A Whole Plant Herbaceous Angiosperm from the Middle Jurassic of China

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Abstract: In contrast to woody habit with secondary growth, truthful herbaceous habit lacking secondary growth is restricted to angiosperms among seed plants. Although angiosperms might have occurred as early as in the Triassic and herbaceous habit theoretically may have been well adopted by pioneer angiosperms, pre-Cretaceous herbs are missing hitherto, leaving the origin of herbs and evolution of herbaceous angiosperms mysterious. Here we report *Juraherba bodae* gen. et sp. nov, a whole plant herbaceous angiosperm, from the Middle Jurassic (>164 Ma) at Daohugou Village, Inner Mongolia, China, a fossil Lagerstätten that is worldwide famous for various fossil finds. The angiospermous affinity of *Juraherba* is ensured by its enclosed ovules/seeds. The plant is small but complete, with physically connected hairy root, stem, leaves, and fructifications. The Middle Jurassic age recommends *Juraherba* as the earliest record of herbaceous seed plants, demanding a refresh look at the evolutionary history of angiosperms.

Key words: seed plant, Jurassic, herbaceous, whole plant, angiosperm.

1 Introduction

Woody plants were thought ancestral among angiosperms in the previous evolutionary theories (Cronquist, 1988; APG, 2009) because the assumed outgroups of angiosperms (fossil and extant gymnosperms) are all woody (Chamberlain, 1957; Bierhorst, 1971; Biswas and Johri, 1997; Taylor et al., 2009). Herbaceous plants are important elements in the current ecosystem, and they supply most of the materials necessary for the human beings and have been playing important roles in the global ecosystem (Jacobs et al., 1999). Considering the so-called Triassic herbaceous conifer actually has, although limited, secondary growth (Rothwell et al., 2000), truthful herbaceous habit is only seen in angiosperms among seed plants so far. Ecophysiological analyses of extant and fossil plants suggest that pioneer angiosperms may well have adopted herbaceous habit as one of their survival strategies (Stebbins, 1981; Taylor and Hickey, 1990, 1992; Carlquist, 1996; Hickey and Taylor, 1996; Royer et al., 2010). How ancient can herbs be is still an open question, partially due to the lower fossilizing potential of herbs (Jacobs et al., 1999). The solution for this problem is emerging as increasing number of claims of pre-Cretaceous angiosperms, including possible Triassic angiosperm pollen (Hochuli and Feist-Burkhardt, 2004, 2013) and Jurassic megafossil angiosperms (*Schmeissneria*, *Xingxueanthus*, and *Euanthus*) (Wang et al., 2007; Wang, 2010a, b; Wang and Wang, 2010; Liu and Wang, 2016), have been recovered in addition to non-woody Early Cretaceous angiosperms (*Chaoyangia* and *Archaefructus*) (Duan, 1998; Sun et al., 1998, 2002; Ji et al., 2004a; Wang, 2010b, 2015). All these make herbaceous angiosperms in the Jurassic rather expected. Although recent studies on Early Cretaceous fossils seem to suggest that herbs are among the pioneer angiosperms (Jud, 2015; Friis et al., 2015), hitherto convincing fossil evidence of herbaceous seed plants in pre-Cretaceous age is still missing. Fossil plants with various parts connected are among the most reliable

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information sources for palaeobotanical studies because reconstructions based on separately preserved parts may be risky and is frequently inflicted by hard-to-detect artifacts and errors (Rothwell et al., 2009; Tekleva and Krassilov, 2009). Here we report an herbaceous angiosperm, *Juraherba bodae* gen. et sp. nov., with all parts physically connected from the Jiulongshan Formation (Jurassic, >164 Ma) of Inner Mongolia, China (Chen et al., 2004; Ji et al., 2005; Zhou et al., 2007; Pott et al., 2012). The herbaceous plant habit and enclosed ovules/seeds pin down the angiospermous affinity for *Jurahbera*. This discovery will re-shape the current thinking on the origin of herbaceous habit in seed plants and its role in the evolution of angiosperms.

2 Geological Settings

One fossil specimen was collected from an outcrop of the Jiulongshan Formation near Daohugou Village. Daohugou Village of Ningcheng City (119.236727ºE, 41.315756ºN) is located on the southeast corner of Inner Mongolia, China, close to the boundaries of Inner Mongolia with Liaoning and Hebei Provinces (Fig. 1). Numerous plant and insect fossils have been found from this locality (Zheng et al., 2003; Ji et al., 2004b; Huang et al., 2006; Zhou et al., 2007; Ren et al., 2009, 2010; Wang et al., 2010; Zheng and Wang, 2010; Wang and Zhang, 2011; Peng et al., 2012). At least most of Ar^{40}/Ar^{39} and SHRIMP U/Pb datings (Chen et al., 2004; Ji et al., 2004b) and biostratigraphy based on fossil plants and animals converge to the same conclusion that the fossiliferous layer of the Formation is at least 164 Ma old, namely, of the Middle Jurassic (Ren et al., 2002, 2009, 2010; Zhang, 2002; Shen et al., 2003; Zheng et al., 2003; Chen et al., 2004; Li et al., 2004; Liu et al., 2004; Ji et al., 2005; Gao and Ren, 2006; Huang et al., 2006, 2008a&b, 2009; Zhang, 2006; Huang and Nel, 2007, 2008; Petrulevicius et al., 2007; Sha, 2007; Zhou et al., 2007; Lin et al., 2008; Liu and Ren, 2008; Selden et al., 2008; Zhang et al., 2008, 2009, 2011; Chang et al., 2009, 2014; Fang et al., 2009; Liang et al., 2009; Shih et al., 2009; Wang et al., 2009a, b, c, 2010, 2014; Wang and Zhang, 2009a&b, 2011; Wang and Ren, 2009; Zheng and Wang, 2010; Pott et al., 2012; Na et al., 2014). Therefore it is safe to adopt the Middle Jurassic age for *Juraherba* reported here.

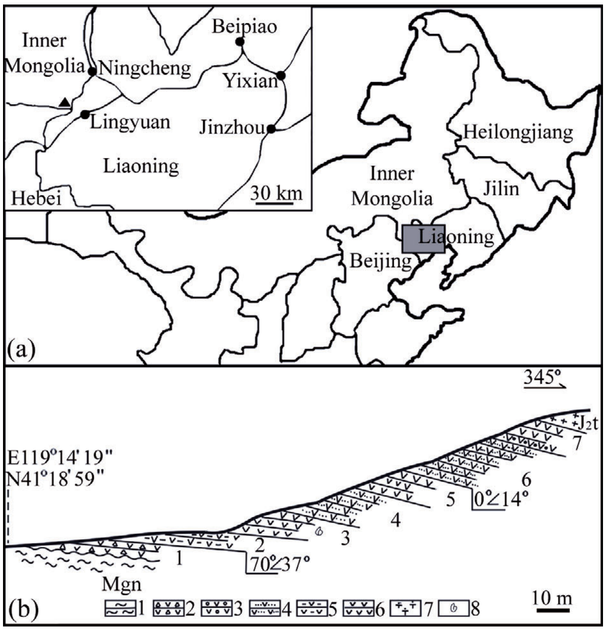

Fig. 1. Geological information of the Jiulongshan Formation at Daohugou Village. Redrawn after Tan and Ren (2009) and Zheng and Wang (2010), with permission.
(a) Geographical position of the fossil locality, Daohugou Village, Ningcheng, Inner Mongolia in northeast China. The rectangular region is shown 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 layer.

3 Samples and Methods

The fossil is preserved as a compression specimen with coalified residues embedded in tuffaceous siltstone, and thus resulting in an impression, too. The specimen was photographed using a Nikon D300 digital camera. Details of the fossil were observed and photographed using a Leica MZ-16A stereomicroscope with a DFC290 digital camera. Afterward replicas of nitro cellulose (Zhu, 1983) 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. The surface of the whole specimen was scrutinized using SEM and Leica fluorescent microscope to search for any trace of *in situ* pollen, but in vain, although many pollen grains were found in the adjacent sediment. One of the fructifications was dissected to expose the internal details (including seed) inside. Fluorescent observation and micrography were performed using a Leica DM5000B using green fluorescent light. All photographs were saved in TIFF format and organized together for publication using Photoshop 7.0.

4 Results

Juraherba Han et Wang, gen. nov.

Generic diagnosis: Herbaceous plant, small, including physically connected roots, stem, leaves, and fructifications. Root minute, borne on the bottom of the plant. Stem straight, bearing helically arranged leaves. Leaves linear, entire margined, with a midvein and an acute tip. Fructification on a long pedicel. Fruits enclosing ovules/seeds, surrounded by foliar parts, with longitudinal ridges and wrinkled surface. Fructification pedicel with scaly leaves and longitudinal ridges.

Type species: *Juraherba bodae* Han et Wang gen. et sp. nov.

Etymology: *Jura-,* for the Jurassic, the age of the fossil; *-herba*, for the herbaceous habit of the plant.

Type locality: the Daohugou Village, Ningcheng, Inner Mongolia, China (119.236727° E, 41.315756°N).

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

Juraherba bodae Han et Wang, sp. nov.
(Figs. 2-7)

Specific diagnosis: as of the genus.

Description: The fossil is preserved as an impression/compression embedded in grey tuffaceous siltstone, with some coalified residue preserved in the lower portion and fructifications (Fig. 2a). The fossil includes physically connected roots, a stem, leaves, fructifications, and is associated with an insect fossil (Fig. 2a) and pollen clumps (Fig. 5n). It is 38 mm long and 12 mm wide, including at least twelve leaves and four fructifications (Fig. 2a). The lower portion is delimited from the above by a constriction, oval-shaped, 0.79 mm high and 1.16 mm wide, with scales and hairy roots (Figs. 2c, 3d-3e, 3g-3h). The scales have integral smooth surfaces and bear vertically inserted hairy roots up to 121 μm long and 33 μm wide (Figs. 3e-3h). The stem bears helically arranged leaves, with irregularly wrinkled surface (Figs. 2a, 2b, 2e, 3i). The leaves are simple, linear, up to 40 mm long and only 1.3 mm wide, with a midvein, entire-margined, with acute tips, usually eclipsing the stem, and older leaves tend to abscise at their bases (Figs. 2a, 2b, 3a-3c, 3i, 3j, 5n). The midvein is 0.3 mm wide and the lateral zone is 0.42 mm wide in the middle portion of the leaves, both

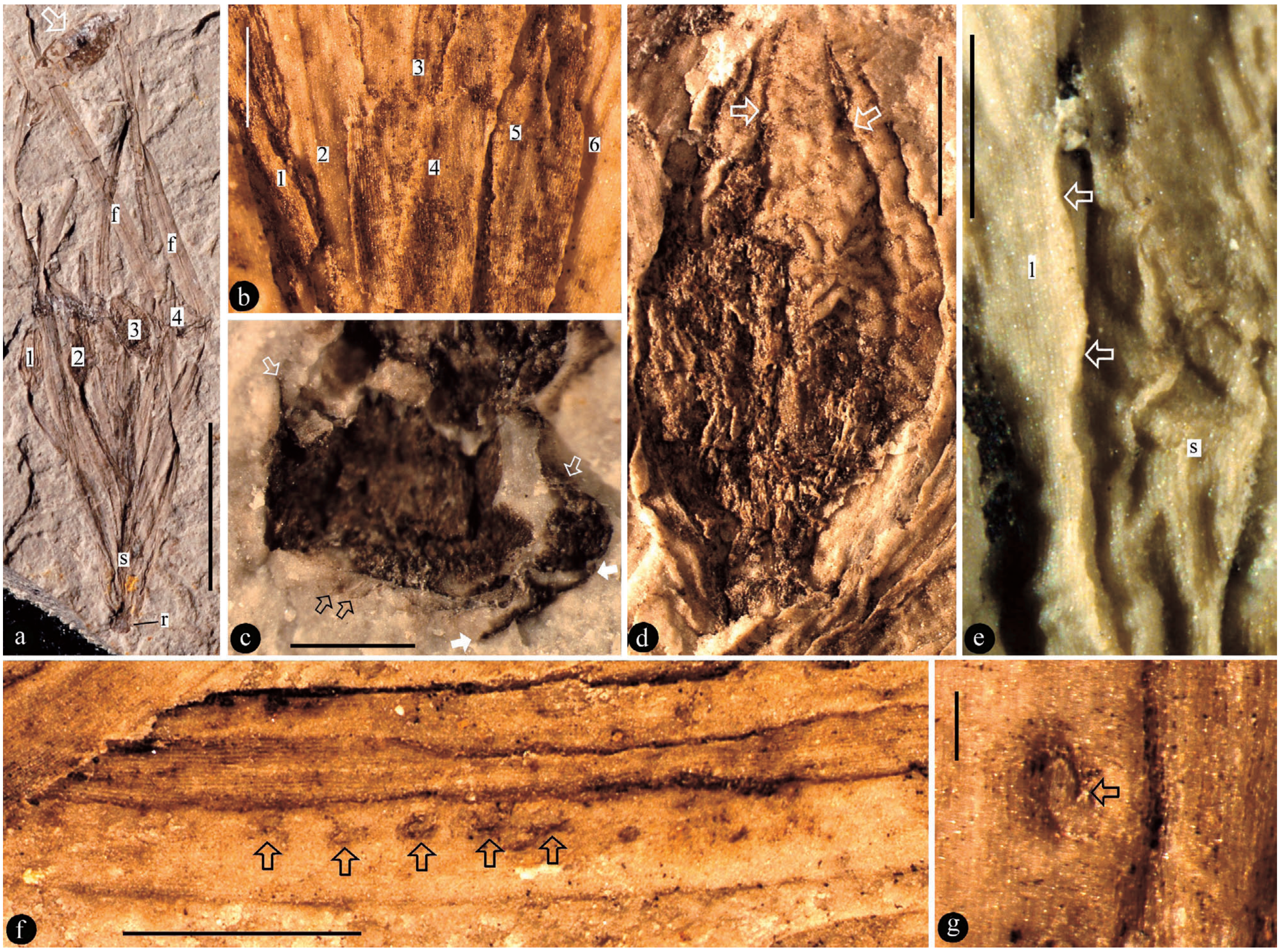

Fig. 2. General morphology and details of *Juraherba*. LM.
(a) Whole plant with physically connected parts including roots (r), stem (s), leaves (f), and fructifications (1-4). Note an associated fossil insect (arrow) at the top. Bar = 10 mm. (b) Helically arranged leaves (1-6). Bar = 0.5 mm. (c) Coalified lower portion with scales (white arrows) and hairy roots (black arrows). Bar = 0.5 mm. (d) Fructification 3 in Fig. 2a, with longitudinal ridges (arrows) and some coalified remains. Bar = 1 mm. (e) Margin (arrows) of a leaf (l) with smooth surface, and the stem (s) with rough surface. Bar = 0.5 mm. (f) One of the leaves with an array of insect damages (arrows). Bar = 1 mm. (g) Detailed view of one (arrow) of the insect damages shown in Fig. 2f. Bar = 0.1 mm.

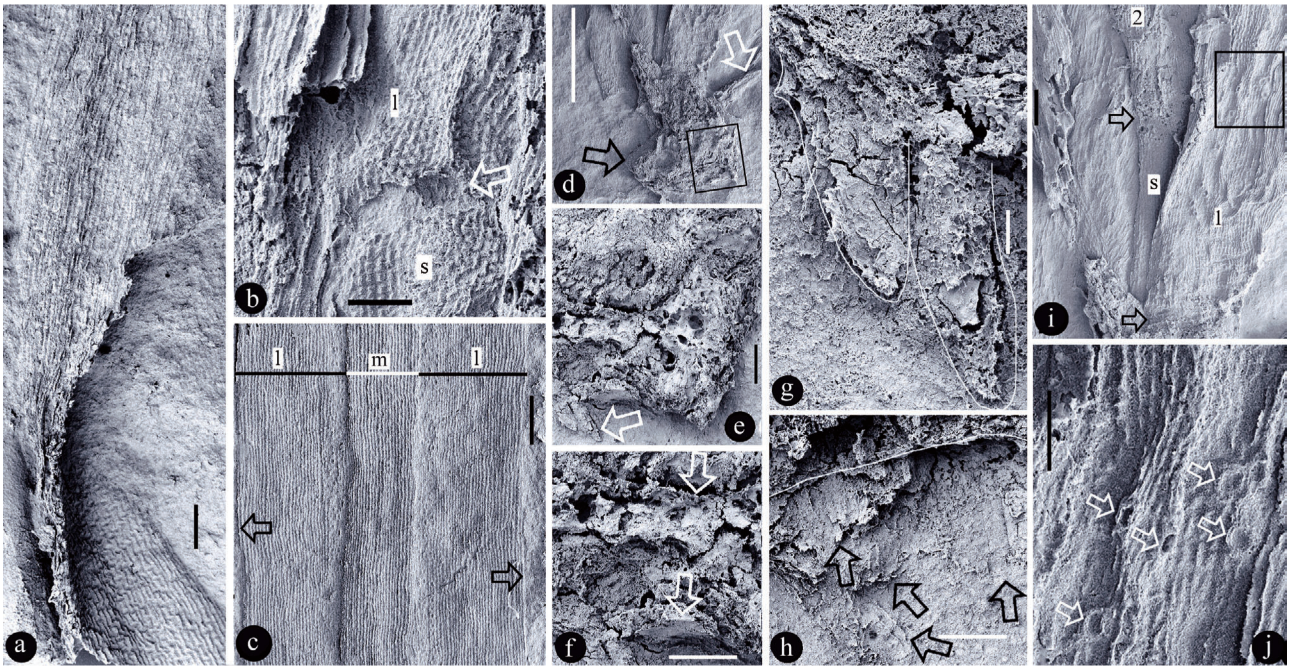

Fig. 3. Stem, leaves, and roots of *Juraherba*, seen on the replica using SEM.
(a) A twisted leaf showing both adaxial (bottom) and abaxial (top) epidermis of the same leaf lamina. Bar = 0.1 mm. (b) A leaf (l) abscising from the stem (s). Note the discontinuity of epidermis (arrow) between the leaf and stem. Bar = 0.1 mm. (c) Abaxial view of the middle portion of a leaf, showing parallel entire margins (arrows), midvein (m), and lateral zones (l). Bar = 0.2 mm. (d) The basal portion of the plant, showing the lower portion (black arrow) and a connected fructification pedicel (white arrow). Refer to Fig. 2c. Bar = 1 mm. (e) Lower-right portion of the roots, enlarged from the rectangle in Fig. 3d, showing a scale (lower-right) and attached hairy roots (arrow). Bar = 100 μm. (f) Integral inner (upper arrow) and outer (lower arrow) surfaces of the scale, enlarged from Fig. 3e. Bar = 100 μm. (g) Hairy roots (line), enlarged from the lower-left of Fig. 3e. Bar = 20 μm. (h) Hairy roots nearly vertically attached to the bottom of the plant (white line). Bar = 50 μm. (i) Leaf arrangement near the base of the plant. Note broken epidermis (arrows) at the nodes on the stem (s) where the leaves (1-2) are attached. Bar = 0.2 mm. (j) Rectangular region in Fig. 3i, showing scattered stomata-like structures (arrows) on the leaf. Bar = 0.1 mm.

tapering distally (Figs. 2a, 3c). Stomata can be seen along both sides of the midvein on the abaxial surface of leaves (Figs. 3i-j, 4a). The adaxial leaf epidermis has rectangular texture (Fig. 3a) while the abaxial one has longitudinal striations, both surfaces are relatively smooth compared to the stem and fructifications (Figs. 2e, 3a, 3c, 4a). Frequently insect damages (DT138, according to Labandeira et al. (2007)) are seen on the leaves (Figs. 2f, 2g, 5o). Four fructifications are inserted basally, arranged nearly at the same horizontal level (Figs. 2a, 3d). The fructifications are fusiform, 2.2–4.1 mm long and 1.4–2.2 mm wide, borne on long pedicels, and surrounded by foliar parts (Figs. 2a, 2d, 5a-c). Different foliar parts distinguish each other by their surface texture and may have stomata (Figs. 4c, 5b). The pedicels are 14–15.5 mm long, longitudinally ridged, with sparsely helically arranged scaly leaves (Figs. 4b, 5a, 5e, 5i). The fructification terminus has an irregular margin, suggestive of an abscised distal part (Fig. 5h). Each fructification has several longitudinal ridges and irregular wrinkles on its surface (Figs. 2d, 5a-5c, 5f, 5g, 5i). Inside one of the fructifications an ovule/seed 339 μm long is seen anchored to an internal structure and embedded in the fructification tissue (Figs. 5c, 5d). Another ovule appears in the same fructification (Fig.

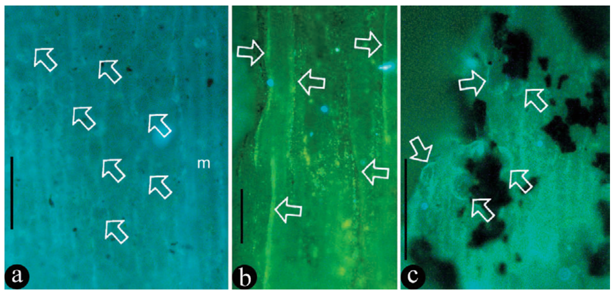

Fig. 4. Fluorescent micrographs of leaf, pedicel, and surrounding foliar parts of *Juraherba*.
(a) Possible stomata (arrows) near the midvein (m) on the abaxial leaf surface. Bar = 0.1 mm. (b) Longitudinal ridges (arrows) on a fructification pedicel. Bar = 0.1 mm. (c) Epidermal cells and possible stomata (arrows) on a foliar part surrounding the fructification. Bar = 0.1 mm.

5m). An oval body (possible seed) is seen in another fructification after removing the covering tissue (Figs. 5i-5l).

Etymology: *bodae,* dedicated to Boda (the Chinese abbreviation of Bohai University), the affiliation of the first author.

Holotype: PB21415, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Remarks: There are limited phyllotactic patterns in plants, including helical, alternate, opposite, decussate,

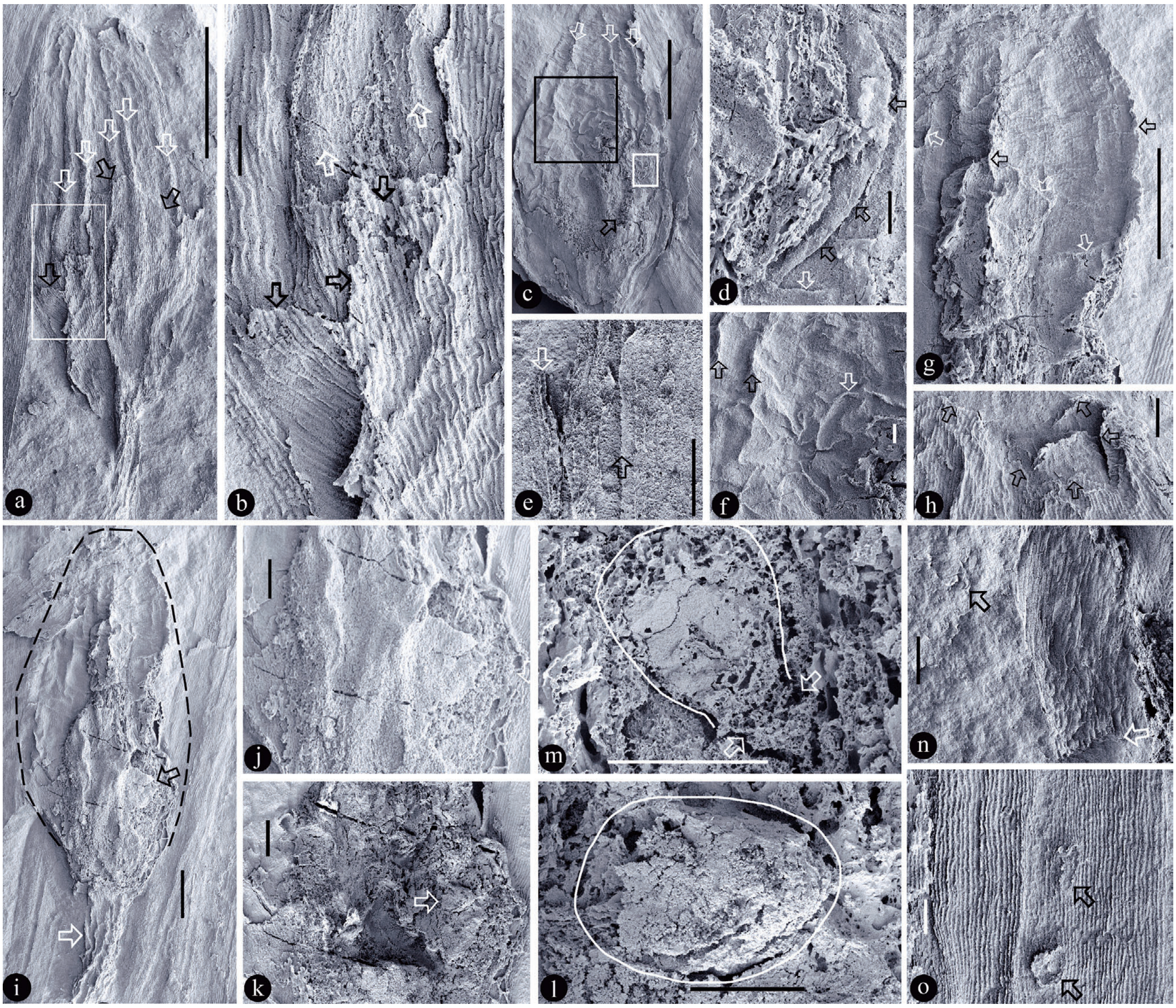

Fig. 5. Fructifications of *Juraherba*, SEM.
(a) Fructification 1 in Fig. 2a, showing its fusiform shape, longitudinal ridges (white arrows), margin of the surrounding foliar parts (black arrows), and a pedicel at the bottom. Bar = 1 mm. (b) Magnification of the rectangular region in Fig. 5a. Note the broken margins (black arrows) of the surrounding foliar part and longitudinal ridges on the fruit (white arrows). Bar = 0.1 mm. (c) Fusiform-shaped fructification 3 in Fig. 2a, with longitudinal ridges (white arrows). Bar = 1 mm. (d) An ovule/seed embedded in the fructification tissue, enlarged from white rectangle in Fig. 5c. Black arrows show the margin of the ovule/seed, and white arrow marks the attachment of the ovule probably to one of the ridges. Bar = 50 μm. (e) The fructification pedicel in Fig. 5a, showing a scaly leaf (white arrow) and ridge (black arrow). Bar = 0.1 mm. (f) Wrinkles (white arrow) and longitudinal ridge (black arrow) on the fructification, enlarged from black rectangle in Fig. 5c. Bar = 0.1 mm. (g) Wrinkles (white arrows) and longitudinal ridges (black arrows) on the fructification 2 in Fig. 2a. Bar = 0.5 mm. (h) Fructification terminus in Fig. 5a, showing the irregular broken margin (arrows) suggestive of an abscission scar. Bar = 0.1 mm. (i) Fusiform-shaped fructification 2 (outlined) in Fig. 2a, with a pedicel at the bottom (white arrow). Bar = 0.5 mm. (j) Detailed view of the portion black-arrowed in Fig. 5i. Bar = 0.2 mm. (k) Internal details of the portion of fructification shown in Fig. 5j, after removing the covering tissue. Bar = 0.2 mm. (l) A possible seed (oval body outlined), enlarged from the arrowed region in Fig. 5k. Bar = 0.1 mm. (m) An ovule (outlined) embedded inside the tissue of fructification and connected by a funiculus (between arrows), enlarged from black-arrowed portion of Fig. 5c. Bar = 0.1 mm. (n) A disarticulated leaf with longitudinal epidermal cells. Note the broken margin at the bottom (white arrow) and associated pollen clump (black arrow). Enlarged from upper-left of Fig. 3d. Bar = 0.2 mm. (*o*) Insect damages (arrow) on a leaf of *Juraherba*. Bar = 0.1 mm.

and whorled ones. The arrangement of the leaves in *Juraherba* (Figs. 2a, 2b) apparently is nothing but the helical one.

The irregularly wrinkled surfaces of the stem and fructifications form a strong contrast against the relatively smooth leaf surface, implying the volume of these parts has been reduced during the fossilization and these parts used to be more or less fleshy in live form.

5 Discussions

5.1 Interpreting structures

The fructifications surrounded by foliar parts without any trace of spores in *Juraherba* are clearly different from sori or sporangia of ferns, in which sori and sporangia are closely related to pinnae except in Salviniales (Haupt, 1953; Smith et al., 2006). Fructification pedicels with scaly leaves are distinct from smooth setae or pseudopodia of bryophytes (Gradstein et al., 2001), therefore the fructifications of *Juraherba* cannot be interpreted as capsules of bryophytes. These differences are sufficient to distinguish *Juraherba* from bryophytes and most ferns.

The general morphology of *Juraherba* might appear similar to a short shoot of Czekanowskiales (including *Phoenicopsis, Czekanowskia*, and *Tianshia*), which are frequently seen in the Mesozoic (Zhou and Zhang, 1998; Sun et al., 2009). However, the single vein and acute leaf tip of *Juraherba* are distinct from the multiple veins and rounded leaf tips of *Phoenicopsis* and *Tianshia* (Zhou and Zhang, 1998). The linear, non-branching leaves of *Juraherba* are distinct from the filiform, branched leaf of *Czekanowskia* (Sun et al., 2009). Furthermore the distinction between the terminal fusiform fructifications surrounded by foliar parts in *Juraherba* and lateral naked bivalvate units in *Leptostrobus* (Czekanowskiales) eliminates any relationship between them. If belonged to Czekanowskiales, then the base of *Juraherba* should be truncated and broken with rough surface and no hairs. However, the base of *Juraherba* has an integral surface (Fig. 3f) and hairy roots (Figs. 3e, 3g, 3h). All these convince us that *Juraherba* is a whole plant rather than a short shoot of any plants.

5.2 Herbaceous habit

The whole plant of *Juraherba* is only 38 mm tall, implying an herbaceous habit. This conclusion is supported by comparison with other big herbaceous and small woody plants. On one hand, primary growth may produce organs bigger than those of *Juraherba*. For example, the early land plant *Rhynia* may produce an axis up to 3 mm in diameter (Edwards, 2003), in contrast to only 1.16 mm wide lower portion of *Juraherba*. This contrast suggests that the size of *Juraherba* is within the scope of primary growth. On the other hand, plants with little secondary growth have axes much thicker than *Juraherba*. The lower portion of *Juraherba* is much smaller than that of the so-called “herbaceous” conifer (*Aethophyllum stipulare,* Rothwell et al., 2000, their Plate I, Fig. 3,), the fertile one of the latter is more than 30 cm tall, suggesting that smaller *Juraherba* has no secondary growth. Similarly, shrubby *Ephedra* (Gnetales) is much bigger than *Juraherba* and does have an active cambium (Martens, 1971). Therefore actually there is no truthful herbaceous gymnosperm without secondary growth. These comparisons indicate that mature *Juraherba* (as implied by its fructifications) is truthfully herbaceous. Thus at least *Juraherba* can be distinguished from all known gymnosperms by its herbaceous habit (Bierhorst, 1971; Biswas and Johri, 1997).

The tiny size and herbaceous habit suggests that *Juraherba* has a short life cycle, an ecological strategy that is paramount for the success of angiosperms (Stebbins, 1981) and adopted by some basal angiosperms such as the Hydatellaceae (Gandolfo et al., 1998; Saarela et al., 2007). This is in line with the ecophysiological analyses of extant and fossil plants, which conclude that herbaceous habit may well have been adopted by early angiosperms (Stebbins, 1981; Taylor and Hickey, 1990, 1992, 1996; Carlquist, 1996; Royer et al., 2010). This conclusion has been favored by recent studies on Early Cretaceous plants (Jud, 2015; Friis et al., 2015). *Juraherba* unequivocally confirms that early angiosperms have already adopted this strategy at least back to the Middle Jurassic (Figs. 7a-7c), although their success did not come until much later. The discovery of *Juraherba* adds first-hand material for studying the origin and evolution of herbs, favoring the Paleoherb Theory that was advanced more than decades ago.

5.3 Affinity

The oval bodies inside the fructification are of crucial importance for the affinity of *Juraherba*. The oval bodies in the fructification seen in Figs. 5d and 5l cannot be interpreted as either microspores or pollen grains because of their large size (over 300 μm long, falling well within the scope of megaspores (Bateman and Dimichele, 1994)), therefore they have to be interpreted as seeds/ovules/megaspores rather than microspores/pollen. Besides seed plants, megaspores are seen in Lycophyta, Sphenophyta, and Salviniales (Scott, 1962; Smith et al., 2006; Taylor et al., 2009). The reproductive organs of Lycophyta and Sphenophyta are usually organized in cone-like structures (Scott, 1962; Taylor et al., 2009), and completely different from *Juraherba*. Salviniales can be easily distinguished from *Juraherba* by their leaf morphology (Smith et al., 2006). Another possibility is insect egg laid inside the fructification. The shape of the oval body in *Juraherba* (Fig. 5d) is not symmetrical, as expected for an insect egg. Instead the oval body is slightly elongated at the bottom, anchored and embedded in the fructification tissue in Fig. 5d. This interpretation is further strengthened by another possible ovule embedded in the same fructification seen in Fig. 5m, in which a mass of dense organic material is anchored by a pedicel and its lack of obvious testa implies that it is either an ovule or a seed in its very early development. Finally, one more oval body that was originally covered inside the fructification became exposed after the covering tissue was removed (Figs. 5i-5l). Its large size (over 200 μm long) comparable to the two above possible ovules (Figs. 5d, 5m) rather than microspores or pollen grains implies that it may be an ovule or a seed. Its spatial position within the fructification (angiospermy) is rather significant because it is a feature expected for angiosperms. The irregular scar at the fructification tip (Fig. 5h) suggests that there used to be a distal part (probably style) in *Juraherba*, in agreement with the occurrence of angiospermy/angio-ovuly in *Juraherba*. Abscised styles are frequently seen in angiosperms after pollination but never in gymnosperms (Goldschmidt and Leshem, 1971; Simons, 1973; Keighery, 2004; Liu et al., 2009), it is logical to state that *Juraherba* is a Middle Jurassic angiosperm. It is noteworthy that, among angiosperms, *Juraherba* resembles Hydatellaceae (one of the basal-most angiosperms) in general morphology and habit (Rudall et al., 2007; Sokoloff et al., 2013), although certain differences do exist between them, too. Lack of both herbaceous growth habit and angio-ovuly in gymnosperms also helps to reinforce the angiospermous affinity for *Juraherba*. Apparently, *Juraherba* is an interesting Jurassic herbaceous angiosperm that deserves further attention.

5.4 Aquatic habitat

The hairy roots of *Juraherba* are very tiny in size, simple in organization, only about one-cell wide, apparently very short and not well-developed (Figs. 2c, 3d-3h, 6). They are even shorter than the earliest known rooting system in the Early Devonian (Hao et al., 2009). These features imply that *Juraherba* most likely lives in an environment with little water stress where strong anchorage and mechanical support are unnecessary. The arrangement of all four fructifications nearly at the same horizontal level in *Juraherba* implies that these reproductive organs might be close to the water surface when pollinated. This assemblage of information suggests that *Juraherba* is most likely aquatic (Figs. 7a-7c).

5.5 Interaction with animals

The wrinkled fructification surface (Figs. 5c, 5f, 5g), in

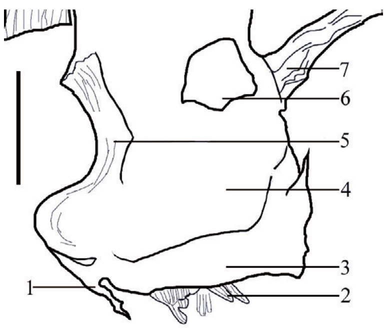

Fig. 6. Sketch showing basal portion of *Juraherba*, refer to Figs. 2c and 3d. 1, 3, scales; 2, hairy roots; 4, core of lower portion; 5, leaf; 6, scar left by a pedicel; 7, fructification pedicel.

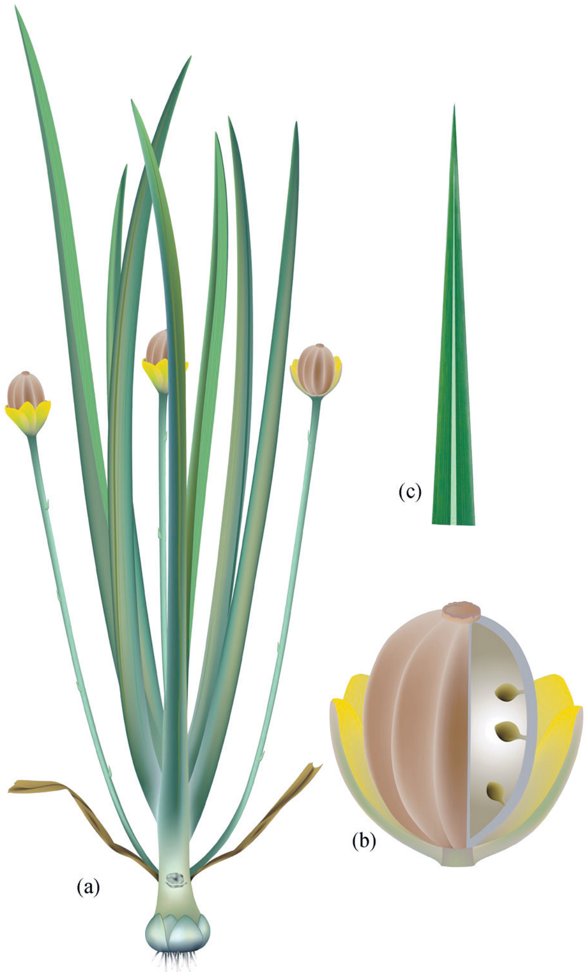

Fig. 7. Reconstruction of whole plant, fructification, and leaf of *Juraherba*. Not to scale.
(a) Reconstruction of *Juraherba* including roots, stem, leaves, and fructifications. (b) Fructification showing surrounding foliar parts, fruit with longitudinal ridges, and ovules/seeds inside the fruit. (c) Leaf with a midvein and lateral zones, tapering distally.

a strong contrast against the smooth leaf surface with little distortion (Fig. 3c) in the same fossil, suggests that *Juraherba*'s fructifications are fleshy. According to the study of early angiosperms (Eriksson et al., 2000), some animals may have involved in the dispersal of fleshy diaspores of angiosperms in the Early Cretaceous. Thus the occurrence of fleshy fructifications in the Jurassic is not too surprising. The Middle Jurassic age of *Juraherba* suggests that the co-evolution between fleshy fructifications of angiosperms and animals can be dated back to the Middle Jurassic. Before this report, Na et al. (2014) reported the first ovipositional scars on *Sphenobaiera* from the same locality, Daohugou Village. Oviposition scars in rows were found on leaves of *Schmeissneria*, the currently known earliest angiosperm (Wang et al., 2007; Wang, 2010a, b), which was, unfortunately, misinterpreted as Ginkgoales (Kirchner and

Van Konijnenburg-Van Cittert, 1994; Van Konijnenburg-Van Cittert and Schmeiβner, 1999; Na et al., 2014). The traces of insect damages on the leaves of *Juraherba* (Figs. 2f, 2g, 5o), in addition to the associated insect fossil (Fig. 2a) and previous record (Van Konijnenburg-Van Cittert and Schmeiβner, 1999), imply that the ecological interaction history between angiosperms and insects may be much longer than previously assumed.

6 Conclusions

(1) *Juraherba bodae* gen. et sp. nov from the Middle Jurassic of Inner Mongolia, China is preserved as a whole plant, including roots, stem, leaves, and fructifications.

(2) The small size of *Juraherba* with fructifications enclosing ovules/seeds and lacking secondary growth indicates that it is a truthful herbaceous angiosperm.

(3) The Middle Jurassic age of *Juraherba* marks the earliest record of herbaceous seed plants and angiosperms.

(4) Analyses indicate that *Juraherba* lived in an aquatic habitat. The unexpected morphology of *Juraherba* undermines the mainstream thinking about angiosperm evolution.

(5) Fleshy fructifications and insect damage seen in *Juraherba* suggest that animal-angiosperm interaction may be much longer than previously assumed.

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