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New records of Jurassic petrified wood in Jianchang of western Liaoning, China and their palaeoclimate implications

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Diverse and rich fossil wood records have been documented from the Mesozoic of Liaoning Province, NE China. The Tiaojishan Formation (mainly distributed in Beipiao, Chaoyang, Fuxin and Jianchang regions) is one of the most significant horizons for the Jurassic petrified wood in Liaoning Province. Previously, wood fossils of this formation were mainly reported in Beipiao and Chaoyang regions, whereas fossil wood record was merely known in Jianchang region. Here we describe new fossil wood specimens from the Tiaojishan Formation in Jianchang County, western Liaoning. Two fossil wood taxa, i.e., *Protaxodioxylon jianchangense* Tian et Wang sp. nov. and *Xenoxylon peidense* Zheng et Zhang were recognized on the basis of anatomical features. These fossil wood records add new data for understanding the fossil wood diversity, floral composition and palaeoclimate of the Tiaojishan Formation. The occurrence of *Xenoxylon* and *Protaxodioxylon* implies a cool temperate, wet and seasonal climate condition with interannual variations during the Middle to Late Jurassic transition in western Liaoning region.

fossil wood, *Xenoxylon*, *Protaxodioxylon*, Middle to Late Jurassic, palaeoclimate, Tiaojishan Formation, western Liaoning

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Diverse wood fossils have been reported in China over the past few decades, ranging in age from the Late Palaeozoic to the Cenozoic (Zhang et al., 2006). The Mesozoic is an important period for fossil wood diversification and radiation in China (Wang et al., 2009; Yang et al., 2013). In particular, the Jurassic fossil wood records are well documented in both the northern and southern phytoprovinces of China (Wang et al., 2009; Feng et al., 2015). In western Liaoning Province of Northeast China, the Tiaojishan Formation with an age of the late Middle Jurassic to early Late Jurassic is considered as one of the most significant fossil Lagerstätten for yielding diverse anatomically preserved petrified plants, including fern rhizomes, cycad stems and conifer wood (Wang et al., 2005; Zhang et al., 2006, 2012; Cheng and Li, 2007; Cheng et al., 2007; Jiang H E et al., 2008; Jiang Z K et al., 2011; Cheng, 2011; Jiang, 2012; Tian et al., 2013, 2014a, 2014b). The Tiaojishan Formation is geographically distributed in Beipiao, Chaoyang, Fuxin and Jianchang regions of western Liaoning Province (Figure 1).

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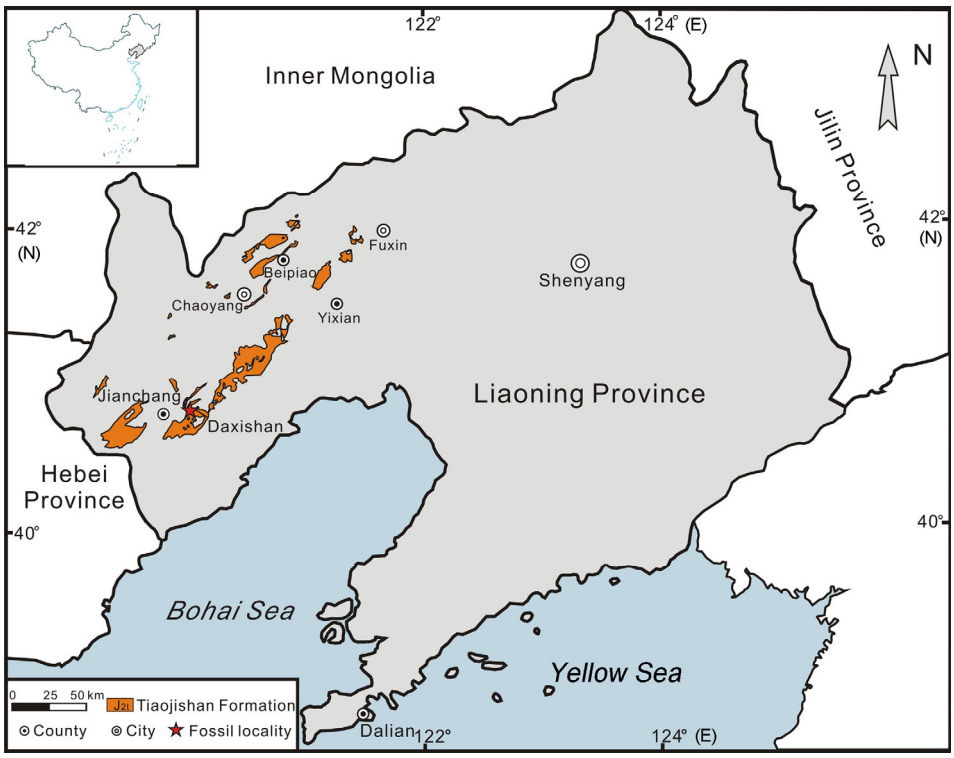


Figure 1 Geographical distribution of the Tiaojishan Formation and fossil wood locality in western Liaoning region, NE China.

However, most of the fossil wood remains reported from this formation were documented in Beipiao and Chaoyang regions. So far, no fossil wood remains have been described from the Tiaojishan Formation in Jianchang region. In this paper, we report some well-preserved petrified wood specimens collected from the Tiaojishan Formation in Jianchang County for the first time. This locality is palaeontologically remarkable for yielding several appealing vertebrate fossils, e.g., the earliest feathered dinosaur (*Anchiornis huxlei* Xu et al.) and earliest eutherian mammal (*Juramaia sinensis* Luo, Yuan, Meng et Ji) (Hu et al., 2009; Luo et al., 2011), which have drawn great attention for revealing the origin of avians and mammals.

The present fossil wood specimens are ascribed to two taxa, i.e., *Protaxodioxylon jianchangense* Tian et Wang sp. nov. and *Xenoxylon peidense* Zheng et Zhang. These fossil remains add new data for understanding the fossil wood diversity and floral composition of the Tiaojishan Formation, and imply a cool temperate, wet and seasonal climate condition with interannual variations during the Middle to Late Jurassic in western Liaoning Province.

1 Material and methods

The new fossil material described here consists of several structurally preserved silicified wood fragments. They were collected from the Tiaojishan Formation in Linglongta Town of Jianchang County, western Liaoning Province (Figure 1). In the Daxishan profile of Linglongta region, the fossil-bearing section of the Tiaojishan Formation is 405.6 m thick, and represented by a set of sediments composed of shales, siltstones and sandstones, sandwiched between andesite volcanic rocks (Duan et al., 2009) (Figure 2). In total of the 29 lithological units recognized in this profile, the fossil wood specimens were collected from the unit 16 (Duan et al., 2009) (Figure 2). In addition to the fossil wood specimens, abundant plant, vertebrate and invertebrate fossils also occurred in this fossil-bearing section. Among them, the plant megafossils are represented by *Neocalamites*, *Equisetum*, *Coniopteris*, *Zamites*, *Czekanowskia*, *Phoenicopsis* and *Sphenobaiera* (Duan et al., 2009). It is noted the earliest known feathered dinosaur *Anchiornis huxlei* occured in the unit 22 of this profile (Figure 2).

Traditionally, the Tiaojishan Formation is considered to be Middle Jurassic in age based on palynological data and floral assemblage (e.g., Zheng and Zhang, 1982; Pu and Wu, 1985; Zhang and Zheng, 1987; Wang et al., 2006). During the last decade, various radioisotopic ages have been proposed using different approaches for the Tiaojishan Formation in western Liaoning and adjacent regions (i.e., northern Hebei and Inner Mongolia) (Liu J et al., 2006; Zhang et al., 2008; Chang et al., 2009; Liu Y Q et al., 2012; Wang et al., 2013). Among these results, the radioisotopic age of the fossil-bearing strata in the Daxishan profile of Jianchang region was dated as 158 to 161 Ma (Liu et al., 2012; Wang et al., 2013). Generally, the Tiaojishan Formation is suggested to be late Middle Jurassic to early Late

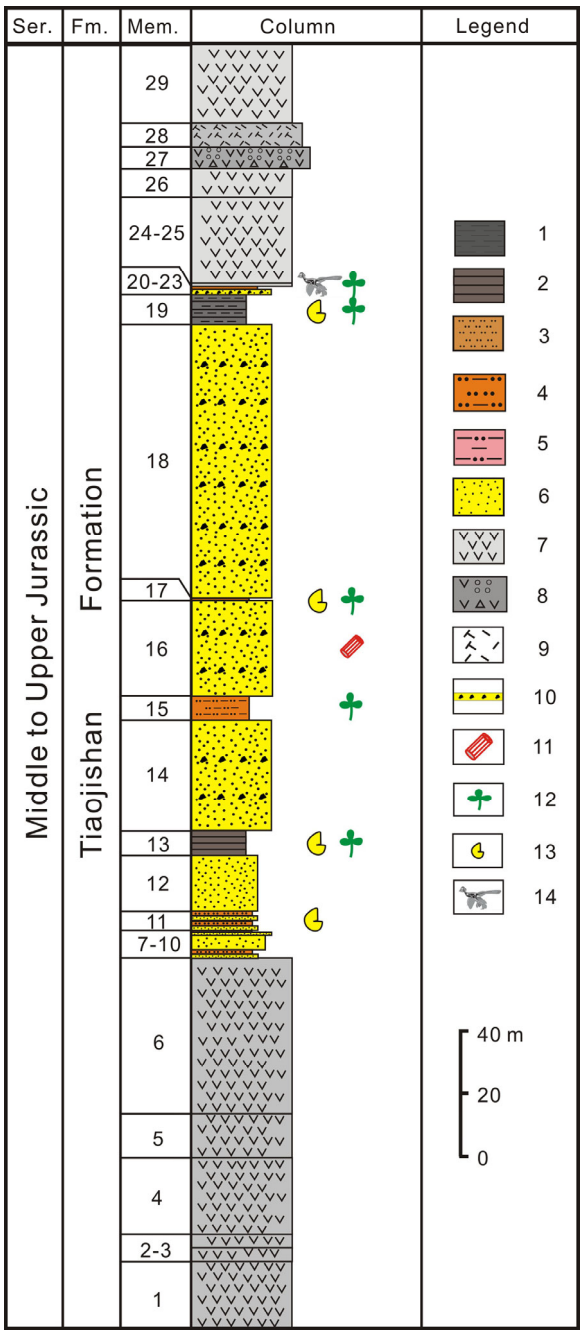


Figure 2 Stratigraphic column of the Tiaojishan Formation in Linglongta of Jianchang County, Liaoning Province, China (Drawing based on lithological descriptions of Duan et al., 2009). 1, mudstone; 2, shale; 3, siltstone; 4, argillaceous siltstone; 5, silty mudstone; 6, sandstone; 7, andesite; 8, tuff breccia; 9, debris coagulation lava; 10, pebbly sandstone; 11, fossil wood; 12, plant fossils; 13, invertebrate fossils; 14, feathered dinosaur (*Anchiornis huxlei*).

Jurassic in age.

The petrified wood specimens were cut transversely, longitudinally and tangentially into several thin sections. These sections were prepared by standard methods, including cutting, grinding and polishing preparations (Hass and Rowe, 1999). These sections were then mounted on slides for microscopic examinations. Photographs were taken with a "Scope Image 9.0 (H3D) Software" adapted to a Yongxin BM2000 transmitted light-microscope. The specimens and slides described in this paper are housed in the Palaeontological Museum of Liaoning, Shenyang, China, with the registration numbers PMOL-B-01397 to PMOL-B-01399.

Additionally, in order to understand the growth pattern, annual sensitivity, and meaning sensitivity of the present fossil wood material, a statistical analysis was applied using the quotation given by Friits (1976) as follows:

$$\mathrm{MS}=1/(n-1)\sum_{t=1}^{t=n-1}\left|2(X_{t+1}-X_t)/(X_{t+1}+X_t)\right|, \qquad (1)$$

where "X_t" is the ring width for a given year (t), "X_{t+1}" is the width of the adjacent younger year and "n" is the total number of rings in the sequence (Friits, 1976).

2 Systematic description

Phylum: Gymnospermae
Class: Coniferopsida
Order: Coniferales
Family: Cupressaceae Gray *sensu* Farjon
Genus: *Protaxodioxylon* Bamford et Philippe
Species: *Protaxodioxylon jianchangense* Tian N. et Wang Y.D. sp. nov.
(Figures 3–5)

Holotype: PMOL-B-01397.

Type locality: Daxishan Village of Linglongta Town, Jianchang County, Liaoning Province.

Horizon and age: Tiaojishan Formation, late Middle Jurassic to early Late Jurassic.

Repository: The specimen and slides are housed in the Palaeontological Museum of Liaoning, Shenyang, China.

Etymology: The specific epithet *jianchangense* refers to the fossil locality Jianchang County.

Specific diagnosis: Secondary xylem with distinct growth rings; false rings present. Early wood tracheids polygonal to semi-circular. Intercellular spaces well-developed. Pits on radial walls of tracheids uniseriate, oval, contiguous and flattened; occasionally circular and separated or not. Cross-field pits mainly taxodioid, occasionally cupressoid. One pit per field. Horizontal and end walls of ray cells smooth and unpitted. Xylem rays uniseriate, 1–16, mostly 2–7 cells high. Axial parenchyma present with end walls smooth or irregularly thickened. Resin canals absent.

Description: The present fossil wood specimen is preserved as a fragment of secondary xylem. In the transverse section, distinct growth rings occur with some false rings present (Figure 3(a), (b)). Tracheids in the transverse section are polygonal to semi-circular. Intercellular spaces are well developed among tracheid cells (Figure 3(c)). The

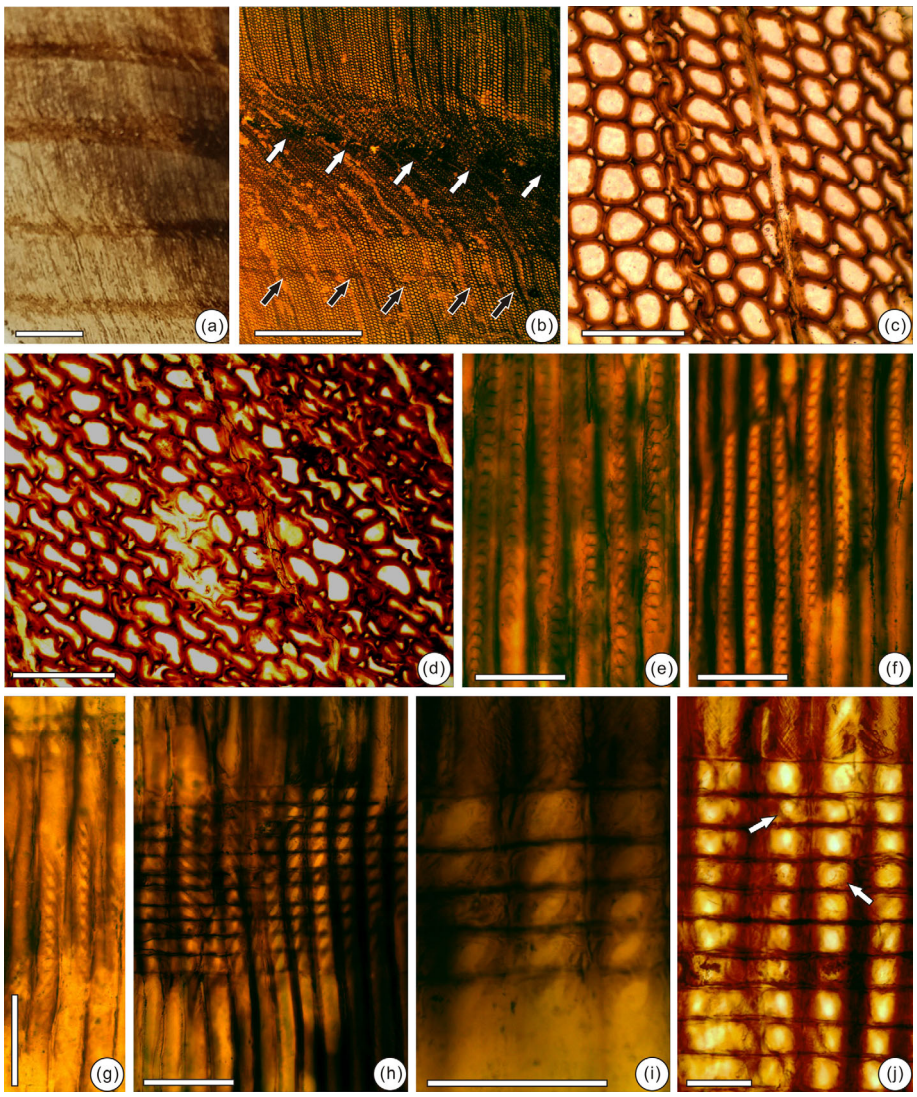


Figure 3 *Protaxodioxylon jianchangense* Tian et Wang sp. nov. from the Tiaojishan Formation in Jianchang of western Liaoning, China. (a) Transverse section, showing the distinct growth rings, scale bar=3.0 mm; (b) transverse section, showing the growth ring (white arrows), the false ring (black arrows) and twisted tracheid cells, scale bar=1.0 mm; (c) transverse section, showing details of the tracheids and ray cells with typical intercellular spaces, scale bar=0.1 mm; (d) transverse section, showing twisted tracheid cells, scale bar=0.1 mm; (e) longitudinal section, showing uniseriate, oval, contiguous and flattened bordered pits, scale bar=0.1 mm; (f) longitudinal section, showing uniseriate bordered pits and helical cracks on the tracheid walls, scale bar=0.1 mm; (g) longitudinal section, showing helical cracks on the tracheid walls, scale bar=0.1 mm; (h) longitudinal section, showing the cross-field, each cross-field bears one taxodioid pit, scale bar=0.1 mm; (i) longitudinal section, showing details of the taxodioid cross-field pits, scale bar=50 μm; (j) longitudinal section, showing the cross-field, white arrows indicate cupressoid pits, scale bar=40 μm.

wood strength appears relatively weak, with many tracheid cells twisted, especially in zones near the growth rings (Figure 3(b), (d)). In the longitudinal section, bordered pits on radial tracheid walls are commonly uniseriate, oval, contiguous and flattened; occasionally circular and separated or not (Figure 3(e), (f)). Typical helical cracks are well developed on the tracheid walls (Figure 3(f), (g)). Cross-field pits are mostly taxodioid in type (Figure 3(h), (i)), occasionally cupressoid in type (Figure 3(j)). Ray cells show smooth horizontal and end walls (Figure 3(i), (j)). Each cross-field bears only one pit, rarely two pits (Figure 3(h)–(j)). In the tangential section, some small holes occur on the tangential wall of the tracheid (Figure 4(d), (e)), but seem to be unbordered. Xylem rays are uniseriate, 1–16 cells high (mean=6, n=250), mostly 2–7 cells high (Figures 4(a)–(c) and 5). Axial parenchyma is present with end walls smooth (Figure 4(f)–(g)) or occasionally irregularly thickened (Figure 4(h)). Resin canals are absent.

Comparison: Mesozoic fossil wood that bears anatomical characters resembling the living taxodiaceous Cupressaceae was previously assigned to the fossil genera *Prototaxodioxylon* Vogellehner and *Taxodioxylon* (Hartig) Gothan (Gothan, 1905; Vogellehner, 1968; Vozenin-Serra et al., 2011). However, Nadjafi (1982) re-examined the original slides of the type specimen of *Prototaxodioxylon*, and claimed that there was a contradiction between the original

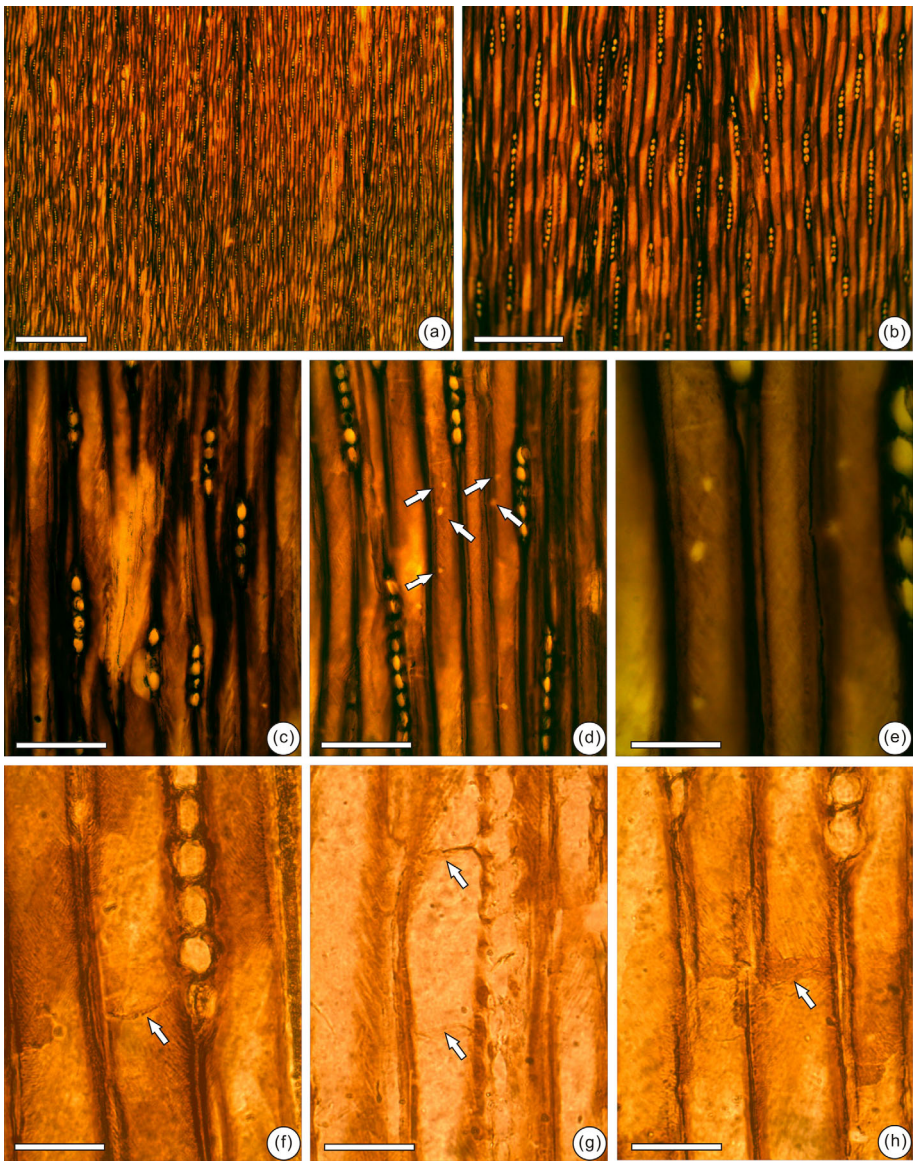


Figure 4 *Protaxodioxylon jianchangense* Tian et Wang sp. nov. from the Tiaojishan Formation in Jianchang of western Liaoning, China. (a)–(h) Tangential sections. (a) The uniseriate rays, scale bar=0.5 mm; (b) the uniseriate rays with a height ranging from 3–19 cells, scale bar=0.25 mm; (c) details of rays, scale bar=0.1 mm; (d) small holes occurring on the tangential walls of the tracheids (arrows), scale bar=0.1 mm; (e) details of the small holes on the tracheid tangential walls, scale bar=25 μm; (f)–(g) the smooth end-wall of the axial parenchyma, scale bar=25 μm; (h) the irregularly thickened end-wall of the axial parenchyma, scale bar=25 μm.

diagnosis and the holotype, which did not have any taxodioid pits in the cross-fields. Consequently, Bamfords and Philippe (2001) suggested that *Prototaxodioxylon* was a taxonomical synonym of either *Protocupressinoxylon* Eckhold or *Brachyoxylon* Hollick et Jeffrey; thus they proposed a new genus name *Protaxodioxylon* Bamford et Philippe to accommodate these tracheidoxyls with mixed radial tracheid pitting and taxodioid cross-field pits. The morphogenus *Taxodioxylon* is distinguished from *Protaxodioxylon* by uniseriate separate or biseriate opposite radial pitting (Gothan, 1905; Yang and Zheng, 2003; Zhang et al., 2006). Considering that the present fossil wood specimen from Liaoning mainly bears uniseriate continuous radial pitting, it should be referable to the genus *Protaxodioxylon.*

So far, three species have been assigned to the genus *Protaxodioxylon*, including *P. romanensis* (Philippe) Bamford et Philippe, *P. mongolense* Ding, Fu, Li et Zhang and *P. turolense* Vozein-Serra (Philippe, 1995; Bamfords and Philippe, 2001; Ding et al., 2010; Vozein-Serra et al., 2011) (Table 1). The new fossil material described here is distinct from these three taxa (Table 1), thus it is assigned to a new taxon, *Protaxodioxylon jianchangense* Tian N. et Wang Y.D. sp. nov..

The present fossil wood from Liaoning differs from the type species *P. romanensis*, by commonly bearing one pit per field, while the latter species has 1–5 pits in each

Table 1 Comparison of the anatomical features (secondary xylem) among species of *Protaxodioxylon* Bamford et Philippe

Species	Growth rings	Pits on the longitudinal wall			Tangential pits	Axial parenchyma	Rays	Cross-field pits	References
		Contiguous / separated	Uniseriate / multiseriate	Opposite / alternate					
Protaxodioxylon jianchangense Tian et Wang sp. nov.	Present	Contiguous, occasionally separated	Uniseriate		Simple holes	Present	Uniseriate; 1–16, mostly 2–7 cells high	1 pit per field; taxodioid, occasionally cupressoid	This paper
P. romanensis (Philippe) Bamford et Philippe	Present	Contiguous or separated	Uniseriate or biseriate	Opposite or alternate	Present, simple or bordered	Present	Uniseriate or biseriate; mean 5 cells high	1–5 pits per field; mixed type and taxodioid	Philippe , 1995; Bamfords and Philippe, 2001; Zhang et al., 2006
P. mongolense Ding, Fu, Li et Zhang	Present	Contiguous	Uniseriate or biseriate	Opposite or alternate	Absent	Present	Uniseriate, locally biseriate to triseriate; 1–57, mostly 8–26 cells high	1–2 pits per field; taxodioid and cupressoid	Ding et al., 2010
P. turolense Vozein-Serra	Absent	Contiguous or separated	Mostly uniseriate	Opposite	Absent	Present	Uniseriate or completely or partially biseriate; 7–26, mostly 12 and 22 cells high	1 or 2, occasionally 3 pits per field; taxodioid	Vozein-Serra et al., 2011

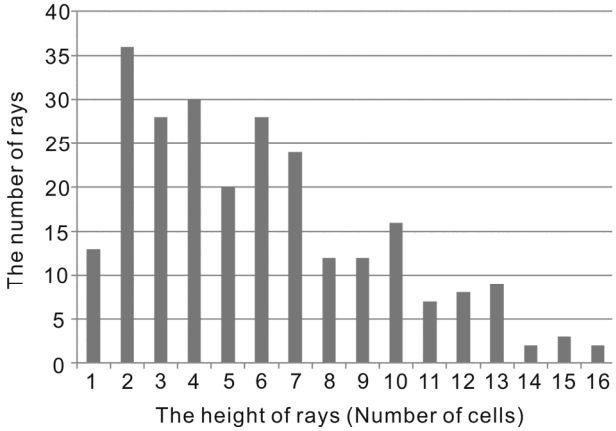


Figure 5 Histogram showing the height frequency distribution of 250 rays in a tangential longitudinal section of *Protaxodioxylon jianchangense* Tian et Wang sp. nov. from the Tiaojishan Formation in Jianchang of western Liaoning, China.

cross-field. *Protaxodioxylon turolense* from the Cretaceous of Spain differs from *P. jianchangense* sp. nov. by lacking distinct growth rings and having araucarioid pits on the radial tracheid walls (Vozein-Serra et al., 2011); additionally, the ray cells of *P. turolense* are locally biseriate or triseriate (Vozein-Serra et al., 2011). Generally, the anatomical structures of *P. jianchangense* sp. nov. are more consistent with *P. mongolense* from the Upper Mesozoic in Mongolia (Ding et al., 2010). However, the ray height of *P. mongolense* is much higher than that of the present new species.

Order: Coniferales
Genus: *Xenoxylon* Gothan
Species: *Xenoxylon peidense* Zheng et Zhang
(Figures 6–8)

1982 *Xenoxylon peidense* Zheng et Zhang, Zheng and Zhang, p. 332, plate 31, figs. 1–10;
1995 *Xenoxylon peidense* Zheng et Zhang, He, p. 15, pl. 15, figs. 1–1d; pl. 16, figs. 2–2a;
2000 *Xenoxylon peidense* Zheng et Zhang, Ding, Zheng and Zhang, p. 240

Material: PMOL-B-01398, 01399.

Description: The fossil wood material is preserved as a piece of fragmented trunk with secondary xylem. Growth rings are distinct. The late wood zone is about 1–2 cells wide, while the early wood zone varies in width (Figure 6(a), (b)). In transverse section, tracheids are transversely square, rectangular, pentagonal or circular to elliptical in transverse view (Figure 6(a), (b)). On radial walls of tracheids, bordered pits are uniseriate, flattened, elliptical and closely arranged, about 20 μm×10 μm in diameter (Figure 6(c)–(f)); pit apertures are rounded or somewhat elliptical (Figure 6(f)). The width of the pits occupies up to 1/2 of total width of tracheid (Figure 6(d), (e)). Septa-like structures and rectangular thickenings are well-developed on both the radial and tangential tracheid walls (Figure 6(i), (k), (l)). Xylem rays are uniseriate, 1–13 cells high (mean=5.5, n=250), mostly 3–8 cells high (Figures 6(j)–(l) and 7). Both the horizontal and end walls of the ray cells are smooth (Figure 6(g), (h)). Cross-field pits are typical window like, mostly one pit per field (Figure 6(g), (h)). No resin canals are observed.

Remarks: The fossil wood specimen described here is characterized by typical xenoxylean radial pittings and xenoxyloid (window-like) cross-field pits, which strongly indicate an affinity with the morphogenus *Xenoxylon* Gothan. To date, more than 20 species have been referred to

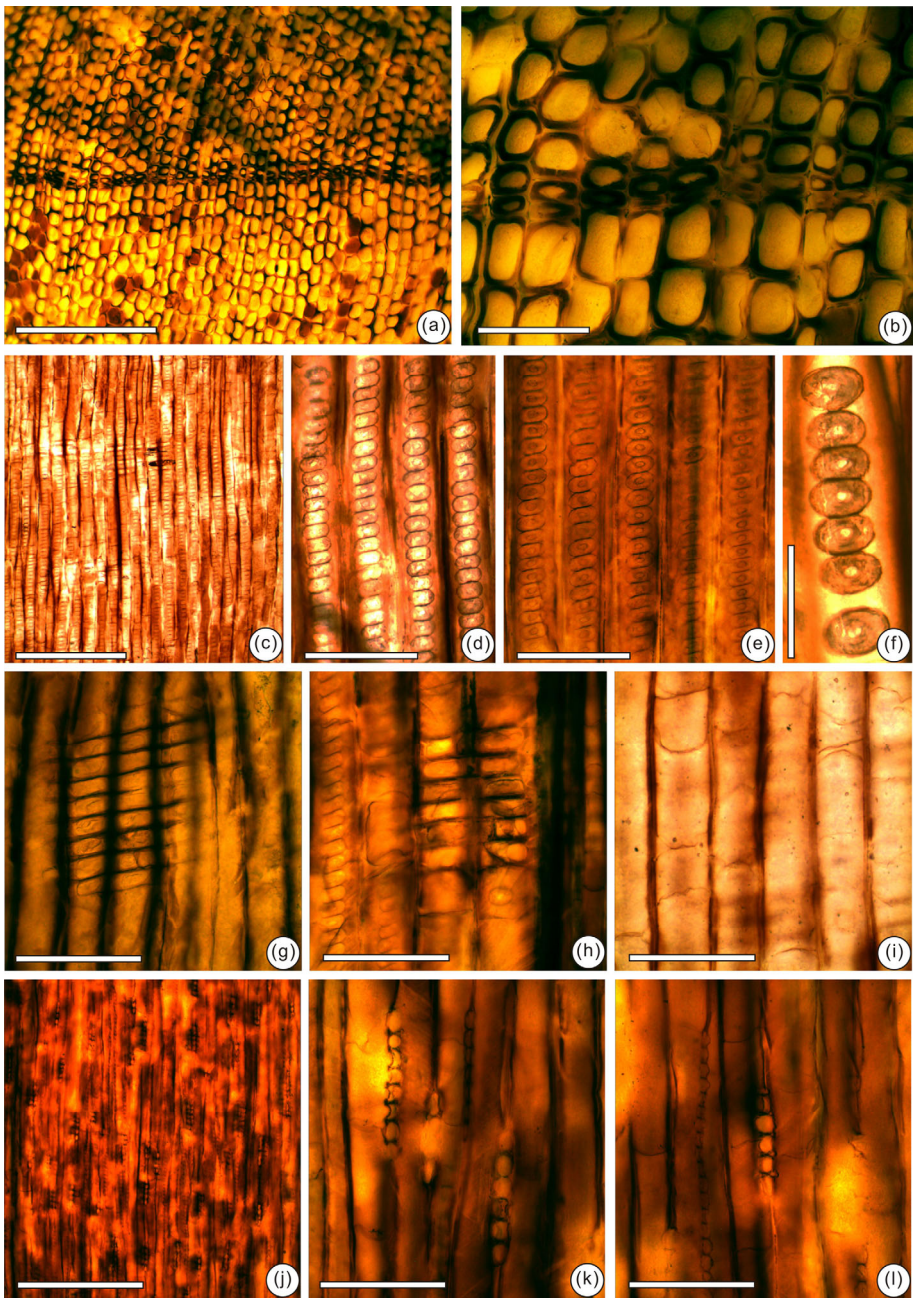


Figure 6 *Xenoxylon peidense* Zheng et Zhang from the Tiaojishan Formation in Jianchang of western Liaoning, China. (a) Transverse section, showing the early wood, narrow late wood and distinct growth ring, scale bar=0.5 mm; (b) transverse section, showing details of the narrow late wood, scale bar=0.1 mm; (c) longitudinal section, showing uniseriate, oval, contiguous and flattened bordered pits, scale bar=0.5 mm; (d), (e) longitudinal section, showing details of uniseriate bordered pits, scale bar=0.1 mm; (f) longitudinal section, showing enlargement of the bordered pits, scale bar=50 μm; (g), (h) longitudinal section, showing the cross-field, each cross-field bears one window-like pit, scale bar=0.1 mm; (i) longitudinal section, showing details of cross-septa on the tracheid longitudinal walls, scale bar=0.1 mm; (j) tangential section, showing the uniseriate rays, scale bar=0.5 mm; (k), (l) tangential section, showing details of rays, scale bar=0.1 mm.

Xenoxylon, stratigraphically ranging from the Upper Triassic to the Upper Cretaceous (Ding et al., 2000; Jiang et al., 2008; Philippe et al., 2009, 2013; Feng et al., 2015). Among them, over 10 species have been described from China (Ding et al., 2000; Feng et al., 2015).

Our specimen is more akin to *X. peidense* Zheng et Zhang, which was originally established for fossil wood from the Lower Cretaceous Dongshengcun Formation in Mishan of Peide, Heilongjiang Province, NE China (Zheng and Zhang, 1982; Zhang et al., 2006). In the type specimen of *X. peidense*, the width of the bordered pits on the tracheid wall occupy 1/2 width of the whole tracheid. This character is also found in the present fossil specimen. Additionally, the well-developed septa-like structures are found in both

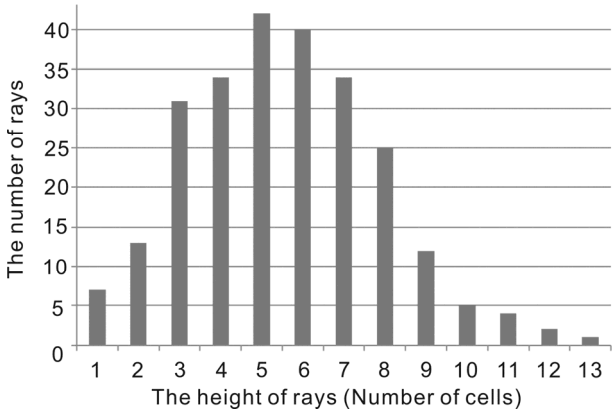


Figure 7 Histogram showing the height frequency distribution of 250 rays in a tangential longitudinal section of *Xenoxylon peidense* Zheng et Zhang from the Tiaojishan Formation in Jianchang of western Liaoning, China.

our specimen and the type specimen of *X. peidense*. Such a structure can also be observed in *X. latiporosum* (Gramer) Gothan and *X. yunnanense* Feng; however, the transition from the early wood to late wood is gradual in *X. latiporosum*, and more or less gradual in *X. yunnanense* (Gothan and Sze, 1933; Feng et al., 2015), whereas it is abrupt in both the present specimen and type specimen of *X. peidense*. The septa-like structures have previously been interpreted as flattened tylose-like structures, cracks or fungal hyphae; however, they are recently proposed to be host cell reactions to fungal attacks or the remains of metabolic products of fungal enzymatic activity (Feng et al., 2015). Interestingly, though no fungal activities have been found in the present fossil wood specimen, some saprotrophic fungal remains were do found in another specimen of *X. peidense* which was also collected from the Tiaojishan Formation in Jianchang region. In China, *Xenoxylon peidense* has also been reported from the Lower Jurassic Beipiao Formation in Kazuo of Liaoning, the Middle Jurassic Yingshugou Formation in Tieling of Liaoning, and the Lower Cretaceous Huolinhe Formation in Inner Mongolia (He, 1995; Zhang et al., 2006).

3 Discussion on palaeoclimate implications

The western Liaoning region is recognized as one of the most significant localities for Jurassic petrified wood in northern China (Zhang et al., 2006; Wang et al., 2009). In this region, the major fossil wood-bearing horizons include the Lower Jurassic Beipiao Formation, the Middle to Upper Jurassic Tiaojishan Formation and the Upper Jurassic Tuchengzi Formation (Zhang et al., 2000, 2006; Ding et al., 2000; Zheng et al., 2001). The present report of *Protaxodioxylon jianchangense* sp. nov. and *Xenoxylon peidense* further increases the fossil wood diversity up to 42 species of 24 genera for the petrified flora of the Tiaojishan Formation. Generally, this petrified flora are mainly represented by osmundaceous fern rhizomes, cycad stems and numerous pycnoxylic gymnosperms (Zhang and Zheng, 1991; Matsumoto et al., 2006; Cheng and Li, 2007; Cheng et al., 2007; Jiang et al., 2008; Cheng, 2011; Jiang, 2012; Zhang et al., 2012; Tian et al., 2013, 2014a, 2014b). Such a high fossil wood diversity makes the western Liaoning region as a unique and remarkable Jurassic fossil wood locality in China.

Petrified wood plays a significant role in understanding the floral composition, terrestrial palaeoclimate and palaeoenvironment of the geological past (Creber and Francis, 1999; Uhl, 2006). *Xenoxylon*, a common genus of Mesozoic fossil wood, has been widely reported in the Northern Hemisphere with more than 20 species (Ding et al., 2000; Philippe et al., 2009, 2013). As a fossil wood genus with distinct palaeoclimatic implications, *Xenoxylon* has been extensively accepted as an indicator of cool and/or wet climate (Philippe and Thévenard, 1996; Philippe et al., 2009; Amoit et al., 2011; Oh et al., 2015). It is further noted that *Xenoxylon* has a typical circumpolar distribution (in the broad sense) with the majority of data from high palaeolatitudes (Philippe and Thévenard, 1996; Philippe et al., 2009). Analysis of European Cretaceous data suggested that the mean annual palaeotemperature at the localities where *Xenoxylon* occurred was generally below 15°C (Philippe and Thévenard, 1996).

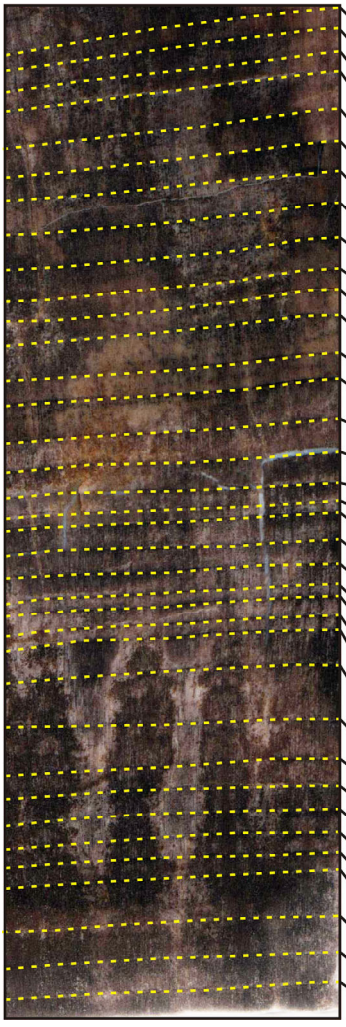
The genus *Xenoxylon* has been widely documented from late Mesozoic deposits in Northeast China. The Tiaojishan Formation is one of the major horizons for the occurrence of *Xenoxylon* in this region. In addition to *X. peidense*, three other species, including *X. hopeiense* Chang, *X. latiporosum* Schultze-Motel and *X. phyllocladoides* Gothan, have also been described from the Tiaojishan Formation in western Liaoning and adjacent regions (Ding et al., 2000; Zhang et al., 2006; Jiang et al., 2008). These fossil records indicate that the genus *Xenoxylon* flourished during the late Middle Jurassic to early Late Jurassic intervals in NE China. The high diversity of *Xenoxylon* demonstrates that the western Liaoning region represents one of the diversification centers for *Xenoxylon* in East Asia. It is therefore inferred that a wet and/or cool climate condition prevailed during the sedimentation period of the Tiaojishan Formation at the Middle to Late Jurassic transition.

This analysis also provides a palaeoclimatic constraint for understanding the associated occurrences of feathered dinosaurs in the Tiaojishan Formation in Jianchang region. The primitive feather of these coetaneous feathered dinosaurs may be a functional response for the cool climate. Besides the Tiaojishan Formation, the Lower Cretaceous Yixian Formation is another major horizon for *Xenoxylon* wood in western Liaoning. Two species of *Xenoxylon* have been reported in this formation (Ding et al., 2000; Zhang et al., 2006). Coincidentally, the Yixian Formation is also well known for bearing feathered dinosaurs (Li et al.,

2010; Zhou, 2014). Interestingly, a recent investigation on oxygen isotopes of dinosaurs revealed that exceptionally cold climate prevailed in the Early Cretaceous of East Asia (Amiot et al., 2011).

Based on marine invertebrate fauna (ammonites) migration and isotopic thermometry, Dromart et al. (2003) proposed a detailed record of sea surface temperatures in the Northern Hemisphere, indicating a severe cooling event at the Middle-Late Jurassic transition, about 160 mya. The magnitude of refrigeration (1–3°C for lower middle latitudes) and its coincidence in time with an abrupt global-scale fall of sea level documented through sequence stratigraphy are both suggestive of continental ice formation at that time (Dromart et al., 2003). Additionally, the paleoatmospheric CO_2 model GEOCARB III indicates that there was a decline of RCO_2 during the transition of the Middle to Late Jurassic (Berner and Kothavala, 2001). This may be a probable inducement leading to the so-called cooling event at that period. Such a climate fluctuation event happened at almost the same period that the Tiaojishan Formation was deposited (158 to 161 mya) (Liu et al., 2012; Wang et al., 2013). The flourishing of *Xenoxylon* in the Tiaojishan Formation is therefore a reasonable interpretation for the terrestrial response to the severe cooling event at the Middle-Late Jurassic transition in western Liaoning and adjacent regions, despite it was situated at mid-latitudes at the time.

On the other hand, the genus *Protaxodixylon* is anatomically similar to some living taxodiaceous Cupressaceae (Vozenin-Serra et al., 2011), such as *Taxodium* Rich. In the present fossil specimen, the tracheid cells are always twisted especially in zones near the growth rings (Figure 3(c)). This may be resulted from the weak wood strength which was easily compressed during the sedimentation; since the wood of extant *Taxodium* is also relatively weak (Zhou and Jiang, 1994). The living *Taxodium* is one of the extremely flood-tolerant conifers in the cypress family Cupressaceae. Lateral roots of *Taxodium* commonly produce erect, irregularly



Growth-ring Number	Growth-ring Width	Annual Sensitivity	Mean Sensitivity
35	1.72		0.33
34	1.75	0.02	
33	1.73	0.01	
32	3.05	0.55	
31	2.44	0.22	
30	3.35	0.31	
29	2.74	0.20	
28	2.72	0.01	
27	2.58	0.05	
26	1.48	0.54	
25	2.11	0.35	
24	2.88	0.31	
23	1.60	0.57	
22	3.10	0.64	
21	2.51	0.21	
20	2.34	0.07	
19	1.46	0.46	
18	0.84	0.54	
17	2.17	0.88	
16	1.78	0.20	
15	1.65	0.08	
14	0.99	0.50	
13	1.57	0.45	
12	1.21	0.26	
11	2.81	0.80	
10	4.38	0.44	
9	3.17	0.32	
8	1.96	0.47	
7	2.23	0.13	
6	1.89	0.17	
5	1.54	0.20	
4	1.65	0.07	
3	3.46	0.71	
2	3.04	0.13	
1	2.61	0.15	

Figure 8 Measurements of growth-ring width, annual and mean sensitivity of *Xenoxylon peidense* Zheng et Zhang from the Tiaojishan Formation in Jianchang of western Liaoning, China.

conic to rounded "knees" in periodically flooded habitats (Zhou and Jiang, 1994). In brief, the similar anatomical wood structures of *Protaxodioxylon jianchangense* sp. nov. to living *Taxodium* are inclined to an interpretation of a wet palaeoclimate condition in the Tiaojishan Formation.

The growth ring pattern analysis is helpful for quantitatively demonstrating terrestrial palaeoclimate (Friits, 1976). The occurrences of clearly defined growth rings in the present fossil wood indicate that the wood growth was controlled by a climate with seasonal variation. In order to reveal the interannual climatic variation, a statistic analysis on 35 growth rings of *Xenoxylon peidense* is applied using the method of Friits (1976) for calculating growth rings. The statistic result shows that the annual sensitivity (AS) of *Xenoxylon peidense* from Jianchang region varies from 0.01 to 0.80, while the mean sensitivity (MS) is 0.33 (Figure 8). For MS, a value of 0.3 is used to divide the population into "sensitive" and "complacent" (Friits, 1976; Creber and Francis, 1999; Wang et al., 2006). The MS of *X. peidense* indicates that the tree inhabited under a sensitive climate with variable interannual water supply.

In addition to fossil wood, plant megafossil assemblages also contribute to understanding the Mesozoic terrestrial palaeoclimate (Deng, 2007). Diverse impressed plant fossils have also been found from the Tiaojishan Formation in Jianchang region, represented by *Neocalamites*, *Equisetum*, *Coniopteris*, *Czekanowskia*, *Phoenicopsis* and *Sphenobaiera* (Duan et al., 2009). Among these fossil plants, *Czekanowskia* and *Phoenicopsis* of the order Czekanowskiales are commonly considered to indicate cool temperate climate (Deng, 2007); *Neocalamites* and *Equisetum* are believed to be indicators of humid environment (Deng, 2007). *Coniopteris* has a cosmopolitan distribution in tropical, subtropical and polar regions during the Middle Jurassic (Deng, 2007); however, the Early Cretaceous *Coniopteris* was restricted in temperate and humid regions, with rare records in tropical and subtropical regions (Deng and Lu, 2006; Deng, 2007). Generally, the floral assemblage of the Tiaojishan Formation in Jianchang region implies a cool temperate humid climate, which is mainly in accordance with the palaeoclimate conditions indicated by the present fossil wood material.

In conclusion, the palaeoclimate of the Tiaojishan Formation is dominated by a cool temperate, wet and seasonal climate condition with interannual variation during the Middle-Late Jurassic transition in western Liaoning. This provides new insights into the relationship between the climatic perturbations and the associated occurrences of the feathered dinosaurs in the Mesozoic of Liaoning, China.

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