

Plant remains from the Middle–Late Jurassic Daohugou site of the Yanliao Biota in Inner Mongolia, China

CHRISTIAN POTT^{1,2*} and BAOYU JIANG³

¹LWL-Museum of Natural History, Westphalian State Museum and Planetarium, Sentruper Straße 285, DE-48161 Münster, Germany; e-mail: christian.pott@lwl.org

²Palaeobiology Department, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

³School of Earth Sciences and Engineering, Nanjing University, 163 Xianlin Avenue, Qixia District, Nanjing 210046, China

Received 29 June 2017; accepted for publication 20 October 2017

ABSTRACT. A late Middle–early Late Jurassic fossil plant assemblage recently excavated from two Callovian–Oxfordian sites in the vicinity of the Daohugou fossil locality in eastern Inner Mongolia, China, was analysed in detail. The Daohugou fossil assemblage is part of the Callovian–Kimmeridgian Yanliao Biota of north-eastern China. Most major plant groups thriving at that time could be recognized. These include ferns, caytonialeans, bennettites, ginkgophytes, czekanowskialeans and conifers. All fossils were identified and compared with species from adjacent coeval floras. Considering additional material from three collections housed at major palaeontological institutions in Beijing, Nanjing and Pingyi, and a recent account in a comprehensive book on the Daohugou Biota, the diversity of the assemblage is completed by algae, mosses, lycophytes, sphenophytes and putative cycads. The assemblage is dominated by tall-growing gymnosperms such as ginkgophytes, czekanowskialeans and bennettites, while seed ferns, ferns and other water- or moisture-bound groups such as algae, mosses, sphenophytes and lycophytes are represented by only very few fragmentary remains. The floral composition underlines the Callovian–Kimmeridgian age of the Yanliao Biota. The Daohugou/Yanliao flora is a typical member of the Middle to Late Jurassic *Coniopteris-Phoenicopsis* assemblage of north-eastern China, differing from the Early Cretaceous Jehol flora. Both floras probably belong to the same cycle of volcanism and sedimentation, although the Daohugou Bed is older than the Yixian Formation. The Yanliao fossil assemblage is placed in a larger palaeo-phytogeographical context and its relationships with Middle–Late Jurassic floras from north-eastern China, north-eastern and eastern Siberia and Japan are evaluated.

KEYWORDS: Daohugou Biota, Haifanggou Formation, Tiaojishan Formation, Liaoning, Hebei, Jehol Biota

INTRODUCTION

The Mesozoic biotas of north-eastern China, including the Middle–Late Jurassic Yanliao Biota (or Daohugou Biota of some authors), constitute exceptionally preserved fossil ecosystems, comprehensive studies of which, carried out during the last few decades, have revolutionized our understanding of animal and plant evolution (see e.g. Chang et al. 2003, Zhou et al. 2003, Benton et al. 2008, Huang 2017). The discoveries of articulated dinosaurs in these strata

are some of the most notable findings (e.g. Sullivan et al. 2014, Xu et al. 2014, Huang 2017), but the deposits have yielded an array of other vertebrate, invertebrate and plant remains, which provide evidence of a number of trophic levels and novel adaptations to specific habitats and selective environmental pressures. The record of vertebrate and invertebrate fossils from the Yanliao Biota has significantly increased during the last decade (e.g. Tan & Ren 2002, Huang et al. 2006, Meng et al. 2006, Wang et al. 2006, Gao et al. 2009, Zheng et al. 2009, Bi et al.

* corresponding author

2014, Sullivan et al. 2014, Xu et al. 2015, 2016), revealing a remarkably diverse and rich late Middle Jurassic fauna, whereas the associated plant fossils have received only scant attention (summarized in Huang 2017).

Plant fossils from Daohugou are well known and not very rare, but until now there has been no published comprehensive report from the Daohugou sites aimed at identifying the fossil plants systematically to place them in well-defined species. One problem hampering a deeper examination of those fossils is the incompleteness or imprecision of information on the provenance (locality, stratum) of many of the plant fossils assigned to “Daohugou” or “Yanliao”, such as that for many from the large museum collections of fossil plants stored in NIGPAS, STMNH and IVPP (for acronyms, see ‘Materials and Methods’), because they were obtained or purchased from local farmers or collectors, and precise information is commonly lacking (see Dong et al. 2017). There are several individual publications reporting on plant fossils from the Yanliao Biota (e.g. Zheng et al. 2003, Li et al. 2004, Zhou et al. 2007, Zheng & Wang 2010, Wang et al. 2007, 2010a, b, Zhang et al. 2011, Pott et al. 2012, 2015, Deng et al. 2014, Heinrichs et al. 2014, Na et al. 2014, Wei et al. 2015, Han et al. 2016, Liu & Wang 2015, 2017; Tab. 1), which all concentrate on single plant taxa or discuss individual aspects of the flora, but so far no comprehensive study of the Yanliao flora as a whole is available (except for the synoptic account in Zhang & Zheng 1987), despite the existence of hundreds of nicely preserved and showy fossils, which are available in different museum exhibitions and collections, and despite apparently ongoing intensive study of the plants as mentioned by Zheng and Wang (2010) or Liu and Wang (2017). Consequently, the plants provide a largely unexploited source of data for reconstruction of the palaeovegetation, habitats or plant-animal interactions in the Yanliao ecosystem. While the present study was being performed, a comprehensive book on the Daohugou Biota was published by Huang (2017), which includes a detailed study of plant fossils (Dong et al. 2017), the majority of them from the NIGPAS collection. However, many of the taxa in the report by Dong et al. (2017) were left in open nomenclature; a considerable number of them were identified by us to be conspecific with the specimens reported here. Thus, in many cases these were identified to species level.

In this paper we present an assemblage of plant fossils obtained during a recent excavation (July 2015) at two sites east of the village of Daohugou in Inner Mongolia, China. The excavation was undertaken to clarify the preservation conditions (diversity, abundance, plan-view orientation, extent of completeness and articulation, and size frequency) and the depositional environments of the Yanliao fossils (ongoing studies of Yang et al. and Wang et al.). In contrast to many other available plant fossils deriving from uncertain “Daohugou” localities and/or strata, the fossils under study here were obtained *in situ* and thus can unequivocally be assigned to the Daohugou locality as well as to definite and well-dated stratigraphic layers within the Daohugou Bed. These plant fossils may thus help in identifying other fossils deriving from that area. This paper is also one of the first more comprehensive reports on a larger collection of plant fossils from the Yanliao Biota within the last decades (see Dong et al. 2017).

MATERIAL AND METHODS

The plant fossils come from the vicinity of Daohugou village, Inner Mongolia, China (Fig. 1). The two excavation sites are the ‘North’ locality at 41°19′19.98″N, 119°14′13.56″E and the ‘South’ locality at 41°19′11.11″N, 119°14′07.24″E. Several hundred slabs were acquired and brought to the School of Earth Sciences and Engineering, Nanjing University, Nanjing, China, where all slabs including those yielding the plant fossils are stored. During the ongoing examination, so far 124 slabs have yielded fossil plant remains. Accession numbers were given to all of them (MES-NJU 57004 to MES-NJU 57127). The plant fossils are preserved as impressions in most cases; some appeared to be preserved as compressions, but attempts to isolate the organic matter and cuticles according to the processes outlined in, for example, Pott (2014, 2016) did not produce any useful results or cuticle remains. The descriptions of the plants are therefore based on the available macrofossils only. Data on epidermal anatomy was included only if it was available from other sources.

The macrofossils were photographed with a Nikon D750/Nikkor AF-SMikro 60-mm 1:2.8G ED system digital camera; to enhance contrast and fine detail, cross-polarization (i.e. polarized light sources together with an analysing filter in front of the camera lens) was used together with oblique lightning.

Larger collections of additional plant fossils from the Daohugou area are stored in the palaeobotanical collections of the Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP), Beijing, China; the Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGPAS), Nanjing, China; and the Shandong Tianyu Museum of Natural History

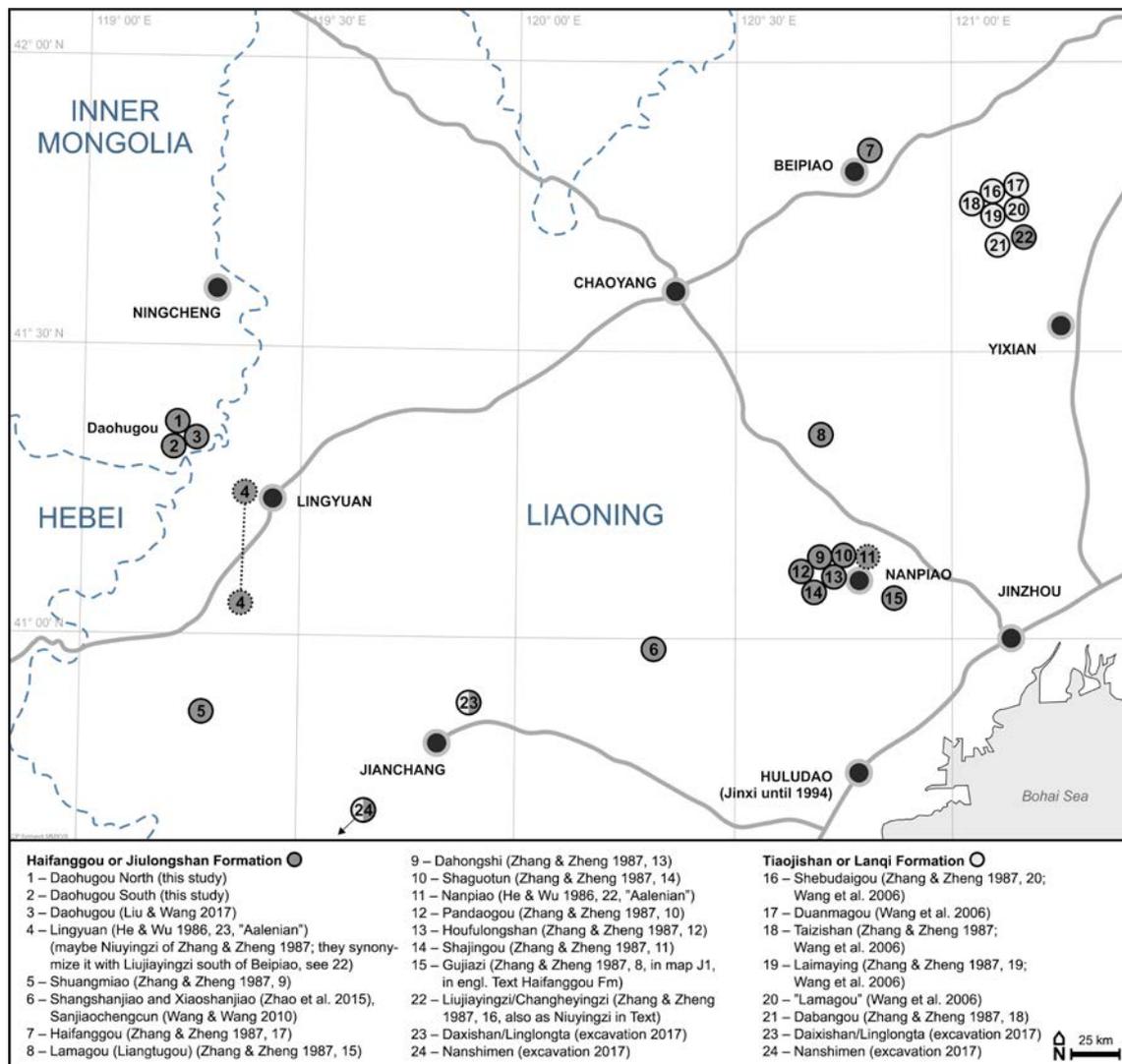


Fig. 1. Sketch map of western Liaoning and eastern Inner Mongolia, with the localities of late Middle to early Late Jurassic floras of the Haifanggou and Tiaojishan formations

(STMNH), Pingyi, Shandong, China. Those fossils should be considered with caution because for many of them the provenance (locality and stratum) is uncertain owing to insufficient, imprecise or absent relevant information accompanying these fossils. Some of them most likely originate from the Daohugou Bed but that is not unequivocally confirmed. In addition, many of the specimens, mainly those at STMNH, are not available for publication. The majority of those plant fossils were photographed by CP during 2009–2014. These fossils were not considered in the body of the present study, but since we have identified all those specimens down to species level as well as possible (Tab. 1) they were used as supporting evidence for the identification and description of the *in situ* fossils.

GEOLOGICAL SETTING

The Daohugou Bed is exposed along the boundaries of Inner Mongolia and Hebei and Liaoning provinces (Fig. 1). The Jurassic–Cretaceous succession in the region consists of, in

ascending order, the Haifanggou, Tiaojishan (or Lanqi of some authors), Tuchengzi and Yixian formations (Jiang et al. 2010). The Daohugou Bed belongs to the Haifanggou Formation. It comprises a 100–150 m thick sequence of greyish to green, very finely laminated tuffaceous silty claystones and tuffs alternating with cm-thick to tens of m-thick tuffs (Fig. 2) (ongoing work of Yang et al.). The individual beds are laterally persistent within the exposures and generally normal-graded, a typical deposition pattern within low-energy lacustrine settings.

Several recent isotope datings using $^{40}\text{Ar}/^{39}\text{Ar}$, SHRIMP U-Pb and LA-ICPMS Zircon U-Pb methods (e.g. Chen et al. 2004, He et al. 2004, Liu et al. 2006b, 2012, Chang et al. 2009) have indicated that the age of the tuff is between late Middle Jurassic and early Late Jurassic, or 165–158 Ma (e.g. Chen et al. 2004: 165–164 Ma; He et al. 2004: 159.8 Ma; Liu

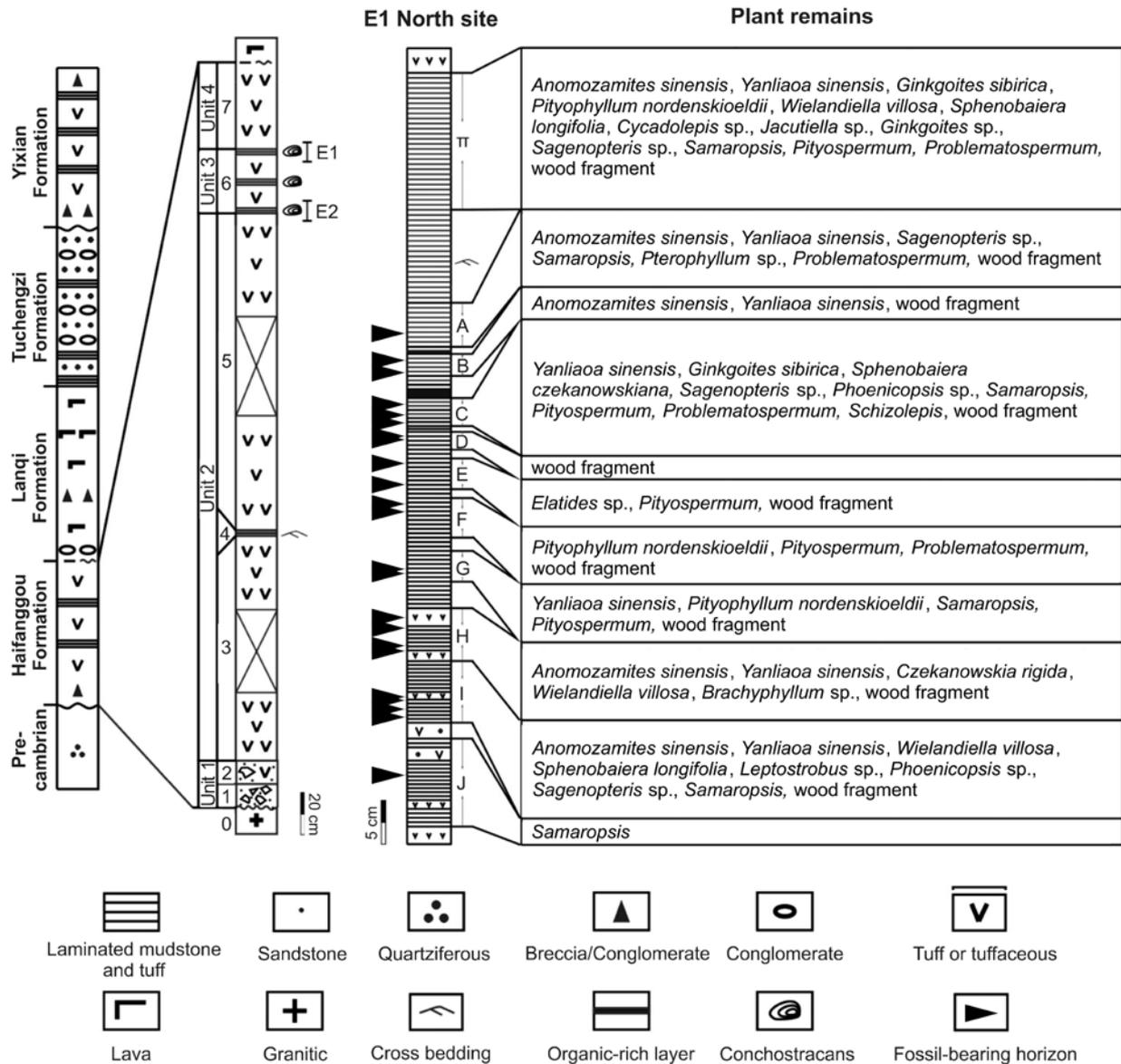


Fig. 2. Lithological succession of the Jurassic–Cretaceous and the Daohugou Bed in the Daohugou area (left), and the occurrence of plant fossils in the northern excavation pit (right; stratigraphic position is labelled E1 in the lithological log of the Daohugou Bed)

et al. 2006b: 164–158 Ma; Chang et al. 2009: 161–159 Ma; Liu et al. 2012: 161–159 Ma; Huang 2015: 168–163.5 Ma; Xu et al. 2016: 168–159 Ma; Zhou & Wang 2017: 160 Ma). Therefore the Daohugou Bed cannot be older than this age and the fossiliferous succession at Daohugou (the Haifanggou Formation) is thus dated as late Middle to early Late Jurassic (Callovian–Oxfordian) (Jiang et al. 2010, Cohen et al. 2013). It is considered to be the local equivalent of either the Jiulongshan Formation or Tiaojishan Formation in northern Hebei (e.g. Ren et al. 2002, Gao & Ren 2006). The precise age and stratigraphic position of the Daohugou Bed have been debated extensively (e.g. He et al. 2004, Wang et al.

2005, Gao & Ren 2006), but the vast majority of results published thus far indicate an early Late Jurassic (Callovian–Kimmeridgian) age for the Yanliao Biota (Ren et al. 2002, Shen et al. 2003, Chen et al. 2004, Liu et al. 2004, 2006a, b, Gao & Ren 2006, Huang et al. 2006, Yang & Li 2008, Zhang et al. 2008, Jiang et al. 2010, Cohen et al. 2013, and references therein).

Despite the lithological similarity between the Daohugou Bed and the Yixian Formation (Jehol Biota), they have yielded two distinctive fossil plant assemblages. They probably belong to the same cycle of volcanism and sedimentation, although the Daohugou Bed is older than the Yixian Formation. It might be argued that

the Yanliao fossil assemblage represents the earliest stage of the evolution of the Jehol Biota.

RESULTS (SYSTEMATIC PALAEOONTOLOGY)

Tracheophyta

Ferns (“Monilophyta”)

Polypodiopsida

Gleicheniales

Dipteridaceae

Clathropteris Brongn.
or *Hausmannia* Dunker

Clathropteris sp. or *Hausmannia* sp.

Pl. 1, fig. 1

Description. One specimen reminiscent of a clathropterid fern was recovered. The lamina portion preserved is 15 mm × 16 mm long and wide, and is derived from a middle portion of a frond segment, as no lamina margins are preserved. It shows the characteristic mesh-type venation pattern of fronds of *Clathropteris*-type ferns. Secondary veins build polygonal–rectangular meshes pervaded by tertiary (the ultimate visible) fine veins again building hexagonal–rectangular meshes. Each of these ultimate meshes is characterized by commonly four embossed spots representing the sori.

Remarks. Since no lamina margin is preserved, it is impossible to assign this specimen to any distinct *Clathropteris* species. The characteristic rectangular venation, however, allows the preserved portion to be recognized as a *Clathropteris* frond portion (see Harris 1961). The most common *Clathropteris* species reported from in and around the study area is *Clathropteris obovata* Ôishi (Wang 1984, He & Wu 1986, see Harris 1961). However, the density of sori per cm² in the specimen from Daohugou is significantly higher (100 sori/cm²) than reported by Harris (1961) for *Clathropteris obovata* (50 sori/cm²). Lee and Shen in Sze et al. (1963) described *Clathropteris pekinensis* Lee et Shen from the Upper Jurassic of the Zhaitang area in the Western Hills of

Beijing, which Duan (1987) deemed different from *Clathropteris obovata* based on the outline of the pinnae. The latter cannot be determined here, so here we refrain from assigning the specimens to a distinct species.

We are not aware of any *Clathropteris*-type fern reported from nearby Upper Jurassic deposits except for *Clathropteris obovata*, which is considered an “elder element” of the Late Jurassic floras in China persisting from the older *Dictyophyllum-Clathropteris* floras (Wang 1984, He & Wu 1986), and also a frond portion that was assigned to *Clathropteris meniscioides* Brongn. by Zhang and Zheng (1987). According to Wang (1984), *Clathropteris obovata* was recorded from the historical Chahar Province (Chahar Right Middle Banner; He & Wu 1986), which is the area where modern-day Daohugou is located, and from nearby Chengde, Hebei. The *Clathropteris meniscioides* specimen is not considered any further in the text by Zhang and Zheng (1987) except for an occurrence in the Haifanggou Formation from close to the town of Dahongshilazi in the vicinity of Nanpiao, Liaoning.

It has to be noted, however, that many different *Hausmannia* species have been described from several Mesozoic floras in northern China and adjacent Russia, including the Tiaojishan Formation and other Upper Jurassic formations, but none so far from the Haifanggou Formation (e.g. Sze 1933, Lebedev 1963, 1965, Zhang & Zheng 1987). *Hausmannia* species have a distinct frond shape that makes them easy to identify. However, if only a portion of the lamina is preserved such as the one under study here, it is difficult to identify as such because the secondary and tertiary venation is very similar in its pattern and architecture to those of *Clathropteris*. The primary veins in *Hausmannia* commonly show a dichotomous branching pattern and are much more prominent than the secondary veins, while they commonly branch pinnately after the initial dipterid branching in *Clathropteris*, and the secondary veins are almost similarly prominent (Schweitzer et al. 2009). In our opinion the present lamina portion thus derives from a *Clathropteris* frond, but it cannot entirely be ruled out that it is from a *Hausmannia* frond, as the preserved portion is relatively small.

Specimen investigated. MES-NJU 57083.

Seed plants (Spermatophyta)

Pteridospermopsida

Caytoniales

Sagenopteris C.Presl in Sternb.

Sagenopteris sp. cf.

Sagenopteris philippsii T.M.Harris

Pl. 1, figs 2–5

Description. Five specimens yield leaflets of *Sagenopteris* compound fronds. The incomplete leaflets are up to 84.2 mm long and 10.3 mm wide at their widest portion. All are elongate–lanceolate, with the acroscopic margin being slightly convex to almost straight or slightly concave and the basiscopic margin strongly convex, and continuously tapering towards the apex and base. They show characteristic *Sagenopteris*-type venation, with secondary veins emerging at very acute angles from the central leaflet vein and commonly bifurcating in the outer portion of the lamina, thereby anastomosing with adjacent veins. Judged from their degree of asymmetry, the smaller leaflets are interpreted to represent basal leaflets of the characteristic four-armed star-shaped outline of *Sagenopteris* leaves, while the long one represents one of the apical leaflets.

Remarks. Except for a few leaflets assigned to different *Sagenopteris* species from the Inner Zone of Japan (Ôishi 1940), we are not aware of any report of *Sagenopteris* leaves from Upper Jurassic deposits of China and eastern Russia. Wang (1984) described *Sagenopteris jinxiensis* Z.Q.Wang from the Western Hills of Beijing ('Lower Cretaceous') and mentioned *Sagenopteris colpodes* T.M.Harris from Qinglong ('Lower Jurassic'), easternmost Hebei, but the leaves assigned to *Sagenopteris jinxiensis* appear very much like the cordiform bracts of *Anomozamites haifanggouensis* (T.Kimura, T.Ohana, L.M.Zhao et B.Y.Geng) S.L.Zheng et L.J.Zhang (Kimura et al. 1994; see below). Dong et al. (2017) reported two species of *Sagenopteris* from the Daohugou Biota but left the nomenclature open (viz. *Sagenopteris* sp. 1 and *Sagenopteris* sp. 2); both leaflet types are identical to the leaflets figured here in Pl. 1, fig. 2 and Pl. 1, figs 3, 4, respectively.

The authors also figured a complete compound leaf of *Sagenopteris* sp. 1. The recognition of two species by Dong et al. (2017) might be justified, but more material would provide more solid evidence for the separation into two species. The leaflets are very similar to *Sagenopteris philippsii* described by Harris (1964) from the Middle Jurassic of Yorkshire, UK. Whether or not the leaflets from Daohugou are conspecific with the species from Yorkshire is difficult to ascertain, due to the small sample size and the very fragmented record from eastern Russia and north-eastern China, but the leaflets give a strong indication.

Specimens investigated. MES-NJU 57004, 57015, 57082, 57100, 57107.

Gymnospermae

Cycadopsida

Bennettitales

Wielandiella (Nath.) Nath.

Wielandiella villosa (C.Pott, McLoughlin, S.Q.Wu et E.M.Friis) C.Pott

Pl. 1, figs 6–8; Pl. 2, fig. 1; Fig. 3d

- 2012 *Anomozamites villosus*, Pott et al., p. 50, pl. 1, figs 1–3, pl. 2, figs 1–3, pl. 3, figs 1–3, pl. 4, figs 1–6.
- 2015 *Wielandiella villosa*, Pott et al., p. 139, text-figs 2–14.
- 2017 *Anomozamites villosus*, Dong et al., p. 270, text-figs 8-23, 8-25.
- 2017 *Anomozamites* sp. 2, Dong et al., p. 271, text-fig. 8-27.

Diagnosis. See Pott et al. (2012, 2015).

Description. Portions of sterile leaves of *Wielandiella villosa* were found on nine specimens. All specimens yield incomplete leaves, the longest of which is almost entirely preserved and reaches 130 mm in length and 32.8 mm in width. The impari-pinnate, small, narrow-oblong to oblanceolate leaves lack an apical leaflet; they are regularly segmented, with subopposite to alternate inserting leaflets. The leaflets are densely arranged, inserted laterally to the rachis at almost 90° and entirely free up to the base; they are falcate to quadrate in outline, with slightly contracted bases and obtusely rounded apices. Several fine

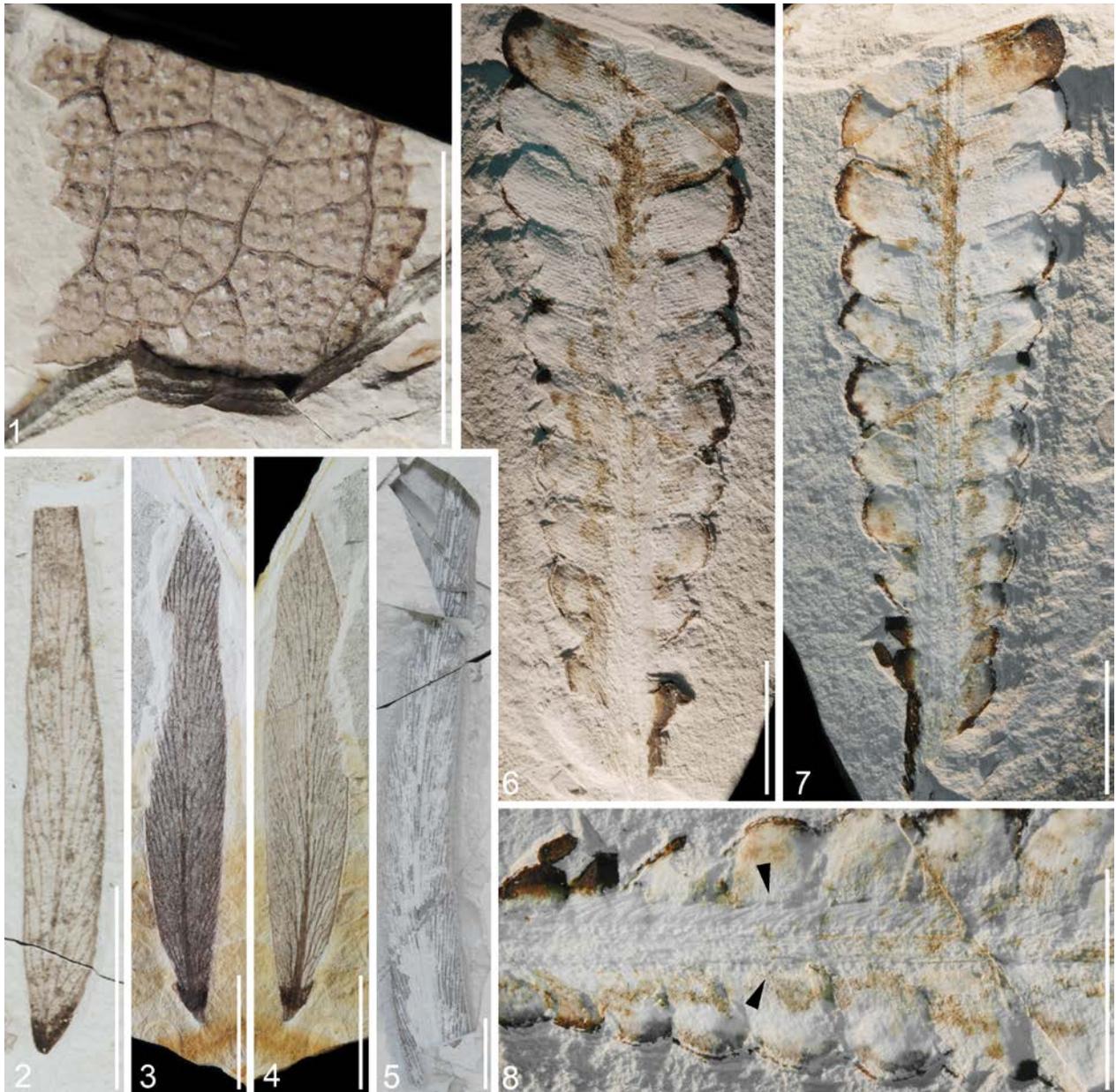


Plate 1. Ferns, seed ferns and bennettites from the Daohugou Bed. 1. *Clathropteris* sp. or *Hausmannia* sp.; 2–5. *Sagenopteris* sp. cf. *Sagenopteris philippsii*; 6–8. *Wielandiella villosa*, note the stiff hairs along the rachis margins (arrowheads). Scale bars – 1 cm

veins enter the leaflets and bifurcate close to the rachis; they then traverse the leaflet perpendicular to the rachis. In two specimens the characteristic dense cover of long and stiff hairs on the abaxial side of the rachis is recognizable (Pl. 1, figs 6–8). The cover with soft and shaggy hairs on the abaxial leaflet surface is hardly recognizable on the specimens at hand, and many are preserved with the adaxial side upwards, obscuring the indumentum.

Remarks. *Wielandiella villosa* was described from Daohugou in detail by Pott et al. (2012) and reconstructed as a shrub-sized bennettite with a divaricate branching system or growth

form (Pott et al. 2015). Dong et al. (2017) included the leaves as *Anomozamites villosus* in their account of the Daohugou Biota. Some of the leaves that were regarded by Dong et al. (2017, i.e. text-fig. 8-23) as belonging to *Anomozamites haifanggouensis* are in our opinion leaves of *Wielandiella villosa*, but their indumentum is not recognizable, probably because the leaves are preserved with their abaxial side downwards. The specimens of Dong et al. (2017, text-fig. 8-27) assigned to *Anomozamites* sp. 2 are clearly identifiable as *Wielandiella villosa*, as they show the characteristic stiff hairs along the rachis, together with the typical outline and shape of the

leaflets. The new specimens are regarded as conspecific with those reported by Pott et al. (2012, 2015). No reproductive structures were found in the present assemblage. Pott et al. (2015) argued that several ovulate cones from Daohugou may derive from the same parent plant as the *Wielandiella villosa* leaves and branches, but no organic connection could prove this association. Similar cones were reported from the Daohugou Biota as *Williamsonia* sp. by Dong et al. (2017, text-fig. 8-32). All those cones are very similar to if not identical with ovulate cones from the Lanqi Formation at Taizishan and Shebudai, close to Beipiao, Liaoning, described by Zhang and Zheng (1987) as *Williamsoniella sinensis* W.Zhang et S.L.Zheng, but they were not known to Pott et al. (2015) at that time. Foliage fitting *Wielandiella villosa* has also been described from the Lanqi Formation at the same localities as *Anomozamites kornilovae* E.R.Orlovskaya, but neither in Zhang and Zheng (1987) nor in the original work by Doludenko and Orlovskaya (1976) were the characteristic trichomes and indumentum of the leaves mentioned or visible in the figures, so we refrain from regarding these as conspecific with *Wielandiella villosa* until further evidence reveals their conspecificity.

Specimens investigated. MES-NJU57014, 57016, 57022, 57049, 57054, 57061, 57074, 57076, 57087, 57092.

Anomozamites Schimp.

Anomozamites sinensis

(W.Zhang et S.L.Zheng) emend. C.Pott

Pl. 2, figs 2–4; Fig. 3a

1987 *Anomozamites sinensis*, Zhang and Zheng, p. 277, pl. 6, figs 2–7, text-fig. 17.

2017 *Anomozamites* sp. 3, Dong et al., p. 271, text-fig. 8-28.

Emended diagnosis. Petiolate leaves, shed as a whole, lanceolate to obovate in outline; lamina regularly segmented into suboppositely positioned leaflets; leaflets twice as wide as long; lamina tapering towards apex and base; leaf apex retuse or emarginated; the two uppermost leaflets variably long, resulting in subopposite leaflet positions; leaflets densely arranged, inserted laterally to the rachis, with straight margins; venation dense, veins entering the lamina at 80°–85°, bifurcating once in

their proximal third and proceeding straight to the leaf margin (translated and emended from Zhang & Zheng 1987).

Description. One of the more common cycadophyte plants and probably the most iconic one from Daohugou is represented by leaves of *Anomozamites sinensis*. Entire leaves are petiolate and lanceolate to obovate in overall outline, with a lamina that is more or less regularly segmented into suboppositely arranged leaflets, which are commonly twice as wide as long. Leaves are up to 150 mm long and 18–20 mm wide in the middle portion. The lamina tapers regularly towards the apex and the base of the leaves. The petiole is prominent and continues into the 1–2-mm-wide rachis. The apex is retuse or emarginate, with the two uppermost leaflets forming a notch; these leaflets are commonly variably long, resulting in the subopposite arrangement of the more proximal leaflets. The common leaflets are more or less of constant width, typically 13 mm long and ca 20 mm wide, inserted to the rachis at almost 90°. The leaflets are inserted laterally to the rachis, and both the acroscopic and the basisopic margins are not decurrent but slightly curved; the margins are commonly straight, however. The leaflets do not overlap but are arranged very densely and may touch each other. The outer margin is straight and slightly rounded according to the overall shape of the leaf. The leaflets are traversed by 20–23 veins per cm, entering the lamina at 80°–85°, bifurcating once in their proximal third and proceeding straight to the leaf margin. Occasional later bifurcations occur but only in veins that remained simple until then.

The leaves are hypostomatic. Zhang and Zheng (1987) described the cuticle as follows: “Cuticle relatively thick, cuticles of both sides of the leaf are of equal thickness. Costal and intercostal fields of the adaxial epidermis comprise elongate rectangular cells, anticlinal walls slightly undulate, periclinal walls coarsely granulate or with striae, the boundaries of lateral walls (dorsal or anticlinal) are not clear; stomata and hair bases absent. Costal fields of the abaxial epidermis comprise slightly elongate rectangular cells, the boundaries between costal and intercostal fields are not entirely clear, round papillae or hair bases are present on the surface; cells in intercostal fields are irregularly arranged, mainly rectangular in outline, also triangular or irregularly polygonal. Anticlinal



Plate 2. Bennettites from the Daohugou Bed. 1. *Wielandiella villosa*; 2–4. *Anomozamites sinensis*; 5. *Pterophyllum* sp.; 6. *Anomozamites* sp.; 7. *Cycadolepis* sp. cf. scale leaves of the plant *Anomozamites haifanggouensis*; 8. *Pterophyllum lamagouense*. Scale bars – 1 cm

cell walls are slightly undulate, the periclinal walls are coarsely granulate or equipped with elongate thick striae; stomata are irregularly oriented and randomly distributed but restricted to the intercostal fields; their number is not very high. The stomatal apparatus is of the brachyparacytic (syndetocheilic) type and of irregular shape, 30–50 μm \times 50–70 μm wide and long, respectively. The guard cells are slightly sunken and unevenly cutinized on the pore side; the inner walls of the subsidiary cells overlap with the guard cells and are occasionally thick. The periclinal walls are straight or slightly undulate, sometimes produce papillae, but are often granulate or striate.”

Remarks. *Anomozamites sinensis* was described by Zhang and Zheng (1987) from the Haifanggou Formation of Liangtugou and Lamagou close to Chaoyang in Liaoning, and from the Tiaojishan Formation at Taizishan. Zhang and Zheng (1987) were able to isolate cuticles and reveal the bennettitalean nature of the species. However, the authors reported only incomplete leaves and were not able to describe the leaf apex, which is here added; we also emend the diagnosis and description of the species accordingly. Additional almost complete leaves were reported by Dong et al. (2017) from the Daohugou Biota as *Anomozamites* sp. 3.

There are many leaves, more or less entire-margined or loosely segmented and of comparable appearance, reported from adjacent Upper Jurassic deposits, many of which have been assigned to *Nilssonia* species due to their lamina that is attached to the upper surface of the rachis. Those that appear very similar to the leaves described here include several leaves assigned to *Nilssonia orientalis* Heer or *Nilssonia schmidtii* (Heer) Seward by authors including Heer (1876a, 1878) and Dobruskina (1965). They agree very much in outline with *Anomozamites sinensis* but the attachment of the leaflets to the rachis as well as the simple venation in *Nilssonia* species discriminates the leaves. Heer (1878) described some plant specimens from Jurassic deposits north-west of Irkutsk, Siberia, as *Anomozamites lindleyanus* Schimp.; they are very similar to the leaves assigned here to *Anomozamites sinensis*. They agree in all dimensions, in venation details and also in leaflet variability with *Anomozamites sinensis*, and may be conspecific, especially since the original leaves assigned to *Anomozamites lindleyanus* from the Middle Jurassic of Yorkshire (Lindley & Hutton 1831–1833) are different from those of Heer (1878) and some of them were assigned by Harris (1969) to *Anomozamites nilssonii* (J. Phillips) Seward, which is characterized by much slender and longer leaflets, and to *Nilssonia compta* (J. Phillips) Göpp., which has similar leaflets that are, however, inserted to the upper side of the rachis. The leaves from the Irkutsk Basin can therefore not be regarded as conspecific with *Anomozamites lindleyanus* but might instead be assigned to *Anomozamites sinensis*. *Anomozamites sinensis* has no apical leaflet but instead a retuse or emarginate leaf apex; Heer (1878, p. 5) reported that there is “no apical leaflet present”, even though he illustrated one specimen with a tiny apical leaflet. The differences between *Anomozamites sinensis* and *Anomozamites latipinnatus* Z.Q. Wang (Wang 1984) are not obvious to us, but we have only seen Xerox copies of Wang (1984) and must refrain from asserting that these species are conspecific. The leaves we obtained better fit *Anomozamites sinensis*, based on the shape and outline of its leaflets.

Specimens investigated. MES-NJU 57002, 57007, 57011, 577012, 57019, 57047, 57051, 57056, 57058, 57085, 57105, 57114.

Anomozamites sp.

Pl. 2, fig. 6; Fig. 3b

Description. One specimen yields a segmented leaf with six pairs of leaflets which have a particular triangular shape. The whole leaf is 63.6 mm long, including a petiole 11 mm long; the leaflets are inserted laterally with their full basal width to a thin rachis 1–2 mm wide, and have a triangular shape, with both margins slightly convex. The basisopic margin is slightly more convex than the acrosopic, which gives the leaflets the appearance of being bent forward. The leaflets are 6–10 mm wide at their base and the longest leaflets are up to 10.0 mm long. Apically, one pair of tiny leaflets is preserved, but it cannot be said whether these are the apical leaflets or rather are only imperfectly preserved. A darker area is visible wherever the incisions between the leaflets reach the rachis. Whether these are incrustations or adcrustations of or to the lamina is difficult to ascertain, but they extend over the rachis and the basal portions of the leaflet lamina. Eleven to thirteen veins enter each leaflet; some bifurcate once close to the rachis. All veins traverse the leaflets straight towards the margin. The latter is obscured by sediment in most leaflets, but the vein courses and a comparison with a number of other specimens from the Daohugou Bed stored at STMNH confirm the leaflet shape as depicted in Fig. 3b.

Remarks. A species that is very similar to if not conspecific with the leaves described here is *Pterophyllum helmersianum* Heer, reported from the Upper Jurassic of the Upper Amur Basin, Siberia, by Heer (1876a). The specimens agree in every detail except that Heer (1876a, p. 104) noted that the Amurian specimens have veins that are “simple throughout”. Whether this is correct or whether Heer (1876a) may have overlooked the tiny bifurcations of some veins close to the rachis cannot be ascertained for certain. The species *Pterophyllum helmersianum*, however, should be transferred to *Anomozamites* on account of its leaflet length/width ratio (see Pott & McLoughlin 2009) and that is why we assigned the specimen to *Anomozamites* sp. The leaves reported by Dong et al. (2017) from the Daohugou Biota as *Anomozamites* sp. 1 might belong here, but this cannot be confirmed unequivocally.

Specimens investigated. MES-NJU 57090, 57119.

***Cycadolepis* sp. cf. scale leaves of the plant
*Anomozamites haifanggouensis***
(T.Kimura, T.Ohana, L.M.Zhao et B.Y.Geng)
S.L.Zheng et L.J.Zhang

Pl. 2, fig. 7

Description. One specimen yields a portion of a scale leaf confidently identified as *Cycadolepis*. The preserved portion of the elongate-ovate scale leaf is 27.0 mm long and 11 mm wide. The entire margin is convex on the lateral edges, perfectly rounded at the apex, and bluntly cut off (abscised) on the proximal end of the scale leaf. Its thick lamina is characterized by the typical longitudinal striae regularly crossed by horizontal striae, the latter of which are commonly interpreted as derivatives of shrinking after abscission.

Remarks. Very similar scale leaves were reported from the Haifanggou Formation of Pandaogou (Nanpiao District, Liaoning) by Zhang and Zheng (1987) as *Cycadolepis nanpiaoensis* W.Zhang et S.L.Zheng. These, however, are usually tapering towards the base, and it cannot be positively determined whether the specimen at hand is abscised as is or if the tapering basal portion is not preserved. Regarding the apex, the specimen at hand fits *Cycadolepis nanpiaoensis* very well. In some cases such scale leaves are connate to the base of a cordiform bract with a particular venation (Zhang & Zheng 1987, Kimura et al. 1994, Zheng et al. 2003). The latter are also found isolated among the plant fossils from Daohugou at STMNH (CP, own observation, 24 October 2014). These scale leaf-bract complexes were formally assigned to *Cycadicotis nilssonervis* Pan *ms.* by Zhang and Zheng (1987). Kimura et al. (1994) regarded *Cycadolepis nanpiaoensis* and *Cycadicotis nilssonervis* as conspecific and introduced the new name *Pankuangia haifanggouensis* T.Kimura, T.Ohana, L.M.Zhao et B.Y.Geng for the species. Later, Zheng et al. (2003) found these organs attached to whorls of *Anomozamites* foliage and included the scale leaf-bract complexes in *Anomozamites haifanggouensis*. Dong et al. (2017) reported several scale leaves from the Daohugou Biota, some with attached bract-like leaves as are typical for *Anomozamites haifanggouensis*, and some with open nomenclature as *Cycadolepis* spp.

Specimen investigated. MES-NJU 57106.

***Pterophyllum* Brongn.**

Pterophyllum lamagouense
W.Zhang et S.L.Zheng

Pl. 2, fig. 8; Fig. 3c

1987 *Pterophyllum lamagouense*, Zhang and Zheng, p. 279, pl. 7, figs 1–8, pl. 26, figs 2, 3, text-fig. 18.

Diagnosis. Leaves lanceolate, lamina segmented, gradually tapering towards apex and base of leaves; rachis prominent in basal part, continuously narrowing towards apex, transversely striate. Leaflets inserted laterally to rachis, slightly expanded basally, in contact with each other, slightly curved towards leaf apex, bluntly rounded apically, basally inserted on rachis at 89°–90°, the more proximal ones slightly bent upwards. Veins obvious, parallel, usually not bifurcating, the outer vein on the acroscopic and basisopic margins ending at leaf margin, the other veins proceeding to apex; each leaflet contains 9–11 veins (translated from Zhang & Zheng 1987).

Description. One specimen yields a complete segmented leaf with cycadophyte appearance, 109 mm long and 21.8 mm wide at its widest portion. The arcuate leaflets with the concave acroscopic margin and the strongly convex basisopic margin are inserted by their whole basal width; their apices are acutely rounded. Leaflets are up to 15.7 mm long and 2.7–3.3 mm wide basally, laterally inserted, and arranged oppositely to slightly suboppositely. Twenty-four pairs of leaflets constitute the petiolate leaf; the petiole is 24.8 mm long. The lowermost leaflets are only up to 4 mm long; leaflet length then increases continuously until the leaf apex except for the apical-most two leaflets, which are again shorter but also bent towards the central rachis. An apical leaflet is not recognizable but probably is obscured by the rock matrix. Venation is hardly observable but some leaflets show a semblance of fine parallel venation, with up to 12 veins per leaflet. The 2.3–2.5-mm-wide rachis tapers towards the leaf apex and is longitudinally striate, with a central 1-mm-wide groove.

The leaves are hypostomatic. The cuticle of *Pterophyllum lamagouense* is, according to Zhang and Zheng (1987), “well-preserved and the cuticles of both sides of the leaf are of equal thickness. Costal and intercostal fields of the adaxial epidermis comprise four to five rows of rectangular, regularly arranged cells;

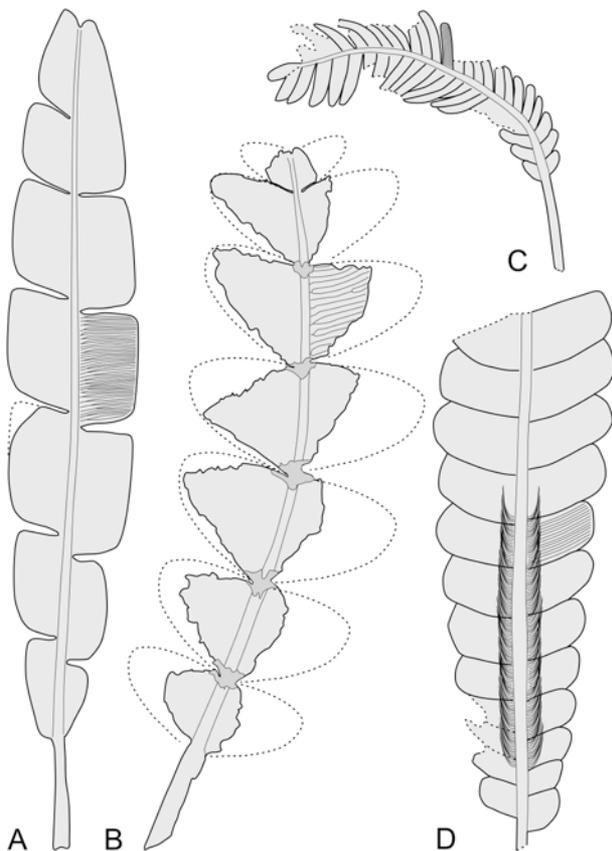


Fig. 3. Line drawings of selected taxa. **A.** *Anomozamites sinensis*; **B.** *Anomozamites* sp.; **C.** *Pterophyllum lamagouense*; **D.** *Wielandiella villosa*, note the stiff hairs along the rachis that have been partly illustrated in the proximal portion

intercostal field cells are mainly polygonal, hardly in line; cell walls are finely undulate; papillae occur occasionally but no stomata. Epidermal cells of the costal fields of the abaxial epidermis are irregularly arranged, anticlinal cell walls are undulate; stomata occur occasionally on the margins but papillae are more common. Intercostal fields of the abaxial epidermis comprise irregularly arranged polygonal cells; a high number of stomata are unevenly distributed, with their pores arbitrarily oriented. Sometimes two to three adjacent stomata are joined in one complex. Stomatal density is 78–84 stomata/mm². The stomatal apparatus is of the brachyparacytic (syndetocheilic) type and 30–60 μm \times 40–70 μm in size. The guard cells are slightly sunken but strongly cutinized; the inner side of subsidiary cells slightly overlaps with the guard cells.”

Remarks. The specimen can be identified with specimens from the Haifanggou Formation at Lamagou in western Liaoning, reported by Zheng and Zhang (1987) as *Pterophyllum lamagouense*. Zhang and Zheng (1987) were able to isolate cuticles from their specimens,

demonstrating the bennettitalean nature and justifying the assignment to *Pterophyllum*. Some specimens from the Upper Jurassic of the Upper Amur Basin assigned to *Pterophyllum helmersianum* by Heer (1876a) appear very similar to *Pterophyllum lamagouense*, but a definite assignment is not possible based on the schematic line drawings of Heer (1876a). Several well-preserved leaves of *Pterophyllum lamagouense* were found in high abundance in the Haifanggou and Tiaojishan formations at Nanshimen and Daxishan/Linglongta in Hebei and Liaoning on a recent excavation by us (June 2017).

Specimen investigated. MES-NJU 57050.

Pterophyllum sp.

Pl. 2, fig. 5

Description. One specimen yields a portion of a cycadophyte leaf with one pair of parallel-sided leaflets preserved. The leaflets are rectangular, inserted by their whole base laterally to the 1-mm-wide rachis, slightly decurrent acroscopically and more decurrent basiscopically. The leaflet apex is truncate. The leaflets are 20.2–22.8 mm long and 8 mm wide and maintain their width from the base up to the apex. The parallel veins bifurcate once close to the rachis and then proceed straight to the apex, with occasional further bifurcations in the lower third of the leaflet. The leaflets contain 19–20 veins, and it is interesting to note that the bifurcation pattern is the same in both oppositely arranged leaflets, but mirror-inverted.

Remarks. Despite being very incomplete, the specimen can be identified with leaflets of *Anomozamites angulatus* Heer reported from the Upper Jurassic of the Upper Amur Basin by Heer (1876a) and from the Lower Cretaceous of the Bureya Basin by Vachrameev and Doludenko (1961), and later by Zheng and Zhang (1987) from the Haifanggou Formation at Pandaogou. However, based on the rather technical classification of bennettitalean leaves deployed by Harris (1969), Watson and Sincock (1992) and later refined by Pott and McLoughlin (2009), the species should be transferred to *Pterophyllum* on account of its leaflet length/width ratio, and that is why we assign the specimen here to the latter. A number of similar segmented leaves are

reported from the Upper Jurassic of western Liaoning and Daohugou (e.g. *Tyrmyia taizishanensis* W.Zhang et S.L.Zheng, *Tyrmyia valida* W.Zhang et S.L.Zheng, *Anomozamites kornilovae* or *Wielandiella villosa*; Heer 1876a, 1878, Zhang & Zheng 1987, Pott et al. 2012, 2015), but none of them has the characteristic rectangular shape of the leaflets. A species from the Middle Jurassic of Europe that is very similar is *Anomozamites nilssonii* from the Middle Jurassic of Yorkshire (Harris 1969).

Specimen investigated. MES-NJU 57009.

Jacutiella Samylyna

Jacutiella sp. cf. *Jacutiella denticulata* W.Zhang et S.L.Zheng

Pl. 3, figs 1, 2

Description. One petiolate, strap-shaped leaf with a prominent rachis is preserved on one specimen. The incomplete leaf is 17.8 cm long and 20.9 mm wide at its widest preserved portion. The rachis is basally 5.1 mm wide and tapers slightly down to 2.8 mm wide along the course of the preserved leaf portion; basally it extends into a petiole 40.6 mm long. The lamina is inserted on the upper side to the rachis close to its margin, leaving the central rachis part exposed. The lamina tapers continuously from the distal end of the preserved portion to the base, and is characterized by several parallel veins arising perpendicularly from the rachis and proceeding straight to the margin. The veins bifurcate once close to the rachis; further bifurcations were not observed. Vein density is 10–11 veins per centimetre. The lamina margin is not preserved in any part of the leaf or is obscured by the rock matrix.

Remarks. *Jacutiella* is a bennettite genus erected by Samylyna (1956) based on specimens from the Lower Cretaceous along the Aldan River in Siberia. It is characterized by a lamina that is attached to the upper side of the rachis but on its edges, leaving the central portion free, by its bifurcating veins that arise perpendicularly from the midrib, and by the bennettitalean type of stomata, although the latter was illustrated neither by Samylyna (1956) nor later by Samylyna (1963), but definitely described. Apart from its type *Jacutiella amurensis* V.A.Samylyna from the Lower Cretaceous of Siberia and *Jacutiella denticulata* from the Upper Jurassic

of Shebudai in Liaoning (Zhang & Zheng 1987), no other species are known so far. It should be mentioned that Krassilov (1973a) made the new combination *Nilssoniopteris amurensis* (V.A.Samylyna) Krassilov based on fossils assigned to *Jacutiella amurensis* by Samylyna (1963). However, we do not agree with this new combination (see Van Konijnenburg-van Cittert et al. 2017). In its macromorphology, the specimen under study here is very similar to those reported by Zhang and Zheng (1987) as *Jacutiella denticulata*. All are very similar to those reported by Samylyna (1956) and therefore the allocation to *Jacutiella* is warranted, even if neither Zhang and Zheng (1987) nor we could provide epidermal details. Whether our specimen is identical with *Jacutiella denticulata* cannot be determined unequivocally, as the leaf margin, the feature separating *Jacutiella denticulata* from *Jacutiella amurensis*, is obscured, but it is very likely that the specimens from Shebudai and Daohugou are conspecific.

Specimen investigated. MES-NJU 57060.

Ginkgoopsida

Ginkgoales

Ginkgoites Seward

Ginkgoites sp. cf. *Ginkgoites huttonii* (Sternb.) Heer

Pl. 3, figs 3, 4

Description. The specimen consists of part and counterpart and shows a typical ginkgoalean leaf, of which only one half is preserved, with one major but deep incision resulting in two basally contracted lobes, which are oblong–ovate in outline with presumably obtusely rounded apices. The lobes are 9.0 mm and 9.5 mm wide at their widest expansion, which is in the upper third of the lobes. The preserved portions of the lobes are 51.3 mm and 52.2 mm long, respectively. Fifteen and 17 veins are recognizable at the widest expansion of each lobe, which arise through several bifurcations occurring in the lower half of the lobes from only three veins that enter the lobes, but all continue until the apex.

Remarks. There is no clear consensus as to whether such foliage is placed in *Ginkgo* or *Ginkgoites*. Current opinions and views were

outlined in Pott et al. (2016); we follow that approach and place the specimen in *Ginkgoites* but with close resemblance to what is commonly described as *Ginkgo(ites) huttonii*. The specimen is very similar in shape, number of veins and measurements to specimens that Heer (1876a) and Vachrameev and Doludenko (1961) described as *Ginkgo(ites) huttonii* from the Irkutsk and Bureya basins in Siberia. The latter, however, is from Cretaceous sediments and later was re-described as *Ginkgoites vachrameevii* Doludenko et Lebedev by Doludenko and Lebedev (1972). Judging from the species reported by Heer (1876a, 1878) and based on later studies of specimens from the same localities (e.g. Vachrameev & Doludenko 1961, Doludenko & Lebedev 1972) and from the Middle Jurassic of Yorkshire (Harris et al. 1974), as well as by comparison with several other specimens from Daohugou at STMNH (CP, own observation, 24 October 2014), we regard this Daohugou specimen as closely resembling *Ginkgoites huttonii*. The main characters for our identification are the rather wide, undivided lobes, the rounded lobe apices and the number of veins, which bifurcate only in the lower half (see Harris et al. 1974). These distinguish it from *Ginkgo(ites) digitata* Nath., *Ginkgo(ites) sibirica* (Heer) Walkom and *Ginkgo(ites) lepida* (Heer) Heer, all of which are also reported from Upper Jurassic deposits of the area (e.g. Heer 1876a, 1878, Vachrameev & Doludenko 1961, Harris et al. 1974). We reserve judgement somewhat on account of the absence of epidermal details, which are crucial in unequivocally identifying the different *Ginkgo/Ginkgoites* species in question (see Vachrameev & Doludenko 1961, Harris et al. 1974, Pott et al. 2016). *Ginkgoites huttonii* is a very widespread species in Late Jurassic floras, occurring more or less all over the Northern Hemisphere in a belt between 40° and 60° latitude (Heer 1876a, 1878, Vachrameev & Doludenko 1961, Harris et al. 1974, Vachrameev 1991, Pott et al. 2016), but see Doludenko and Lebedev (1972) and Krassilov (1972), who concluded that *Ginkgo(ites) huttonii* did not occur in the Mesozoic of Russia; Krassilov (1972) erected *Ginkgo jampolensis* (Lebedev) Krassilov and placed *Ginkgo vachrameevii* and the *Ginkgo huttonii* specimens of Vachrameev and Doludenko (1961) in its synonymy. Zhang and Zheng (1987) figured specimens assigned to *Ginkgo(ites) huttonii*

from the Haifanggou Formation at Lamagou, but the authors do not consider the species further in the text; the specimens fit very well but are only half the size (we assume that the figure is only reproduced half the size). Dong et al. (2017) placed similar specimens from the Daohugou Biota in *Ginkgoites* sp. 1; they very likely belong here.

Specimens investigated. MES-NJU57024, 57101, 5727.

Ginkgoites sibirica (Heer) Walkom

Pl. 3, figs 5, 6

- 1876a *Ginkgo sibirica*, Heer, p. 61, pl. 7, fig. 6, pl. 9, fig. 5b, pl. 11, figs 1–8.
 1987 *Sphenobaiera colchica*, Zhang and Zheng, p. 305, pl. 29, fig. 2.
 2017 *Ginkgoites* sp. 2, Dong et al., p. 278, text-fig. 8-35.

Diagnosis. See Harris et al. (1974).

Description. One specimen yields an incomplete ginkgoalean leaf, which is deeply incised into two lobes that again are deeply incised into two slender lobes each. The lobes are elongate and lanceolate in outline, with one showing an acutely rounded apex. The longest preserved lobe portions are 33 mm and 43 mm long and 4.4 mm and 5.1 mm wide at their widest expansion. Up to ten inconspicuous veins are recognizable in the lobes, bifurcating at the base of the lobes and running to the apex.

Remarks. The specimen from Daohugou, even though incomplete, can be assigned with confidence to *Ginkgoites sibirica* based on its overall outline, lobe shape, incisions, measurements and vein number (see remark above on the use of *Ginkgo* and *Ginkgoites*). Heer (1876a) described *Ginkgo(ites) sibirica* and *Ginkgo(ites) lepida* from the Middle Jurassic of the Irkutsk Basin. Both species agree very much with one another, and even Heer (1876a) initially had difficulty separating the two species based on the specimens available to him. In fact the only difference the author gave is the more acute lobe apices in *Ginkgo(ites) lepida*. Comparing the leaves figured by Heer (1876a, 1880), however, it seems difficult to separate the two species, and even Harris et al. (1974) were not able to convincingly distinguish the two when measuring and summarizing the most obvious characters. Given the overall variability

of *Ginkgo* and *Ginkgoites* leaves, and the fact that in Heer's (1876a, 1880) illustrations a definite boundary between the "round" lobe apices of *Ginkgo(ites) sibirica* and the "more acute" ones in *Ginkgo(ites) lepida* cannot be recognized (see also Pott et al. 2016), we here regard *Ginkgo(ites) sibirica* and *Ginkgo(ites) lepida* of Heer (1876a, 1880) as conspecific with *Ginkgoites sibirica* (see Dobruskina 1965). Harris et al. (1974) apparently were of the same opinion when they united several Jurassic specimens from eastern Asia and Europe under *Ginkgo(ites) sibirica*, including several reports that initially distinguished between *Ginkgo(ites) sibirica* and *Ginkgo(ites) lepida*. Epidermal details of Heer's specimens are unavailable. The specimen reported here from Daohugou lacks information on its epidermal anatomy as well, but based on its shape, measurements and vein number, it is confidently placed in *Ginkgoites sibirica*. This identification is confirmed by even more specimens from Daohugou investigated at STMNH (CP, own observation, 24 October 2014). The specimen reported as *Sphenobaiera colchica* (Pryn.) G.V.Delle from the Haifanggou Formation at Lamagou by Zhang and Zheng (1987) belongs here as well. Dong et al. (2017) placed similar specimens from the Daohugou Biota in *Ginkgoites* sp. 2; they very likely belong here too.

Specimens investigated. MES-NJU57041, 57110.

Sphenobaiera Florin

Sphenobaiera longifolia (Pomel) Florin

Pl. 3, fig. 7

1847 *Dicropteris longifolia*, Pomel, p. 339.

1876a *Baiera longifolia*, Heer, p. 52, pl. 10, figs 1–5, pl. 7, fig. 1.

Diagnosis. Leaves broadly petiolate, split dichotomously into 4, 5 und 6 linear, parallel-sided segments with bluntly rounded apices; 3–7 parallel, longitudinal veins, which do not bifurcate (based on Heer 1876a).

Description. The preserved portion is from the basi-central part of a leaf, with one bifurcation almost in the middle. The preserved portion of the deeply incised leaf is 79 mm long. At its proximal end the leaf is 5.7 mm wide, expanding to 11.7 mm at the bifurcation and

then incised into two slightly tapering lobes, which initially are 5.8 mm and 6.6 mm wide but expanding slightly to 8.0 mm and 7.4 mm, respectively, towards their distal ends. Ten to eleven veins traverse the lobes up to the apex; longitudinal striae between them suggest further venation. At the proximal end, towards the leaf base, 5–6 veins are recognizable, which immediately bifurcate continuously to support the venation of the lobes.

Remarks. The specimens are confidently identified with specimens reported by Heer (1876a, 1880) as *Baiera longifolia* Heer from the Upper Jurassic of the Upper Amur Basin, with which they agree in outline, measurements and number of veins. Florin (1936) erected *Sphenobaiera* to accommodate such leaves without a distinct petiole, and transferred *Baiera longifolia* to *Sphenobaiera* (see Dobruskina 1965). *Sphenobaiera longifolia* is, according to Heer (1876a, 1880), one of the most common and a quite variable species in the Upper Jurassic of Siberia and the Upper Amur Basin.

Specimen investigated. MES-NJU 57102.

Sphenobaiera czekanowskiana

(Heer) Florin

Pl. 3, fig. 8

1876a *Baiera czekanowskiana*, Heer, p. 56, pl. 10, figs 1–5, pl. 7, fig. 1.

2017 *Baiera* sp., Dong et al., p. 279, text-fig. 8-38.

Diagnosis. Leaves broadly petiolate, split dichotomously into 6–8 linear segments, slightly tapering towards the acutely rounded apices (based on Heer 1876a).

Description. The preserved portion of this deeply incised leaf is 13.8 cm long. The bifurcation of the leaf is at 50 mm measured from the base of the leaf, resulting in two very thin, parallel-sided lobes, which are 3.5 mm and 4.0 mm wide, and 88 mm and 43 mm long, respectively. The first has a preserved apex that is acutely rounded; the second is incomplete. The leaf is not petiolate. Four to six veins traverse the lobes to the apex, arising from two that enter each lobe at the bifurcation point.

Remarks. The specimens are confidently identified with specimens reported by Heer (1876a, 1880) as *Baiera czekanowskiana* from the Middle Jurassic of Ust-Balej in the Irkutsk Basin,

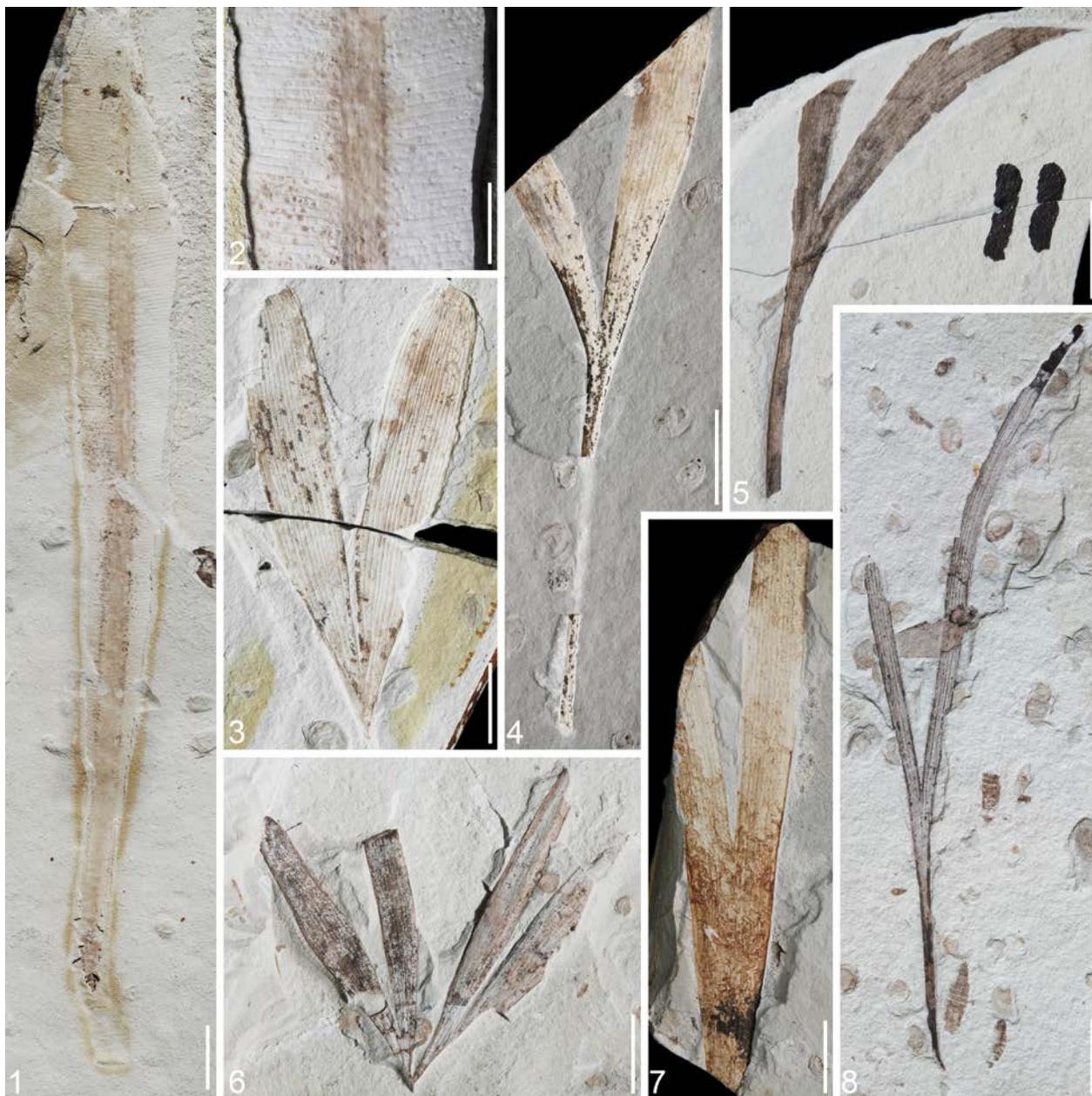


Plate 3. Bennettites and ginkgophytes from the Daohugou Bed. **1, 2.** *Jacutiella* sp. cf. *Jacutiella denticulata*; **3, 4.** *Ginkgoites* sp. cf. *Ginkgoites huttonii*; **5, 6.** *Ginkgoites sibirica*; **7.** *Sphenobaiera longifolia*; **8.** *Sphenobaiera czekanowskiana*. Scale bars – 1 cm

with which they agree in outline, measurements and number of veins. Florin (1936) erected *Sphenobaiera* to accommodate such leaves without a distinct petiole, and *Baiera czekanowskiana* is consequently transferred to *Sphenobaiera*. Zhang and Zheng (1987) illustrated one specimen as *Baiera czekanowskiana* and one as *Sphenobaiera angustiloba* from the Haifanggou Formation in western Liaoning (Pandaogou and Liujiaying, Beipiao, Liaoning). Both are here regarded as conspecific with the Daohugou specimens. *Sphenobaiera angustiloba* (Heer) Florin was erected by Heer (1878) based on very few specimens, said to differ from *Sphenobaiera czekanowskiana* in having even narrower lobes,

fewer veins and deeper incisions. However, the specimens illustrated by Heer (1878, pl. 3; 1880) for *Sphenobaiera angustiloba* and *Sphenobaiera czekanowskiana* are, despite being illustrated on the same plate, not distinguishable. There are no differences in vein number, nor in lobe width or length, nor in incision patterns. Therefore, *Sphenobaiera angustiloba* should be regarded as junior synonym of *Sphenobaiera czekanowskiana*. Dong et al. (2017) placed a similar specimen from the Daohugou Biota in *Baiera* sp.; it very likely belongs here.

Specimens investigated. MES-NJU 57026, 57032, 57079.

Incertae classis

Czekanowskiales

Phoenicopsis Heer

Phoenicopsis sp.

cf. ***Phoenicopsis speciosa*** Heer

Pl. 4, figs 1, 2

Description. Two specimens yield strap-shaped leaves with parallel venation. The apex of the lanceolate leaves is acutely rounded and the leaf tapers at the base, continuing into a very short petiole or abscission area. The leaves are 6.5 mm and 10.0 mm wide at their widest portion, and 11.2 cm and 15.3 cm long, respectively. Eight and ten veins traverse the leaves, arising from a few bifurcations in the lowermost portion of the leaves.

Remarks. These leaves very likely represent disintegrated parts of short shoots of *Phoenicopsis*, of which *Phoenicopsis speciosa* is the most common species in the Upper Jurassic in the surroundings of the study area (Heer 1876a, 1878, Vachrameev & Doludenko 1961, Dobruskina 1965). The leaves agree in outline, size and venation pattern very well with those described for *Phoenicopsis speciosa* by Heer (1876a). Zhang and Zheng (1987) described similar leaves from the Haifanggou Formation at Liujiaying and Changheying, Beipiao, Liaoning), which they assigned to *Phoenicopsis speciosa* as well.

Specimens investigated. MES-NJU57018, 57055.

Czekanowskia Heer

Czekanowskia rigida Heer

Pl. 4, fig. 3

1876a *Czekanowskia rigida*, Heer, p. 70, pl. 5, figs 8–11, pl. 6, fig. 7, pl. 10, fig. 2b.

2017 *Solenites* sp., Dong et al., p. 282, text-fig. 8-39.

Diagnosis. *Czekanowskia* with very slender leaves, 1 mm wide, with slender central depression (Heer 1876a, p. 70).

Description. *Czekanowskia*-like, caducous short shoots with long needle-like leaves are found on two specimens. The whole short shoot is 127 mm long, producing remnants of at least

two highly dissected leaves. At about half of their length the leaves are dissected into at least two recognizable portions each. The leaves are 1 mm wide along their entire length; the longest leaf is 121 mm long. All leaves are pervaded by a single central vein along their entire length; the vein builds a spiny tip at the leaf apex. The base of the shoot, the spur shoot, is 5 mm in diameter and built of scale-like leaves, the tips of two of which can be recognized in the specimens.

Remarks. The short shoots preserved here are very similar to specimens that Heer (1876a, p. 26, 1878, 1880) illustrated from the Upper Jurassic of the Upper Amur (“very common”) and Irkutsk basins, and can without doubt be regarded as conspecific. *Czekanowskia rigida* is distinguished from the co-occurring *Czekanowskia setacea* by the leaves, which are only 0.5 mm wide in the latter but 1 mm wide in the former. *Czekanowskia rigida* is known from the Upper Jurassic of the Upper Amur and Bureya basins (Vachrameev & Doludenko 1961, Dobruskina 1965), Transcaucasia (Delle 1967) and western Liaoning (Zhang & Zheng 1987), and from many more Late Jurassic floras of eastern Asia, rendering it an excellent index fossil of these Late Jurassic floras. However, the specimens from the Bureya Basin were regarded as different from *Czekanowskia rigida* and are identified as *Czekanowskia aciculata* Krassilov by Krassilov (1972). Dong et al. (2017) placed similar specimens from the Daohugou Biota in *Solenites* sp. 1; in our opinion they belong to *Czekanowskia rigida* as well.

Specimens investigated. MES-NJU57046, 57089.

Leptostrobus Heer

Leptostrobus sp.

cf. ***Leptostrobus laxiflora*** Heer

Pl. 4, figs 4, 6

Description. One specimen yields a reproductive structure that can be identified from its overall architecture, shape and habit as a *Leptostrobus* cone. The preserved portion of the cone is 107 mm long. It bears pairs of capsules placed at regular distances of 5–6 mm in a decussate arrangement. The scale-like capsules are 7–9 mm long and 4–5 mm wide, bearing two or three lobes at their apex and only faintly distinguishable ribs; the middle



Plate 4. Czekanowskiales and conifers from the Daohugou Bed. 1, 2. *Phoenicopsis* sp. cf. *Phoenicopsis speciosa*; 3. *Czekanowskia rigida*; 4–6. *Leptostrobus* sp. cf. *Leptostrobus laxiflora*; 7, 8. cf. *Ixostrobus* sp.; 9, 10. *Yanliaoa sinensis*; 11. *Brachyphyllum* cf. *Brachyphyllum longispicum*; 12, 13. *Pityophyllum nordenskiöldii*; 14. *Elatides* sp. cf. *Elatides falcata*. Scale bars – 1 cm

lobe is emphasized, giving the scale a keeled appearance at the base. The outer surface of the capsules is characterized by faint longitudinal striae. The cone axis is 1.0–1.5 mm wide, reaching almost 2 mm in width in its more proximal portion.

Remarks. This reproductive structure is identified as a *Leptostrobus* cone based on its architecture and the typical capsules, which have the same shape as in other cones attributed to *Leptostrobus*. The specific allocation is indeed much more difficult. Harris et al. (1974) made the point that epidermal details gained

from cuticles provide characters required for proper species allocation. *Leptostrobus cancer* T.M.Harris from the Middle Jurassic of Yorkshire, for example, is distinguished from the almost identical *Leptostrobus laxiflora* through epidermal details and stomata characteristics such as the much thicker cutinized subsidiary cells in *Leptostrobus laxiflora*, as well as the “strong papillate border” (Harris et al. 1974, p. 123). Information on the epidermal anatomy of our specimen is not available. Zhang and Zheng (1987) assigned one similar cone from the Haifanggou Formation in western Liaoning to *Leptostrobus cancer*, which might

be justified based on its small capsules; the authors pointed to its difference from the more robust *Leptostrobus laxiflora* with larger capsules. However, from the size range of the capsules, the few prominent lobes, the loose architecture of the cone and the width of the rachis, it is more likely that our cone is conspecific with *Leptostrobus laxiflora* (see Heer 1876a, 1880, Vachrameev & Doludenko 1961, Krassilov 1968). Support also comes from its distribution and the attribution of the cones to sterile foliage: *Leptostrobus laxiflora* has repeatedly been recorded from the Middle Jurassic to Lower Cretaceous of China and Siberia and then attributed to *Czekanowskia rigida* (Heer 1876a, 1880, Vachrameev & Doludenko 1961, Krassilov 1968, 1970, Harris et al. 1974, Duan 1987), which is present in the Daohugou floras as well, while *Leptostrobus cancer* is known from Western Europe and commonly occurred together with *Solenites* (Harris et al. 1974). Based on this evidence, we assign the cone to *Leptostrobus laxiflora* but with some reservations. Whether the specimen of Zhang and Zheng (1987) should be transferred to *Leptostrobus laxiflora* as well should be evaluated based on the original material, which was not at hand here. Dong et al. (2017) placed similar specimens from the Daohugou Biota in *Leptostrobus* sp.; in our opinion they are conspecific with the specimens reported here.

Specimen investigated. MES-NJU 57017.

***Ixostrobus* Racib.**

cf. *Ixostrobus* sp.

Pl. 4, figs 7, 8

Description. The preserved portion of the cone is 18.1 mm long and 4.85 mm wide at its widest portion. On a ca 0.5-mm-wide central axis the structure bears numerous scales at regular distances of ca 1 mm; whether they are borne spirally or in whorls is not definitely ascertained, but the arrangement is probably spiral. The appendices have a very thin stalk and widen distally to a head, continuing into a small pointed scale. Pollen sacs are adumbrated by paler brown matrix between the stalks of the appendices.

Remarks. The reproductive structure might be identified from its overall architecture, shape and habit as an *Ixostrobus* cone, but the

specimen can only be tentatively placed here, as more evidence from, for example, the form of epidermal anatomy or the outline of proper pollen sacs and appendices might be needed for further identification. Our identification is based on its architecture and the typical appendices, which have the same shape as other cones ascribed to *Ixostrobus*. The specific allocation is difficult. Harris et al. (1974) argued that only epidermal details gained from cuticles provide the information needed for a proper species allocation. Heer (1876a, 1880) assigned several very similar cones to different species of *Ginkgo*, *Baiera* and *Antholithus*, on the assumption that the proximity of the cones and foliage indicates that they belong to the same parent plant. Many of Heer's cones were identified by Harris et al. (1974) as probably belonging to *Ixostrobus*, which these authors placed among *Czekanowskia*les. We here refrain from assigning the cone at hand to any particular species reported from the Upper Jurassic of Siberia, the Upper Amur Basin or north-eastern China (e.g. Heer 1876a, 1880, Harris et al. 1974, Zhang & Zheng 1987, Sun et al. 2001), as it does not yield enough information. Whether or not the cone is conspecific with any of the reported ginkgoalean or *czekanowskia*lean leaves may be clarified when more material becomes available. Dong et al. (2017) assigned similar specimens from the Daohugou Biota to *Ixostrobus* sp.; in our opinion they are conspecific with the specimens reported here.

Specimen investigated. MES-NJU 57096.

Coniferopsida

Pinales

***Yanliaoa* Pan**

***Yanliaoa sinensis* Pan**

Pl. 4, figs 9, 10

1977 *Yanliaoa sinensis*, Pan, p. 70, pl. 1, figs 1–4.

2017 *Yanliaoa* sp., Dong et al., p. 287, text-figs 8–48, 8–49.

Diagnosis. See Pan (1977).

Description. The most common plant fragments are short conifer branches densely covered with needle-like leaves characterized by a central double-vein entirely traversing the leaves from base to apex. The leaves are densely arranged and inserted alternately; it

appears that they are inserted to the upper side of the rachis but at the edge, leaving the central part of the rachis free. The elongate, almost parallel-sided leaves are 7.5–9.0 mm long and 1.0–1.5 mm wide and inserted at 18°–25°. The leaf apices are bluntly rounded; at their base the leaves taper very abruptly and are slightly decurrent. The longest preserved shoot fragment is 74 mm long and carries 24 leaves on either side. No cones attached to any shoot fragments were found.

Remarks. The branch fragments are identical to branches described as *Yanliaoa sinensis* by Pan (1977) from the Late Jurassic Yanliao Biota in western Liaoning. Pan (1977) described branches with attached male and female cones. The fragments found here have no cones preserved, but can, based on the shape, arrangement and architecture of the branches and leaves, be confidently identified with *Yanliaoa sinensis*. Similar shoot fragments were described by Zhang and Zheng (1987) from Pandaogou in western Liaoning. Pan (1977) argued that *Yanliaoa* and *Elatides* are two closely allied genera, based mainly on the female cones and scales, but in *Elatides* the leaves are borne helically around the axes, while in *Yanliaoa* they are borne in two rows above the lateral margin of the rachis. In this character they may be much closer to leaves assigned to the form-genus *Elatocladus* (Harris 1979). The shoot fragments that Heer (1876a, 1880) assigned to *Lycopodites tenerimus* Heer might belong here, but this cannot be verified from the schematic drawings given by Heer (1876a). Many of the leaves have bluntly rounded apices, while all species assigned to *Elatocladus* from the Middle Jurassic of Yorkshire are characterized by having leaves with spiny or acute apices (Harris 1979). Pan (1977) compared the leafy shoots with extant *Sequoia sempervirens* Endl., and indeed they show great similarities, leading Pan (1977) to suggest *Yanliaoa* as an ancestor of modern Taxodiaceae. Dong et al. (2017) assigned several similar specimens from the Daohugou Biota to *Yanliaoa* sp.; in our opinion they are conspecific with the specimens reported here.

Specimens investigated. MES-NJU57008, 57013, 57021, 57033, 57038, 57039, 57042, 57045, 57048, 57057, 57059, 57062, 57063, 57066, 57067, 57077, 57099, 57103, 57108, 57111, 57115, 57118, 57120, 57121, 57123, 57124.

Brachyphyllum Brongn.

Brachyphyllum **cf. *Brachyphyllum longispicum***

G.Sun, S.L.Zheng et S.W.Mei

Pl. 4, fig. 11

Description. One specimen yields a coniferous leafy shoot entirely covered with spirally arranged, close-fitting rhombic scaly leaves. The preserved branch portion is 72.5 mm long and 9–11 mm wide. The scaly leaves are keeled and have an acutely pointed apex; they are 5–6 mm long and 2.0–2.5 mm wide.

Remarks. The shoot at hand is poorly preserved, making identification down to species level almost impossible, but from its nature it can confidently be placed in *Brachyphyllum* (see Harris 1979). However, there are identical shoots on additional specimens from Daohugou at STMNH (CP, own observation, 24 October 2014), which suggests that the shoot under study here can be assigned to *Brachyphyllum longispicum*, a species erected by Sun et al. (2001) from the Lower Cretaceous of western Liaoning. It is interesting to note that no similar species were reported from the Jurassic of Siberia and the Upper Amur Basin by Heer (1876a, 1880) or from the Haifanggou Formation of western Liaoning by Zhang and Zheng (1987). Dong et al. (2017), however, found some similar specimens from the Daohugou Biota and assigned them to *Brachyphyllum* sp.; in our opinion they are conspecific with the specimens reported here.

Specimen investigated. MES-NJU 57122.

Pityophyllum (Nath.) Seward

Pityophyllum nordenskiöldii (Heer) Nath.

Pl. 4, figs 12, 13

1876b *Pinus nordenskiöldii*, Heer, p. 45, pl. 9, figs 1, 3–5.

1897 *Pinites (Pityophyllum) nordenskiöldii*, Nathorst, p. 68.

2017 *Taxus* sp., Dong et al., p. 290, text-fig. 8–53.

Diagnosis. *Pinus* with single, firm, flattened and long linear leaves with one vein, barely narrowing towards the acuminate apex, base bluntly rounded (translated from Heer 1876b).

Description. Several specimens yield nee-

dle-like leaves characterized by having a single prominent vein. The parallel-sided leaves are up to 55 mm long and 3–4 mm wide at their widest portion; they taper abruptly at their proximal and distal ends to form an acute apex and a very slender, contracted leaf base. In many specimens the tip and base of the leaves are darker-stained, perhaps indicating desiccation effects, as that is not uncommon in modern conifers. One specimen shows a leafy shoot bearing several of these needle-like leaves, arranged in a decussate manner around a central axis. In this shoot the longest leaves reach 11.6 mm in length.

Remarks. The leaves and the shoot at hand are confidently identified with specimens from the Upper Jurassic of the Upper Amur and Bureya basins that Heer (1876a, 1880) assigned to *Pinus nordenskiöldii* Heer. The species was later transferred to *Pityophyllum* (the foliage of *Pinites*) by Nathorst (1897), a decision confirmed by Dobruskina (1965). *Pityophyllum nordenskiöldii* apparently had a rather extended distribution; it is known from the Upper Jurassic of Svalbard and Japan (Nathorst 1897), but so far no such leaves have been described from Inner Mongolia and western Liaoning (Zhang & Zheng 1987), except for one specimen assigned to *Pityophyllum staratschinskii* (Heer) Nath. by Zhang (1976) from the Upper Jurassic of Wuchuan in Inner Mongolia and Daqingshan in Heilongjiang. The specimens from the Daohugou Biota reported by Dong et al. (2017) as *Taxus* sp. are, in our opinion, better placed in *Pityophyllum nordenskiöldii* as well.

Specimens investigated. MES-NJU57065, 57084, 57104, 57117 + three specimens without numbers.

Elatides Heer

Elatides sp. cf. *Elatides falcata* Heer

Pl. 4, fig. 14

Description. Three specimens yield leafy conifer shoots resembling species commonly attributed to *Elatides*. The longest preserved portion is a 51.6 mm long shoot entirely covered by slender needle-like leaves, which appear to be arranged spirally around the axes. The leaves are 4–5 mm long and appear to be keeled and with a spiny apex. The leaves

roll outwards in their proximal half but then bend in again in their apical portion. Small scale leaves may cover the rachis but this is difficult to observe.

Remarks. The shoots at hand are poorly preserved and further identification is impossible. Zhang and Zheng (1987) did not report any specimen or species that can be regarded as similar. Neither did Vachrameev and Doludenko (1961) or Dong et al. (2017). Heer (1876a) described some *Elatides* species from the Upper Jurassic of the Upper Amur and Irkutsk basins, of which *Elatides falcata* appears very similar if not conspecific in its habit, dimensions and shape. Another similar species is *Elatides williamsonii* T.M.Harris from the Middle Jurassic of Yorkshire (Harris 1979), but as Harris (1979) correctly stated, much more information, such as on cones and leaf anatomy, is needed for a sound species identification. Consequently, we keep the identification with some reservations until more material from Daohugou becomes available.

Specimens investigated. MES-NJU57034, 57043, 57088, 57113.

Seeds

In this section we describe disarticulated seeds found in the assemblage. For each seed type a possible allocation to a plant group is discussed, but since this is in many cases debatable, we have kept the seed descriptions separate from the systematics section above.

Single-winged seeds

Pl. 5, figs 1–6

Description. Single-winged seeds are found on 14 specimens excluding counterparts. They can be grouped into two size categories but in general have the same architecture and appearance. The smaller seeds are 2.8–3.2 mm × 6.0–8.5 mm in size and have an ovate wing, an ovate grain (1.0 mm × 1.5 mm in size), and a prominent rim. The larger seeds are up to 6.5–9.0 mm × 19.0–20.5 mm in size and have an elongate–triangular wing and a roundish grain (4.0–5.0 mm in diameter) but also a prominent rim. The wing, in both size categories, is traversed by faint striae radiating from the grain and proceeding to the margin of the wing. The seeds appear robust; the wing probably was delicate and membranous.

Remarks. Comparable seeds were reported by Heer (1876a) as *Pinus maakiana* Heer from the Upper Jurassic of the Upper Amur and Irkutsk basins. The seeds illustrated by Heer (1876a) are intermediate between the two size categories described above, and members of those also show transitions. Consequently, it is possible that all these seeds come from the same parent plant species and that their variability is attributable to their location (origin) in the cone. In modern *Pinus* species the seeds show considerable variation in size depending on the placement of the producing scale in the cone. Sun et al. (2001) reported *Pityospermum* sp. from the Lower Cretaceous of Liaoning. Zhang and Zheng (1987) assigned similar seeds to *Pityospermum* cf. *Pityospermum maakianum* (Heer) Nath. and *Pityospermum* cf. *Pityospermum moelleri* Seward from the Haifanggou Formation at Pandaogou. Similar seeds were reported from the Daohugou Biota by Dong et al. (2017) and collectively assigned to *Pityospermum* spp.

Specimens investigated. MES-NJU57025, 57028, 57035, 57036, 57037, 57064, 57068, 57069, 57072, 57073, 57075, 57078, 57080, 57093, 57094, 57097, 57098, 57112, 57116, 57126.

Seed pappi attributable to
Problematospermum Turut.-Ket.

Pl. 5, figs 7, 8

Description. Two specimens provide remnants of seeds that can be attributed to *Problematospermum*. The specimens at hand yield only the hairy appendix (pappus) of the seeds, but their shape, structure and arrangement of the hairs confirm the affiliation. The hairy appendixes are 18 mm and 20 mm long and are preserved in the typical fan-shaped manner. The individual hairs are less than or up to a tenth of a millimetre in width.

Remarks. Since only the pappi of the seeds are preserved, we cannot assign the seeds to any species, which are commonly identified by the shape and size of the grains. Seeds with this type of pappi were reported from Upper Jurassic deposits of western Liaoning (Wang et al. 2010b) but are more common in Lower Cretaceous deposits (e.g. *Problematospermum beipiaoense* G. Sun et S.L. Zheng, *Problematospermum ovale* Turut.-Ket.) (Wu 1999, Sun et al. 2001,

Friis et al. 2011). The seeds are also commonly known from Upper Jurassic deposits (e.g. Turutanova-Ketova 1930a, Krassilov 1973b, 1997), including several records from Daohugou (Wang et al. 2010b). Krassilov (1973b, 1997) suggested a bennettitalean affinity of these pappose seeds; this view has since then been emphasized in several later studies (e.g. Sun et al. 2001, Friis et al. 2011, Pott & McLoughlin 2014). Similar Early Cretaceous seeds have been assigned to presumed angiosperm-like *Typhaera fusiformis* Krassilov by, for example, Krassilov (1982) and Wu (1999), but Wang et al. (2010b) regarded these as congeneric since there are no recognizable differences between these seeds. Similar seeds were reported from the Daohugou Biota by Dong et al. (2017) and collectively assigned to *Problematospermum ovale*.

Specimens investigated. MES-NJU57006, 57031, 57095.

Seeds with lateral flanges attributable to
Samaropsis Göpp.

Pl. 5, figs 9–11

Description. Three seeds are characterized by a profound lateral flange. The roundish to ovate grains appear robust and are 6.5 mm × 11.0 mm to 4.5 mm × 5.5 mm in size. The elongate grain is surrounded by a less robust flange up to 2 mm wide, which forms two characteristic bulges at the apical end of the seed. One of the seeds has remnants of an indumentum.

Remarks. The seeds can be attributed to *Samaropsis* based on their characteristic shape (see Heer 1876a, 1880, Krassilov 1982), which is known from Middle Jurassic to Lower Cretaceous deposits from eastern Siberia and throughout northern China. Affiliation of these seeds with conifers has been asserted (Krassilov 1982). A specific assignment cannot be made due to the paucity of information, but the seeds most probably belonged to two different parent species. Similar seeds include *Samaropsis rotundata* Heer and *Samaropsis kajensis* Heer from the Jurassic of the Upper Amur and Irkutsk basins (Heer 1876a, 1880). It should be noted that Heer (1880) figured a very similar seed as a seed of *Baiera longifolia* (Pomel) Heer on plate 2, figure 6b. Similar seeds were reported from the Daohugou Biota by Dong et al. (2017) and collectively assigned to *Carpolithes* spp.; in our opinion these are better placed in *Samaropsis*.

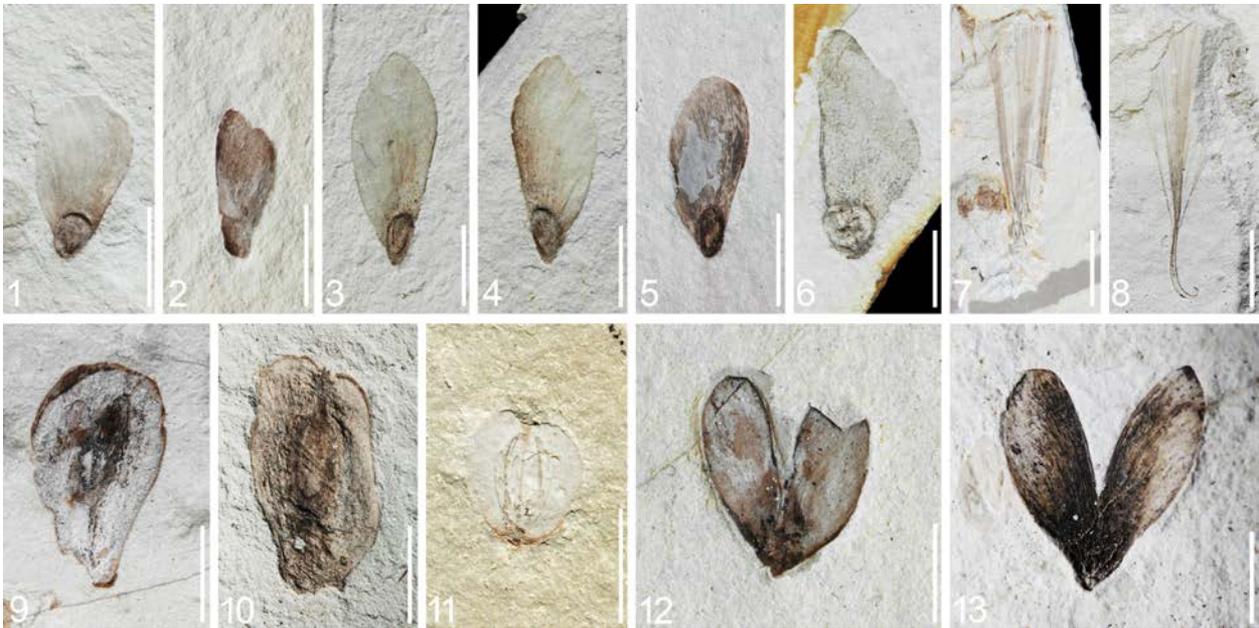


Plate 5. Dispersed seeds from the Daohugou Bed. **1–6.** Single-winged seeds attributable to *Pityospermum* (see text); **7, 8.** Seed pappi attributable to *Problematospermum* (see text); **9–11.** Seeds with lateral flanges attributable to *Samaropsis* (see text); **12, 13.** Double-winged seeds attributable to *Schizolepis* (see text). Scale bars – 1 cm

Specimens investigated. MES-NJU57052, 57071, 57109, 57125.

Double-winged seeds attributable
to *Schizolepidopsis* Doweld

Pl. 5, figs 12, 13

Description. Among the seeds found in this assemblage are two double-winged seeds. The seed-scale-complex has a short stalk and is deeply divided into two lobes. The lobes are lanceolate to ovate in shape, 12 mm and 14 mm long and 4.0–4.5 mm wide. Each seed bears a grain in its proximal portion, which is ovate with a flat surface, and 2.5 mm × 4.5 mm in size. The wings in both are membranous and traversed by faint striae radiating from the grain and proceeding to the margin of the wing

Remarks. The fossil *Schizolepis* was transferred in *Schizolepidopsis* by Doweld (2001), because the generic name was preoccupied by an extant angiosperm genus. The seeds are confidently identified with similar seeds from the Lower Cretaceous of western Liaoning assigned to *Schizolepis* (Sun et al. 2001). The form genus apparently has a long range from the Upper Triassic to the Lower Cretaceous. It is difficult to determine whether the seeds from Daohugou are of the same (parent) species as the Lower Cretaceous seeds assigned to *Schizolepis jeholensis* H.Yabe et S.Endô by Sun et al. (2001), but they are very similar

if not conspecific. Information on cones is so far unavailable from Daohugou. Neither Heer (1876a, 1880) nor Vachrameev and Doludenko (1961) mentioned similar specimens from any of the Middle–Upper Jurassic localities in that area, but Zhang and Zheng (1987) illustrated one similar isolated seed as *Schizolepis* sp. from the Haifanggou Formation at Pandaogou, as well as seeds attached to a cone, as *Schizolepis dabangouensis* W.Zhang et S.L.Zheng from the slightly younger Tiaojishan Formation at Dabangou. Conspecificity with the latter can be neither proven nor excluded, but is very likely. Dong et al. (2017) reported several *Schizolepis* seeds from the Daohugou Biota that are organically connected to cones. The authors placed these in two different species such as *Schizolepis daohugouensis* J.Zhang, A.d’Rozario, J.Yao, Z.Wu et L.Wang and *Schizolepis moelleri* Seward. The seeds reported here cannot be assigned to either species unequivocally.

Specimens investigated. MES-NJU57027, 57030.

DISCUSSION

During a recent excavation close to Daohugou village, Inner Mongolia, we collected the assemblage of plant fossils presented here. These fossils were obtained *in situ*, so their locality and stratigraphic position are known

precisely. Consequently, they can be confidently assigned to the Callovian–Oxfordian (165–158 Ma) Haifanggou Formation underlying the slightly younger Kimmeridgian (≥ 157 Ma) Tiaojishan Formation (e.g. Chen et al. 2004, He et al. 2004, Liu et al. 2006b, 2012, Chang et al. 2009, Jiang et al. 2010, Huang 2015, Xu et al. 2016, Zhou & Wang 2017), both of which, however, are known to have produced the Yanliao Biota. The assemblage of plant fossils presented here may thus serve for the identification of other fossils from that area.

COMPOSITION OF THE DAOHUGOU FLORA

Our examination revealed that at the time the Yanliao Biota thrived in what now is north-eastern China, all major plant groups present at that time were represented in the Daohugou flora. These include algae, mosses, lycophytes, sphenophytes, ferns, seed ferns, cycadophytes, ginkgophytes and conifers. Reports of several species of so-called “undercover angiosperms” (Wang et al. 2007, Zheng & Wang 2010, Deng et al. 2014, Liu & Wang 2015, Han et al. 2016, Dong et al. 2017) should be considered with caution, as the identification of these fossils as angiosperms is not unequivocally accepted (e.g. Deng et al. 2014, Herendeen et al. 2017).

Table 1 shows a synoptic overview of the species reported so far from the Yanliao Biota, including a list of preliminary, value-free identifications of fossils photographed by CP at IVPP, NIGPAS and STMNH, which most likely derive from the Yanliao Biota. The account of Zhang and Zheng (1987) was not strictly limited to the Yanliao Biota but it reported and identified a good share of the species; later the report was not considered in much detail. Zheng and Wang (2010) and Liu and Wang (2015, 2017) published limited surveys in the form of synoptic lists of genera and species names and groups (Tab. 2); the identification of many of them cannot be validated or verified independently due to the lack of figures, descriptions and referencing, or due to the omission of names and identifications from older literature. In any case, many of those identifications disagree with our present ones. The most comprehensive account of the Daohugou flora was published recently by Dong et al. (2017).

All reports agree well in the composition of the flora, which appeared to be dominated by cycadophytes (mainly bennettites) and

ginkgophytes (Tab. 1). The species of all specimens presented here and those provisionally analyzed from photographs could be identified with already known species from Jurassic deposits of the area (see Figs 1, 4, 5); no new genera or new species were found. For this reason, the preliminary generic and specific identifications given by Zheng and Wang (2010) and Liu and Wang (2015, 2017) need more detailed investigation and may have to be revised. No publication upon which those proposed identifications were made could be accessed; Dong et al. (2017) left many of the species in open nomenclature.

The new *in situ* assemblage is dominated, in both species richness and number of fossils, by gymnosperms, most of which are bennettites, ginkgophytes and conifers, together with a few czezanowskialeans. Ferns are represented by only a single fragment, and caytonialeans by a few fragments. The information in previously published reports (see above; Tab. 1; Dong et al. 2017, and references therein) adds single reports of mosses, lycophytes and sphenophytes to the composition of the Daohugou/Yanliao flora. The information from preliminary identifications made from photographs of further material assigned to ‘Daohugou’ (see above) confirms the general picture as given here. Additional taxa entering the list include an alga, a sphenophyte, a few more ferns and putative cycads (Tab. 1; see also Dong et al. 2017).

POSSIBLE REASONS FOR THE PARTICULAR COMPOSITION OF THE FLORA FROM THIS ASSEMBLAGE

A large, continuous portion of slabs from a single locality was collected. Every slab was then completely browsed for plant fossils and every plant fragment was recorded. It is safe to assume that the composition of the examined assemblage reflects its natural configuration. Bias generated through selective sampling or selective collecting is absent or negligible.

The composition of the flora, which derived from freshwater lake sediments, is dominated by bennettites, conifers and ginkgophytes, together with only very few fern, sphenophyte, algae and moss fragments. In a freshwater lake community, however, many more water-related plants such as large monotypic stands of sphenophytes, mosses or ferns would

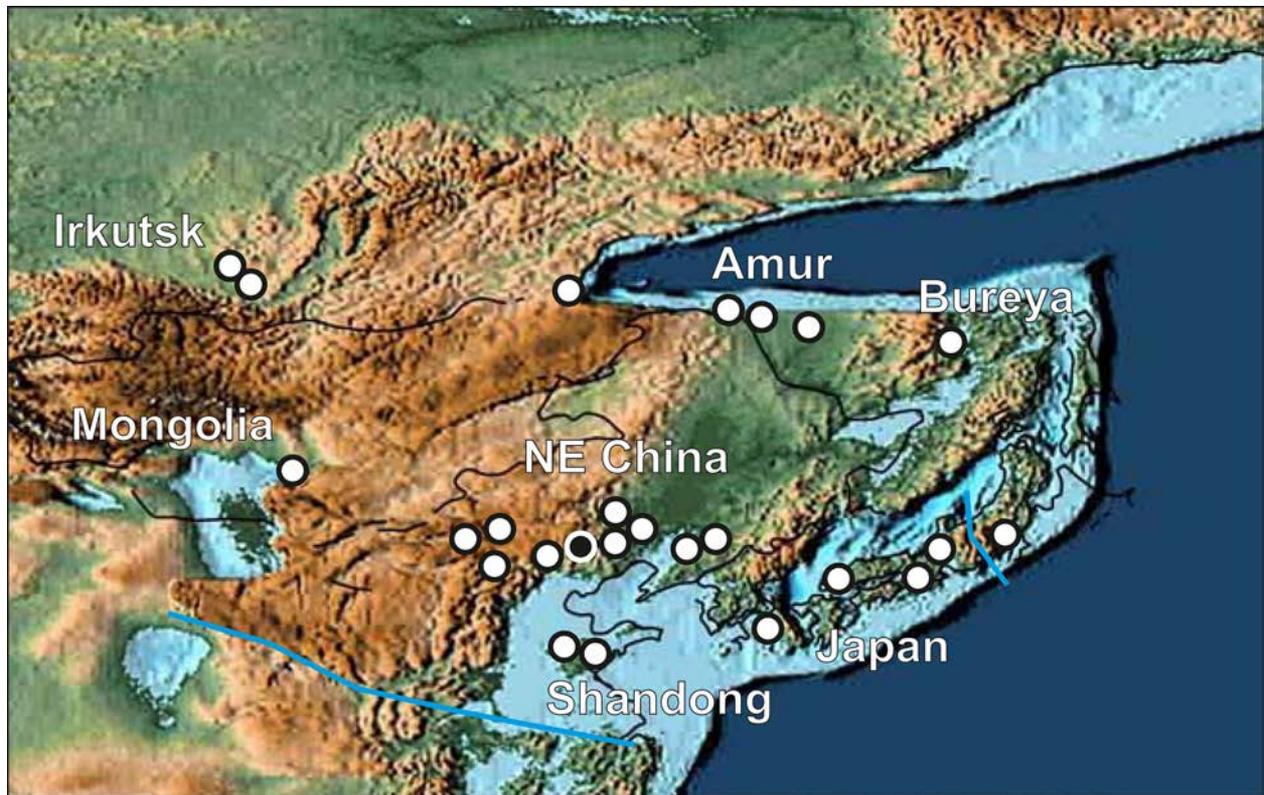


Fig. 4. Palaeogeographic map of the region under study, depicting the palaeo-locations of the Middle to early Late Jurassic floras mentioned in the text, including the Yanliao Biota in north-eastern China. Daohugou is indicated by a black dot with white circle; blue lines mark the borders between the Northern and Southern Floristic Regions of China, and between the Inner and Outer Zone of Japan. Base map: PALEOMAP Project, C. R. Scotese, Arlington, Texas, USA

be expected; instead, the assemblage reflects dominance by larger land plants, which in at least some groups indicate drier environments of the hinterland. We can offer certain reasons for the particular composition of this fossil assemblage. The fossils collected here derive from near the centre of the lake, assumed to have been moderately deep. All fossil plant fragments must have been transported to that area and thus embedded allochthonously. As there are only fragments, and entire leaves or organs are the exception, most of the plant material presumably was removed from living plants in the surroundings of the lake and introduced into the lake by natural abortion/abscission or wind/storm. Under these circumstances it is very likely that the assemblage would be dominated by plants that grow to a certain height (such as ginkgophytes, conifers, and to some extent also bennettites), fragments of which are more likely to be blown into the middle of the lake than fragments of low-growing ferns and sphenophytes thriving at the lake shores. Remains of the latter are more likely to be embedded autochthonously at the shallower shores (CP and BJ, own observations at new excavations at Nanshimen and

Daxishan/Linglongta, June 2017). In or near its centre the lake may have been too deep to provide a habitat for plants that stand in water or thrive entirely in water, which could have been embedded autochthonously.

From the composition of the gymnosperm portion of the flora it can be inferred that many of the plants thrived in water- or moisture-related environments that may have surrounded the lake (wet or boggy soil, humid conditions, osmotic/acidic soils), thus in the close vicinity of the lake. Especially for bennettites, it has often been suggested that these plants grew in more or less monotypic stands in deltaic or lacustrine environments or in habitats with slightly reduced osmotic potential (e.g. Pott et al. 2008, Pott 2014, Pott & McLoughlin 2014); similar interpretations have been made for some larger-leaved and phylloclade conifers (e.g. Farjon 2010), the modern relatives of many of which (e.g. *Phyllocladus*, *Podocarpus*) live from sea level up to 700–800 m a.s.l. on acidic soils, or in evergreen rainforests. Some Triassic–Jurassic ginkgophytes probably grew under similar conditions (e.g. Pott et al. 2007), but there is only one extant species left that naturally occurs on reduced-pH soils. This does

not explain the nearly total absence of sphenophyte and fern remains but it does explain the dominance of bennettites, larger-leaved conifers such as *Yanliaoa* or *Podozamites*, and several ginkgophytes.

Another reason for the biased composition of the flora may be the different degrees of preservation potential of the diverse plant fragments introduced into the lake. Ligneous or lignified material (e.g. seeds, wood, branches, ‘cones’ and other reproductive organs) as well as plant organs furnished with thick cuticles (leathery leaves, young branches, reproductive organs), all of which commonly characterize gymnosperm plants such as those identified here, have a higher preservation potential than leaves and other plant portions with no or only very thin cuticles, thin or filmy tissues, or nonlignified seeds such as those of the ferns that are very common in adjacent and related floras [e.g. *Coniopteris hymenophylloides* (Brongn.) Seward or *Eboracia lobifolia* (J. Phillips) H.H. Thomas] or of mosses, algae and lycophytes. The almost complete absence of sphenophytes is difficult to explain, as they have high preservation potential due to the incorporation of silicon as a replacement for lignin in their cell walls. However, these are commonly embedded authochthonously; most likely they thrived near the lake shore and thus outside the excavated area (CP and BJ, own observations, June 2017). The preservation potential of the plant fragments might also be strongly influenced by the properties of the lake water: if very acidic, for example, it would boost the speed and rate of decomposition or decay; the absence of oxygen might slow decay. Since the plant assemblage is rather small and it is not known how large the lake was and from exactly which area of the lake the plant fossils derived, we refrain from discussing this issue further and await upcoming results of an ongoing analyses of the Daohugou lake community (see Dong et al. 2017; ongoing studies of Yang et al. and Wang et al.).

THE AGE OF THE DAOHUGOU BED

The Daohugou Bed was discovered in the late 1990s and was thought to be part of the Yixian Formation (e.g. Wang 2000, Wang et al. 2000). Subsequent palaeontological studies showed that the bed belongs to the Haifanggou Formation. The bed produces abundant invertebrate

fossils indicative of the Middle–Late Jurassic in Central Asia, Siberia and the Urals, such as the conchostracans *Euestheria ziliujingensis* Chen, *Euestheria haifanggouensis* Chen, *Euestheria jingyuanensis* Chen and *Euestheria luanpingensis* Shen et Niu (Shen et al. 2003), the bivalve *Ferganoconcha sibirica* Tschernyshev (Jiang 2006), and numerous insects belonging to the Ephemeroptera, Odonata, Blattaria, Orthoptera, Dermaptera, Grylloblattodea, Plecoptera, Psocoptera, Hemiptera, Megaloptera, Raphidioptera, Neuroptera, Mecoptera, Coleoptera, Trichoptera, Diptera, Hymenoptera, and Lepidoptera (Huang et al. 2006, Huang 2017). This conclusion is also supported by radiometric datings from both the bed and the overlying Tiaojishan Formation, which gave an age range of 165–158 Ma, belonging mainly to the Callovian of the Middle Jurassic to the Oxfordian of the Late Jurassic (e.g. Chen et al. 2004, He et al. 2004, Liu et al. 2006b, 2012, Chang et al. 2009, Huang 2015, Xu et al. 2016, Zhou & Wang 2017).

COMPARISON OF THE DAOHUGOU FLORA WITH ADJACENT LATE MIDDLE–EARLY LATE JURASSIC FLORAS

A comparison of the Daohugou flora with adjacent floras is hampered by discrepancies and disagreements in the age determination and correlation of many deposits in China, not only regarding the Yanliao or Jehol biotas as outlined above. The excavated assemblage comes from the Haifanggou (Jiulongshan) Formation, which has been confidently dated to the late Middle to early Late Jurassic (Callovian–Oxfordian). There have been a number of fossil floras reported from Chinese deposits called the Haifanggou Formation or Jiulongshan Formation, or from formations underlying or overlying these (e.g. Li & Hu 1984, Wang 1984, He & Wu 1986, Duan 1987, Zhang & Zheng 1987, Wang et al. 2006, Jiang et al. 2010, Wang & Wang 2010, Zhao et al. 2015, Liu & Wang 2015, 2017). In many of these reports those assemblages were placed in the Middle Jurassic at the time the reports were published. There has also been some dispute about the plant fossil deposits of the Upper Amur and Bureya basins, but these have been dated and widely accepted as Late Jurassic–Early Cretaceous in age (Callovian–Aptian; e.g. Krassilov 1973a, Markevich & Bugdaeva 2009, 2014).

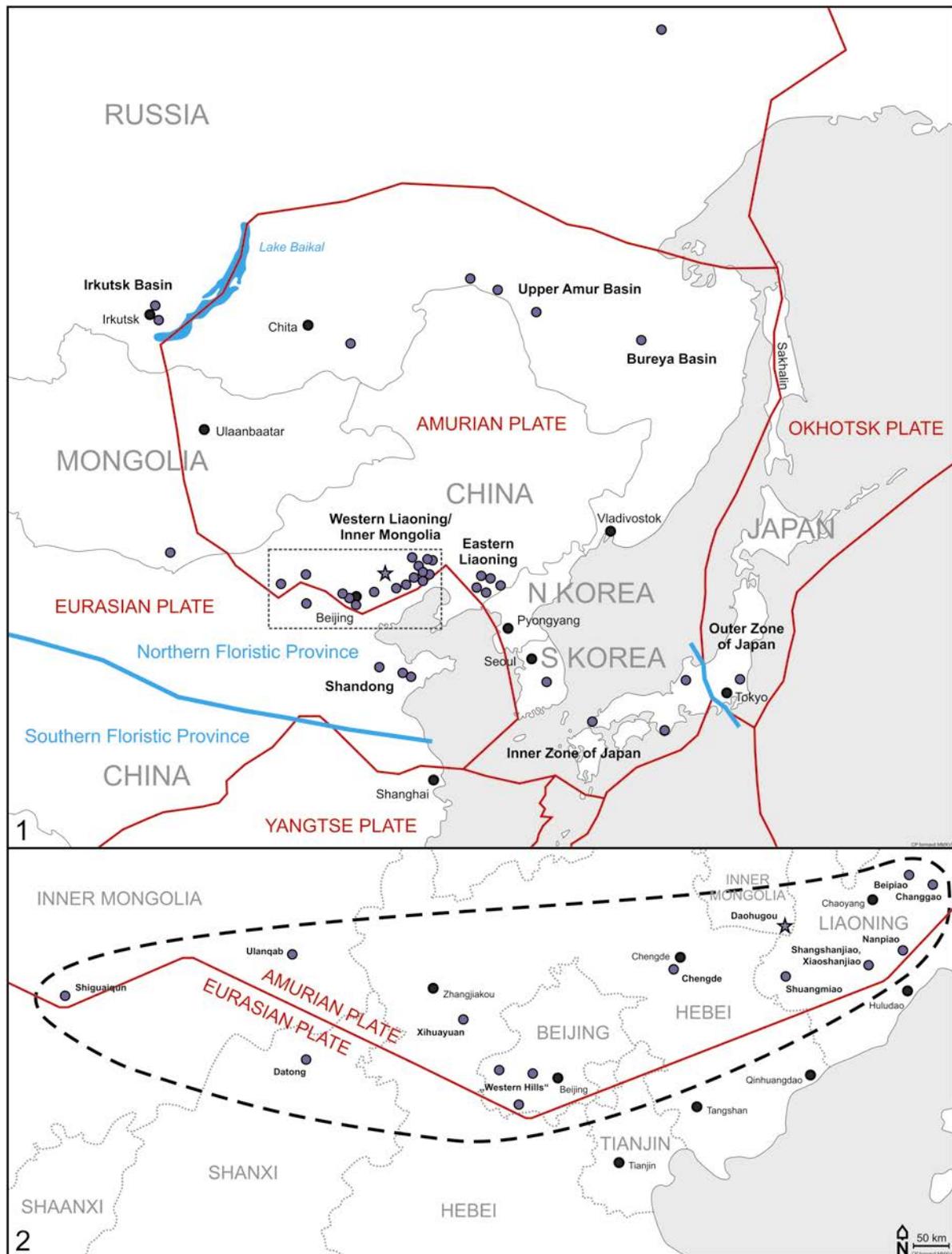


Fig. 5. 1. Map of eastern Asia, depicting the borders of the Amurian Tectonic Plate and the distribution of late Middle to early Late Jurassic floras in the region. 2. Detail map showing the so-called *Coniopteris-Phoenicopsis* floras from the Haifanggou (Jiulongshan) and over- and underlying formations. The Daohugou site is marked with a star. Information obtained from available literature (e.g. Li & Hu 1984, Wang 1984, He & Wu 1986, Duan 1987, Zhang & Zheng 1987, Wang et al. 2006, Zhao et al. 2015, Liu & Wang 2015, 2017)

The species identifications of many fossils under study here, and the preliminary identifications made for the collections of IVPP, NIG-PAS and STMNH were based mostly on species

described elsewhere from the Haifanggou Formation and the Upper Jurassic of eastern Russia (Figs 1, 4, 5). This means that the Haifanggou Formation (and the Jiulongshan

Formation) elsewhere in China (e.g. western Liaoning, Western Hills of Beijing, Datong Coalfield, Inner Mongolia) may be regarded as Callovian–Oxfordian in age instead of Middle Jurassic. It appears that the Daohugou flora comprises a number of taxa regarded as key taxa from this geographical region characterizing the floras of geological stages commonly referred to as *Coniopteris-Phoenicopsis* floras (Vachrameev 1964, Wu et al. 1980). These include *Coniopteris hymenophylloides*, *Eboracia lobifolia*, *Phoenicopsis angustifolia*, *Ginkgoites sibirica*, *Sphenobaiera czekanowskiana*, *Czekanowskia rigida*, *Pityophyllum nordenskioldii*, and *Podozamites lanceolatus*; they seem to appear in many floras if not all, and consequently can be used to correlate these floras and those of adjacent regions. Unfortunately, the Late Jurassic plant assemblages of the Northern Floristic Province in China are treated only marginally in the extensive synopsis of Zhou (1995).

The flora from the Haifanggou Formation of western Liaoning in the surroundings of Nanyang (He & Wu 1986, Zhang & Zheng 1987, Jiang et al. 2010, Wang & Wang 2010, Zhao et al. 2015) (Fig. 1, Tab. 2) is very similar in composition to the Daohugou flora. Within the examined collection of plant fossils, the Daohugou flora shares 17 of 25 taxa (68%) with the flora from western Liaoning; if the preliminarily identified taxa are included, the Daohugou flora shares 39 of 49 taxa (80%) with the western Liaoning flora. However, the flora from western Liaoning is much more diverse than the Daohugou flora, as many more plant species (especially ferns) have been reported, though this difference could be biased, due, for example, to differences between the preservation environments. These two floras might consequently be regarded as similar if not identical; at least, active exchange between the two may be presumed. Their modern localities are also not too far away from each other (≈ 250 km). Already at the beginning of the 20th century, plant fossils (probably) from the Haifanggou Formation were described from the surroundings of Shenyang, Liaoning, from a small town called Taojiatun, by Yabe (1908), yielding a composition almost identical to the Daohugou/Yanliao flora, comprising such key taxa as *Pityophyllum nordenskioldii*, *Podozamites lanceolatus*, *Ginkgoites sibirica*, *Sphenobaiera czekanowskiana*, and *Czekanowskia*

rigida. Later, Yabe and Ôishi (1928) described a comparable fossil floral assemblage from Fangtzu, Shandong.

The flora from the Western Hills of Beijing (Zhaitang; e.g. Duan 1987) was obtained from the Longmen and Yaopo formations, which underlie the Jiulongshan Formation, and was dated as Middle Jurassic (Duan 1987) [see Ren et al. 2002 and Zhou et al. 2007 for the correlation of the Daohugou Bed with the Chiulongshan (=Jiulongshan) Formation in the Western Hills of Beijing]. However, the flora shows many connections to the early Late Jurassic floras from Daohugou and western Liaoning, in its composition and in the occurrence of similar genera and a number of identical species including several key taxa such as *Coniopteris hymenophylloides*, *Eboracia lobifolia*, *Phoenicopsis angustifolia*, and *Czekanowskia rigida*; thus it might be interpreted as younger, probably uppermost Middle Jurassic. Duan (1987, p. 6) interpreted the Zhaitang flora as “the end of the Yanliao aulacogen system”, that is, belonging to the Yanliao Biota. The flora from the ‘Middle’ Jurassic Yongdingzhuang Formation of the Datong Coalfield in northern Shanxi (Li & Hu 1984) shows a similar composition, with identical key taxa such as *Coniopteris hymenophylloides*, *Phoenicopsis angustifolia*, and *Czekanowskia rigida*.

Zhang and Zheng (1987) reported an additional flora from the Tiaojishan Formation north-east of Yixian County (Fig. 1), which overlies the Haifanggou Formation. Like the flora from the Western Hills of Beijing, the composition of this flora shows several connections to the Daohugou flora, though many species placed in the same genera have been described as different from those in the Daohugou flora. Based on their composition, the floras of the Daohugou Bed and the Tiaojishan Formation can be differentiated but also greatly overlap. In any event, all fossils from the Callovian–Oxfordian Haifanggou Formation and the overlying Tiaojishan Formation are regarded as belonging to the Callovian–Kimmeridgian Yanliao Biota, which is thought to be distributed throughout northern China, including the Aalenian–Kimmeridgian floras from north-eastern China.

In its floristic composition the Daohugou/Yanliao flora is a typical member of the Middle to Late Jurassic *Coniopteris-Phoenicopsis* assemblage of north-eastern China; it

differs from the Early Cretaceous Jehol flora (Wu 1999, 2003, Sun et al. 2001) but can be regarded as strongly correlated. Despite the lithological similarity between the Daohugou Bed and the Yixian Formation (Jehol Biota), they have yielded two distinctive fossil plant assemblages. They probably belong to the same cycle of volcanism and sedimentation, although the Daohugou Bed is older than the Yixian Formation. It might be argued that the Yanliao fossil assemblage represents the earliest stage of the evolution of the Jehol Biota.

The Daohugou/Yanliao flora also shows considerable overlap and might have had active exchange (Fig. 4) with the Jurassic floras from the Upper Amur Basin and eastern Siberia (Bureya Basin) (Heer 1876a, 1880, Vachrameev & Doludenko 1961, Lebedev 1963, 1965, Dobruskina 1965, Vachrameev 1991), based on the occurrence of many identical taxa such as *Coniopteris hymenophylloides*, *Coniopteris burejensis*, *Anomozamites angulatus*, *Podozamites lanceolatus*, *Phoenicopsis speciosa*, *Phoenicopsis angustifolia*, *Sphenobaiera longifolia*, *Ginkgoites sibirica*, *Czekanowskia rigida*, and *Pityophyllum nordenskiöldii*, among others. Further to the north-east and east, the flora from the Upper Jurassic at the Aldan River (Samylina 1963, Vachrameev 1991) and the Callovian–Oxfordian Kuzuryu flora of the Tetori Group in the Inner Zone of Japan (e.g. Yokoyama 1889, Kimura 1958, Yamada & Uemura 2008), and the Upper Jurassic floras of the Utano and Kiyosue formations (Ôishi 1940, Takahashi 1957, Kimura 1958, 1988, Kawamura 2010) show some similarities to the Daohugou/Yanliao flora, again sharing key taxa such as *Coniopteris hymenophylloides*, *Coniopteris burejensis*, *Ginkgo sibirica*, *Czekanowskia rigida*, *Phoenicopsis speciosa*, and *Podozamites lanceolatus*, and thus may be related floras with active exchange as well (Fig. 4), whereas the flora of the Soma Formation in the Outer Zone of Japan considerably differs (Figs 4, 5) (Kimura 1958). In the west, the ‘Middle’ Jurassic flora of southern Mongolia also shows some overlap, revealing a relation of exchange with the floras from north-eastern China (e.g. Kostina & Herman 2013). On the other hand, floras more to the north, such as those from the Irkutsk Basin, differ substantially from the southern Mongolian, Upper Amur and Bureya basins and Daohugou/Yanliao floras (Figs 4, 5) (see e.g. Vachrameev

1991). Heer (1876a) had already noted that the flora of the Upper Amur and Bureya basins differed greatly from the flora obtained from the Irkutsk Basin (Kaya and Baley rivers). Even key taxa such as *Coniopteris hymenophylloides*, *Anomozamites angulatus* and *Phoenicopsis speciosa* were absent, while others such as *Phoenicopsis angustifolia*, *Sphenobaiera longifolia*, *Ginkgoites sibirica*, *Czekanowskia rigida*, and *Pityophyllum nordenskiöldii* were found but in very low numbers.

It is interesting to note that the Daohugou/Yanliao flora thrived at the southern margin of the so-called Amurian Tectonic Plate (Fig. 5) (Savostin et al. 1982, 1983, Wei & Seno 1998, Bird 2003, Guo et al. 2017). Plotting the Amurian Plate on a map reveals that almost all mentioned floras of the so-called *Coniopteris-Phoenicopsis* type in north-eastern China and adjacent areas are more or less restricted to the proposed Amurian Plate (Fig. 5). Floras outside the western, northern and eastern borders of this tectonic plate (e.g. Georgia, Kazakhstan, Uzbekistan, Kirgizstan, western and northern Siberia, Irkutsk Basin, western Mongolia, Outer Zone of Japan) differ much in their composition from the Daohugou/Yanliao flora (Heer 1876a, 1880, Turutanova-Ketova 1930a, 1930b, Prynada 1931, Teslenko 1970, Doludenko & Svanidze 1969, Doludenko & Orlovskaya 1976, Krassilov 1982, Kimura & Ohana 1988, Kimura et al. 1988, 1992, Vachrameev 1991, Yabe et al. 2003), but they still reveal some exchange between the floras through overlapping species ranges (e.g. Doludenko & Orlovskaya 1976). In floras adjacent to the southern edge of the Amurian Plate [e.g. the Late Jurassic flora of southern Mongolia (Kostina & Herman 2013) and the Datong and Fangzi floras], the differences are less abrupt and more gradational; apparently, exchange between the floras within the Chinese Northern Floristic Region and the Daohugou/Yanliao Biota was more active than it was between the ‘Amurian floras’ and the more northerly floras (Figs 4, 5) (Yabe & Ôishi 1928, Li & Hu 1984). Reasons for the differences and similarities might be found in the natural conditions, owing to the geographical relief. Mountain ranges and island isolation might act as natural borders, impeding active exchange between the floras (e.g. from the Irkutsk Basin, western Mongolia, Outer Zone of Japan), while vast plains might have

the opposite effect, enhancing the exchange (e.g. from north-eastern China, the Amur and Bureya basins, Inner Zone of Japan) (Fig. 4).

CONCLUSIONS

We made a detailed analysis of a recently found *in-situ* assemblage of plant fossils from two sites at the Daohugou fossil site in Inner Mongolia, China. Exact dating of the tuff layers containing the plant assemblage place it in the late Middle–early Late Jurassic (Callovian–Oxfordian). It can be regarded as part of the Callovian–Kimmeridgian Yanliao Biota. The composition of the examined assemblage is dominated by tall-growing gymnosperms such as ginkgophytes, conifers, czezanowskialeans and bennettites. Low-growing and water-bound plants such as ferns are represented only by a few fragmentary remains. When additional material available in museum collections is considered, the picture of the flora is completed by mosses, algae, sphenophytes, lycophytes and additional ferns, many of which are also preserved only as fragmentary remains, and the above-mentioned gymnosperms still dominate the assemblage. Our interpretation of this bias relates it potentially to preservation potential, position in the lake, the preservational environment, taphonomy, or the habitat composition and distribution of the plants during their lifetime in different local areas in and around the Daohugou Lake. The flora is part of the East Asian *Coniopteris-Phoenicopsis* type floras; comparison with several Middle–Late Jurassic floras from north-eastern China, north-eastern and eastern Siberia and Japan reveals relationships and active exchange but also differences; the Yanliao fossil assemblage is part of the larger palaeo-phytogeographical context of the area.

ACKNOWLEDGEMENTS

We thank all the people who were involved in the excavation at Daohugou village in July 2015, especially Wang Shengyu, Yang Zixiao, Tian Qingyi (NJU, Nanjing University, Nanjing, China) and Manja Hethke (Freie Universität, Berlin, Germany), who obtained the fossils in Inner Mongolia and later separated the fossil plant fragments at NJU. Eugenia Bugdaeva (Institute of Biology and Soil Science FEB RAS, Vladivostok, Russia) provided help with Russian localities and Russian literature. Peng Jungang (Nanjing Institute of Geology and Palaeontology CAS, Nanjing,

China) is thanked for help in translating portions of Chinese literature. CP acknowledges funding from the Swedish Research Council, Stockholm, Sweden (grant no. 621-2012-4375). BJ is supported by the National Science Foundation of China (grant no. 41672010) and the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS), Nanjing, China (grant no. 153104). We thank Eugenia Bugdaeva and an anonymous reviewer for their constructive reviews of the manuscript.

REFERENCES

- BENTON M.J., ZHOU Z., ORR P.J., ZHANG F. & KEARNS S.L. 2008. The remarkable fossils from the Early Cretaceous Jehol Biota of China and how they have changed our knowledge of Mesozoic life. *Proc. Geologist. Assoc.*, 119: 209–228.
- BI S., WANG Y., GUAN J., SHENG X. & MENG J. 2014. Three new Jurassic euharamiyidan species reinforce early divergence of mammals. *Nature*, 514: 579–584.
- BIRD P. 2003. An updated digital model of plate boundaries. *Geochem. Geophys. Geosyst.* 4.3 SCOPUS-Web; accessed 25 November 2016.
- CHANG M., CHEN P., WANG Y., WANG Y. & MIAO D. 2003. The Jehol Biota. The emergence of feathered dinosaurs, beaked birds and flowering plants. Scientific & Technical Publishers, Shanghai, China.
- CHANG S., ZHANG H., RENNE P.R. & FANG Y. 2009. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ age constraints on the basal Lanqi Formation and its implications for the origin of angiosperm plants. *Earth Planet. Sci. Lett.*, 279: 212–221.
- CHEN W., JI Q., LIU D., ZHANG Y., SONG B. & LIU X. 2004. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geol. Bull. China*, 23: 1165–1169.
- COHEN K.M., FINNEY S.C., GIBBARD P.L. & FAN J. 2013; updated. The ICS International Stratigraphic Chart. *Episodes*, 36: 199–204.
- DELLE G.V. 1967. The Middle Jurassic flora of the Tkvarchelian Coal Basin (Transcaucasia). Nauka, Leningrad.
- DENG S., HILTON J., GLASSPOOL I.J. & DEJAX J. 2014. Pollen cones and associated leaves from the Lower Cretaceous of China and a re-evaluation of Mesozoic male cycad cones. *J. Syst. Palaeontol.*, 12: 1001–1023.
- DOBRUSKINA I.A. 1965. Revision of the Jurassic flora described by O. Heer from the River Amur. *Palaeontol. J.*, 3: 110–118.
- DOLUDENKO M.P. & LEBEDEV E.L. 1972. *Ginkgoites sibirica* and “*G. huttonii*” of Eastern Siberia. *Trans. Geol. Inst. Acad. Sci. USSR.*, 230: 82–101.
- DOLUDENKO M.P. & ORLOVSKAYA E.R. 1976. The Jurassic flora of the Karatau. *Transactions* 284, Nauka, Moscow.

- DOLUDENKO M.P. & SVANIDZE T.I. 1969. The Late Jurassic flora of Georgia. Trudi GIN AN SSSR 178, Nauka, Moscow.
- DONG C., YANG X. & ZHOU Z. 2017. The plants: 252–302. In: Huang D. (ed.), *The Daohugou Biota*. Shanghai Science and Technology Publishing House, Shanghai.
- DOWELD A.B. 2001. *Schizolepidopsis*, a new substitute generic name for Mesozoic plants. Byulleten' Moskovskogo Obshchestva Ispytateley Prirody. Otdel Geologicheskii, 76: 86–88.
- DUAN S. 1987. The Jurassic flora of Zhaitang, Western Hills of Beijing. PhD thesis, Palaeobotany Department, Swedish Museum of Natural History, Stockholm, Sweden.
- FARJON A. 2010. *A Handbook of the World's Conifers*. Brill, Leiden.
- FLORIN R. 1936. Die fossilen Ginkgophyten aus Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters. I. Spezieller Teil. *Palaeontographica*, B, 81: 71–173.
- FRIIS E.M., CRANE P.R. & PEDERSEN K.R. 2011. *Early Flowers and Angiosperm Evolution*. Cambridge University Press, Cambridge.
- GAO K. & REN D. 2006. Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou Beds. *Acta Geol. Sinica*, 80: 42–45.
- GAO T., REN D. & SHIH C. 2009. *Abrotaxyela* gen. nov. (Insecta, Hymenoptera, Xyelidae) from the Middle Jurassic of Inner Mongolia, China. *Zootaxa*, 2094: 52–59.
- GUO Z., YANG Y., ZYABREV S. & HOU Z. 2017. Tectonostratigraphic evolution of the Mohe-Upper Amur Basin reflects the final closure of the Mongol-Okhotsk Ocean in the latest Jurassic–earliest Cretaceous. *J. Asian Earth Sci.* DOI: 10.1016/j.jseae.2017.06.020
- HAN G., LIU Z., LIU X., MAO L., JACQUES F.M.B. & WANG X. 2016. A whole plant herbaceous angiosperm from the Middle Jurassic of China. *Acta Geol. Sinica (English Edition)*, 90: 19–29.
- HARRIS T.M. 1961. The Yorkshire Jurassic flora. I. Thallophyta–Pteridophyta. Trustees of the British Museum (Natural History), London.
- HARRIS T.M. 1964. The Yorkshire Jurassic flora. II. Caytoniales, Cycadales & Pteridosperms. Trustees of the British Museum (Natural History), London.
- HARRIS T.M. 1969. The Yorkshire Jurassic flora. III. Bennettiales. Trustees of the British Museum (Natural History), London.
- HARRIS T.M. 1979. The Yorkshire Jurassic flora. V. Coniferales. Trustees of the British Museum (Natural History), London.
- HARRIS T.M., MILLINGTON W. & MILLER J. 1974. The Yorkshire Jurassic flora. IV. Ginkgoales & Czekanowskiales. Trustees of the British Museum (Natural History), London.
- HE H., WANG X., ZHOU Z., ZHU R., JIN F., WANG F., DING X. & BOVEN A. 2004. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of ignimbrite from Inner Mongolia, north-eastern China, indicates a post-Middle Jurassic age for the overlying Daohugou Bed. *Geophys. Res. Letters*, 31: L20609.
- HE Y. & WU X. 1986. Middle Jurassic Aalenian flora of China. *Acta Palaeontol. Sinica*, 25: 591–601.
- HEER O. 1876a. Beiträge zur Jura-Flora Ostsibiriens und des Amurlandes. *Mém. Acad. Imp. Sci. St. Pétersbourg*, 22: 1–122.
- HEER O. 1876b. Beiträge zur fossilen Flora Spitzbergens. *Kongl. Sv. Vet.-Akad. Handl.*, 14: 1–141.
- HEER O. 1878. Beiträge zur fossilen Flora Sibiriens und des Amurlandes. *Mém. Acad. Imp. Sci. St. Pétersbourg*, 25: 1–58.
- HEER O. 1880. Nachträge zur Juraflora Sibiriens. *Mém. Acad. Imp. Sci. St. Pétersbourg*, 27: 1–34.
- HEINRICH S., WANG X., IGNATOV M.S. & KRINGS M. 2014. A Jurassic moss from northeast China with preserved sporophytes. *Rev. Palaeobot. Palynol.*, 204: 50–55.
- HERENDEEN P.S., FRIIS E.M., PEDERSEN K.R. & CRANE P.R. 2017. Palaeobotanical redux: Revisiting the age of the angiosperms. *Nature Plants*, 3: 17015.
- HUANG D. 2015. Yanliao Biota and Yanshan Movement. *Acta Palaeont. Sinica*, 54: 501–546.
- HUANG D. 2017. *The Daohugou Biota*. Shanghai Science and Technology Publishing House, Shanghai.
- HUANG D., NEL A., SHEN Y., SELDEN P.A. & LIN Q. 2006. Discussions on the age of the Daohugou fauna – evidence from invertebrates. *Progr. Nat. Sci.*, 16: 309–312.
- JIANG B. 2006. Non-marine Ferganoconcha (Bivalvia) from the Middle Jurassic in the Daohugou area, Ningcheng County, Inner Mongolia, China. *Acta Palaeontol. Sinica*, 45: 259–264.
- JIANG B., YAO X., NIU Y., RAO X. & LI Q. 2010. Outline of the Jurassic and Cretaceous systems in western Liaoning, NE China. University of Science & Technology of China Press, Hefei.
- KAWAMURA H. 2010. Stratigraphic revision of the Jurassic Toyora Group of the southern part of the Tabe Basin, Yamaguchi Prefecture, southwest Japan. *Jour. Geol. Soc. Japan*, 116: 27–44.
- KIMURA T. 1958. On the Tetori flora (Part 1). Mesozoic plants from the Kuzuryu Sub-Group, Tetori Group, Japan. *Bull. Senior High School Tokyo Univ. Educ.*, 2: 1–47.
- KIMURA T. 1988. Jurassic macrofloras in Japan and palaeophytogeography in East Asia. *Bull. Tokyo Gakugei Univ. Sect. IV*, 40: 147–164.
- KIMURA T. & OHANA T. 1988. Late Jurassic plants from the Tochikubo Formation (Oxfordian), Somanakamura Group, in the Outer Zone of northeast Japan. II. *Bull. National Sci. Mus., Ser. C*, 14: 151–185.
- KIMURA T., LEBEDEV E.L., MARKOVICH E.M. & SAMYLINA V.A. 1992. Macrofloras of eastern

- Asia and other circum-Pacific areas: 311–316. In: Westermann G.E.G. (ed.), *The Jurassic of the circum-Pacific*. Cambridge University Press, Cambridge.
- KIMURA T., OHANA T., ZHAO L.M. & GENG B.Y. 1994. *Pankuangia haifanggouensis* gen. et sp. nov., a fossil plant with unknown affinity from the Middle Jurassic Haifanggou Formation, western Liaoning, northeast China. *Bull. Kilakyushu Mus. Nat. Hist.*, 13: 255–261.
- KIMURA T., OHANA T., TAKIMOTO H., IKEHARA K., AIBA H. & FURUOYA H. 1988. Late Jurassic plants in the Outer Zone of northeast Japan. *Proc. Japan Acad., Ser. B*, 64: 217–220.
- KOSTINA E.I. & HERMAN A.B. 2013. The Middle Jurassic flora of South Mongolia: Composition, age and phytogeographic position. *Rev. Palaeobot. Palynol.*, 193: 82–98.
- KRASSILOV V.A., 1968. A new group of Mesozoic gymnosperms: Czekanowskiales. *Dokl. Acad. Nauk. SSSR*, 168: 942–945.
- KRASSILOV V.A. 1970. Approach to the classification of Mesozoic “ginkgoalean” plants from Siberia. *Palaeobotanist*, 18: 12–19.
- KRASSILOV V.A. 1972. Mesozoic Flora of the Bureya River (Ginkgoales and Czekanowskiales). *Nauka, Moscow*.
- KRASSILOV V.A. 1973a. Materials on the stratigraphy and taphofloras of the coal-bearing strata of the Bureya Basin: 28–51. In: Krassilov V. (ed.), *Fossil Floras and Phytostatigraphy of the Far East*. Akademia NAUK SSSR, Vladivostok.
- KRASSILOV V.A. 1973b. The Jurassic disseminules with pappus and their bearing on the problem of angiosperm ancestry. *Geophytol.*, 3: 1–48.
- KRASSILOV V.A. 1982. Early Cretaceous flora of Mongolia. *Palaeontographica, B*, 181: 1–43.
- KRASSILOV V.A. 1997. *Angiosperm Origins: Morphological and Ecological Aspects*. Pensoft, Sofia.
- LEBEDEV E.L. 1963. Upper Jurassic flora of the Zeya River and its significance to the boundary of the Upper Jurassic and Lower Cretaceous continental deposits in the Amur River Basin. *Dokl. Akad. Nauk SSSR*, 150: 149–152.
- LEBEDEV E.L. 1965. Late Jurassic flora of Zeya River and the Jurassic–Cretaceous boundary. *Nauka, Moscow*.
- LI B. & HU B. 1984. Fossil plants from the Yongdingzhuang Formation of the Datong Coalfield, northern Shanxi. *Acta Palaeontol. Sinica*, 23: 135–147.
- LI N., LI Y., WANG L., ZHENG S. & ZHANG W. 2004. A new *Weltrichia* Braun in north China with a special bennettitalean male reproductive organ. *Acta Bot. Sinica*, 46: 1269–1275.
- LINDLEY J. & HUTTON W. 1831–1833. *The Fossil flora of Great Britain, or Figures and Descriptions of the Vegetable Remains Found in a Fossil State in the Country*. Volume I. J. Ridgway and Sons, London.
- LIU Y., LIU Y. & ZHANG H. 2006b. LA-ICPMS Zircon U–Pb Dating in the Jurassic Daohugou beds and correlative strata in Ningcheng of Inner Mongolia. *Acta Geol. Sinica*, 80: 733–742.
- LIU Y., LIU Y., JI S. & YANG Z. 2006a. U–Pb zircon age for the Daohugou Biota at Ningcheng of Inner Mongolia and comments on related issues. *Chin. Sci. Bull.*, 51: 2634–2644.
- LIU Y., KUANG H., JIANG X., PENG N., XU H. & SUN H. 2012. Timing of the earliest known feathered dinosaurs and transitional pterosaurs older than the Jehol Biota. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 323–325: 1–12.
- 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. *Geol. Bull. China*, 23: 1181–1187.
- LIU Z. & WANG X. 2015. A perfect flower from the Jurassic of China. *Hist. Biol.*, 27: 707–719.
- LIU Z. & WANG X. 2017. *Yuhania*: a unique angiosperm from the Middle Jurassic of Inner Mongolia, China. *Hist. Biol.*, 4: 431–441.
- MARKEVICH V.S. & BUGDAEVA E.V. 2009. Palynological evidence for dating Jurassic–Cretaceous boundary sediments in the Bureya Basin, Russian Far East. *Russ. J. Pacific Geol.*, 3: 284–293.
- MARKEVICH V.S. & BUGDAEVA E. 2014. Late Jurassic–Early Cretaceous coal-forming plants of the Bureya Basin, Russian Far East. *Stratigr. Geol. Correl.*, 22: 239–255.
- MENG J., HU Y., WANG Y., WANG X. & LI C. 2006. A Mesozoic gliding mammal from north-eastern China. *Nature*, 444: 889–893.
- NA Y., SUN C., LI T. & LI Y. 2014. The insect oviposition firstly discovered on the Middle Jurassic Ginkgoales leaf from Inner Mongolia, China. *Acta Geol. Sinica (English Edition)*, 88: 18–28.
- NATHORST A.G. 1897. Zur mesozoischen Flora Spitzbergens gegründet auf die Sammlungen der schwedischen Expeditionen. *Kungl. Sv. Vetenskapsakad. Handl.*, 30: 1–77.
- ÔISHI S. 1940. The Mesozoic floras of Japan. *J. Fac. Sci., Hokkaido Imp. Univ., Sect. IV*, 5: 123–480.
- PAN K. 1977. A Jurassic conifer, *Yanliaoa sinensis* gen. et sp. nov. from the Yanliao region. *Acta Phytotaxon. Sinica*, 15: 69–71.
- POMEL A. 1847. Matériaux pour servir à la flore fossile des terrains jurassiques de la France. *Amtl. Ber. Versamml. Gesellsch. dt. Naturf. Aachen*: 1–24.
- POTT C. 2014. A revision of *Wielandiella angustifolia* – a shrub-sized bennettite from the Rhaetian–Hettangian of Scania, Sweden, and Jameson Land, Greenland. *Internat. J. Plant Sci.*, 175: 467–499.
- POTT C. 2016. *Westersheimia pramelreuthensis* from the Carnian (Upper Triassic) of Lunz, Austria: More evidence for a unitegmic seed coat in early Bennettitales. *Internat. J. Plant Sci.*, 177: 771–791.

- POTT C. & MCLOUGHLIN S. 2009. Bennettitalean foliage from the Rhaetian–Bajocian (latest Triassic–Middle Jurassic) floras of Scania, southern Sweden. *Rev. Palaeobot. Palynol.*, 158: 117–166.
- POTT C. & MCLOUGHLIN S. 2014. Divaricate growth habit in Williamsoniaceae: Unravelling the ecology of a key Mesozoic plant group. *Palaeobiodiv. Palaeoenvir.*, 94: 307–325.
- POTT C., KRINGS M. & KERP H. 2007. A surface micro-relief on the leaves of *Glossophyllum florinii* (?Ginkgoales) from the Upper Triassic of Lunz, Austria. *Bot. J. Linn. Soc.*, 153: 87–95.
- POTT C., KRINGS M. & KERP H. 2008. The Carnian (Late Triassic) flora from Lunz in Lower Austria: Palaeoecological considerations. *Palaeoworld*, 17: 172–182.
- POTT C., VAN DER BURGH J. & VAN KONIJNENBURG-VAN CITTERT J.H.A. 2016. New ginkgo-phytes from the Upper Triassic–Lower Cretaceous of Spitsbergen and Edgeøya (Svalbard, Arctic Norway): The history of Ginkgoales on Svalbard. *Internat. J. Plant Sci.*, 177: 175–197.
- POTT C., WANG X. & ZHENG X. 2015. *Wielandiella villosa* comb. nov. from the Middle Jurassic of Daohugou, China: More evidence for divaricate plant architecture in Williamsoniaceae. *Bot. Pacifica*, 4: 137–148.
- 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 defense against herbivorous arthropods? *Rev. Palaeobot. Palynol.*, 169: 48–60.
- POTT C., BOUCHAL J.M., CHOO T.Y.S., YOUSIF R. & BOMFLEUR B. in press. Ferns and fern allies from the Carnian (Upper Triassic) flora of Lunz am See, Lower Austria: a melting pot of Mesozoic fern vegetation. *Palaeontographica*, B.
- PRYNADA V.D. 1931. Contribution towards the knowledge of the Mesozoic flora of Central Asia. *Trans. Geol. Prosp. Serv. USSR*, 122: 19–56.
- 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. *Geol. Bull. China*, 21: 584–591.
- SAMYLINA V.A. 1956. New cycadophytes in Mesozoic deposits of the Aldan River. *Bot. Zh.*, 41: 1334–1339.
- SAMYLINA V.A. 1963. Mesozoic flora from the lower reaches of the Aldan River. *Palaeobotanika*, 4: 57–139.
- SAVOSTIN L.A., VERZHBITSKAYA A.I. & BARANOV B.V. 1982. Holocene plate tectonics of the Sea of Okhotsk region, *Dokl. Akad. Nauk. USSR, Earth Sci. Ser., Engl. Transl.*, 266: 62–65.
- SAVOSTIN L.A., ZONENSHAIN L. & BARANOV B.V. 1983. Geology and plate tectonics of the Sea of Okhotsk, geodynamics of the western Pacific-Indonesian Region, *Geodyn. Ser.*, 11: 189–221.
- SCHWEITZER H.-J., SCHWEITZER U., KIRCHNER M., VAN KONIJNENBURG-VAN CITTERT J.H.A., VAN DER BURGH J. & ASHRAF R.A. 2009. The Rhaeto–Jurassic flora of Iran and Afghanistan. 14. Pteridophyta–Leptosporangiateae. *Palaeontographica*, B, 279: 1–108.
- SHEN Y., CHEN P. & HUANG D. 2003. Age of the fossil conchostracans from Daohugou of Ningcheng, Inner Mongolia. *J. Stratigr.*, 27: 311–314.
- SULLIVAN C., WANG Y., HONE D.E., WANG Y., XUA X. & ZHAN F. 2014. The vertebrates of the Jurassic Daohugou Biota of north-eastern China. *J. Vertebr. Palaeontol.*, 34: 243–280.
- SUN G., ZHENG S., DILCHER D.L., WANG Y. & MEI S. 2001. Early Angiosperms and Their Associated Plants from Western Liaoning, China. Shanghai Scientific and Technological Education Publishing House, Shanghai.
- SZE H. 1933. Beiträge zur mesozoischen Flora von China. *Palaeontol. Sinica*, Ser. A, 4: 1–92.
- SZE H., LI X., LI P., ZHOU Z., YE M., WU S. & SHEN G. 1963. Mesozoic plants from China. Science Press, Beijing.
- TAN J. & REN D. 2002. Palaeoecology of insect community from Middle Jurassic Jiulongshan Formation in Nincheng County, Inner Mongolia, China. *Acta Zootaxon. Sinica*, 27: 428–434.
- TAKAHASHI E. 1957. Fossil flora of the Toyora and the Toyonishi Groups, Yamaguchi Prefecture. *Yamaguchi J. Sci.*, 8: 55–60.
- TESLENKO Y.V. 1970. Stratigraphy and floras of Jurassic deposits of western and southern Siberia and Tuva. Nedra, Moscow.
- TURUTANOVA-KETOVA A.I. 1930a. The Jurassic flora of the Karatau. *Trav. Mus. Géol. Acad. Sci. URSS*, 6: 131–172.
- TURUTANOVA-KETOVA A.I. 1930b. Materials to the knowledge of the Jurassic flora of the Lake Issyk-Kul Basin in Kirgizstan. *Trav. Mus. Géol. Acad. Sci. URSS*, 8: 311–356.
- VACHRAMEEV V.A. 1964. Jurassic and Early Cretaceous Floras of Eurasia and Contemporary Palaeofloristic Provinces. Nauka, Moscow.
- VACHRAMEEV V.A. 1991. Jurassic and Cretaceous Floras and Climates of the Earth. Cambridge University Press, Cambridge.
- VACHRAMEEV V.A. & DOLUDENKO M.P. 1961. The Upper Jurassic and Lower Cretaceous flora from the Bureya Basin and their stratigraphic significances. *Trud. Geol. Inst. Akad. Nauk SSSR*, 54: 1–136.
- VAN KONIJNENBURG-VAN CITTERT J.H.A., POTT C., CLEAL C.J. & ZIJLSTRA G. 2017. Differentiation of the fossil leaves assigned to *Taeniopteris*, *Nilssoniopteris* and *Nilssonia* with a comparison to similar genera. *Rev. Palaeobot. Palynol.*, 237: 100–106.
- WANG X. & WANG S. 2010. *Xingxueanthus*: An enigmatic Jurassic seed plant and its implications for the origin of angiospermy. *Acta Geol. Sinica (English Edition)*, 84: 47–55.

- WANG X., KRINGS M. & TAYLOR T.N. 2010a. A thaloid organism with possible lichen affinity from the Jurassic of north-eastern China. *Rev. Palaeobot. Palynol.*, 162: 591–598.
- WANG X., ZHENG S. & JIN J. 2010b. Structure and relationships of *Problematospermum*, an enigmatic seed from the Jurassic of China. *Internat. J. Plant Sci.*, 171: 447–456.
- WANG X., DUAN S., GENG B., CUI J. & YANG Y. 2007. *Schmeissneria*: A missing link to angiosperms? *BMC Evol. Biol.*, 7: 14.
- WANG X., WANG Y., ZHANG F., ZHANG J., ZHOU Z., JIN F., HU Y., GU G. & ZHANG H. 2000. Vertebrate biostratigraphy of the Lower Cretaceous Yixian Formation in Lingyuan, western Liaoning, and its neighbouring southern Nei Mongol (Inner Mongolia), China. *Vertebr. Palasiatica*, 38: 95–101.
- WANG X., ZHOU Z., HE H., JIN F., WANG Y., ZHANG J., WANG Y., XU X. & ZHANG F. 2005. Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. *Chin. Sci. Bull.*, 50: 2369–2376.
- WANG Y. 2000. A new Salamander (Amphibia: Caudata) from the Early Cretaceous Jehol Biota. *Vertebr. Palasiatica*, 38: 100–103.
- WANG Y., KEN S., ZHANG W. & ZHENG S. 2006. Biodiversity and palaeoclimate of the Middle Jurassic floras from the Tiaojishan Formation in western Liaoning, China. *Progr. Nat. Sci.*, 16: 222–230.
- WANG Z. 1984. Flora: 223–296. In: Tianjin Institute of Geology and Mineral Resources (d.), *Palaeontological Atlas of North China. II. Mesozoic Volume*. Geological Publishing House, Beijing.
- WATSON J. & SINCOCK C.A. 1992. Bennettitales of the English Wealden. *Monogr. Palaeontogr. Soc. Lond.*, 588: 1–228.
- WEI D. & SENO T. 1998. Determination of the Amurian Plate motion: 337–346. In: Flower M.J.F., Chung S., Lo C., Lee T. (eds.), *Mantle Dynamics and Plate Interactions in East Asia*. *Geodyn. Ser.* 27, AGU, Washington, DC.
- WEI H., SUN C., WANG H., NA Y., LI Y. & LI T. 2015. New *Phoenicopsys* leaves (Czekanowskiales) from the Middle Jurassic Daohugou Biota, China, and their roles in phytogeographic and paleoclimatic reconstruction. *Palaeoworld*, 25: 388–398.
- WU S. 1999. A preliminary study of the Jehol flora from western Liaoning. *Palaeoworld*, 11: 7–37.
- WU S. 2003. Land plants: 166–177. In: Chang M., Chen P., Wang Y., Wang Y., Miao D. (eds.), *The Jehol Biota: The Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants*. Scientific and Technical Publishers, Shanghai.
- WU S., YE M. & LI B. 1980. Upper Triassic and Lower and Middle Jurassic plants from the Hsiangchi Group, western Hubei. *Mem. Nanjing Inst. Geol. Palaeontol., Acad. Sinica*, 14: 63–131.
- XU X., ZHOU Z., SULLIVAN C., WANG Y. & REN D. 2016. An updated review of the Middle–Late Jurassic Yanliao Biota: Chronology, taphonomy, paleontology and paleoecology. *Acta Geol. Sinica*, 90: 2229–2243.
- XU X., ZHOU Z., DUDLEY R., MACKEM S., CHUONG C.M., ERICKSON G.M. & VARRICCHIO D.J. 2014. An integrative approach to understanding bird origins. *Science*, 346: 1341–1351.
- XU X., ZHENG X., SULLIVAN C., WANG X., XING L., WANG Y., ZHANG X., O'CONNOR J.K., ZHANG F. & PAN Y. 2015. A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. *Nature*, 521: 70–73.
- YABE H. 1908. Jurassic plants from T'ao-chia-T'un, China. *Bull. Imp. Geol. Sur. Japan*, 21: 1–8.
- YABE H. & ÔISHI S. 1928. Jurassic plants from the Fang-tzu coal-field, Shantung. *Japan. J. Geol. Geogr.*, 6: 1–14.
- YABE A., TERADA K. & SEKIDO S. 2003. The Tetori-type flora, revisited: A review. *Mem. Fukui Pref. Dinosaur Mus.*, 2: 23–42.
- YAMADA T. & UEMURA K. 2008. The plant fossils from the Kaizara Formation (Callovian, Jurassic) of the Tetori Group in the Izumi district, Fukui Prefecture, Central Japan. *Palaeontol. Res.*, 12: 1–17.
- YANG W. & LI S. 2008. Geochronology and geochemistry of the Mesozoic volcanic rocks in Western Liaoning: Implications for lithospheric thinning of the North China Craton. *Lithos*, 102: 88–117.
- YOKOYAMA M. 1889. Jurassic plants from Kaga, Hida and Echizen. *J. Coll. Sci. Imp. Univ. Japan*, 3: 1–66.
- 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 Geol. Sinica*, 85: 471–481.
- ZHANG H., WANG M. & LIU X. 2008. Constraints on the upper boundary age of the Tiaojishan Formation volcanic rocks in West Liaoning–North Hebei by LA-ICP-MS dating. *Chin. Sci. Bull.*, 53: 3574–3584.
- ZHANG W. & ZHENG S. 1987. Early Mesozoic fossil plants in western Liaoning, northeast China: 239–338. In: Yu X., Wang W., Liu X., Zhang W., Zheng S., Zhang Z., Yu J., Ma F., Dong G., Yao, P. (eds.), *Mesozoic Stratigraphy and Palaeontology of Western Liaoning*. Geological Publishing House, Beijing.
- ZHANG Z. 1976. Fossil plant kingdom: 179–211. In: Nei Mongol Autonomous Region Bureau of Geology (ed.), *Paleontological Atlas of North China, Inner Mongolia. Volume II. Mesozoic and Cenozoic*. Geological Publishing House, Beijing.
- ZHAO M., SUN C., DILCHER D.L., ZHAO Z. & NA Y. 2015. *Anomozamites* (Bennettitales) from Middle Jurassic Haifanggou Formation, western Liaoning, China. *Global Geol.*, 18: 75–87.
- ZHENG S. & WANG X. 2010. An undercover angiosperm from the Jurassic of China. *Acta Geol. Sinica*, 84: 895–902.

- ZHENG S., ZHANG L. & GONG E. 2003. A discovery of *Anomozamites* with reproductive organs. Acta Bot. Sinica, 45: 667–672.
- ZHENG X., YOU H., XU X. & DONG Z. 2009. An early Cretaceous heterodontosaurid dinosaur with filamentous integumentary structures. Nature, 458: 333–336.
- ZHOU Z. 1995. Jurassic floras: 343–410. In: Li X. (ed.), Fossil Floras of China Through the Geological Ages. Guangdong Science and Technology Press, Gunagzhou.
- ZHOU Z. & WANG Y. 2017. Vertebrate assemblages of the Jurassic Yanliao Biota and the Early Cretaceous Jehol Biota: Comparisons and implications. Palaeoworld, DOI: 10.1016/j.palwor.2017.01.002.
- ZHOU Z., BARRETT P.M. & HILTON J. 2003. An exceptionally preserved Lower Cretaceous ecosystem. Nature, 421: 807–814.
- ZHOU Z., ZHENG S. & ZHANG L. 2007. Morphology and age of *Yimaia* (Ginkgoales) from Daohugou Village, Ningcheng, Inner Mongolia, China. Cretac. Res., 28: 348–362.

Table 1. Synopsis of genera and species identified and reported for the flora from the Daohugou Bed (Haifanggou Formation), based on the present study, preliminary identifications made from photographs of hundreds of specimens from IVPP, NIGPAS and STMNH (the latter of which in large part are not available for publication), and available literature

Species name	Plant group	Specimens available at			Remarks
		NJU	STMNH	IVPP NIGPAS	
Species identified from material collected for the present study (MES-NJU)					
<i>Clathropteris</i> sp. or <i>Hausmannia</i> sp.	Fern	+			see text
<i>Sagenopteris</i> sp. cf. <i>Sagenopteris philippsii</i>	Caytoniales	+	+	+	see text
<i>Wielandiella villosa</i>	Bennettite	+	+	+	see text
<i>Anomozamites sinensis</i>	Bennettite	+	+	+	see text
<i>Anomozamites</i> sp. cf. <i>Anomozamites helmersianus</i>	Bennettite	+	+	+	see text
<i>Cycadolepis</i> sp. (= <i>Anomozamites haifanggouensis</i>)	Bennettite	+	+	+	see text
<i>Pterophyllum lamagouense</i>	Bennettite	+		+	see text
<i>Pterophyllum</i> sp. cf. <i>Pterophyllum angulatum</i>	Bennettite	+			see text
<i>Jacutiella</i> sp. cf. <i>Jacutiella denticulata</i>	Cycadophyte	+			see text
<i>Ginkgoites</i> sp. cf. <i>Ginkgoites huttonii</i>	Ginkgophyte	+	+		see text
<i>Ginkgoites sibirica</i>	Ginkgophyte	+	+	+	see text
<i>Sphenobaiera longifolia</i>	Ginkgophyte	+			see text
<i>Sphenobaiera czekanowskiana</i>	Ginkgophyte	+	+		see text
<i>Phoenicopsis</i> sp. cf. <i>Phoenicopsis speciosa</i>	Ginkgophyte	+	+		see text
<i>Czekanowskia rigida</i>	Czekanowskiales	+	+	+	see text
<i>Leptostrobus</i> sp. cf. <i>Leptostrobus laxiflora</i>	Czekanowskiales	+			see text
cf. <i>Ixostrobus</i> sp.	Czekanowskiales	+		+	see text
<i>Yanliaoa sinensis</i>	Conifer	+	+	+	see text
<i>Brachyphyllum</i> sp. cf. <i>Brachyphyllum longispicum</i>	Conifer	+	+	+	see text
<i>Pityophyllum nordenskiöldii</i>	Conifer	+	+	+	see text
<i>Elatides</i> sp. cf. <i>Elatides falcata</i>	Conifer	+			see text
<i>Pityospermum maakiana</i>	Conifer	+	+	+	see text
<i>Problematospermum</i> sp.	Bennettite	+			see text
<i>Samaropsis</i> sp.	Conifer?	+		+	see text
<i>Schizolepis</i> sp.	Conifer?	+	+	+	see text
Preliminary identifications of additional specimens from IVPP, NIGPAS, STMNH, based on photographs at hand					Identification based on
<i>Daohugouthallus ciliiferus</i>	Algae			+	Wang et al. 2010a
<i>Thallites clarus</i>	Moss			+	Zhang & Zheng 1987
<i>Lycopodites tenerrimus</i>	Lycophyte		+	+	Heer 1876, Frolov & Mashchuk 2014
<i>Equisetites lamagouense</i> / <i>Phyllothea sibirica</i>	Sphenophyte			+	Zhang & Zheng 1987
<i>Scytopyllum chaoyangensis</i>	Fern			+	Zhang & Zheng 1987
<i>Coniopteris hymenophylloides</i>	Fern		+	+	Zhang & Zheng 1987
<i>Eboracia lobifolia</i> (<i>Thyrsopteris</i>)	Fern		+	+	Zhang & Zheng 1987

Table 1. Continued

Species name	Plant group	Specimens available at			Remarks
		NJU	STMNH	IVPP NIGPAS	
<i>Cladophlebis asiatica</i> (<i>Asplenium whitbyense</i>)	Fern			+	Zhang & Zheng 1987
<i>Tyrmia valida</i>	Bennettite		+	+	Zhang & Zheng 1987
<i>Tyrmia grandifolia</i>	Bennettite		+	+	Zhang & Zheng 1987
<i>Tyrmia pterophylloides</i>	Bennettite			+	Vachrameev & Doludenko 1961
<i>Weltrichia daohugouensis</i>	Bennettite			+	Li et al. 2004
<i>Williamsoni(ella) sinensis</i>	Bennettite		+	+	Zhang & Zheng 1987
<i>Pterophyllum</i> sp. cf. <i>P. pumilum</i>	Bennettite			+	Zhang & Zheng 1987
<i>Podozamites lanceolatus</i>	Conifer		+	+	Heer 1876
<i>Yuccites decus</i>	Conifer			+	Zhang & Zheng 1987
<i>Nilssonia orientalis</i>	Cycadophyte			+	Heer 1878
<i>Pityocladus</i> sp.	Conifer		+	+	Sun et al. 2001
Reproductive structure similar to “ <i>Schmeissneria sinensis</i> ”	Ginkgophyte		+	+	Wang et al. 2007
Cone similar to <i>Ixostrobus</i> spp.	Ginkgophyte			+	Harris 1974
Cone similar to <i>Leptostrobus</i> spp. but not fitting in the genus	Conifer			+	Heer 1876
<i>Cephalotaxopsis</i> cf. <i>Cephalotaxopsis sinensis</i>	Conifer		+	+	Sun et al. 2001
<i>Aegianthus daohugouensis</i>	Cycadophyte			+	Deng et al. 2014
<i>Caytonanthus</i> sp. cf. <i>Antholithus yangshugouensis</i>	Caytoniales			+	Zhang & Zheng 1987

Additional taxa from available papers					Paper by
<i>Selaginellites chaoyangensis</i>	Lycophyte				Zheng & Li 1978
<i>Tyrmia taizishanensis</i> *	Bennettite				Li et al. 2004
<i>Problematospermum ovale</i>	Bennettite				Wang et al. 2010b
<i>Cladophlebis</i> sp. (<i>Osmunda</i>)*	Fern				Zheng & Wang 2010
<i>Coniopteris burejensis</i> *	Fern				Zheng & Wang 2010
<i>Anomozamites</i> sp.*	Bennettite				Zheng & Wang 2010
<i>Zamites gigas</i> *	Bennettite				Zheng & Wang 2010
<i>Pterophyllum</i> spp.*	Bennettite				Zheng & Wang 2010
<i>Williamsonia</i> sp.*	Bennettite				Zheng & Wang 2010
<i>Cycadolepis</i> spp.*	Bennettite				Zheng & Wang 2010
<i>Ginkgoites</i> sp.*	Ginkgophyte				Zheng & Wang 2010
<i>Yimaia capituliformis</i> *	Ginkgophyte				Zheng & Wang 2010
<i>Pityocladus</i> sp.*	Conifer?				Zheng & Wang 2010
<i>Aegianthus daohugouensis</i> (previously <i>Solaranthus daohugouensis</i>)	Cycadophyte				Deng et al. 2014
<i>Williamsonia</i> sp.	Bennettite				Pott et al. 2012
<i>Ningchengia jurassica</i>	Moss				Heinrichs et al. 2014
<i>Sphenobaiera</i> sp.	Ginkgophyte				Na et al. 2014
<i>Juraherba bodae</i>	“Undercover angiosperm”				Han et al. 2016
<i>Yuhania daohugouensis</i>	“Undercover angiosperm”				Liu & Wang 2016
<i>Phoenicopsis daohugouensis</i>	Ginkgophyte				Wei et al. 2015
<i>Anomozamites haifanggouensis</i>	Bennettite				Zheng et al. 2003

Note: *said to occur at Daohugou but not independently verified due to incomplete referencing

Dong et al. (2017) list					Our identification
<i>Ulothrix</i> sp.	Algae				
<i>Daohugouthallus ciliiferus</i>	Moss				<i>Daohugouthallus ciliiferus</i>
<i>Metzgerites</i> sp.	Moss				
<i>Muscites</i> sp. 1	Moss				<i>Lycopodites tenerrimus</i>
<i>Muscites</i> sp. 2, <i>Muscites</i> sp. 3	Moss				
<i>Ningchengia jurassica</i>	Moss				<i>Ningchengia jurassica</i>

Table 1. Continued

Species name	Plant group	Specimens available at			Remarks
		NJU	STMNH	IVPP NIGPAS	
<i>Lycopodites</i> sp.	Fern				
<i>Annulariopsis</i> sp.	Fern				
<i>Equisetites lamagouense</i>	Fern				<i>Equisetites lamagouense</i>
<i>Coniopteris</i> sp.	Fern				<i>Coniopteris hymenophylloides</i>
<i>Eboracia</i> sp. 1, <i>Eboracia</i> sp. 2	Fern				<i>Eboracia lobifolia</i> (<i>Thyrsopteris</i>)
<i>Cladophlebis</i> sp. 1, <i>Cladophlebis</i> sp. 3	Fern				<i>Eboracia lobifolia</i> (<i>Thyrsopteris</i>)
<i>Cladophlebis</i> sp. 2	Fern				<i>Cladophlebis asiatica</i> (<i>Asplenium whitbyense</i>)
<i>Caytonia</i> sp.	Caytoniales				(Fern sporangia)
<i>Sagenopteris</i> sp. 1, <i>Sagenopteris</i> sp. 2	Caytoniales				<i>Sagenopteris</i> sp. cf. <i>Sagenopteris philippsii</i>
<i>Pterophyllum</i> sp.	Bennettite				(<i>Tyrmia grandifolia</i>)**
<i>Anomozamites haifanggouensis</i>	Bennettite				some leaves: <i>Wielandiella villosa</i>
<i>Anomozamites villosus</i>	Bennettite				<i>Wielandiella villosa</i>
<i>Anomozamites</i> sp. 1	Bennettite				<i>Anomozamites</i> sp. cf. <i>Anomozamites helmersianus</i>
<i>Anomozamites</i> sp. 2	Bennettite				<i>Wielandiella villosa</i>
<i>Anomozamites</i> sp. 3	Bennettite				<i>Anomozamites sinensis</i>
? <i>Anomozamites</i> sp. 4	Bennettite				
? <i>Nilssoniopteris</i> sp.	Bennettite				<i>Nilssonia orientalis</i>
<i>Weltrichia daohugouensis</i>	Bennettite				<i>Weltrichia daohugouensis</i>
<i>Williamsonia</i> sp.	Bennettite				<i>Williamsoni(ella) sinensis</i>
<i>Cycadolepis</i> spp.	Bennettite				<i>Cycadolepis</i> sp.
<i>Yimaia captuliformis</i>	Ginkgophyte				<i>Yimaia captuliformis</i>
<i>Ginkgoites</i> sp. 1	Ginkgophyte				<i>Ginkgoites</i> sp. cf. <i>Ginkgoites huttonii</i>
<i>Ginkgoites</i> sp. 2	Ginkgophyte				<i>Ginkgoites sibirica</i>
<i>Ginkgoites</i> sp. 3	Ginkgophyte				<i>Yuccites decus</i>
<i>Baiera</i> sp.	Ginkgophyte				<i>Sphenobaiera czekanowskiana</i>
<i>Solenites</i> sp.	Czekanowskiales				<i>Czekanowskia rigida</i>
<i>Leptostrobus</i> sp.	Czekanowskiales				<i>Leptostrobus</i> sp. cf. <i>Leptostrobus laxiflora</i>
<i>Ixotrobus</i> sp.	Czekanowskiales				cf. <i>Ixotrobus</i> sp.
<i>Pityocladus</i> sp. 1, <i>Pityocladus</i> sp. 2, <i>Pityocladus</i> sp. 3	Conifer				<i>Pityocladus</i> sp.
<i>Pityospermum</i> spp.	Conifer				<i>Pityospermum</i> cf. <i>Pityospermum maakianum</i>
<i>Schizolepis daohugouensis</i>	Conifer				<i>Schizolepidopsis</i>
<i>Schizolepis molleri</i>	Conifer				<i>Schizolepidopsis</i>
? <i>Yanliaoa</i> sp.	Conifer				<i>Yanliaoa sinensis</i>
<i>Araucarites</i> sp. 1, <i>Araucarites</i> sp. 2	Conifer				
<i>Amentotaxus</i> sp.	Conifer				<i>Cephalotaxopsis</i> cf. <i>Cephalotaxopsis sinensis</i>
<i>Taxus</i> sp.	Conifer				<i>Pityophyllum nordenskiöldii</i>
<i>Nageiopsis</i> sp.	Conifer				<i>Podozamites lanceolatus</i>
<i>Cephalotaxopsis</i> cf. <i>leptophylla</i>	Conifer				
<i>Frenelopsis</i> sp.	Conifer				
<i>Brachyphyllum</i> sp.	Conifer				<i>Brachyphyllum</i> cf. <i>Brachyphyllum longispicum</i>
<i>Elatocladus</i> sp. 1, <i>Elatocladus</i> sp. 2, <i>Elatocladus</i> sp. 3	Conifer				<i>Cephalotaxopsis</i> cf. <i>Cephalotaxopsis sinensis</i>
<i>Solaranthus daohugouensis</i>	Incertae sedis				(<i>Solaranthus daohugouensis</i>)
<i>Juraherba bodae</i>	Incertae sedis				(<i>Juraherba bodae</i>)
<i>Yuhania daohugouensis</i>	Incertae sedis				(<i>Yuhania daohugouensis</i>)
<i>Conites</i> spp.	Incertae sedis				<i>Conites</i> sp. / <i>Schmeissneria</i> sp.
<i>Problematospermum ovale</i>	Incertae sedis				<i>Problematospermum</i>
<i>Carpolithes</i> spp.	Incertae sedis				<i>Samaropsis</i>

Note: **The placement in *Tyrmia* is questionable

Table 2. Additional reports ('surveys') on the composition of the Daohugou flora and Haifanggou Formation, with lists of taxa names, some of which are not convincingly documented or verifiable so far (Liu & Wang 2017, Dong et al. 2017)

According to Liu & Wang (2016), the Daohugou Flora includes:	
Algae 1 genus, 1 species	Chlorophyceae
Bryophytes 4 genera, 6 species	<i>Daohugouthallus</i> , <i>Metzgerites</i> , <i>Muscites</i> , <i>Ningchengia</i>
Lycopodaceae 2 genera, 2 species	<i>Lycopodites</i> , <i>Selaginellites</i>
Sphenophytes 2 genera, 2 species	<i>Annularia</i> , <i>Equisetites</i>
Filicales 4 genera, 6 species	<i>Coniopteris</i> , <i>Osmunda</i> , <i>Eboracia</i> , <i>Sphenopteris</i>
Cycads 7 genera, 12 species	<i>Pterophyllum</i> , <i>Anomozamites</i> , <i>Nissoniopteris</i> , <i>Williamsonia</i> , <i>Weltrichia</i> , <i>Cycadolepis</i> , <i>Tyrmia</i>
Czekanowskiales 4 genera, 4 species	<i>Czekanowskia</i> , <i>Solenites</i> , <i>Leptostrobus</i> , <i>Ixostrobus</i>
Ginkgoales 4 genera, 6 species	<i>Yimaia</i> , <i>Ginkgoites</i> , <i>Baiera</i> , <i>Sphenobaiera</i>
Coniferales 13 genera, 20 species	<i>Pityocladus</i> , <i>Pityospermum</i> , <i>Schizolepis</i> , <i>Austrohamia</i> (<i>Yanliaoa</i>), <i>Brachyphyllum</i> , <i>Elatocladus</i> , <i>Amentotaxus</i> , <i>Taxus</i> , <i>Nageiopsis</i> , <i>Podocarpites</i> , <i>Cephalotaxopsis</i> , <i>?Pseudofrenelopsis</i> , <i>Podozamites</i>
Caytoniales 2 genera, 2 species	<i>Caytonia</i> , <i>Sagenopteris</i>
Seeds/fruits with unknown affinities 3 genera, 3 species	<i>Conites</i> , <i>Problematospermum</i> , <i>Carpolithus</i>
Angiosperms 2 genera, 2 species	<i>Solaranthus</i> , <i>Juraherba</i>
References cited: Zheng et al. 2003, Li et al. 2004, Zhou et al. 2007, Zheng & Wang 2010, Wang et al. 2010a, b, Pott et al. 2012, Heinrichs et al. 2014, Han et al. 2016, Dong et al. 2017	

The Haifanggou Formation at Sanjiaochengcun contains:

<i>Selaginellites</i> , <i>Equisetites</i> , <i>Coniopteris</i> , <i>Cladophlebis</i> , <i>Pterophyllum</i> , <i>Nilssonina</i> , <i>Anomozamites</i> , <i>Zamites</i> , <i>Ctenis</i> , <i>Cycadolepis</i> , <i>Taeniopteris</i> , <i>Ginkgoites</i> , <i>Baiera</i> , <i>Sphenobaiera</i> , <i>Cephalotaxopsis</i> , <i>Podocarpites</i> , <i>Brachyphyllum</i> , <i>Pagiophyllum</i> , <i>Pityophyllum</i> , <i>Cupressiocladius</i> , <i>Schizolepis</i> , <i>Carpolithus</i> , <i>Yanliaoa</i> , <i>Xingxueanthus</i>	Wang & Wang 2010, no evidence provided; citing Pan (1977, 1983), Wang et al. (1997), Zheng et al. (2003), which only report on single species); ignoring Zhang & Zheng (1987), but citing Zheng et al. (2003) who report on Daohugou in fact.
<i>Schmeissneria sinensis</i>	Wang et al. 2007
<i>Problematospermum ovale</i>	Wang et al. 2010b
<i>Anomozamites sanjiaocunensis</i>	Zhao et al. 2015