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NEW MIDDLE MIOCENE FOSSIL WOOD OF *WATARIA* (MALVACEAE) FROM SOUTHWEST CHINA

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ABSTRACT

This paper describes a new species of fossil wood, *Wataria yunnanica* Li *et* Oskolski, from the Dajie Formation of the middle Miocene in southern Yunnan province, China. This species shows the greatest similarity to the modern genus *Reevesia* Lindl. from the subfamily Helicteroideae of Malvaceae. The fossil specimen is ascribed to the genus *Wataria* Terada & Suzuki based on its combination of ring-porous wood and the presence of tile cells. It differs from other *Wataria* species because vessel groups are common in its latewood. This is the first record of *Wataria* in China. Other species of this genus have been reported from Oligocene and Miocene deposits in Japan, and from Miocene deposits in Korea. The occurrence of ring-porous wood in the Dajie Formation suggests that there may have been a seasonal (probably monsoonal) climate in southern Yunnan during the middle Miocene.

Keywords: Tile cells, ring-porous wood, Dajie Formation, *Reevesia*, Helicteroideae, monsoon climate, Yunnan.

INTRODUCTION

The extinct genus *Wataria* (Malvaceae) was established by Terada and Suzuki (1998) based on fossil woods discovered in strata of the Oligocene and Miocene in Japan, at sites in Iragawa, Koinoura, Nigoriike, Nametaki, Minamihora and the Kiso River. This genus is similar to extant *Reevesia* of the same family, which is considered as its closest living relative. Three species of *Wataria* have been reported: *W. miocenica* (Wadari) Terada & Suzuki and *W. parvipora* Terada & Suzuki from the Miocene strata of Japan and Korea (Wadari 1952; Suzuki & Wadari 1994; Terada & Suzuki 1998; Jeong *et al.* 2003, 2004, 2009; Lim *et al.* 2010); and *W. oligocenica* (Suzuki) Terada &

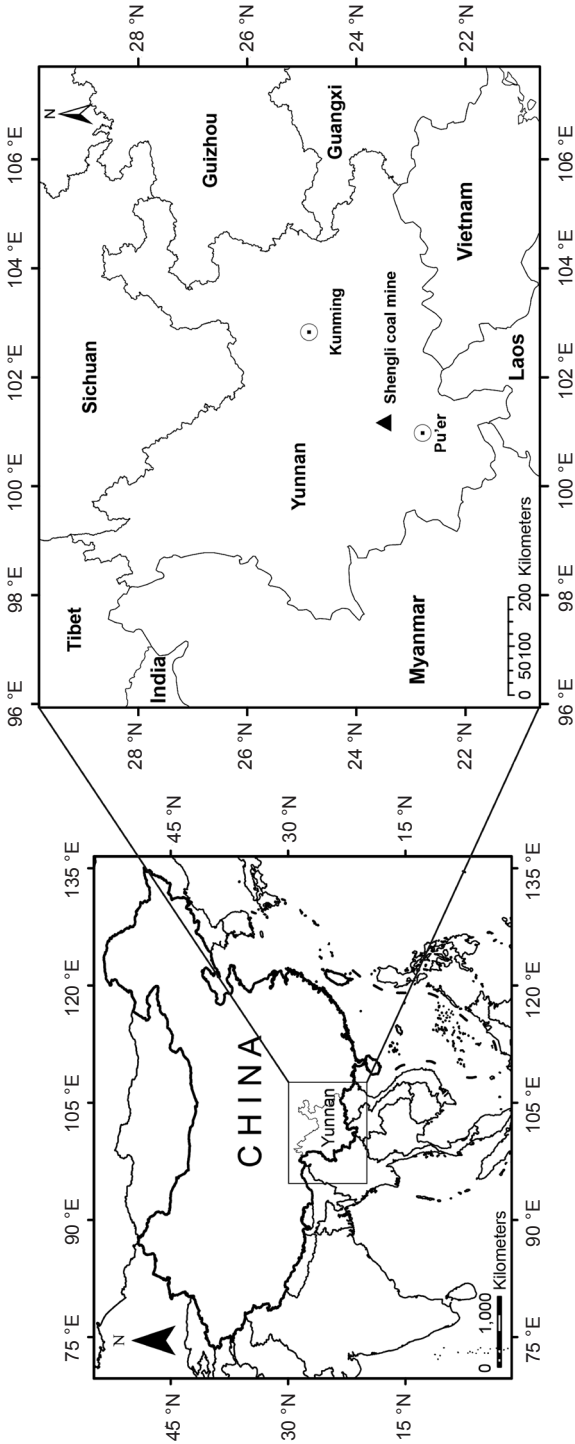


Figure 1. The locality of the fossil site. ▲ = Shengli coal mine, Pu'er, Yunnan, China.

Suzuki from the Oligocene deposits of Japan (Suzuki 1976). The first two species were originally assigned to *Reevesia* (*R. miocenica* Watari and *R. oligocenica* Suzuki, respectively), but Terada and Suzuki (1998) proposed that they should be considered as a new genus, *Wataria*.

The species of *Wataria* share an unusual combination of ring-porous wood and rays with tile cells. Tile cells are a distinct wood trait that characterizes many genera of Malvaceae (Chattaway 1933; Manchester 1979, 1980; Cheng *et al.* 1992; InsideWood 2004-onwards; Manchester *et al.* 2006; Wheeler 2011), but that has also been reported in a few species of *Hopea* Roxb. of the Dipterocarpaceae (Cheng *et al.* 1992; InsideWood 2004-onwards; Wheeler 2011). Terada and Suzuki (1998) ascribed the extinct genus *Wataria* to the family Sterculiaceae. Later molecular phylogenetic analyses have shown that Sterculiaceae is not monophyletic, and all of its members have been included into Malvaceae *s.l.* (Bayer *et al.* 1999; Bayer & Kubitzki 2003; APG III 2009).

Although many fossil wood specimens collected from Cretaceous to Miocene strata in different regions of the world have been ascribed to Malvaceae *s.l.* (Suzuki 1976; Manchester 1979, 1980; Awasthi 1981; Suzuki & Watari 1994; Terada & Suzuki 1998; Jeong *et al.* 2003, 2004, 2009; InsideWood 2004-onwards; Gregory *et al.* 2009; Estrada-Ruiz *et al.* 2010; Lim *et al.* 2010; Jeong *et al.* 2013; Licht *et al.* 2014; Rodríguez-Reyes *et al.* 2014), no such records for China have been reported to date. Recently, we collected 59 fossil wood specimens dated as the middle Miocene from the Shengli coal mine in southwestern Yunnan, China. The majority of these fossil woods can be convincingly assigned to a few morphotypes of Lauraceae, but one sample (SL002) is distinct because it is ring porous and has tile cells. This sample is described in the present paper as the holotype of a new species of *Wataria*. The anatomy and systematics of the Lauraceae woods from the Shengli coal mine will be the subject of another paper.

MATERIALS AND METHODS

The fossil wood specimens were collected from the Shengli coal mine in Meizi town, Zhenyuan County, Pu'er city, Yunnan Province, Southwest China (101° 09' 49.7" E, 23° 30' 29.1" N; Fig. 1). This mining area consists of Quaternary, Neogene and Jurassic deposits (Ge & Li 1999). The Neogene deposits belong to the Dajie Formation, which is dated to the middle Miocene (Ge & Li 1999; Zhang *et al.* 2012). This formation is subdivided into a sand and mudstone group (N13), a coal group (N12) and a Glutenite group (N11); the calcified fossil woods were found in N13 (Ge & Li 1999; Fig. 2).

A single sample of the fossil wood (SL002) was studied, measuring 20 cm in length × 20 cm in diameter. Thin-sectioned slides were prepared according to standard methods of cutting, grinding and polishing, using different grades of Carborundum power (Lacey 1963). The slides were examined using a Carl Zeiss Axio Imager A2 light microscope. Microphotographs were taken using a Zeiss AxioCamHRc digital camera fitted with the ZEN 2012 photographing program. The anatomical characters of the wood were described and measured in accordance with recommendations of the IAWA Committee (1989).

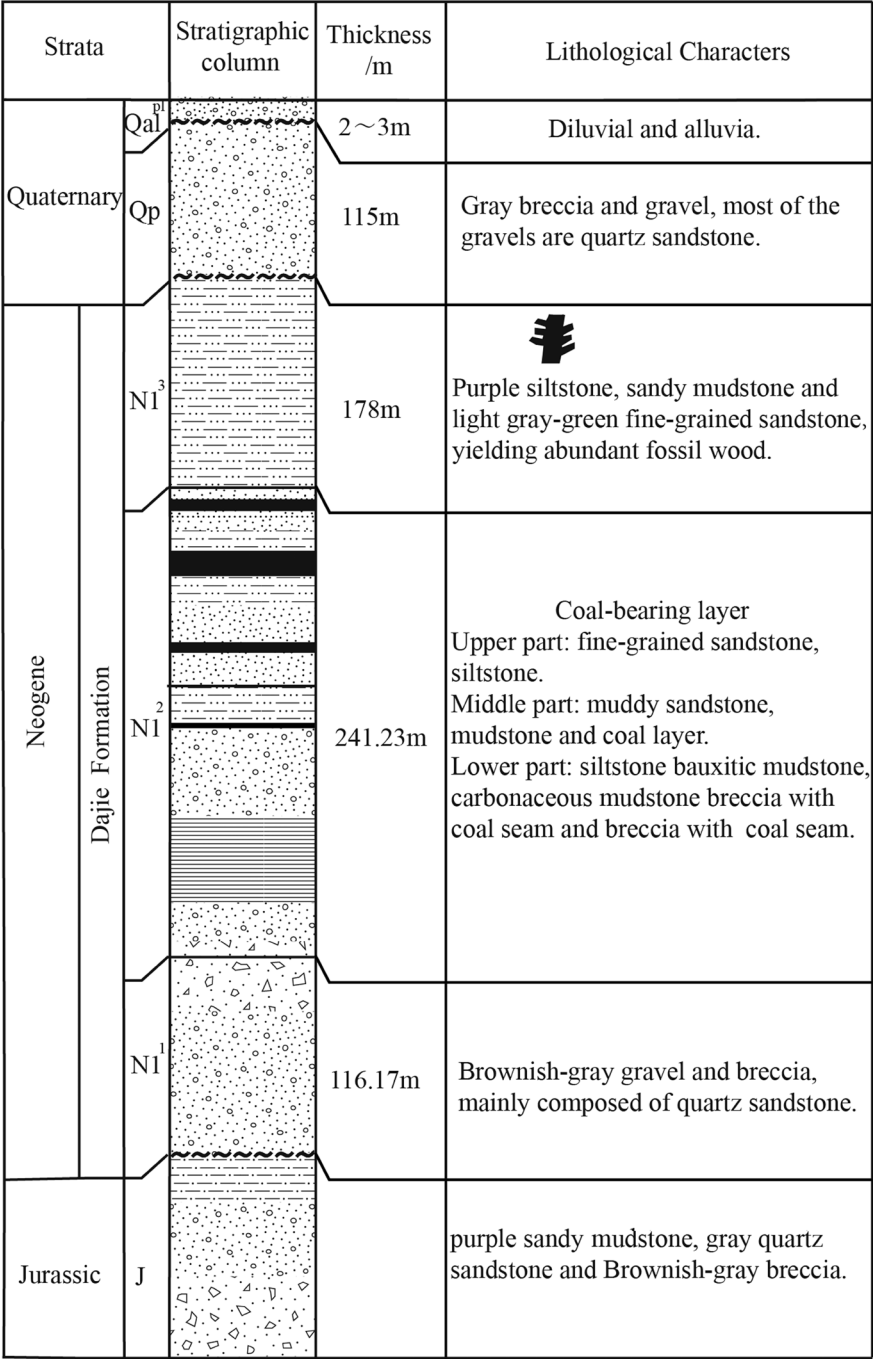


Figure 2. The schematic strata of Shengli coal mine. The fossil woods were collected from the layer marked by a sketch of a branch (Ge & Li 1999).

RESULTS

Systematic description

Order: Malvales.

Family: MALVACEAE.

Genus: *Wataria* Terada & Suzuki.

Species: *Wataria yunnanica* Li et Oskolski, *sp. nov.*

Holotype: SL002.

Type locality: Shengli coal mine, Pu'er, Yunnan, China.

Stratigraphic horizon: middle Miocene.

Etymology of specific name: after Yunnan province where the fossil wood was collected.

Repository: Fossil wood samples and microscopic slides are deposited in Kunming Institute of Botany, Kunming, Yunnan, China.

Diagnosis: Wood ring-porous. Earlywood vessels wide (tangential diameter can exceed 200 μm), mostly solitary, whereas the latewood vessels mostly in groups. Vessel element length averages < 350 μm . Perforation plates are exclusively simple. Intervessel pits alternate, minute. Helical thickenings absent on vessel walls. Axial parenchyma fusiform and in strands, occasionally storied. Prismatic crystals rare, present in axial parenchyma cells and ray cells. Rays heterocellular, 1–12 cells wide, uniseriate rays occasionally storied. Tile cells present.

Description:

Wood ring-porous (Fig. 3A, B). Growth rings distinct, 1.3–2.5 mm (mean 1.8 mm) wide and marked by wide (8–12-seriate) bands of axial parenchyma embedding the earlywood vessels. Earlywood vessels mostly solitary (occasionally in groups of two to three), commonly arranged in one to two layers (sometimes in three), rounded in outline, very thin-walled, 166–370 μm (mean 270 μm) in tangential diameter. Latewood vessels (Fig. 3B) mostly in groups of two to four (up to five), sometimes solitary, rounded (rarely angular) in outline, thin-walled, with tangential diameter of 54–135 μm (mean 94 μm).

Vessel elements 144–569 μm (mean 280 μm) long; end walls horizontal or somewhat oblique. Perforation plates exclusively simple. Intervessel pits alternate (Fig. 3E), mostly polygonal in outline, 2.6–3.1 μm (mean 2.8 μm) in horizontal diameter. Vessel-ray pits (Fig. 3F) with reduced borders, somewhat larger than intervessel pits (horizontal diameter 3.5–4.8 μm , mean 4.2 μm) but similar to them in shape. Helical thickenings on vessel walls absent. Tyloses not observed. In some wide vessels, roots of extraneous plant(s) visible that apparently grew on the fallen tree (Fig. 3B, D).

Fibers libriform, mostly polygonal in cross section, 7.0–28.5 μm (mean 18 μm) in tangential diameter, with thin walls (4.1–8.9 μm thick, mean 6.5 μm), nonseptate, with minute simple pits on tangential and radial walls.

Axial parenchyma fusiform and in strands of two to four (up to six) cells, occasionally storied (Fig. 4B). In earlywood, axial parenchyma in wide (8–12-seriate)

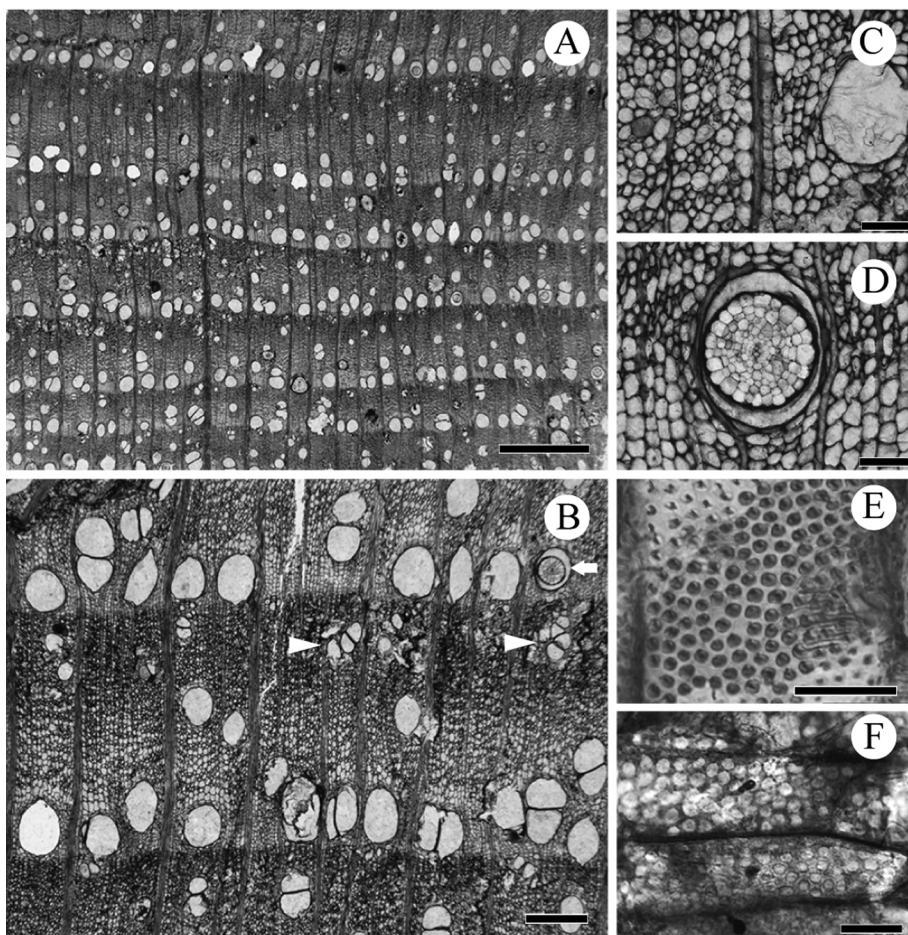
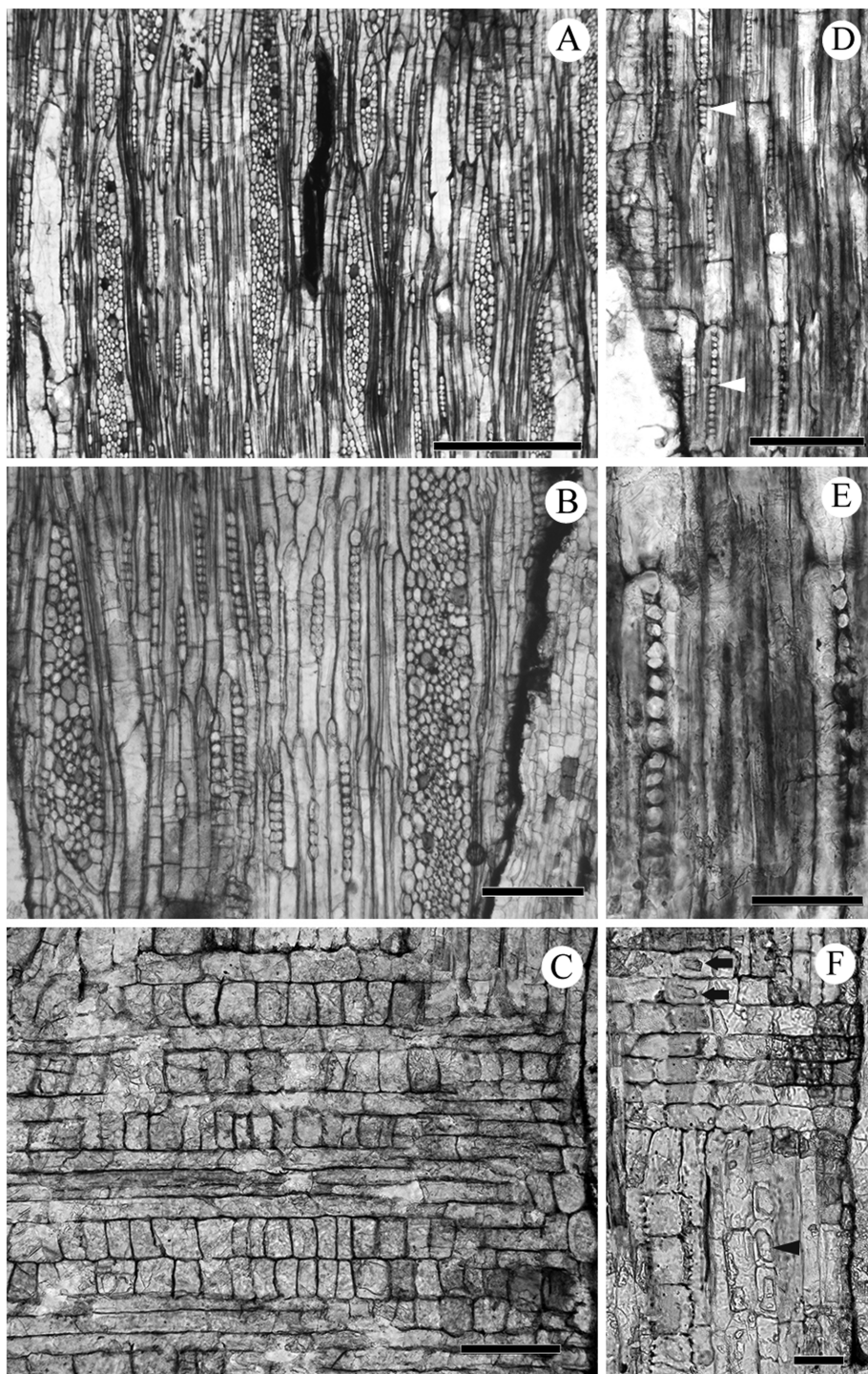


Figure 3. *Wataria yunnanica* Li et Oskolski, *sp. nov.*, SL002. – A: Ring-porous wood. – B: Growth rings, with groups of narrow latewood vessels (white arrowheads), diffuse-in-aggregate axial parenchyma, roots of extraneous plant in earlywood vessel (white arrow). – C: Diffuse-in-aggregate axial parenchyma. – D: Root of extraneous plant in earlywood vessel. – E: Alternate intervessel pits. – F: Vessel-ray pits with reduced borders. — Transverse section (TS): A, B, C, D; radial longitudinal section (RLS): E, F. — Scale bars: A = 4 mm; B = 1 mm; C & D = 100 μ m; E & F = 20 μ m.

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Figure 4. *Wataria yunnanica* Li et Oskolski, *sp. nov.*, SL002. – A: Heterocellular rays, storied axial parenchyma strands and uniseriate rays. – B: Wide heterocellular rays, storied axial parenchyma strands and uniseriate rays. – C: Tile cells of *Pterospermum* type. – D: Strands of axial parenchyma with apparently chambered crystaliferous cells (white arrowheads). – E: Prismatic crystals in apparently chambered axial parenchyma cells. – F: Prismatic crystals in non-chambered axial parenchyma cells (black arrowhead) and ray cells (black arrows). — Tangential longitudinal section (TLS): A, B; radial longitudinal section (RLS): C, D, E, F. — Scale bars: A = 1 mm; B = 400 μ m; C = 100 μ m; D = 200 μ m; E & F = 50 μ m.



marginal bands embedding the earlywood vessels, sometimes also vasicentric, forming 1–3-seriate sheaths. In latewood, axial parenchyma diffuse-in-aggregates (Fig. 3B, C) and vasicentric, in 1–2-seriate sheaths. Parenchyma cells 11–51 μm (mean 29 μm) in tangential diameter; fusiform cells and strands 247–436 μm (mean 368 μm) long. Prismatic crystals rarely occur in apparently chambered (Fig. 4D, E) or non-chambered (Fig. 4F) axial parenchyma cells.

Rays heterocellular, 1–12-seriate (mostly 4–6-seriate). Uniseriate rays occasionally storied (Fig. 4B), 9–36 μm (mean 20 μm) wide, 81–287 μm (mean 178 μm) tall, consisting of procumbent cells. Multiseriate rays are 2–12 cells (23–170 μm , mean 75 μm) wide, by 11–72 cells (193–2037 μm , mean 873 μm) tall, and composed mostly of procumbent and square cells mixed throughout the ray; upright cells occur in one to a few (up to five) marginal rows and in incomplete sheaths. Tile cells (Fig. 4C) of the *Pterospermum* type commonly occur, although some were also of an intermediate type.

Prismatic crystals occur very rarely in non-chambered ray cells (Fig. 4F).

DISCUSSION

Comparison with modern plant taxa

The presence of tile cells was the key trait that determined placement of the fossil wood specimen in the Malvaceae *s.l.* (Metcalfe & Chalk 1950; IAWA Committee 1989; Carlquist 2001; InsideWood 2004-onwards). Although some species of *Hopea* Roxb. (Dipterocarpaceae) are reported to have tile cells, the Miocene sample from Shengli is distinct from members of this genus by the absence of axial secretory canals (Gottwald & Parameswaran 1966; Kribs 1968; InsideWood 2004-onwards). Thus, we are confident that the fossil wood described here is a representative of Malvaceae.

The specimen had a combination of ring-porous wood, very wide earlywood vessels (mean diameter > 200 μm), simple perforation plates, minute alternate intervessel pitting, and tile cells. Within the modern plants, this suite of wood traits has been reported only in *Reevesia* Lindl. (Kanehira 1921; Terada & Suzuki 1998; InsideWood 2004-onwards), a member of the subfamily Helicteroideae (Malvaceae). This genus is centered in southeast and east Asia, with a single Meso-American species *R. clarkii* (Monach. & Moldenke) S.L. Solheim, which some authors consider to be a monospecific genus, *Veeresia* Monach. & Moldenke (Monachino 1940; Solheim 1987; Terada & Suzuki 1998). The Miocene wood from Shengli differs from present-day *Reevesia* species (*R. clarkii*, *R. formosana* Sprague, *R. pubescens* Mast., *R. thyrsioidea* Lindley and *R. wallichii* Benn.) in the absence of helical thickenings on its vessel walls, and axial parenchyma strands composed of more numerous cells, with up to four cells in *Reevesia* species (Kanehira 1921; Terada & Suzuki 1998) versus up to six cells in the fossil wood.

In summary, this Miocene wood sample from Shengli can be classified as a member of the Malvaceae *s.l.* The sample is most similar to the modern genus *Reevesia* from the subfamily Helicteroideae of Malvaceae.

Table 1. Anatomical comparison of fossil wood from Shengli coal mine (SL002) to other fossil species of the genus *Wataria*, *Reevesia* and *Triplachitoxylon* (Manchester 1979; Terada & Suzuki 1998; Jeong et al. 2003).

Botanical name	Sample no.	RP	TD (µm)	VEL (µm)	LV	NV	HT	NAP	RH (µm)	RW (µm)	TT	CAP	CR	Source
Fossil from Shengli coal mine (W. yunnanica)	SL002	+	166–370 (270)	144–569 (280)	1–3	groups	–	6	193–2037 (873)	23–170 (75)	P	+	+	
<i>Wataria miocenica</i> (Watar)	35252	+	200–350 (294)	70–350 (234)	2–3	solitary	–	10	150–1150 (621)	70–150 (105)	I	–	+	Terada & Suzuki (1998)
<i>W. miocenica</i>	53108	+	200–300 (265)	?	2–3	solitary	–	?	175–1950 (870)	20–75 (50)	I	–	+	Terada & Suzuki (1998)
<i>W. miocenica</i>	53219	+	200–300 (257)	?	1–3	solitary	–	?	100–2200 (1280)	40–70 (54)	P	–	+	Terada & Suzuki (1998)
<i>W. miocenica</i>	KNU 0010	+	195–325 (252)	200–345 (257)	1–3	solitary	–	10	140–1900 (985)	30–125 (84)	I	–	+	Jeong et al. (2003)
<i>Wataria oligocenica</i> (M. Suzuki)	71189	+	140–260 (210)	75–325 (219)	3–5	solitary	–	10	200–1000 (688)	30–75 (59)	I	–	+	Terada & Suzuki (1998)
<i>Wataria parvipora</i> K. Terada et M. Suzuki	59044	+	100–250 (176)	65–290 (185)	1–2	solitary	–	10	100–2000 (716)	10–100 (36)	P	–	+	Terada & Suzuki (1998)
<i>W. parvipora</i>	59061	+	125–220 (167)	?	1–3	solitary	–	?	unmeasurable		I	–	+	Terada & Suzuki (1998)
<i>W. parvipora</i>	59082	+	110–275 (171)	?	1–2	solitary	–	?	550–1200 (803)	70–140 (112)	I	–	+	Terada & Suzuki (1998)
<i>W. parvipora</i>	59098	+	90–200 (150)	?	1–2	solitary	–	?	unmeasurable		I	–	+	Terada & Suzuki (1998)
<i>W. parvipora</i>	KNU 0008, 0019, 0044	+	125–250 (181)	125–250 (178)	1–3	solitary	–	10	120–900 (558)	25–115 (67)	I	–	+	Jeong et al. (2003)
<i>Reevesia japonoxyla</i>	59019	+	110–210 (162)	150–330 (264)	2–5	groups	+	4	550–1200 (803)	40–70 (54)	P	–	–	Terada & Suzuki (1998)
<i>Triplachitoxylon oregonensis</i> S.R. Manchester	NBW-50	±	49–287 (185)	273–502 (403)	?	solitary	–	4	?	?	I	–	+	Manchester (1979)

RP = ring-porous (+) or semi-ring-porous to diffuse-porous (±) wood; TD = range (mean) of tangential diameter of vessel lumina; VEL = range (mean) of vessel element length; LV = number of layers of wide vessels in earlywood; NV = narrow vessels; HT = presence of helical thickenings on vessel walls (+ present / – absent); NAP = maximum number of cells in axial parenchyma strand; RH = range (mean) of multiseriate ray height; RW = range (mean) of multiseriate ray width; TT = type of tile cells; P = *Pterospermum* type; I = intermediate between *Durio* and *Pterospermum* type. CAP = crystals in axial parenchyma cells (+ present / – absent); CR = crystals in ray cells (+ present / – absent).

Comparison with fossil plant taxa

For fossil woods, the combination of ring- or semi-ring-porous wood, exclusively simple perforation plates, wide vessels (mean diameter > 200 µm), and tile ray cells has been reported for *Triplochitioxylon oregonensis* Manchester (Malvaceae) from the middle Eocene strata of Oregon, USA (Manchester 1979), and in several species from Oligocene to Miocene strata of Japan and Korea. Such specimens have been ascribed to the genera *Wataria* K. Terada *et al.* Suzuki and/or *Reevesia* in the Malvaceae (Watari 1952; Terada & Suzuki 1998; InsideWood 2004-onwards). *Triplochitioxylon oregonensis* differs from this Shengli Miocene wood because it has diffuse-porous wood, longer mean vessel element (mean length 403 µm), mostly solitary latewood vessels (Manchester 1979). Some wood anatomical traits of *W. miocenica*, *W. oligocenica*, *W. parvipora* and *R. japonoxyla* and the Miocene wood from Shengli, are summarized in Table 1. As this comparison suggested, our sample differs from all species of *Wataria* due to its narrow latewood vessels that were mainly grouped, rather than solitary, and also by the occurrence of crystals in the axial parenchyma cells. Grouped latewood vessels are also reported for *R. japonoxyla*, but this species has helical thickenings on its vessel walls that makes it distinct from the fossil wood from the Shengli coal mine. Crystals rarely occur in ray cells of the *Wataria* species and of *Triplochitioxylon oregonensis* as well, but they have not been reported from the axial parenchyma cells of these taxa (Manchester 1979; Terada & Suzuki 1998; Jeong *et al.* 2003). Therefore, the Shengli wood sample can be placed in the genus *Wataria* with confidence. On the basis of the differences mentioned above, we consider it to be a new species, *Wataria yunnanica* sp. nov.

Biogeographical and paleoclimatological implications

This is the first report of *Wataria* in China – it extends the distribution of this genus in the Miocene further south and west from Japan and Korea, where the other species in this genus have been found. Concurrently, this fossil wood was found within the range of the modern genus *Reevesia*, whose distribution covers Southeast Asia from the Himalayas to China, Indochina, and Java (Ivanov 2004; Fang *et al.* 2011). The modern genus *Reevesia* has wood structure similar to that of *Wataria*, so we consider the genus likely to be related to *Wataria*. *Reevesia*-like pollen has been recorded in western Europe (Belgium and France) from the early Paleogene (Muller 1981). *Reevesiapollis* Krutzsch pollen has been reported in central, south and southeastern Europe from Oligocene to Pliocene (Petrov & Drazheva-Stamatova 1972; Sadowska 1973, 1977; Bertoldi *et al.* 1994; Nagy 1985; Dyjor & Sadowska 1986; Petrescu & Givulescu 1986; Hristova & Ivanov 2009). Moreover, fossil fruits of *Reevesia*, along with *Reevesia* pollen were found in Early Miocene strata of the Most Basin in North Bohemia, Czech Republic (Kvaček 2006). To date in China, *Reevesia* pollen is not known in the fossil record. However, fossil leaves that are similar to *R. pubescens* Mast. var. *pubescens* have been recorded from the late Miocene in Lincang, Yunnan (Guo 2011). Therefore, the finding of *W. yunnanica* in the middle Miocene of Yunnan corresponds with the temporal and spatial distribution of *Reevesia*.

Ring-porosity – the most prominent wood feature of *Wataria* and *Reevesia* – has adaptive value in seasonal climates (Baas & Wheeler 2011). Ring-porous woods occur in seasonal temperate climates (mostly in the northern hemisphere) and, very rarely, in some monsoonal forest species in the tropics. The modern species of *Reevesia* are one such rare case: they grow in subtropical and tropical seasonally dry vegetation, and sometimes in montane forests up to 1500–2000 m (Ivanov 2004; Tang *et al.* 2007; Fang *et al.* 2011). The occurrence of ring-porous wood in our sample may therefore be an indicator that south Yunnan had a seasonal (probably monsoonal) climate during the middle Miocene. Some palynological studies suggest that a weak monsoon climate existed since the Middle Miocene in Southwest China (Zhang *et al.* 2012; Li *et al.* 2015).

The characteristic of ring porosity is restricted almost exclusively to deciduous trees and shrubs (Boura & De Franceschi 2007). In *Reevesia*, the combination of ring-porous wood and deciduous habit has been reported for *R. formosana* (Terada & Suzuki 1998; Tang *et al.* 2007). Thus, it seems probable that *W. yunnanica* and other *Wataria* species were also deciduous.

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