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Two New Species of *Protocedroxylon* Gothan (Pinaceae) from the Middle Jurassic of Eastern Inner Mongolia, NE China

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Abstract: Two new coniferous wood taxa, *Protocedroxylon zhangii* sp. nov. and *P. zhalantunense* sp. nov., are described from the Middle Jurassic Wanbao Formation in Zhalantun City, Inner Mongolia, NE China. The new discovery represents the first record of petrified wood in the Wanbao Formation, and contributes to further understanding the floral composition, especially that of the forest, of the Wanbao Formation. Anatomically, the two new species are characterized by having a mixed type of radial pitting and Abietineentüpfelung. In extant conifers, Abietineentüpfelung is considered to be characteristic of the wood of Pinaceae. The new discovery further indicates that the first occurrence of Abietineentüpfelung in conifer-like wood should be earlier than the Kimmeridgian. The palaeolatitudinal distribution pattern of *Protocedroxylon* indicates that the genus is a palaeobiogeographically consistent group, which was probably restricted to wetter and cooler temperate climates. In combination with distinct growth rings, the occurrence of *Protocedroxylon* suggests that a cool temperate and seasonal climate might have prevailed during the sedimentation period of the Wanbao Formation in eastern Inner Mongolia, NE China. Such a view is also in agreement with the palaeoclimatic conditions indicated by the plant megafossils of the Wanbao Formation.

Key words: *Protocedroxylon*, Pinaceae, Wanbao Formation, Middle Jurassic, Inner Mongolia

1 Introduction

Abundant and diverse petrified woods have been described in China ranging in time from the Late Palaeozoic to the Cenozoic (Zhang Wu et al., 2006). As of 2006, 181 species referred to 106 genera of petrified wood have been reported in China (Zhang Wu et al., 2006). Amongst them, 33 species referred to 17 genera of petrified wood were reported from Jurassic deposits in China (Wang et al., 2009). Thereafter, an increasing number of Jurassic petrified woods were reported from both Northern and Southern Phytoprovinces of China during the past decade (e.g., Jiang et al., 2008; Fu Junyu et al., 2012; Jiang Zikun et al., 2012, 2016a, b; Zheng Yuejuan et al., 2013; Feng et al., 2015; Tian Ning et al., 2015; Zhang Feng et al., 2015, 2016; Wang Yongdong et al., 2017). Palaeogeographically, most of the Jurassic petrified woods were reported in northern China, especially in Northeast China (e.g., Liaoning, Jilin and Heilongjiang Provinces). However, Jurassic petrified wood records had yet to be documented in eastern Inner Mongolia, which is also located in Northeast China.

The Middle Jurassic Wanbao Formation, known as a coal-bearing stratum, is well developed and widely distributed in Northeast China. Diverse plant megafossils have been described from this formation, represented by Sphenophyllales, Filicales, Bennettitales, Cycadales and Coniferales (Yang Xuelin and Sun Liwen, 1985). All these plant remains are represented by leaf impressions/ compressions. No permineralized plant fossils have so far

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been reported from this formation. During our recent geological survey in the Longjiang Basin, northeastern China, some well-preserved, petrified wood remains were collected from the Middle Jurassic Wanbao Formation in Zhalantun City, Inner Mongolia. Two new wood species of Pinaceae, i.e., *Protocedroxylon zhalantunense* sp. nov. and *P. zhangii* sp. nov., are recognized. The new discoveries represent the first record of petrified wood in the Wanbao Formation, as well as the first record of Jurassic petrified wood in Inner Mongolia, and they contribute to a greater understanding of the floral composition and palaeoclimatic conditions of the Wanbao Formation in the Middle Jurassic.

2 Materials and Methods

The studied fossil wood material consists of two well-preserved silicified wood fragments, collected from the Middle Jurassic Wanbao Formation in Aiguo Village of Moguqi Town, Zhalantun City, Inner Mongolia, Northeast China (47º26′52"N, 122º27′20"E) (Fig. 1). The fossil locality of Zhalantun City is localized to the northwestern edge of the Longjiang Basin. The fossil wood bearing strata lithologically consist of conglomerates, pebbly sandstones, medium-fine sandstones and siltstones, and represent a set of fluvio-lacustrine clastic sedimentary deposits. In the fossil locality, the Wanbao Formation is lithologically divided into 14 beds, and the fossil wood remains were collected from layer 5 (Fig. 2). Originally, the fossil wood-bearing deposits were considered to belong to the Lower Cretaceous Damoguaihe Formation. Then Ding Qiuhong et al., (2010) proposed that it should be treated as the Middle Jurassic Wanbao Formation, based on evidence of regional stratigraphic correlations. During our recent geological survey in this region, in addition to petrified wood, numerous well-preserved plant and sporopollen fossils were also found in these deposits. Preliminary investigation shows that both the floral assemblage (*Coniopteris-Pheonicopsis-Raphaelia*) and the palynological assemblage (*Cyclogranisporites-Alisporites*) are of typical Early to Middle Jurassic character (Zhang Yujin et al., 2018). The radioisotope dating data (165.2±1.7 Ma and 162.1±1.6 Ma) for two tuff samples from two layers of the Wanbao Formation at the current fossil locality indicate that the Wanbao Formation is late Middle Jurassic in age (Zhang Yujin et al., 2018).

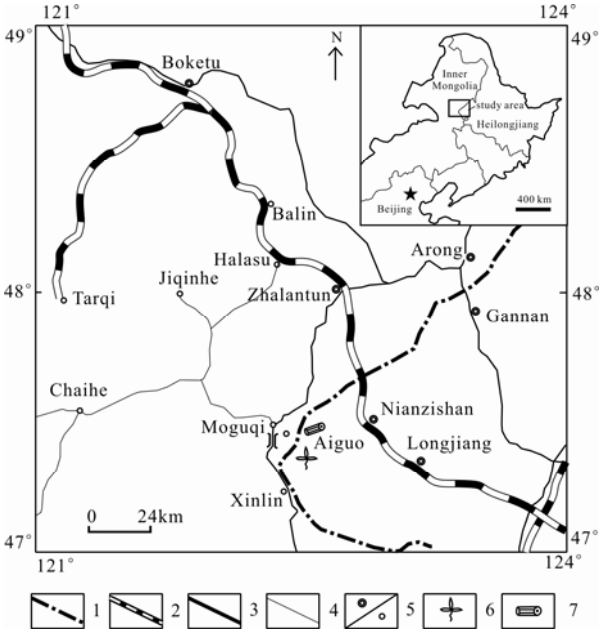


Fig. 1. Geographic position of the fossil locality in Zhalantun City, Inner Mongolia, NE China.
(1), provincial boundary; (2), railway; (3), national highway; (4), county road; (5), county, town and village; (6), plant fossil; (7), fossil wood.

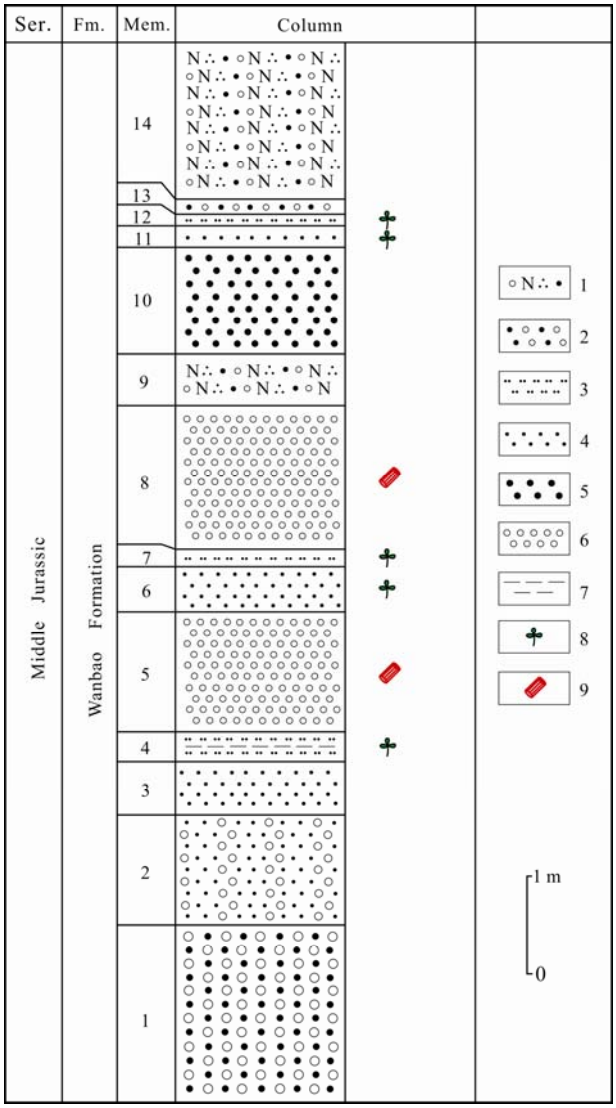


Fig. 2. Stratigraphic column of the Middle Jurassic Wanbao Formation in Zhalantun City, Inner Mongolia, NE China.
(1), feldspar-quartz sandstone; (2), pebbly sandstone; (3), siltstone; (4), fine sandstone; (5), coarse sandstone; (6), conglomerate; (7), mudstone; (8), plant fossil; (9), fossil wood.

Therefore, the age of the present fossil wood is considered to be Middle Jurassic.

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). Photographs were taken with Scope Image 9.0 (H3D) Software adapted to a Yongxin BM2000 Microscope. The fossil wood specimens and correlated slides described in this paper are housed in the Shenyang Center of the Geological Survey, CGS, Shenyang, China, with the registration numbers AGC-02 (A-F) and AGC-03 (A-C). Fossil wood description follows the standardized terminologies of the IAWA Committee (2004) and Philippe and Bamford (2008).

3 Systematics

Class Coniferopsida

Order Coniferales

Family Pinaceae

Genus *Protocedroxylon* Gothan 1910

Type species: *Protocedroxylon araucarioides* Gothan 1910

Species: *Protocedroxylon zhangii* sp. nov. Zhang, Tian et Wang

Holotype: AGC–02 (A–F).

Type locality: Aiguo Village of Moguqi Town, Zhalantun City, Inner Mongolia.

Horizon and age: Wanbao Formation, Middle Jurassic.

Repository: The specimen and slides are housed in the Shenyang Center of the Geological Survey, CGS, Shenyang, China.

Etymology: The specific epithet *zhangii* honors the late Prof. Zhang Wu from the Shenyang Center of the Geological Survey, CGS, who outstandingly contributed to the study of Mesozoic fossil wood in China.

Specific diagnosis: Homoxylous secondary xylem with distinct growth rings; tracheid radial wall pitting mostly uniseriate and separated, or occasionally biseriate alternate; early wood cross-fields usually with 1–4 (mostly 1–2) cupressoid pits; ray cell walls strongly pitted; axial traumatic resin canals present; Abietineentüpfelung (pitted transverse ray cell walls) present.

Description: The present fossil wood specimen (AGC-02) is preserved as a fragment of secondary xylem. In transverse section, the growth rings are distinct, ca. 1.2–3.0 mm wide, with differentiated early wood and late wood (Fig. 3a). The transition from early to late wood is gradual (Fig. 3b), late wood zone being usually narrow (3–5 tracheid layers). Within the early wood zone, the tracheid cells are large, polygonal and thin-walled (Fig. 3b). Meanwhile, the late wood zone consists of rectangular and thick-walled tracheid cells (Fig. 3b). Axial traumatic resin canals are well-developed, and commonly occur within the early wood zone near the growth rings (Fig. 3c–e). The resin canals with an irregular polygonal outline are generally tangentially arranged to form a line with a maximum length of over 6 mm (Fig. 3c). The epithelial cells of the axial resin canal are thick-walled (Fig. 3f).

In longitudinal radial section, the bordered pits on the tracheid walls are mixed type. The pits, 10–15 μm in diameter, are mostly rounded and distant (Fig. 4a–b), and locally biseriate alternate (Fig. 4c–d). Each cross-field contains 1–4 (mostly 1 or 2) pits, arranged in one horizontal row (Fig. 5b, d). The cross-field pits are mostly cupressoid (Fig. 5d). Rays are homogeneous, with strongly pitted horizontal walls and nodular end walls (Fig. 5a, c). In radial view, the axial traumatic resin canals have a width of 0.15–0.25 mm (Fig. 4e–g). Helical thickenings are absent on the tracheid walls.

In longitudinal tangential section, the rays are mostly uniseriate with a height of 1–17 (mostly 1–8) cells (Figs. 5e–f; 6a). Intercellular spaces occur between adjacent ray cells (Fig. 5f). Typical Abietineentüpfelung (pitted transverse ray cell walls) are present (Fig. 5g).

Species: *Protocedroxylon zhalantunense* sp. nov. Zhang, Tian et Wang

Holotype: AGC–03 (A–C).

Type locality: Aiguo Village of Moguqi Town, Zhalantun City, Inner Mongolia.

Horizon and age: Wanbao Formation, Middle Jurassic.

Repository: The specimen and slides are housed in the Shenyang Center of the Geological Survey, CGS, Shenyang, China.

Etymology: The specific epithet *zhalantunense* is named after the fossil locality Zhalantun City in Inner Mongolia.

Specific diagnosis: Homoxylous secondary xylem with distinct growth rings; tracheid radial wall pitting mixed type, mostly uniseriate continuous or bi-triseriate alternate, occasionally uniseriate distant or biseriate opposite; early wood cross-fields containing 2–4 cupressoid pits arranged in 1–2 horizontal rows; ray cells homogeneous, with pitted horizontal walls and nodular end walls; axial traumatic resin canals present; Abietineentüpfelung present.

Description: The present fossil wood specimen (AGC–03) is preserved as a fragment of secondary xylem. In transverse section, the growth rings are distinct, with a relatively narrow width ranging from 0.1 to 0.5 mm (Fig. 7a–b). The transition from early to late wood is abrupt (Fig. 7a–b). The tracheid cells of the early wood are rectangular, square or irregularly polygonal in shape, with

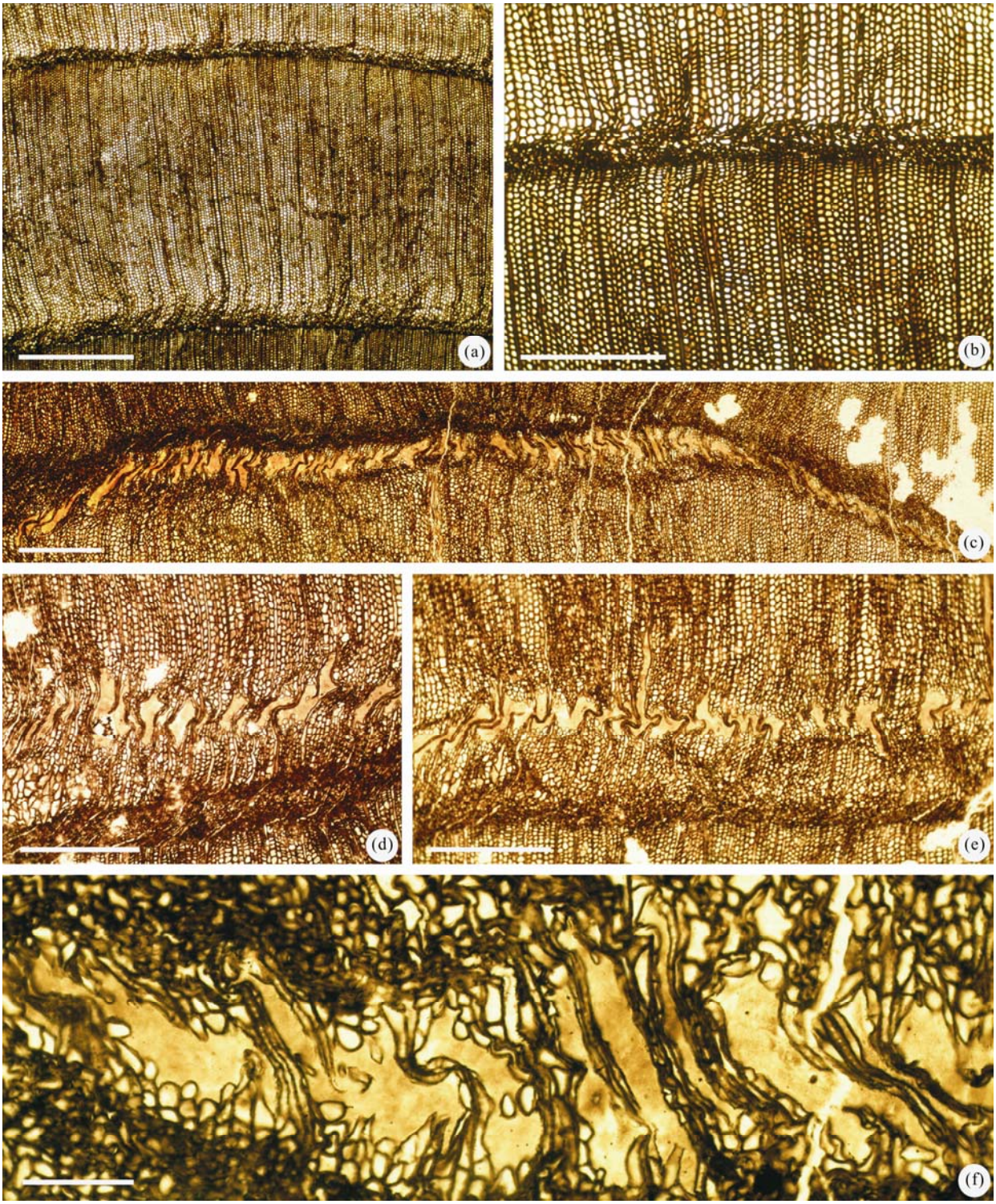


Fig. 3. *Protocedroxylon zhangii* sp. nov. (AGC–02–A, B) from the Jurassic Wanbao Formation in Inner Mongolia, NE China.
(a), transverse section, showing distinct growth rings, scale bar=1 mm; (b), transverse section, showing the gradual transition from early to late wood, scale bar=0.5 mm; (c–e), transverse section, showing tangentially arranged axial traumatic resin canals in the early wood zone, scale bar=0.5 mm. (f), transverse section, showing details of the axial traumatic resin canal, scale bar=0. 1 mm.

a size from 10×20 μm to 30×50 μm (Fig. 7c). The late wood zone is quite narrow with only 1–3 layers of tracheid cells (Fig. 7c). Axial traumatic resin canals are well-developed, and commonly occur within the early wood zone (Fig. 7d). These resin canals are generally ordered in a tangential line (Fig. 7b). The resin canals are mostly rounded in transverse view, with a diameter ranging from 15 to 60 μm (Fig. 7d).

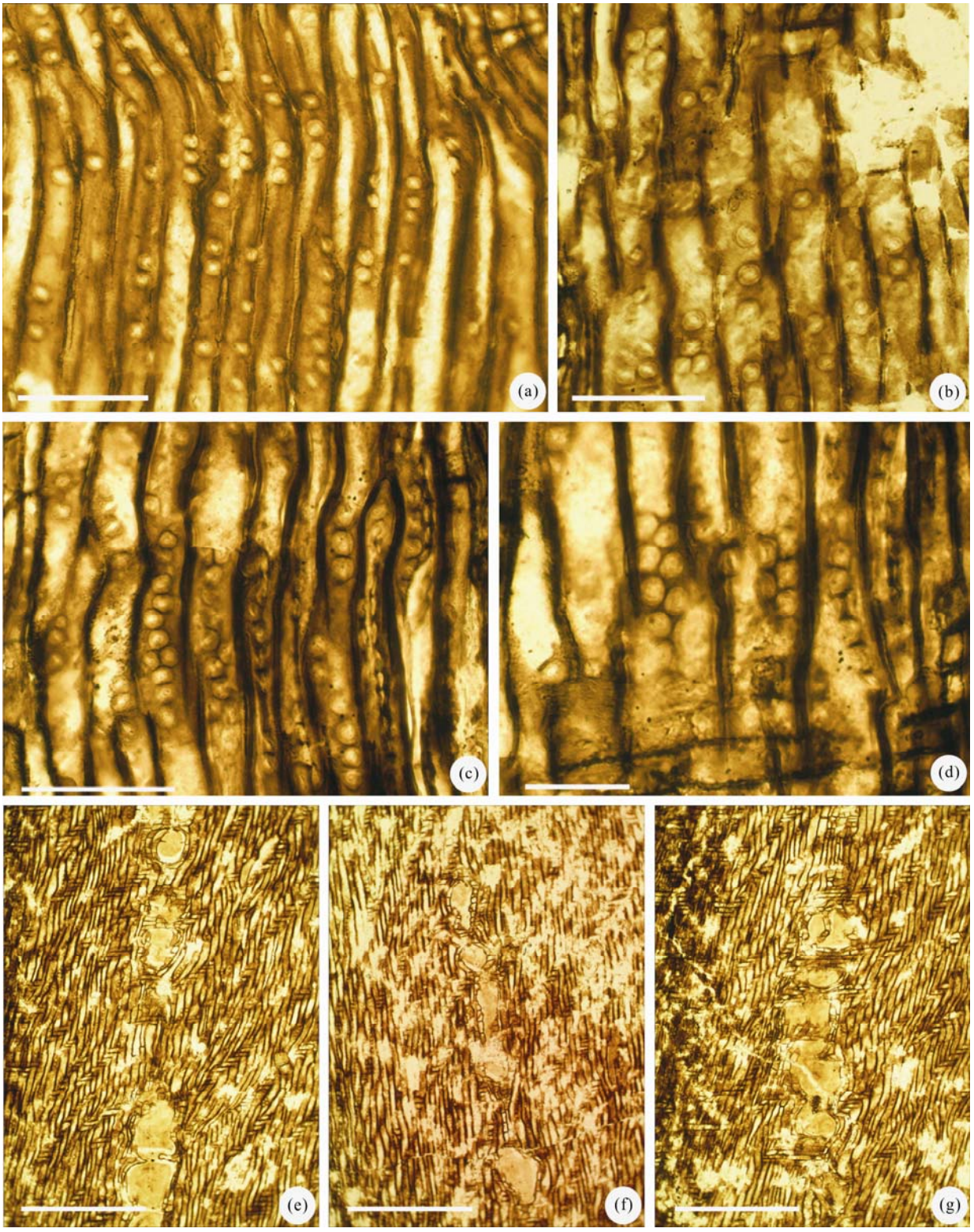


Fig. 4. *Protocedroxylon zhangii* sp. nov. (AGC–02–C, D) from the Jurassic Wanbao Formation in Inner Mongolia, NE China.
(a), radial section, showing uniseriate distant bordered pits, scale bar=0.1 mm; (b), radial section, showing uniseriate distant and locally biseriate opposite bordered pits, scale bar=0.1 mm; (c), radial section, showing uniseriate and contiguous bordered pits; scale bar=0.1 mm; (d), radial section, showing biseriate alternate bordered pits; scale bar=0.05 mm; (e-g), radial section, showing the radial view of the axial traumatic resin canal, scale bar=0.5 mm.

In longitudinal radial section, the bordered pits on the tracheid walls are uni-triseriate with a diameter of 13–15 μm (Fig. 7e–h). The uniseriate ones are mostly continuous (Fig. 7e), and locally distant (Fig. 7g); while the bi-triseriate ones are mostly rounded and alternate (Fig. 7e–f), occasionally opposite (Fig. 7h). The cross-field pits are

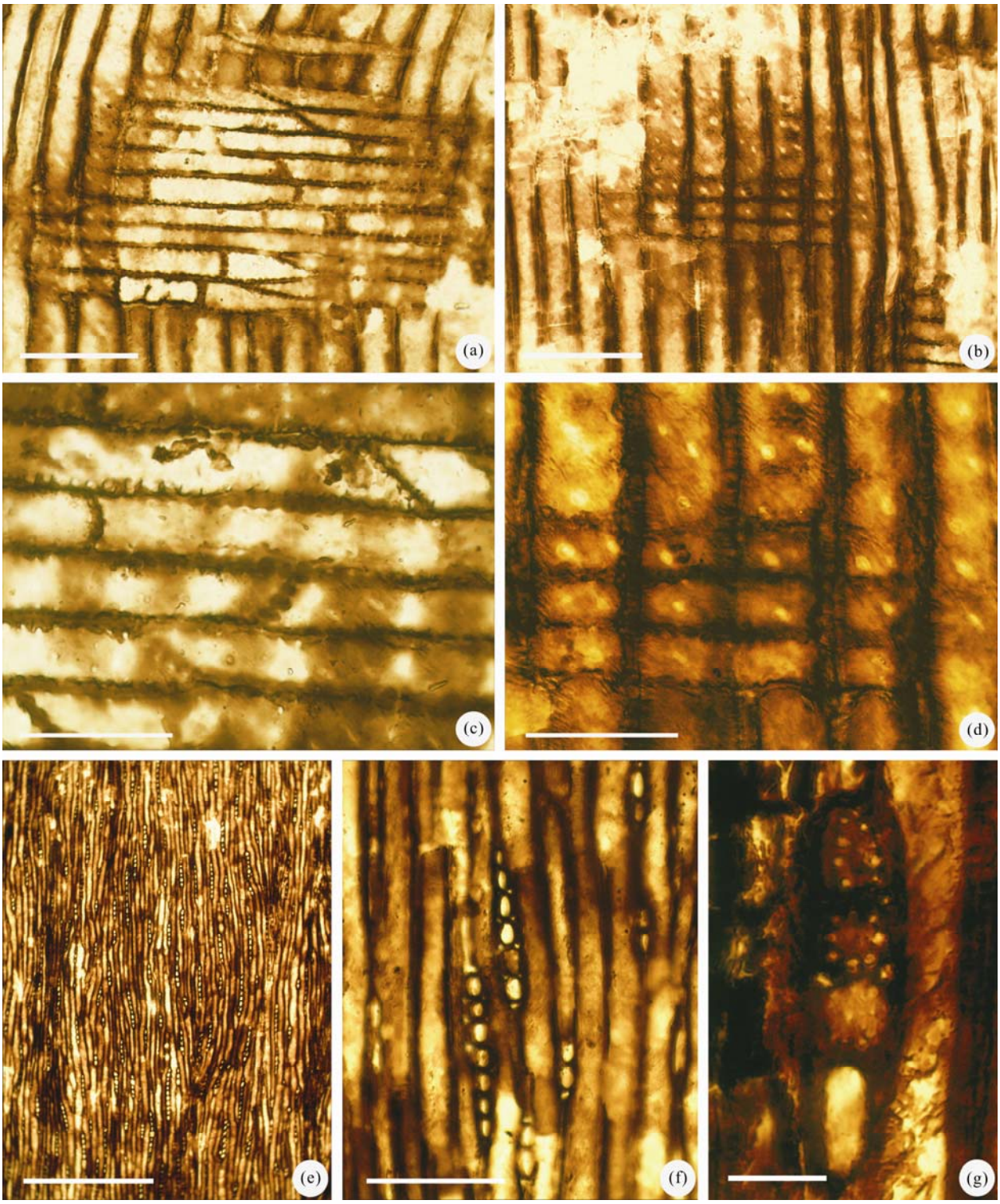


Fig. 5. *Protocedroxylon zhangii* sp. nov. (AGC–02–D, E) from the Jurassic Wanbao Formation in Inner Mongolia, NE China. (a), radial section, showing the ray cells, with pitted horizontal walls and nodular end walls, scale bar=0.1 mm; (b), radial section, showing the cross-field with 1-4 cupressoid pits arranged in one horizontal row, occasionally taxodioid, scale bar=0.1 mm; (c), radial section, showing details of pitted horizontal walls and the nodular end walls of the ray cells, scale bar=0.05 mm; (d), radial section, showing details of the cross-field, each cross-field bears 1-4 cupressoid pits, scale bar=0.05 mm; (e), tangential section, showing the ray cells, scale bar=0.5 mm; (f), tangential section, showing details of the ray cells with intercellular space, scale bar=0.1 mm; (g), tangential section, showing typical Abietineentüpfelung, scale bar=25 μm.

mostly cupressoid (Fig. 8c). Each cross-field contains 2–4 pits, which are arranged in one to two horizontal rows (Fig. 8b, c). Helical thickenings are absent in the tracheid walls. Ray cells are homogeneous, with strongly pitted horizontal walls and nodular end walls (Fig. 8a–b).

In longitudinal tangential section, the rays are mostly

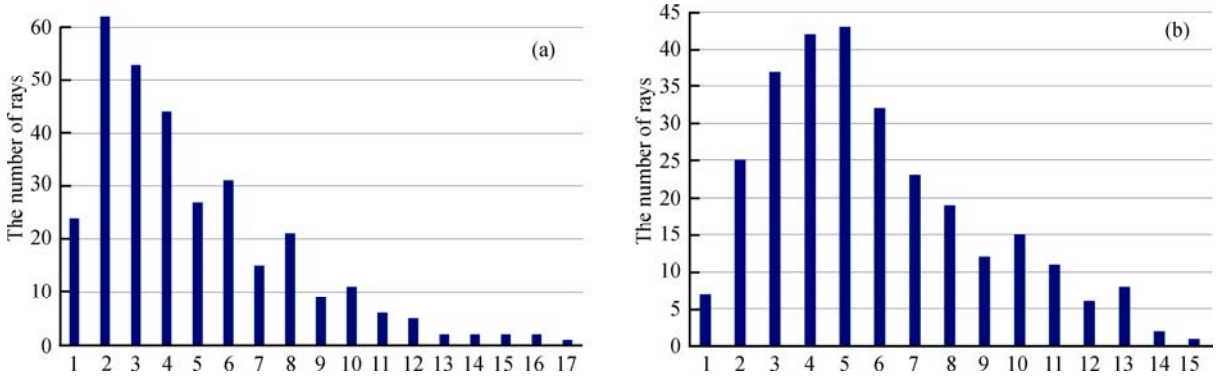


Fig. 6. Histogram showing the height frequency distribution of *Protocedroxylon zhangii* sp. nov. (AGC–02) and *P. zhalantunense* sp. nov. (AGC–03) from the Jurassic Wanbao Formation in Inner Mongolia, NE China.
(a), height frequency distribution of 293 rays in tangential longitudinal section of *Protocedroxylon zhangii* sp. nov.; (b), height frequency distribution of 260 rays in tangential longitudinal section of *P. zhalantunense* sp. nov.

uniseriate with a height of 1–15 (mostly 2–11) cells (Figs. 6b; 8d). Axial parenchyma occasionally occurs with smooth or slightly nodular transverse walls (Fig. 8e). Abietineentüpfelung (pitted transverse ray cell walls) are present (Fig. 8f).

4 Systematic Affinity and Comparisons

4.1 Systematic affinity

The present fossil wood specimens (AGC–02 & 03) are anatomically characterized by their mixed type of radial pitting and Abietineentüpfelung (pitted transverse ray cell walls). Such a combination of anatomical characters is typical of the so called '*Protocedroxylon*' type of wood (fossil wood with mixed type of radial pitting and Abietineentüpfelung), including *Protocedroxylon* Gothan, *Araucariopitys* Hollick et Jeffrey, *Pityoxylon* Kraus, *Planoxylon* Stopes and *Protopiceoxylon* Gothan (Philippe and Bamford, 2008; Philippe and Hayes, 2010). All these generic names were proposed more than 100 years ago, and have been widely used for Mesozoic wood. However, the naming of the '*Protocedroxylon*' type of wood is problematic (Philippe and Hayes, 2010)

The genus *Araucariopitys* was not validly published by Jeffrey (1907) for short shoots together with both primary structures and secondary xylem, as it was not wholly accepted by the author in the original publication (Art. 34.1). Then, in Jeffrey's paper with Hollick (Hollick and Jeffrey, 1909), Jeffrey unambiguously and completely accepted the genus *Araucariopitys* Hollick et Jeffrey at the generic level. The genus *Protocedroxylon* was proposed by Gothan (1910) based on fossil wood from West Spitsbergen having the combination of characters of abietineous and araucarian conifers. Kräusel (1919) pointed out that *Araucariopitys* was a taxonomic synonym of *Protocedroxylon* Gothan (1910), at least as long as only the secondary xylem was considered. Eckhold (1923) suggested that *Araucariopitys* and *Protocedroxylon* were taxonomical synonyms; however, he retained the younger name *Protocedroxylon*. Edwards (1925) pointed out that if these two genera were considered as taxonomic synonyms, the genus *Araucariopitys* Jeffrey should have priority. The genus *Planoxylon* was established by Stopes (1916) based on fossil wood material from New Zealand. Vogellehner (1968) further added *Metacedroxylon* Holden (1913) and *Planoxylon* Stopes (1916) to this synonymy. It should be noted that, Medlyn and Tidwell (1986) separated the genus *Planoxylon* from *Protocedroxylon* based on the difference in tracheal pitting. Philippe (2002) pointed out that *Metacedroxylon* Holden was an illegitimate junior nomenclatural synonym of *Protocedroxylon* Gothan. Additionally, on the basis of a detailed reinvestigation of a topotype of *Araucariopitys americana* Hollick et Jeffrey, Philippe and Hayes (2010) proposed that *Araucariopitys* Hollick et Jeffrey, *Protocedroxylon* Gothan and *Planoxylon* Stopes should not be considered as taxonomical synonyms, since *Araucariopitys* should be used only for short shoots with preserved pith and araucarioid cross-field pits (Philippe and Hayes, 2010). On the other hand, *Planoxylon* could be distinguished from *Protocedroxylon* by having usually more than five oculipores per early wood cross-field, as compared to rarely more than four small and distant oculipores in *Protocedroxylon* (Philippe and Hayes, 2010).

Then, with reference to the genus *Pityoxylon* Kraus, its lectotype from the Triassic of Germany bears both axial and radial resin canals (Andrews, 1955), which are otherwise unknown prior to the latest Jurassic (Creber, 1972). Philippe and Bamford (2008) proposed that this taxon needed further revision, and should not be used until this was done. The genus *Palaeopiceoxylon* is characterized by having both horizontal and vertical resin canals.

Based on the above discussion, it is reasonable for the

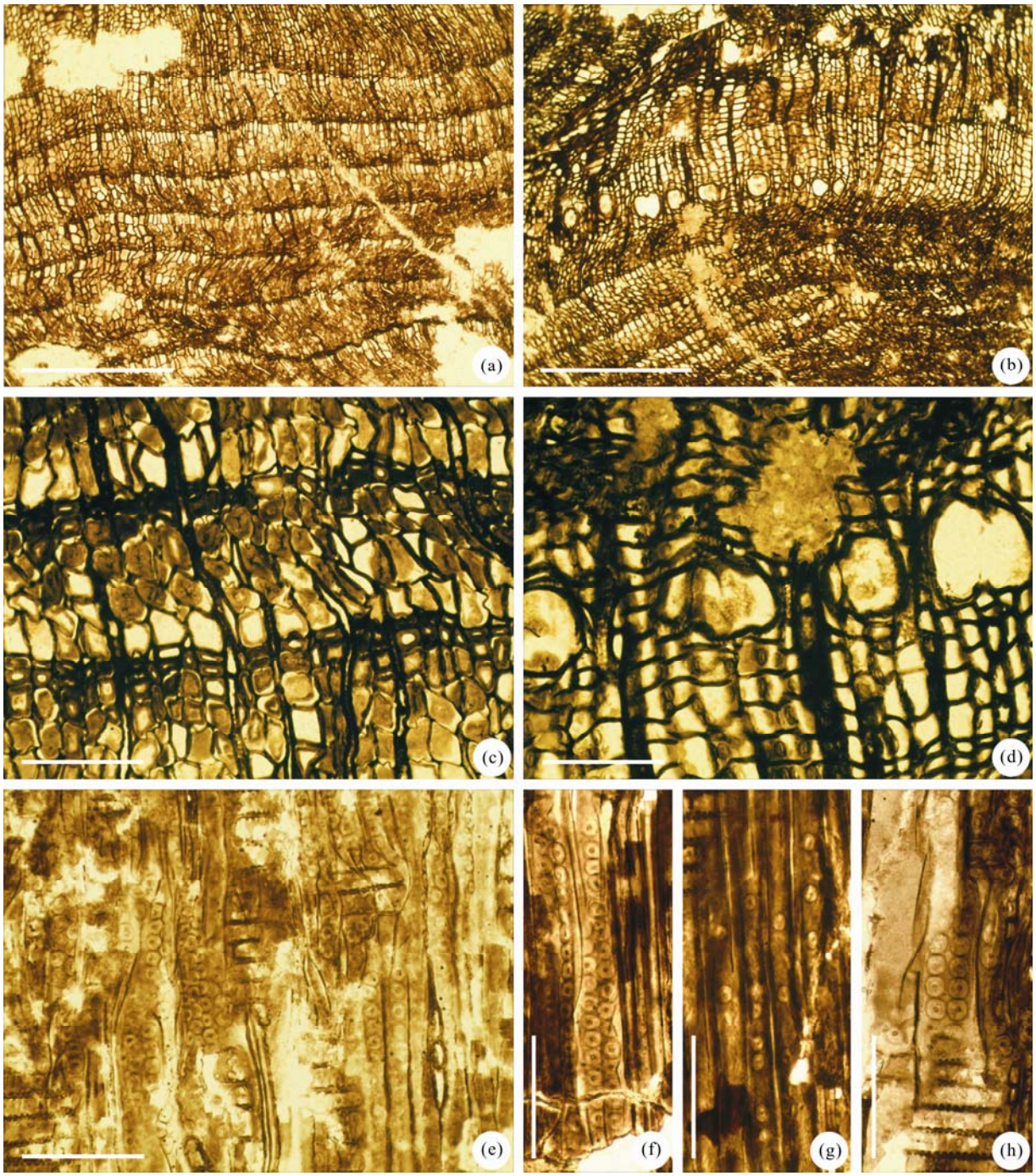


Fig. 7. *Protocedroxylon zhalantunense* sp. nov. (AGC–03–A, B) from the Jurassic Wanbao Formation in Inner Mongolia, NE China

(a), transverse section, showing distinct growth rings, axial traumatic resin canals, scale bar=0.5 mm; (b), transverse section, showing axial traumatic resin canals, scale bar=0.5 mm; (c), transverse section, showing details of the growth rings, scale bar=0.1 mm; (d), transverse section, showing details of the axial traumatic resin canal, scale bar=0.1 mm; (e), radial section, showing uni-triseriate bordered pits, scale bar=0.1 mm; (f), radial section, showing biseriate alternate bordered pits, scale bar=0.1 mm; (g), radial section, showing uniseriate and distant bordered pits, scale bar=0.1 mm; (h), radial section, showing biseriate sub-opposite bordered pits, scale bar=0.1 mm.

present two fossil wood specimens (AGC-02 & 03) to be assigned to the genus *Protocedroxylon* Gothan.

4.2 Comparisons

So far, an estimated 20 species have been reported worldwide referrable to the genus *Protocedroxylon* (Afonin, 2012; Ding et al., 2016), stratigraphically ranging from the Lower Triassic to the Upper Cretaceous (e.g., Shilkina and Khudayberdyev, 1971; Blokhina, 1975; Zhang Wu et al., 2006; Harland et al., 2006; Afonin, 2014) (Table 1). A detailed comparison is given between the present fossil material from Inner Mongolia and other

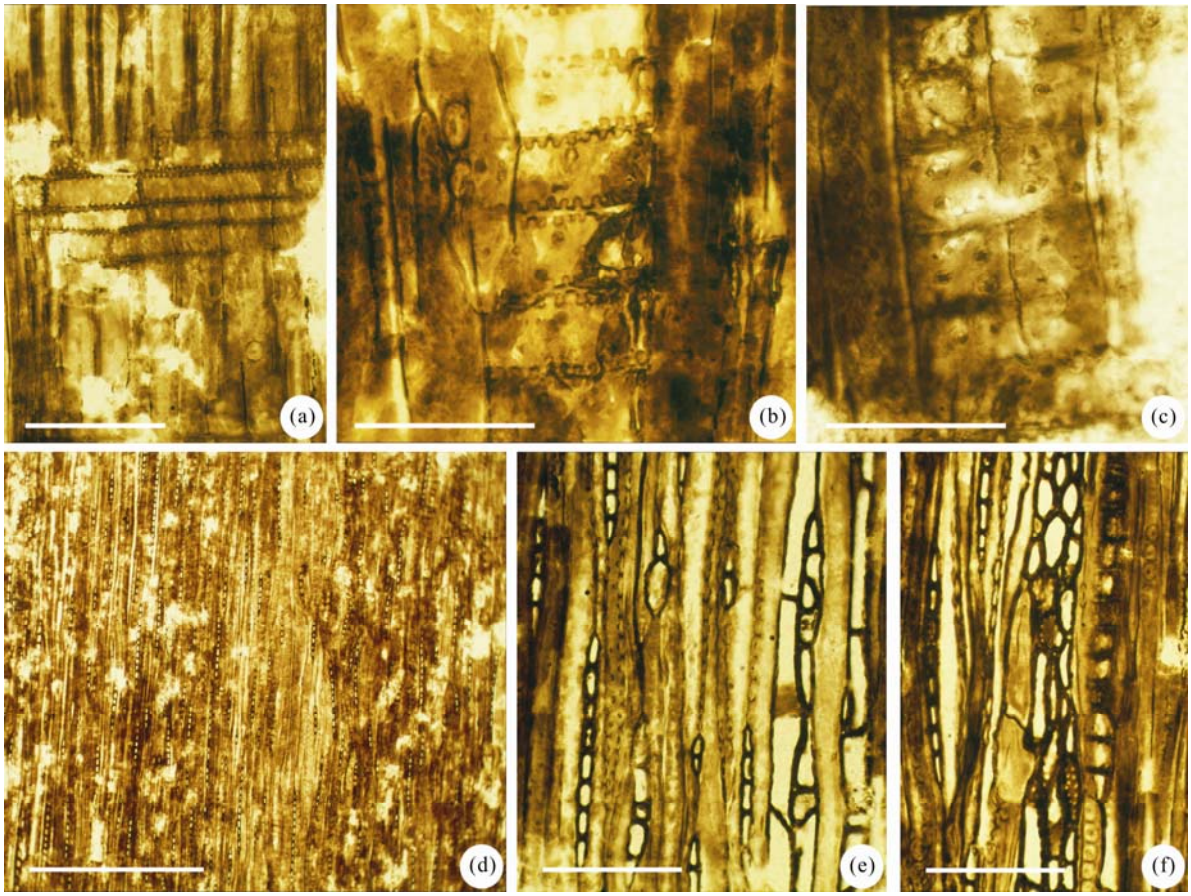


Fig. 8. *Protocedroxylon zhalantunense* sp. nov. (AGC–03–B, C) from the Jurassic Wanbao Formation in Inner Mongolia, NE China

(a), radial section, showing the ray cells, with pitted horizontal walls and the nodular end walls, scale bar=0.1 mm; (b), radial section, showing details of pitted horizontal walls and the nodular end walls of the ray cells, scale bar=50 μm; (c), radial section, showing the cross-field, each cross-field bears 2–4 cupressoid pits arranged in 1–2 horizontal row, scale bar=50 μm; (d), tangential section, showing uniseriate ray cells, scale bar=0.5 mm; (e), tangential section, showing details of the ray cells and axial parenchyma, scale bar=0.1 mm; (f), tangential section, showing the typical Abietineentüpfelung, scale bar=0.1 mm.

Protocedroxylon species, which demonstrates pronounced differences in anatomical details (Table 1). Therefore, two new species, *Protocedroxylon zhangii* sp. nov. and *P. zhalantunense* sp. nov. are established for fossil specimens from Inner Mongolia, NE China.

For the present two specimens described here, they resemble each other in having the mixed type of tracheid pitting, Abietineentüpfelung and axial traumatic resin canals. However, they are distinct from one another in a series of anatomical features. For instance, the annual ring width of the *Protocedroxylon zhangii* sp. nov. is more than 2 mm, while that of *P. zhalantunense* sp. nov. is no more than 0.5 mm. The transition of early to late wood is gradual in *Protocedroxylon zhangii* sp. nov., while it is abrupt in *P. zhalantunense* sp. nov. For *P. zhangii* sp. nov., the radial tracheid pits are mostly uniseriate and distant; for *P. zhalantunense* sp. nov., they are uni-triseriate. Additionally, typical intercellular spaces occur between the ray cells of *P. zhangii* sp. nov., whereas, they are absent in *P. zhalantunense* sp. nov. Overall, the present two fossil wood specimens represent two distinct species of the genus *Protocedroxylon*.

When compared to the types species, *Protocedroxylon araucarioides*, *P. zhangii* sp. nov. differs from it by having a relatively larger growth ring width and mostly uniseriate distant radial pits. *Protocedroxylon zhalantunense* sp. nov. resembles the type species in gross morphology, such as a relatively narrower growth ring width and radial pitting. However, the radial pits of *P. araucarioides* are 20–24 μm in diameter, while those of *P. zhalantunense* sp. nov. are just 13–15 μm in diameter. Additionally, the cross-field pits are arranged in 1–2 horizontal rows in *P. zhalantunense* sp. nov.; they are commonly arranged in one horizontal row in *P. araucarioides*.

In China, three species of *Protocedroxylon*, i.e., *P. lingwuense* He, *P. orientale* He and *P. shengjinbeigouense* Tian, Wang, Zhang et Zheng, have been reported from the Middle Jurassic of Ningxia, the Lower Cretaceous of Inner Mongolia, and the Lower Cretaceous of Liaoning,

Table 1 Comparisons of anatomical features between species of *Protocedroxylon* Gothan

Species	Locality	Age	Radial pits	Cross-field pits	Rays	Traumatic resin canals	References
P. zhangii sp. nov.	Inner Mongolia, China	J_2	Mixed type, mostly uniseriate distant	1–4 (mostly 1–2) cupressoid or taxodoid pits arranged in 1–2 rows	Uniseriate, locally biseriate; 1–17 (mostly 1–8) cells high	present	In this paper
P. zhalantunense sp. nov.	Inner Mongolia, China	J_2	Mixed type, uni-triseriate, mostly uniseriate contacted or biseriate alternate	1–4 (mostly 2–4) cupressoid or taxodoid pits arranged in 1–2 rows	Uniseriate, locally biseriate; 1–15 (mostly 2–11) cells high	present	In this paper
P. araucarioides Gothan	Spitsbergen	J_3	uniseriate, or biseriate, alternate	1–3 pits per field; simple or demi-bordered	uniseriate, low; cell wall with abietoid pits	present or absent	Gothan, 1910
P. scoticum (Holden) Seward	Helmsdale, Scotland	J_3	uniseriate, contacted and flattened	1 large pits per field, rarely 2 pits;	uniseriate, occasionally biseriate; 2–20 cells high; cell wall pitted	absent	Seward, 1919
P. transiens (Gothan) Eckhold	Spitsbergen	K_1	biseriate	3 small pits per field	uniseriate; 1–12 cells high; pits horizontal walls pitted	absent	Eckhold, 1922
P. irregular (Gothan) Eckhold	Spitsbergen	J_3-K_1	uniseriate, or biseriate, alternate	early wood: 2–3 pits per field; late wood: one pit	uniseriate to biseriate, occasionally triseriate; horizontal wall mightily pitted	present	Eckhold, 1922
P. latiporosum (Holden) Eckhold	Yorkshire, Britain	J	uniseriate contacted, or biseriate alternate	1 small pit per field, rarely 2 pits	uniseriate with a low height; horizontal wall mightily pitted	absent	Eckhold, 1922
P. japonicum Nishida	Chiba, Japan	K	uniseriate continuously or often separate, or biseriate alternate	2─6 pits per field; semi-bordered, arranged in 1─2 rows	uniseriate, 1–4, rarely 6 cells high	absent	Nishida, 1967
P. brisbanense (Sahni) Vegellegner	Australia	T_3	uniseriate, contacted and flattened	3–5 pits large per field	uniseriate; 1–15 cells high; cell wall pitted	absent	Shilkina and Khudayberdyev, 1971
P. cedroides (Gothan) Shilkina et Khudayberdyev	Spitsbergen	K_1	uniseriate to biseriate; mixed type	1–5 small pits per field; simple (unbordered?)	uniseriate, locally biseriate; horizontal walls pitted	absent	Shilkina and Khudayberdyev, 1971
P. dibneri (Shilkina) Shilkina et Khudayberdyev	Franz Josef Land	T_3	biseriate to triseriate; mixed type; uniseriate in late wood	2–3 unbordered pits per field	uniseriate, locally biseriate; 1–19 cells high	absent	Shilkina and Khudayberdyev, 1971
P. gregussii (Shilkina) Shilkina et Khudayberdyev	Franz Josef Land	T_3	uniseriate contacted or biseriate alternate	1–2 large pits per field, locally 4 pits	uniseriate, locally biseriate; 5–12 cells high	absent	Shilkina and Khudayberdyev, 1971
P. haraulachica (Shilkina) Vegellegner	Arctic	J_1	uniseriate to biseriate; mixed type	2–5 pits per field; pinoid	uniseriate; 1-8 cells high; horizontal walls pitted	absent	Shilkina and Khudayberdyev, 1971
P. holdenae (Kräusel) Shilkina et Khudayberdyev	Yorkshire, Britain	J	uniseriate; mixed type	2 or more small pits per field	uniseriate, locally biseriate	occasionally present	Shilkina and Khudayberdyev, 1971
P. polyporosum (Shilkina) Shilkina et Khudayberdyev	Franz Josef Land	K_1	uniseriate, contacted and flattened	1–2 pits per field; cupressoid	uniseriate, locally biseriate; 2–45 cells high; cell wall pitted	absent	Shilkina and Khudayberdyev, 1971
Protoeedroxylon pseudoaraucarioides Nishida	Chiba, Japan	K	uni-triseriate, auracarian type,	1 single large or 3–6 small pits	Uniseriate, locally biseriate; 2–22 cells high	absent	Nishida, 1973
P. bojarense Shilkina et Blokhina	Siberia	J	uniseriate to triseriate; mixed type	1–3 pits per field; podocarpoid	uniseriate, locally biseriate; 1–30 cells high; cell wall pitted	present	Blokhina, 1975
P. mineense (Ogura) Nishida et Oishi	Yamaguchi, Japan	T_3	uni-biseriate, auracarian type, rarely protopinoid type	1–2 large ovoid pits, rarely several small crowded pits	usually uniseriate, and often biseriate, 1–42 cells high	absent	Nishida and Oishi, 1982
P. okafujii Nishida et Oishi	Yamaguchi, Japan	T_3	usually araucarian type, uni-biseriate, alternate and continous, rarely separated	1–2 large ovoid pits	usually uniseriate, and often biseriate, 1–40 cells high	absent	Nishida and Oishi, 1982
P. yezoense Nishida et Nishida	Hokkaido, Japan	K_2	Protopinoid, uniseriate , continuous, sometimes septate	1–2 half bordered pits,	1–28 (mostly 3–15) cells high	absent	Nishida and Nishida, 1984
P. kryshtofovichii Shilkina	Kirovgrad, Russia	K_1	biseriate to triseriate; mixed type, araucarioid	unknown	uniseriate, occasionally biseriate; 1–10 cells high; cell wall pitted	present	Shilkina, 1986
P. ronkinii Shilkina	East Siberia, Russia	J_3	uniseriate to triseriate; alternate and opposite (mixed type)	1–4 simple circular pits per field	uniseriate, locally biseriate; 2–20 cells high; cell wall pitted	absent	Shilkina, 1986
P. macgregorii	British Columbia, Canada	J	1-4 seriate	1–3 pits per field	uniseriate, occasionally biseriate,1–40 (mostly 12–25) cells high	present	Medlyn and Tidwell, 1986

Continued Table 1

Species	Locality	Age	Radial pits	Cross-field pits	Rays	Traumatic resin canals	References
P. lingwuense He et Zhang,	Ningxia, China	J_2	uniseriate to triseriate; when biseriate or triseriate, circular pits alternate and contacted	1–6 small pits per field, arranged in row	uniseriate, 1–30 cells high; horizontal wall mightily pitted	absent	He Dechang and Zhang Xiuyi, 1993
P. orientale He	Inner Mongolia, China	K_1	uniseriate to biseriate, occasionally triseriate; alternate, locally opposite	2–5 pits per field, mostly 2–4; piceoid type	uniseriate; 1–30 cells high	absent	He Dechang, 1995
P. primoryense Afonin	Southern Primorye, Russia	K_1	uniseriate to biseriate, occasionally triseriate	1–4 pits per field; cupressoid and taxodioid	uniseriate, occasionally biseriate,1–22(35) cells high	present	Afonin, 2012
P. shengjinbeigouense Tian, Wang, Zhang et Zheng	Liaoning, China	K_1	uniseriate, contacted; or biseriate, alternate	1–3 pits per field; mostly cupressoid, rarely taxodioid	uniseriate; 1–16 cells high; horizontal walls pitted	present	Ding et al., 2016

Note: Modified after Ding et al. (2016); **Abbreviations**: T_3=Late Triassic; J=Jurassic; J_1=Early Jurassic; J_2=Middle Jurassic; J_3=Late Jurassic; K= Cretaceous; K_1=Early Cretaceous.

respectively (He Dechang and Zhang Xiuyi, 1993; He Dechang, 1995; Ding et al., 2016). *Protocedroxylon lingwuense* is anatomically characterized by having bi-triseriate alternate radial pits, piceoid cross-field pits, an absence of traumatic resin canals and a relatively higher ray height (1–30 cells) (Table 1). The present two new species differ from it in having a traumatic resin canal, and a relatively lower ray height (no more than 20). Then for *P. orientale*, the transition of early to late wood is gradual, which resembles that of *P. zhangli* sp. nov., but differs from that of *Protocedroxylon zhalantunense* sp. nov. However, its piceoid cross-field pits, the absence of the traumatic resin canal and relatively higher ray height (1–30) (Table 1) also distinguish it from the two new species from Inner Mongolia. Generally, the two new species are most similar to *P. shengjinbeigouense* in cross-field pits and ray height. However, *P. shengjinbeigouense* differs from *P. zhalantunense* sp. nov. through having a relatively larger annual ring width and a gradual early to late wood transition. When compared to *P. zhangii* sp. nov., *P. shengjinbeigouense* differs from it by having mostly uniseriate contacted or biseriate alternate radial tracheid pits.

Judging from the presence of typical axial traumatic resin canals, the present two new species resemble the following taxa, including *Protocedroxylon bojarense* Shilkina et Blokhina (Jurassic, Siberia), *P. holdenae* (Kräusel) Shilkina et Khudayberdyev (Jurassic, Yorkshire), *P. irregular* (Gothan) Eckhold (Upper Jurassic to Lower Cretaceous, Spitsbergen), *P. kryshtofovichii* Shilkina (Lower Cretaceous, Kirovgrad), and *P. primoryense* Afonin (Lower Cretaceous, Southern Primorye) (Eckhold, 1922; Shilkina and Khudayberdyev, 1971; Blokhina, 1975; Shilkina, 1986; Afonin, 2012) (Table 1). Meanwhile, many other *Protocedroxylon* species, e.g., *P. transiens* (Gothan) Eckhold, *P. latiporosum* (Holden) Eckhold, *P. japonicum* Nishida, *P. brisbanense* (Sahni) Vegellegner, *P. cedroides* (Gothan) Shilkina et Khudayberdyev, *P. dibneri* (Shilkina) Shilkina et Khudayberdyev, *P. gregussii* (Shilkina) Shilkina et Khudayberdyev, and *P. haraulachica* (Shilkina) Vegellegner do not have the traumatic resin canals (Table 1).

When compared to the new species *Protocedroxylon zhangii* sp. nov., *P. bojarense* bears triseriate araucarioid radial pits and podocarpoid cross-field pits (Table 1); both *P. holdenae* and *P. irregular* bear axial wood parenchyma, through which they can be distinguished from the new species (Table 1); *P. kryshtofovichii* has bi-triseriate radial tracheid pits and a relatively lower ray height (Table 1), whereas *Protocedroxylon zhangii* sp. nov. bears mostly uniseriate radial pits; *P. primoryense* has a relatively higher ray height and bi-triseriate radial tracheid pits (Table 1).

In contrast, when compared to the new species *Protocedroxylon zhalantunense* sp. nov., *P. bojarense* bears podocarpoid cross-field pits and a higher ray height (Table 1); the presence of axial wood parenchyma in *P. holdenae* and *P. irregular* distinguishes them from the present new species (Table 1); *P. kryshtofovichii* has a relatively lower ray height (Table 1); in differing from the new species, *P. primoryense* has a relatively higher ray height and marginal ray cells resembling ray tracheids (Table 1).

5 Discussion

As mentioned, besides petrified wood, diverse compressed/impressed leaf fossils have also been described from the Middle Jurassic Wanbao Formation in the southern Great Khingan Ranges (Yang Xuelin and Sun Liwen, 1985). A systematic study of the Wanbao flora indicated that the whole flora is composed of 52 species of 24 genera, represented by sphenophytes, pteridophytes, ginkgophytes and coniferophytes. Among them, coniferophytes are represented by 12 species of 7 genera, including *Pityophyllum lindstroemi*, *P. staratschini*, *Podozamites lanceolatus*, *P. angustifolia*, *Schizolepis*

moelleri, *Elatides* ? sp., *Elatocladus* sp., *Strobilites*. sp. 1, *S*. sp. 2, *S*. sp. 3 and *Carpolithus* sp. The discovery of *Protocedroxylon zhalantunense* sp. nov. and *P*. *zhangii* sp. nov. represents the first record of petrified wood in the Middle Jurassic Wanbao Formation, and contributes further to the understanding of the floral composition of the Wanbao Formation, especially with respect to the coniferophytes, which represent the forest components of the flora.

The wood character 'Abietineentüpfelungen' is a term coined by Gothan (1905) to describe pits on the transversal wall of ray cells similar to that of modern *Abies* (Philippe and Cantrill, 2007). In extant conifers Abietineentüpfelung is considered to be characteristic of the wood of Pinaceae, though it also occasionally occurs in the traumatic wood of the Taxodiaceae (Holden, 1913; Kräusel, 1921). The oldest occurrence of Abietineentüpfelung in conifer-like wood was originally hypothesized to be within the Kimmeridgian (Late Jurassic) (Philippe, 1995; Philippe and Bamford, 2008). However, fossil wood referred to *Protocedroxylon* from the Toarcian of Eastern Greenland and the Liassic of Yorkshire, UK, indicates that the fossil record of petrified wood with Abietineentüpfelung can be traced back to the Early Jurassic (Philippe and Hayes, 2010). The discovery of the two new *Protocedroxylon* species with Abietineentüpfelung from the Middle Jurassic of China provides additional evidence for the viewpoint that the first occurrence of Abietineentüpfelung in conifer-like wood should be earlier than the Kimmeridgian. Additionally, the new discovery also helps to understand the evolution of the coniferous family Pinaceae in China.

As important plant fossil components, petrified wood plays a significant role in understanding the terrestrial palaeoclimate and palaeoenvironment in the geological past (Creber and Francis, 1999; Uhl, 2006). Philippe et al. (2017) addressed the potential of using the latitudinal distributions of fossil wood genera as a proxy for Jurassic terrestrial climate conditions. The genus *Protocedroxylon* is known as a palaeobiogeographically consistent group, which was restricted to the middle to high palaeolatitudes of Laurasia (Philippe and Hayes, 2010; Philippe et al., 2017). The palaeolatitudinal distribution of *Protocedroxylon* in western Laurasia indicates that the genus was probably limited to wetter and cooler temperate climates (Philippe et al., 2017). The occurrence of well-defined growth rings in the present fossil wood specimens indicates that the wood growth was controlled by a climate with seasonal variation. Growth ring analysis on fossil wood is helpful for demonstrating terrestrial palaeoclimate, especially for interannual climate variation (Friits, 1976). For revealing the interannual climatic variation, a statistical analysis on growth rings of *Protocedroxylon zhangii* sp. nov. and *P*. *zhalantunense* sp. nov. was applied using the method of Friits (1976) for calculating their annual sensitivity (AS) and mean sensitivity (MS). As is known, the more growth rings that are counted, the more precise the analysis result will be. However, due to preservation conditions, only a few continuous growth rings can be found in the present two fossil wood specimens. For *P*. *zhangii* sp. nov., nine (AGC -02-A) and seven (AGC-02-B) continuous growth rings were counted for AS and MS, respectively. Then, for *P*. *zhalantunense* sp. nov., only six continuous growth rings (AGC-03-A) were counted. The statistical result shows that the AS of *P*. *zhangii* sp. nov. varies from 0.01 to 0.52, with a MS value of 0.279(AGC-02-A) and 0.066(AGC- 02 -B) (Table 2). Then for *P*. *zhalantunense* sp. nov., the annual sensitivity (AS) varies from 0.02 to 0.09, with a mean sensitivity (MS) of 0.056 (Table 2). Generally, for the MS of wood, a value of 0.3 is used to divide the population into 'sensitive' and 'complacent' (Friits, 1976; Creber and Francis, 1999; Wang Yongdong et al., 2006; Tian Ning et al., 2015). The MS value of both *Protocedroxylon zhangii* sp. nov. and *P*. *zhalantunense* sp. nov. indicates that the trees grew under a complacent climate with a relatively stable interannual water supply. In conjunction with distinct growth rings, the occurrence of *Protocedroxylon* suggests that a cool temperate and seasonal climate might have prevailed during the sedimentation period of the Wanbao Formation in eastern Inner Mongolia, NE China. It is noted that plant megafossil assemblages are also of importance for understanding the terrestrial palaeoclimate of the Mesozoic (Deng Shenghui, 2007). Just as mentioned, diverse compressed/impressed leaf fossils have also been reported from the Wanbao Formation (Yang Xuelin and Sun Liwen, 1985; Zhang Yujin et al., 2018), represented by *Neocalamites*, *Todites*, *Coniopteris*, *Raphaelia*, *Czekanowskia*, *Phoenicopsis*, *Pityophyllum*, *Pityocladus* and *Elatocladus*. Among these fossil plants, *Todites* and *Raphaelia*, as representatives of the fern family Osmundaceae, are commonly considered to be indicators of a warm and humid climate (Deng Shenghui, 2007). *Neocalamites* are believed to be indicators of a humid environment (Deng Shenghui, 2007). Palaeogeographically, the genus *Coniopteris* has a cosmopolitan distribution during the Middle Jurassic; however, they are restricted in temperate and humid regions, with rare records in tropical and subtropical regions in the Early Cretaceous (Deng Shenghui and Lu Yuanzheng, 2006; Deng Shenghui, 2007). Then, as members of the order Czekanowskiales, *Czekanowskia* and *Phoenicopsis* are commonly considered to indicate a cool temperate climate with seasonal

Table 2 Measurements of growth-ring width, annual and mean sensitivity of *Protocedroxylon zhangii* sp. nov. and *P. zhalantunense* sp. nov. from the Middle Jurassic Wanbao Formation in Zhalantun City, Inner Mongolia, NE China

Species	Specimen number	Growth-ring Number	Growth-ring width (mm)	Annual sensitivity	Mean sensitivity
Protocedroxylon zhangii sp. nov.	AGC-02-A	9	0.91		0.279
		8	1.92	0.70	
		7	1.81	0.05	
		6	1.56	0.14	
		5	1.92	0.21	
		4	2.03	0.06	
		3	2.25	0.10	
		2	1.42	0.45	
		1	2.42	0.52	
	AGC-02-B	6	2.07		0.066
		5	2.10	0.01	
		4	1.94	0.08	
		3	1.88	0.03	
		2	2.24	0.17	
		1	2.33	0.04	
P. zhalantunense sp. nov.	AGC-03-A	6	0.16		0.056
		5	0.15	0.06	
		4	0.147	0.02	
		3	0.14	0.05	
		2	0.154	0.09	
		1	0.164	0.06	

variations (Deng Shenghui, 2007); For conifers, *Elatocladus* is interpreted as indicating warm and humid climates, and *Pityocladus* and *Pityophyllum* indicate a cool, temperate climate (Deng Shenghui, 2007). Generally, the megafossil floral assemblage of the Wanbao Formation also implies a cool, temperate, humid climate, which is generally in agreement with the palaeoclimatic conditions indicated by wood fossils of the Wanbao Formation.

6 Conclusion

In conclusion, two new coniferous wood taxa, *Protocedroxylon zhangii* sp. nov. and *P. zhalantunense* sp. nov., are described from the Middle Jurassic Wanbao Formation in Inner Mongolia, NE China, which represents the first record of petrified wood in the Wanbao Formation. The existence of Abietineentüpfelung in the present Inner Mongolia fossil wood indicates that the first occurrence of Abietineentüpfelung in coniferous wood should be prior to the Kimmeridgian. The new discoveries provide new evidence for understanding the floral composition and palaeoclimatic conditions of the Wanbao Formation. The occurrence of *Protocedroxylon* indicates that a cool temperate and seasonal climate might have prevailed during the sedimentation period of the Wanbao Formation in eastern Inner Mongolia, NE China. Such a view is also consistent with the palaeoclimatic conditions indicated by the plant megafossils of the Wanbao Formation.

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