **26**, 173–77.
Zhang, K., Li, J., Yang, D. & Ren, D. 2009. A new species of *Archirhagio* Rohdendorf, 1938 from the Middle Jurassic of Inner Mongolia of China (Diptera: Archisargidae). *Zootaxa* **1984**, 61–65.
Zhang, X., Liu, W. & Wang, X. 2017. How the ovules get enclosed in magnoliaceous carpels. *PLOS One* **12**, e0174955.
Zhang, X.-W., Ren, D., Pang, H. & Shih, C.-K. 2008. A water-skiing chresmodid from the Middle Jurassic in Daohugou, Inner Mongolia, China (Polyneoptera: Orthopterida). *Zootaxa* **1762**, 53–62.
Zheng, S. & Wang, X. 2010. An undercover angiosperm from the Jurassic in China. *Acta Geologica Sinica* **84**, 895–902.
Zheng, S.-L., Zhang, L.-J. & Gong, E.-P. 2003. A discovery of *Anomozamites* with reproductive organs. *Acta Botanica Sinica* **45**, 667–72.
Zhou, Z., Zheng, S. & Zhang, L. 2007. Morphology and age of *Yimaia* (ginkgoales) from Daohugou Village, Ningcheng, Inner Mongolia, China. *Cretaceous Research* **28**, 348–62.

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