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# Revision of the so-called ‘*Reevesia*’ fossil woods from the Tertiary in Japan — a proposal of the new genus *Wataria* (Sterculiaceae)

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## Abstract

The Tertiary so-called ‘*Reevesia*’ fossil woods from the Oligocene and Miocene in Japan are characterized by distinct ring porosity and tile cells in rays. Comparison of these ‘*Reevesia*’ fossil woods with extant woods showed that only one specimen has characteristics of *Reevesia*, while the others differ from all extant genera of the Malvales, and so are regarded as belonging to an extinct genus of Sterculiaceae, most similar to the extant genus *Triplochiton* Schumann and the fossil genus *Triplochitioxylon* Manchester, and the new genus *Wataria* K. Terada et M. Suzuki, gen. nov. is proposed for those fossil woods. *Reevesia miocenica* Watari and *R. oligocenica* M. Suzuki are transferred into *Wataria* as *W. miocenica* K. Terada et M. Suzuki, comb. nov. and *W. oligocenica* K. Terada et M. Suzuki, comb. nov., respectively, and one new species, *Wataria parvipora*, is described here. The specimen with characteristics of *Reevesia* is described as a new species *Reevesia japonoxyla* K. Terada et M. Suzuki, sp. nov. © 1998 Elsevier Science B.V. All rights reserved.

*Keywords:* fossil wood; *Reevesia*; Sterculiaceae; Tertiary; tile cells; *Triplochiton*; *Wataria*

## 1. Introduction

Tile cells are a distinctive wood anatomical feature. They are defined as a special type of apparently empty upright (or rarely square) ray cells occurring in horizontal series usually interspersed among the procumbent cells of rays (IAWA Committee, 1989). Tile cells are restricted to the order Malvales (Chattaway, 1933; Carlquist, 1988; IAWA Committee, 1989). Tile cells are classified into two extreme types, the *Durio* and *Pterospermum* types, and an intermediate of the two is also present (Chattaway, 1933).

Watari (1952) discovered three fossil woods that are characterized by distinct ring porosity and the presence of tile cells in rays from the Miocene of Yamagata Prefecture, northern Honshu (Fig. 1, a–c). Because Kanehira (1921), who worked on Formosan woods, indicated that only the extant species *Reevesia formosana* Sprague of Sterculiaceae had ring porosity and intermediate tile cells, he assigned the fossil woods to *Reevesia*. Watari (1952) named the fossil woods *Reevesia miocenica* Watari and considered them closely related to *R. formosana*.

Subsequently, *Reevesia oligocenica* Suzuki, which is very similar to *Reevesia miocenica*, was described from the Oligocene of Fukuoka Prefecture, northern Kyushu (Fig. 1, i; Suzuki, 1976). Additional specimens of *R. miocenica* were reported from the Lower

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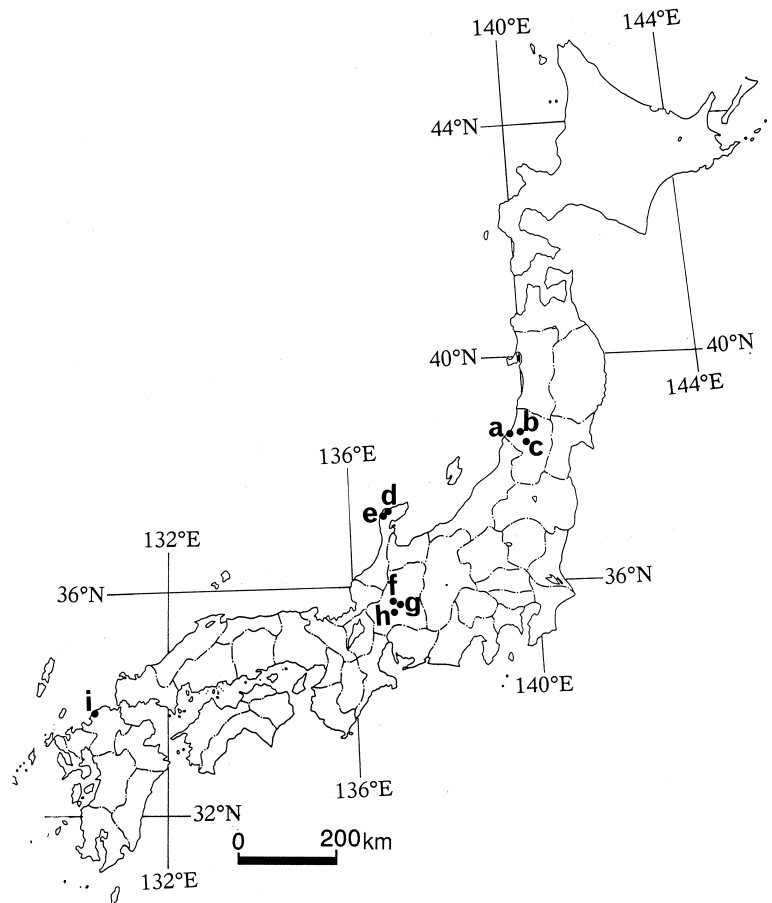


Fig. 1. Locality map of so-called '*Reevesia*' fossil woods in Japan. *a* = Iragawa, Atsumi-machi, Nishitagawa-gun, Yamagata Prefecture; *b* = Isagodani, Tsuruoka City, Yamagata Prefecture; *c* = Tamugimata, Higashi-mura, Yamagata Prefecture; *d* = Nametaki, Wajima City, Ishikawa Prefecture; *e* = Nigoriike, Monzen-machi, Ishikawa Prefecture; *f* = Minamihora, Kawabe-machi, Kamo-gun, Gifu Prefecture; *h* = the river bed of Kiso River at a border of Minokamo and Kani Cities, Gifu Prefecture; *i* = Koinoura, Tsuyazaki-machi, Fukuoka Prefecture.

Miocene of Noto Peninsula, Ishikawa Prefecture, central Honshu (Fig. 1, e; Suzuki and Watari, 1994).

Recently, Lower Miocene fossil forests composed of many erect stumps were found on the river bed of Kiso River, Gifu Prefecture, central Honshu (Fig. 1, h; Shikano, 1995). A preliminary observation of the wood structure of those stumps revealed that most of them had ring porosity and tile cells, and were quite similar to *Reevesia miocenica* (Terada, 1995). Furthermore, two fossil woods with ring porosity and tile cells were also found from the Lower Miocene Hachiya Formation of Kawabe-machi near the fossil forests (Fig. 1, f, g).

The so-called '*Reevesia*' fossil woods characterized by distinct ring porosity and tile cells were known from various areas and ages in the Tertiary of Japan (Fig. 1). This fact suggests that '*Reevesia*' trees had flourished during the Tertiary of Japan, although they are now extinct in Japan.

During a study on Tertiary fossil woods in Japan, it was noticed that most '*Reevesia*' fossil woods differed in some features from the genus *Reevesia* and from other extant genera of Malvales. Therefore, we re-examined all '*Reevesia*' fossil woods from Japan and revised them systematically.

## 2. Materials and methods

Nine specimens were examined in detail (Table 1). The specimen of no. 35252 is the syntype of *Reevesia miocenica* Watari, which is one of the three specimens reported by Watari (1952) and deposited in the University Museum, University of Tokyo (TI). It was collected from the Lower Miocene at Iragawa, Atsumi-machi, Nishitagawa-gun, Yamagata Prefecture (38°40'N, 139°38'E; Fig. 1, a). No. 71189 is the holotype of *Reevesia oligocenica* Suzuki, which is one of the two specimens reported by Suzuki (1976), and collected from the Lower Oligocene Tsuyazaki Formation at Tsuyazaki, Fukuoka Prefecture (33°49'N, 130°27'E; Fig. 1, i; Sakai, 1994). No. 53108 is one of the five specimens reported as *Reevesia miocenica* from the Lower Miocene Nawamata Formation of Noto Peninsula, Ishikawa Prefecture (37°20'N, 136°48'E; Fig. 1, e; Suzuki and Watari, 1994). No. 53219 is collected from the Lower Miocene Nawamata Formation at Nametaki, Wajima City, Ishikawa Prefecture (37°21'N, 136°48'E; Fig. 1, d). No. 59019 is collected in the volcanic breccia of the Lower Miocene Hachiya Formation on the right riverside of Hida River at Kawabe Dam, Kawabe-machi, Kamo-gun, Gifu Prefecture (35°28'N, 137°04'E; Fig. 1, g; Nomura, 1986, 1992). No. 59044 is also collected from the Hachiya Formation at Minamihora, Kawabe-machi, Kamo-gun, Gifu Prefecture (35°29'N, 137°03'E; Fig. 1, f), about 3 km north-

west of the Kawabe Dam. Nos. 59061, 59082 and 59098 are the representatives of 27 fossil stumps which were collected from the fossil forests on the river bed of Kiso River at a border of Minokamo and Kani Cities, Gifu Prefecture (35°26'N, 137°02'E; Fig. 1, h; Terada, 1995). The horizon of the forests is the Lower Miocene Nakamura Formation (Shikano, 1995).

All the fossil specimens examined are silicified wood. Ground cross, tangential and radial thin sections were prepared by the conventional technique. Excepting for the loaned specimens of *Reevesia miocenica* (nos. 35252, 53108) from TI, all the other fossil specimens examined in this paper are deposited in the Wood Collection of the Herbarium, Faculty of Science, Tohoku University, Sendai, Japan (TUSw).

A comparison of wood structure of those fossils with extant species of the Malvales was made using samples deposited in TUSw and loaned from FU (Forest Products Department, Kyushu University, Fukuoka, Japan), Kw (Royal Botanic Garden, Kew, England), Lw (Rijksherbarium, Leiden, Netherlands), MADw or SJRW (U.S. Forest Products Laboratory, Madison, USA), Tw (Royal Museum for Central Africa, Tervuren, Belgium) and TWTw (Forestry and Forest Products Research Institute, Tsukuba, Japan). For searching candidates which may have affinity with the fossil woods, the Fossil Dicotyledonous Wood Database (Wheeler, 1991) was used.

Table 1  
List of the examined specimens of the so-called '*Reevesia*' fossil woods

Specimen No.	Locality	Formation	Horizon <sup>c</sup>
35252	Iragawa, Atsumi, Yamagata Pref. (Fig. 1a) <sup>a</sup>	Atsumi F. <sup>d</sup>	L. Mio.
71189	Koinoura, Tsuyazaki, Fukuoka Pref. (Fig. 1i) <sup>b</sup>	Tsuyazaki F.	L. Oligo.
53108	Nigoriike, Monzen, Ishikawa Pref. (Fig. 1e) <sup>c</sup>	Nawamata F.	L. Mio.
53219	Nametaki, Wajima, Ishikawa Pref. (Fig. 1d)	Nawamata F.	L. Mio.
59019	Kawabe, Kamo, Gifu Pref. (Fig. 1g)	Hachiya F.	L. Mio.
59044	Minamihora, Kamo, Gifu Pref. (Fig. 1f)	Hachiya F.	L. Mio.
59061	Kiso River, Minokamo-Kani, Gifu Pref. (Fig. 1h)	Nakamura F.	L. Mio.
59082	Kiso River, Minokamo-Kani, Gifu Pref. (Fig. 1h)	Nakamura F.	L. Mio.
59098	Kiso River, Minokamo-Kani, Gifu Pref. (Fig. 1h)	Nakamura F.	L. Mio.

<sup>a</sup> Syntype specimen of *Reevesia miocenica* Watari (1952) in TI.

<sup>b</sup> Holotype specimen of *Reevesia oligocenica* Suzuki (1976) in TUSw.

<sup>c</sup> *R. miocenica* in Suzuki and Watari (1994) in TI.

<sup>d</sup> The formations are deduced by us from the locality.

<sup>e</sup> L. Mio = Lower Miocene; L. Oligo. = Lower Oligocene.

## 2.1. Taxonomic treatments

MALVALES

STERCULIACEAE

***Wataria*** K. Terada et M. Suzuki, gen. nov.

*Type: Wataria miocenica* (Watari) K. Terada et M. Suzuki, comb. nov.

*Diagnosis of genus:* Wood distinctly ring porous with wide vessels at beginning of growth rings in cross section. Growth rings distinct. Wide vessels in earlywood mostly solitary, round. Narrow vessels in latewood solitary, and in groups of 2–5 with vasicentric parenchyma; very thick-walled. Vessel elements short; perforation plates exclusively simple; intertracheary pitting alternate; helical thickenings absent; thin-walled tyloses often present in wide vessels; gum-like deposits rarely present in narrow vessels. Axial parenchyma abundant, apotracheal and paratracheal; apotracheal in uni- or biseriate tangential bands alternating with 1–3 rows of fibers in latewood; paratracheal abundant, vasicentric forming 1–3-seriate sheath; conspicuously storied; fusiform and in strands of 2–10 cells or more; crystals absent. Rays heterocellular; uni- or multiseriate. Multiseriate rays 2–10-seriate, composed of tile cells and procumbent cells. Tile cells *Pterospermum* type or intermediate to the *Durio* type; brown-colored substances rarely observed in the tile cells; crystals rarely present.

*Etymology:* The genus *Wataria* is named for the late Dr. Shunji Watari for his pioneer work on this taxon.

***Wataria miocenica*** (Watari) K. Terada et M. Suzuki, comb. nov.

*Basionym:* *Reevesia miocenica* Watari, 1952, J. Fac. Sci. Univ. Tokyo, Sect. 3 Bot. 6, 126–129 photos 8C–D, 9A–E.

*Typification:* Although Watari (1952) originally described three specimens as *Reevesia miocenica* and indicated no holotype, we designated a lectotype in this paper according to the article 9 of ICBN (Greuter et al., 1994) as Watari's description is chiefly based on the specimen of no. 35252.

*Lectotype:* No. 35252; Slides: 35252-1 to -6.

*Repository:* University Museum, University of Tokyo, Japan.

*Type locality:* Iragawa, Atsumi-machi, Nishitagawa-gun, Yamagata Prefecture (38°40'N, 139°38'E; Fig. 1, a).

*Type stratum and stratigraphic horizon:* Atsumi Formation (deduced from the locality), Lower Miocene (Sato et al., 1989; Yamaji, 1989).

*Diagnosis:* This species is distinguished from other species in the genus by: (1) wide vessels arranged in 1–3 layers in earlywood; and (2) very wide earlywood vessels of about 270 µm in mean tangential diameter (Table 2).

*Comments:* Although Watari (1952) described *Reevesia miocenica* as having faint helical thickenings in some vessels, our re-examination of *R. miocenica* including the type specimens, revealed that helical thickenings were absent. The character described by Watari (1952) is mutated herein.

*Syntypes:* No. 35008 in TI, collected from the Lower Miocene at Isagodani, Tsuruoka City, Yamagata Prefecture (38°39'N, 139°46'E; Fig. 1, b). No. 35213 in TI, collected from the Lower Miocene at Tamugimata, Higashi-mura, Yamagata Prefecture (38°34'N, 139°56'E; Fig. 1, c).

*Additional specimens:* Nos. 53103, 53108, 53110, 53117 and 53123 in TI, collected from the Lower Miocene Nawamata Formation at Nigoriike, Monzen-machi, Ishikawa Prefecture (37°26'N, 136°48'E; Fig. 1, e) (Suzuki and Watari, 1994). No. 53219, a new specimen reported in this paper, collected from the Lower Miocene Nawamata Formation at Nametaki, Wajima City, Noto Peninsula, Ishikawa Prefecture (37°21'N, 136°48'E; Fig. 1, d), and deposited in TUSw.

***Wataria oligocenica*** (M. Suzuki) K. Terada et M. Suzuki, comb. nov.

*Basionym:* *Reevesia oligocenica* M. Suzuki, 1976, Bot. Mag. Tokyo 89, 65–68, fig. 4A–G.

*Holotype:* No. 71189; Slides: 71189-1 to -6.

*Paratype:* No. 71208; Slides: 71208-1 to -3.

*Repository:* Herbarium, Faculty of Science, Tohoku University, Sendai, Japan.

*Type locality:* Koinoura, Tsuyazaki-machi, Fukuoka Prefecture, northern Kyushu Japan (33°49'N, 130°27'E; Fig. 1, i).

*Type stratum and stratigraphic horizon:* Tsuyazaki Formation, Lower Oligocene (Sakai, 1994).

Table 2

Anatomical characters of the so-called 'Reevesia' fossil woods

Specimen (No.)	Wide vessels in earlywood			Narrow vessels in latewood			Rays		
	TD <sup>a</sup> (μm)	RD <sup>a</sup> (μm)	LV	NV	WT (μm)	HT <sup>b</sup>	MRH <sup>a</sup> (μm)	MRW <sup>a</sup> (μm)	TT
<i>Wataria miocenica</i> comb. nov.									
35252	200–350 (287)	200–350 (294)	2–3	solitary	5.0	–	150–1150 (621)	70–150 (105)	I
53108	220–350 (265)	300–450 (376)	2–3	solitary	5.8	–	175–1950 (870)	20–75 (50)	I
53219	200–300 (257)	250–320 (288)	1–3	solitary	6.8	–	100–2200 (1280)	40–70 (54)	P
<i>Wataria oligocenica</i> comb. nov.									
71189	140–260 (210)	150–250 (199)	3–5	solitary	4.2	–	200–1000 (688)	30–75 (59)	I
<i>Wataria parvipora</i> sp. nov.									
59044	100–250 (176)	105–285 (187)	1–2	solitary	8.3	–	100–2000 (716)	10–100 (36)	P
59061	125–220 (167)	125–250 (187)	1–3	solitary	7.1	–	unmeasurable		I
59082	110–275 (171)	100–250 (185)	1–2	solitary	6.8	–	550–1200 (803)	70–140 (112)	I
59098	90–200 (150)	125–275 (196)	1–2	solitary	6.7	–	unmeasurable		I
<i>Reevesia japonoxyla</i> sp. nov.									
59019	110–210 (162)	170–290 (235)	2–5	cluster	2.9	+	550–2700 (1392)	40–70 (54)	P

TD = tangential vessel diameter; RD = radial vessel diameter; LV = layers of wide vessels in earlywood.

NV = narrow vessels; WT = mean wall thickness of narrow vessel; HT = helical thickenings on vessel walls.

MRH = multiseriate ray height; MRW = multiseriate ray width.

TT = type of tile cells: P = *Pterospermum*-type; I = intermediate of *Durio*- and *Pterospermum*-types.<sup>a</sup> Range (mean). <sup>b</sup> – = absent; + = present.

**Diagnosis:** This species is distinguished by following features from other species in the genus: (1) wide vessels arranged in 3–5 layers in earlywood; and (2) earlywood vessels of about 210 μm in mean tangential diameter (Table 2).

***Wataria parvipora*** K. Terada et M. Suzuki, sp. nov.

**Holotype:** No. 59044; Slides: 59044-1, 2, 3, 4, 5, 6 and 7. This hand-sample is a stem wood about 5 cm in diameter, 11 cm long.

**Repository:** Herbarium, Faculty of Science, Tohoku University, Sendai, Japan.

**Type locality:** Minamihora, Kawabe-machi, Kamogun, Gifu Prefecture (35°29'N, 137°03'E; Fig. 1, f).

**Type stratum and stratigraphic horizon:** Hachiya Formation, Lower Miocene (Nomura, 1986, 1992)

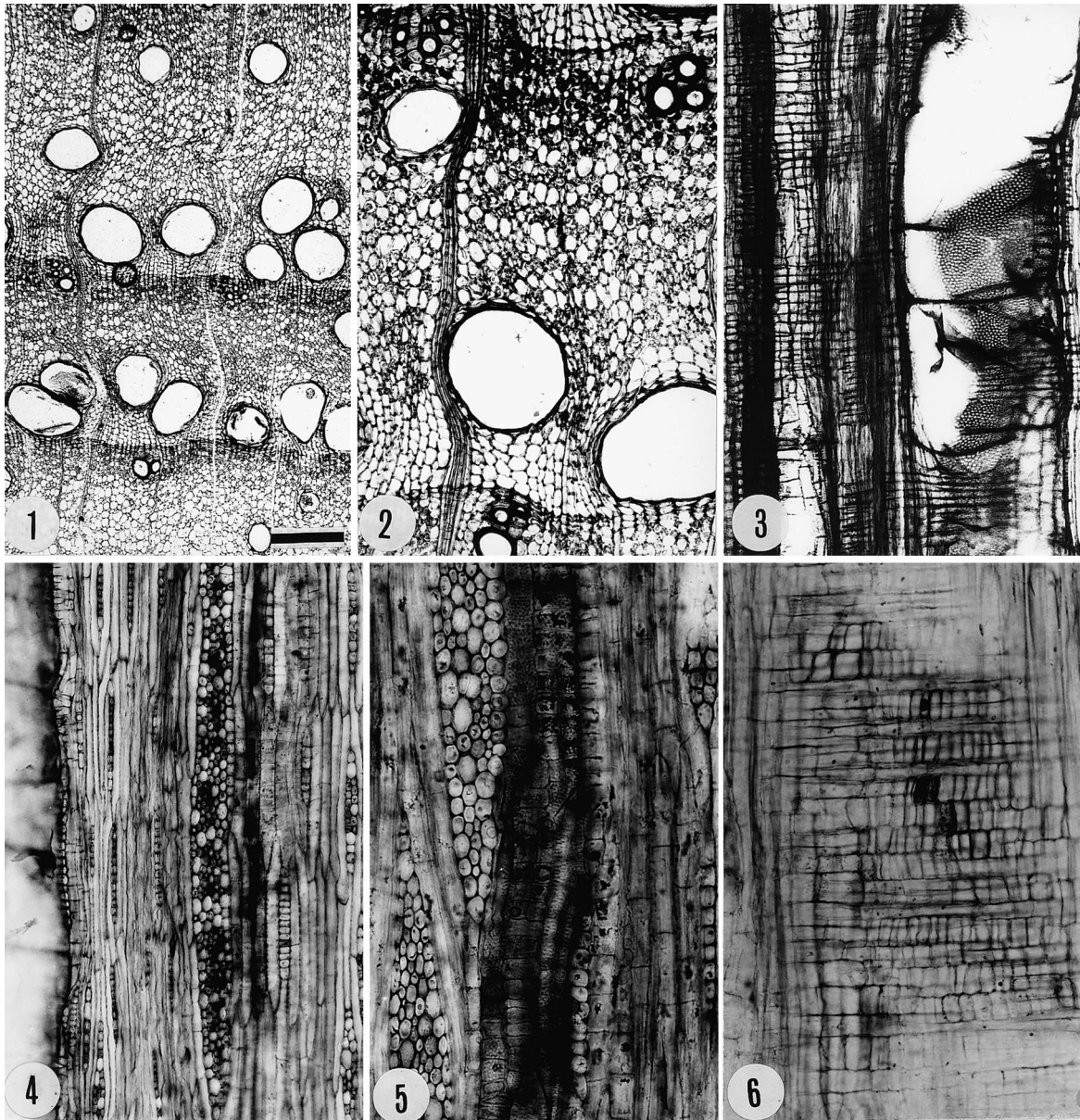
**Paratypes:** 27 specimens, nos. 59058–59066, 59077–59084, 59089–59095, 59097–59099, in TUSw, were collected from the fossil forests of the Lower Miocene Nakamura Formation on the river bed of Kiso River at a border of Minokamo and Kani cities, Gifu Prefecture (35°26'N, 137°02'E; Fig. 1, h; Shikano, 1995). Most of them were compressed and deformed during burial.

**Etymology:** The specific epithet, *parvipora*, is derived that this species has much narrower vessels in earlywood than that of *Wataria miocenica*.

**Description:** Wood distinctly ring porous (Plate I, 1, 2). Growth rings distinct; 0.5–1.5 mm wide (Plate I, 1, 2).

Wide vessels arranged in one or two layers in earlywood in cross section, mostly solitary and sometimes in radial or oblique multiples of two to three; solitary vessels round, 100–250 (mean 176) × 105–285 (mean 187) μm in tangential × radial diameters; walls slightly thickened (about 4 μm) (Plate I, 1, 2). Narrow latewood vessels solitary in cross section, not in multiples nor in clusters; forming groups of 2–5 vessels with vasicentric parenchyma in latewood; circular or angular especially at the end of growth rings, 15–100 (mean 50) μm in tangential diameter; walls 8.3 μm thick (Plate I, 1, 2). Vessel elements short, 65–290 (mean 184.8) μm long in earlywood, 145–210 (mean 175.6) μm long in latewood; end walls horizontal or somewhat oblique in earlywood, and oblique in latewood (Plate I, 3). Perforation plates exclusively simple (Plate I, 3). Intertracheary pits alternate, dense, circular or polygonal in outline, about 5 μm in diameter, with horizontally elongated aper-

## PLATE I



*Wataria parvipora* K. Terada et M. Suzuki, *sp. nov.* Holotype: no. 59044. Scale bars indicated in 1. The bar is 250  $\mu\text{m}$  in 1, 100  $\mu\text{m}$  in 2–4, 50  $\mu\text{m}$  in 5 and 6.

1. Cross section showing ring porous wood with distinct growth rings.
2. Cross section showing wide vessels in earlywood, thick-walled solitary narrow vessels in latewood and uniseriate banded parenchyma in latewood.
3. Radial section showing wide vessel with simple perforation and alternate intertracheary pitting.
4. Tangential section showing both uniseriate rays and multiseriate rays with tile cells, and storied structure of fibers, axial parenchyma and narrow rays.
5. Tangential section showing multiseriate rays with tile cells and densely pitted vasicentric parenchyma around vessels.
6. Radial section showing tile cells and procumbent cells of a multiseriate ray.

tures (Plate I, 3). Helical thickenings not observed. Thin-walled tyloses often present (Plate I, 1). Gum-like deposits rarely observed only in narrow vessels.

Fibers consisting ground mass of the latewood with axial parenchyma; square or polygonal in cross section, 7–25 (mean 15.5)  $\mu\text{m}$  in diameter; walls about 3.5  $\mu\text{m}$  thick; not septate; storied (Plate I, 2).

Axial parenchyma abundant, apotracheal and paratracheal; conspicuously storied (Plate I, 4); fusiform and in strands of 2–10 cells, up to 18 cells (Plate I, 5), 225–325 (mean 261)  $\mu\text{m}$  in length (Plate I, 2, 4); polygonal to round in cross section, 10–40 (mean 21.5)  $\mu\text{m}$  in diameter. Apotracheal parenchyma in uni- or biseriate tangential bands alternating with 1–3 rows of fibers in latewood (Plate I, 2). Paratracheal parenchyma abundant and vasicentric forming 1–3-seriate sheaths (Plate I, 2). Vessel-parenchyma pits small circular, alternate, dense (Plate I, 5). Crystals absent.

Rays heterocellular, 1–7-seriate (Plate I, 4, 5). Uniseriate rays 5–12.5 (mean 8.3)  $\mu\text{m}$  wide and 37.5–275 (mean 146.5)  $\mu\text{m}$  tall. Multiseriate rays mostly 3–5 cells and 10–100 (mean 36.1)  $\mu\text{m}$  wide, and 100–2000 (mean 715.9)  $\mu\text{m}$  tall; composed of tile cells and procumbent cells (Plate I, 6). Tile cells *Pterospermum* type to intermediate (Plate I, 5, 6); 7.5–20 (mean 13.5)  $\times$  15–45 (mean 25.5)  $\times$  5–27.5 (mean 15.8)  $\mu\text{m}$  in tangential  $\times$  vertical  $\times$  radial diameters. Procumbent cells 3–10 (mean 6)  $\times$  5–17.5 (mean 10.4)  $\times$  15–37.5 (mean 26.3)  $\mu\text{m}$  in tangential  $\times$  vertical  $\times$  radial diameters. Ray-vessel pits alternate and dense. Brown-colored substances sometimes observed in tile cells (Plate I, 6). Crystals not observed, but rarely with swollen cells which may suggest the occurrence of crystals.

Genus *Reevesia* Lindley, 1827

### *Reevesia japonoxyla*

K. Terada et M. Suzuki, sp. nov. (Plate II)

*Holotype*: No. 59019; Slides: 59019-1 to -5. This sample is a trunk with estimated diameter of 30 cm.

*Repository*: Herbarium, Faculty of Science, Tohoku University, Sendai, Japan.

*Type locality*: the right riverside of Hida River at Kawabe Dam, Kawabe-machi, Kamo-gun, Gifu Prefecture (35°28'N, 137°04'E; Fig. 1, g).

*Type stratum and stratigraphic horizon*: Hachiya Formation, Lower Miocene (Nomura, 1986, 1992)

*Etymology*: From Japan.

*Description*: Wood distinctly ring porous (Plate II, 7). Growth rings distinct 0.5–1.5 mm wide (Plate II, 7).

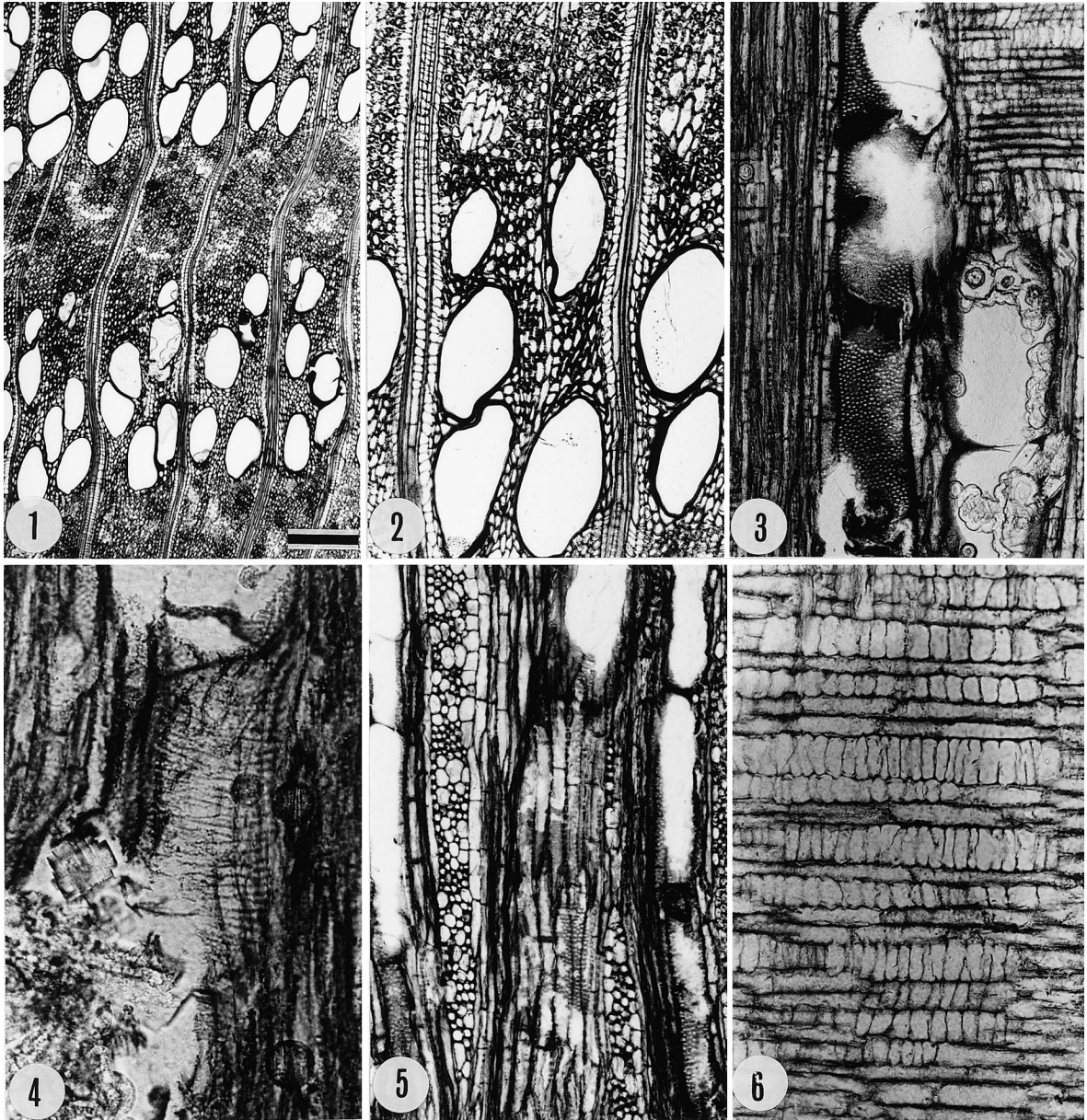
Wide vessels arranged in two to five layers in earlywood, mostly solitary and sometimes in radial or oblique multiples of two to three in cross section; solitary vessels radially elongated oval, 110–210 (mean 162)  $\times$  170–290 (mean 234.5)  $\mu\text{m}$  in tangential  $\times$  radial diameters; walls thin (about 3  $\mu\text{m}$ ) (Plate II, 1, 2). Narrow vessels in latewood commonly in clusters of 5–20 vessels; each vessel polygonal in cross section, 10–50 (mean 24.1)  $\mu\text{m}$  in diameter; walls 2.9  $\mu\text{m}$  thick (Plate II, 2). Latewood vessels distributed in ulmiform or in tangential bands (Plate II, 1, 2). Vessel elements 150–330 (mean 263.8)  $\mu\text{m}$  long; end walls horizontal or somewhat oblique in earlywood, and oblique in latewood (Plate II, 3–5). Perforation plates exclusively simple (Plate II, 3–5). Intertracheary pits alternate, dense, circular or polygonal in outline, about 5  $\mu\text{m}$  in diameter, with horizontally elongated apertures (Plate II, 3). Helical thickenings distinct on narrow vessel walls (Plate II, 4). Tyloses not observed. Gum-like deposits often present in vessels (Plate II, 1).

Fibers forming the ground mass of the latewood; square or polygonal in cross section (Plate II, 2), 10–20 (mean 15.1)  $\mu\text{m}$  in diameter; walls about 4  $\mu\text{m}$  thick; not septate.

Axial parenchyma apotracheal and paratracheal (Plate II, 2); conspicuously storied; fusiform and in strands with 2–4 cells (Plate II, 5). Apotracheal parenchyma diffuse-in-aggregates in latewood and paratracheal vasicentric scanty (Plate II, 2). Parenchyma cells 10–25 (mean 16.4)  $\mu\text{m}$  in diameter in cross section (Plate II, 2) and 250–375 (mean 322.6)  $\mu\text{m}$  in length (Plate II, 5). Crystals absent.

Rays heterocellular, 1–7-seriate (Plate II, 5). Uniseriate rays 15–20 (mean 17.5)  $\mu\text{m}$  wide, 92.5–500 (mean 205.5)  $\mu\text{m}$  tall. Multiseriate rays mostly 3–5 cells and 40–70 (mean 54.3)  $\mu\text{m}$  wide and 550–2700 (mean 1392)  $\mu\text{m}$  tall; composed of tile cells and procumbent cells (Plate II, 5, 6). Tile cells *Pterospermum* type (Plate II, 5, 6); 10–25 (mean 16.7)  $\times$  15–57.5 (mean 32.6)  $\times$  4–20 (mean 11.2)

## PLATE II



*Reevesia japonoxyla* K. Terada et M. Suzuki, *sp. nov.* Holotype: no. 59019. Scale bars indicated in 1. The bar is 250  $\mu\text{m}$  in 1, 100  $\mu\text{m}$  in 2, 3 and 5, 50  $\mu\text{m}$  in 4 and 6.

1. Cross section showing ring porous wood with 3–5 layers of wide vessels and sporadic gum-like dark contents in vessels in earlywood.
2. Cross section showing wide earlywood vessels and narrow latewood vessels in clusters.
3. Radial section showing wide vessels with simple perforation and alternate intertracheary pitting.
4. Radial section showing helical thickenings on vessel walls.
5. Tangential section showing multiseriate rays with tile cells and storied structure.
6. Radial section showing *Pterospermum*-type tile cells in multiseriate rays.



$\mu\text{m}$  in tangential  $\times$  vertical  $\times$  radial diameters. Procumbent cells 7.5–15 (mean 10.3)  $\times$  7.5–17.5 (mean 12.9)  $\times$  35–85 (mean 60.6)  $\mu\text{m}$  in tangential  $\times$  vertical  $\times$  radial diameters. Ray-vessel pits alternate, minute and dense. Brown-colored substance and crystals invisible.

### 3. Affinities and discussions

#### 3.1. Comparison with extant *Reevesia*

All '*Reevesia*' fossil woods examined have in common the following characteristics: (1) distinct ring porosity; (2) exclusively simple perforation plates; (3) alternate intertracheary pitting; (4) storied structure; and (5) heterocellular multiseriate rays with tile cells. They can be divided into two groups by features of the latewood vessels (Table 2). One group has mostly solitary and thick-walled latewood vessels without helical thickenings. Specimens reported as *Reevesia miocenica* Watari or *R. oligocenica* Suzuki, and newly obtained specimens, nos. 53219, 59044, 59058–59066, 59077–59084, 59089–59095, 59097–59099, belong to this group. The other group is represented by only one specimen, no. 59019, which has latewood vessels in clusters and helical thickenings on vessel walls. As discussed below, the former group is designated as a new fossil wood genus, *Wataria*, of Sterculiaceae, and the latter group is a new species of *Reevesia*, *R. japonoxyla* (Table 2).

When Watari (1952) described *Reevesia miocenica* (= *Wataria miocenica* comb. nov.), he found only extant species *Reevesia formosana* Sprague has ring porosity and tile cells based on a description of wood anatomy by Kanehira (1921). As tile cells of his fossil woods and *Reevesia formosana* are intermediate between the *Durio* and the *Pterospermum* type, he described his fossils as a new species of *Reevesia* closely related to *R. formosana* (Watari, 1952).

Although Kanehira (1921) described *Reevesia formosana* as ring porous wood, its ring porosity is not well developed and is quite different from that of Watari's fossils. Distinct ring porosity is one of the common features common to all fossil woods of *Wataria*. We re-examined Kanehira's wood sample

(FU-A50) of *Reevesia formosana* (Plate III, 1–3), an additional wood sample (TUSw-10584) of *R. formosana* obtained from Taiwan, and fossil woods of *Wataria* including the syntype specimen of Watari's *Reevesia miocenica* (Table 3).

As a result, we found many wood anatomical differences between *Reevesia formosana* and *Wataria* fossil woods (Table 3; Plate III, 1–3): (1) *Wataria* has distinct ring porosity while *R. formosana* does not; (2) latewood vessels of *Wataria* are mostly solitary while those of *R. formosana* are usually in clusters; (3) helical thickenings on vessel walls are not observed in *Wataria* but distinct in *R. formosana*; (4) vessel occlusions are thin-walled tyloses in *Wataria* and gum-like deposits in *R. formosana*; (5) vasicentric parenchyma is abundant in *Wataria*, while only scanty in *R. formosana*; (6) apotracheal parenchyma in *Wataria* is distinct and in uni- or biseriate tangential bands while that of *R. formosana* is in diffuse-in-aggregates; (7) storied structure is distinct in *Wataria*, while indistinct in *R. formosana*; and (8) the number of cells in a parenchyma strand is 2–10 cells or more cells in *Wataria*, while only 2–4 cells in *R. formosana*. These anatomical differences suggest that *Wataria* has no direct affinity to *Reevesia formosana*.

There are about 18 extant species (Hsue, 1984) of *Reevesia* distributed in the subtropical to warm-temperate regions of Taiwan (Li and Lo, 1993), southern China (Hsue, 1984), eastern Himalaya (Masters, 1875) and Java (Backer and Bakhuizen van den Brink, 1963). In addition, Monachino (1940) reported a new genus with only one species, *Veeresia clarkii* Monachino et Moldenke, from Hidalgo, Mexico, as being closely related to *Reevesia*. Solheim (1987) placed *Veeresia* in synonymy with *Reevesia* and reported a new species from Chiapas and Nicaragua, central America. However, he has not yet effectively published about it because it is only in an abstract. So in this paper we treat these two species as *Veeresia*.

Of about 18 species of *Reevesia*, only a few descriptions of wood anatomy are available. Our observations and the descriptions by Tang (1932, 1936) of Chinese *Reevesia pubescens* Masters [= syn. *R. cavaleriei* Léveille (Hsue, 1984)] indicate that it has semi-ring or indistinct ring porosity, latewood vessels in clusters, and helical thickenings in latewood

Table 3  
Anatomical comparison of 'Reevesia' fossil woods with extant woods and fossil records

Botanic name	Specimen (No.)	Porosity	Vessels				Parenchyma				Rays		
			MTD	VEL <sup>a</sup>	occlusion	NV	HT <sup>b</sup>	PL	NS	storied	CP <sup>b</sup>	TT	CR <sup>b</sup>
'Reevesia' fossil woods													
<i>Wataria miocenica</i> comb. nov.	35252	ring	350	70–350 (234)	tylosis	solitary	–	250–425 (332)	2–10	distinct	–	IP	–/+
<i>Wataria oligocenica</i> comb. nov.	71189	ring	260	75–325 (219)	tylosis	solitary	–	225–360 (291)	2–10	distinct	–	I	–
<i>Wataria parvipora</i> sp. nov.	59044	ring	250	65–290 (185)	tylosis	solitary	–	225–325 (261)	2–10	distinct	–	IP	–/+
<i>Reevesia japonoxyla</i> sp. nov.	59019	ring	210	150–330 (264)	gum	cluster	+	250–375 (322)	2–4	distinct	–	P	–
Extant species													
<i>Reevesia formosana</i>	FU-A50	ring	250	225–450 (347)	gum	cluster	+	250–475 (380)	2–4	indistinct	–	I	–
	TUSw-10584	semi-ring	170	220–440 (320)	gum	cluster	+	270–400 (343)	2–4	indistinct	–	I	–
<i>Reevesia pubesens</i>	SJRw-21786	ring	210	320–500 (403)	gum	cluster	+	320–480 (417)	2–4	distinct	–	P	–
	SJRw-21895	semi-ring	100	280–540 (457)	gum	cluster	+	350–520 (463)	2–4	distinct	–	I	+
<i>Reevesia thyrsoides</i>	Kw-38115	ring	200	500–740 (624)	?	cluster	+	500–750 (625)	2–4	distinct	–	P	–
<i>Reevesia wallichii</i>	TUSw-10585	semi-ring	140	230–590 (443)	gum	cluster	+	430–600 (497)	2–4	indistinct	–	I	–
<i>Veesia clarkii</i>	MADw-42819	ring	170	200–470 (371)	?	multiple of 2–3	+	330–450 (412)	2–4	indistinct	+	I	+
	MADw-42820	ring	200	230–520 (388)	?	multiple of 2–3	+	310–480 (406)	2–4	indistinct	+	I	+
	MADw-44043	ring	190	240–500 (390)	?	multiple of 2–3	+	300–600 (421)	2–4	indistinct	+	I	+
<i>Triplochiton scleroxylon</i>	TWTw-2772	semi-ring	325	75–335 (230)	tylosis	solitary	–	225–385 (298)	2–4	distinct	+	I	+
	TWTw-4265	diffuse	300	100–350 (272)	tylosis	solitary	–	210–360 (302)	2–4	distinct	+	I	+
	TWTw-5622	semi-ring	270	100–350 (247)	tylosis	solitary	–	250–360 (304)	2–4	distinct	+	I	+
<i>Triplochiton zambesiacus</i> <sup>c</sup>	PRFw-26601	diffuse	130	129–230 (163)	tylosis	solitary	–	130–201 (165)	2–4	distinct	?	I	+
Fossil records													
<i>Triplochitioxylon oregonensis</i> <sup>c</sup>	NBW-50	semi-ring to diffuse	287	273–502 (403)	tylosis	solitary	?	431–660 (532)	2–4	distinct	?	I	+

MTD = maximum tangential vessel diameter; VEL = vessel element length; NV = narrow vessels; HT = helical thickenings.

PL = axial parenchyma length; NS = number of cells in a parenchyma strand; CP = crystal in axial parenchyma.

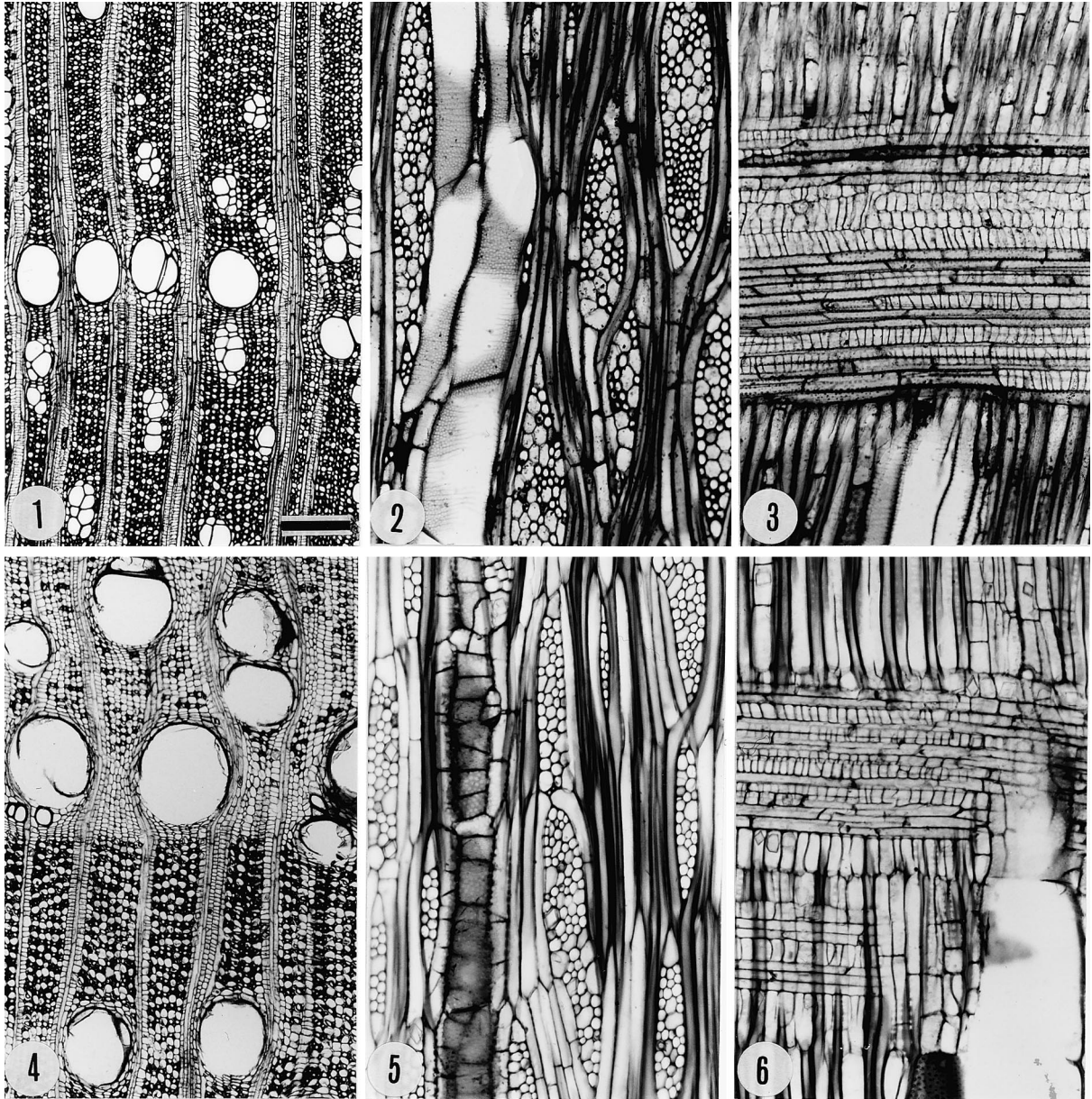
TT = type of tile cells; I = intermediate of *Durio* and *Pterospermum* types; P = *Pterospermum* type; CR = crystal in ray cells.

<sup>a</sup> Range (mean).

<sup>b</sup> – = absent; + = present.

<sup>c</sup> Data from Manchester (1979).

## PLATE III



Scale bars indicated in 1. The bar is 250  $\mu\text{m}$  in 1 and 4, 100  $\mu\text{m}$  in 2, 3, 5 and 6.

1–3. Microphotographs of extant *Reevesia formosana* (FU-A50).

1. Cross section showing semi-ring porous wood and thin-walled narrow vessels in clusters.

2. Tangential section showing multiseriate rays with tile cells, helical thickenings in vessels and unstoried structure of axial elements.

3. Radial section showing tile cells.

4–6. Microphotographs of extant *Triplochiton scleroxylon* (TWTw-2772).

4. Cross section showing semi-ring porous wood with thin-walled tyloses in vessels.

5. Tangential section showing multiseriate rays with tile cells, vasicentric parenchyma and storied structure of fibers, axial parenchyma and rays.

6. Radial section showing rays with tile cells and crystals in both rays and axial parenchyma.

vessels (Table 3). *Reevesia thyrosidea* Lindley of China is diffuse to ring porous wood with latewood vessels in clusters and distinct helical thickenings (Table 3; Cheng et al., 1992; our observations). Moll and Janssonius (1906), cited in Metcalfe and Chalk (1950), described *Reevesia wallichii* Brown from western Java as it did not have vessels in clusters, helical thickenings on vessel walls or tile cells. Our study of the specimen (SJRw-30221) described by Moll and Janssonius (1906) indicates, however, that it has typical tile cells and vessels in multiples of 2–5. Metcalfe and Chalk (1950) suggested that the differences in wood anatomy of *R. wallichii* from other *Reevesia* species might be due to the difference of habitat. However, our observation on an additional specimen of *R. wallichii* (TUSw-10585) reveals that the wood anatomy of the species is quite different from the Moll and Janssonius' description as follows: it has semi-ring to diffuse porosity with latewood vessels in clusters, distinct helical thickenings and typical tile cells. Solereder (1908) also reported that *Reevesia wallichii* has helical thickenings in vessels. Furthermore, *Reevesia wallichii* occurs only in the eastern Himalaya region (Masters, 1875; Stainton, 1988; Long and Rae, 1991), and does not reach to Java where Moll and Janssonius' specimen was collected (Backer and Bakhuizen van den Brink, 1963). This suggests that the description of Moll and Janssonius (1906) was based on incorrectly identified material.

There is no description of the wood anatomy of *Veeresia*. According to our observation on three specimens (MADw-42819, 42820, 44043) of *Veeresia clarkii* from Mexico, it shows more distinct ring porosity than the above mentioned *Reevesia* species and has latewood vessels in radial multiples of 2–3, helical thickenings on vessel walls, tile cells in rays and numerous crystals in both axial parenchyma and rays (Table 3). Although there are some differences of wood anatomy between *Veeresia* and *Reevesia*, *Veeresia* is quite similar in gross anatomical features to *Reevesia*.

In conclusion, the wood structure of *Reevesia* including *Veeresia* is quite uniform, i.e., (1) the wood is mostly semi-ring or rarely ring porous, (2) latewood vessels are usually in clusters or in multiples, (3) helical thickenings are distinct on latewood vessel walls, and (4) tile cells are present (Table 3). Thus it

is apparent that *Wataria* does not belong to *Reevesia* or to *Veeresia*, because *Wataria* has thick-walled solitary latewood vessels and lacks of helical thickenings on the vessel walls. Other differences are (1) *Wataria* has thin-walled tyloses in wide vessels, while *Reevesia* has gum-like deposits; and (2) *Wataria* has much shorter vessel elements and axial parenchyma strands than *Reevesia* and *Veeresia* (Table 3).

### 3.2. Comparison within the Malvales

The most outstanding feature of *Wataria* is the presence of tile cells in rays. Species with tile cells are restricted to species in four families of Malvales: Sterculiaceae, Tiliaceae, Bombacaceae and Malvaceae (Table 4). In the Sterculiaceae, species

Table 4  
Tile cells occurrence among extant genera

<i>Durio</i> type	Intermediate	<i>Pterospermum</i> type
Sterculiaceae		
<i>Reevesia</i> <sup>a</sup>	<i>Reevesia</i> <sup>a</sup>	<i>Reevesia</i> <sup>a</sup>
<i>Triplochiton</i> <sup>a</sup>	<i>Triplochiton</i> <sup>a</sup>	<i>Triplochiton</i> <sup>a</sup>
<i>Guazuma</i> <sup>a</sup>	<i>Guazuma</i> <sup>a</sup>	
<i>Leptonychia</i>		<i>Pterospermum</i>
<i>Scaphopetalum</i>		<i>Melochia</i>
<i>Kleinhovia</i>		
Tiliaceae		
<i>Microcos</i>	<i>Grewia</i> <sup>a</sup>	<i>Grewia</i> <sup>a</sup>
<i>Mortoni dendron</i> <sup>a</sup>		<i>Mortoni dendron</i> <sup>a</sup>
<i>Colona</i>		<i>Duboscia</i>
<i>Luehea</i>		<i>Trichospermum</i>
<i>Lueheopsis</i>		
<i>Mollia</i>		
<i>Vinticina</i>		
Bombacaceae		
<i>Durio</i>		<i>Hampea</i>
<i>Boshia</i>		<i>Ochroma</i>
<i>Neesia</i>		
<i>Coelosstegia</i>		
Malvaceae		
<i>Kydaia</i>		<i>Malvaviscus</i>
		<i>Montezuma</i>
		<i>Pavonia</i>
		<i>Urena</i>

Drawn based on Chattaway (1933), Metcalfe and Chalk (1950), Manchester and Miller (1978), Carlquist (1988) and IAWA Committee (1989).

<sup>a</sup> Genera with different types of tile cells within the genus.

with tile cells are restricted to four tribes, Theobromaceae, Helicteraceae, Hermannieae and Mansonieae, in the Tiliaceae to the tribes Grewieae and Tiliaceae, in the Bombacaceae to the tribes Durioneae and Matisieae, and in the Malvaceae, to the tribes Kydieae and Ureneae. In these four families, tile cells are known in 29 genera of ten tribes in total (Table 4). In these genera with tile cells, no species has the distinctly ring porosity. The only species in the Malvales that has such distinct ring porosity as *Wataria* is *Firmiana simplex* (L.) Wight in Japan, Taiwan and China, but it does not have tile cells.

Chattaway (1933) recognized two extreme types of tile cells, the *Durio* and *Pterospermum* types, although there is intermediate between the two types. The most obvious difference between the two types is the height of tile cells. The tile cells of the *Durio* type have the same height as the procumbent cells and the tile cells of the *Pterospermum* type are higher than the procumbent cells. Most genera have either of the two types of tile cells. In the Bombacaceae and the Malvaceae, the tile cell type is the same within the tribes, e.g. in the Bombacaceae the *Durio* type is restricted to the tribe Durioneae and the *Pterospermum* type to the tribe Matisieae. However, three genera of the Sterculiaceae and two genera of the Tiliaceae have intermediate tile cells and/or both types (Table 4). *Reevesia* has both types and intermediate one, and *Guazuma* of the Sterculiaceae has the *Durio* type and also intermediate one (Chattaway, 1933). *Triplochiton* of the Sterculiaceae is considered as *Durio* type by Chattaway (1933), but Metcalfe and Chalk (1950) and Manchester (1979) regarded it as intermediate while Carlquist (1988) considered it as *Pterospermum* type (Table 4). *Grewia* of Tiliaceae has either the intermediate or the *Pterospermum* type (Chattaway, 1933; IAWA Committee, 1989). *Mortonioidendron* of the Tiliaceae also has either of the two types (Carlquist, 1988). As *Wataria* has both the intermediate and the *Pterospermum* type (Table 2), *Wataria* may have affinities with the above mentioned genera.

Axial parenchyma is an important feature in assessing taxonomic relationships among dicotyledonous woods (Metcalfe and Chalk, 1983). Axial parenchyma of *Wataria* is apotracheal banded and paratracheal vasicentric. Apotracheal parenchyma is in uni- or biseriate tangential bands alternating with

1–3 rows of fibers. Paratracheal parenchyma is abundant and in vasicentric 1–3-seriate sheaths around the vessels. The distribution pattern of axial parenchyma is usually constant throughout genera in Sterculiaceae (Chattaway, 1932) as well as among dicotyledonous woods (Metcalfe and Chalk, 1983). Among the 29 genera with the tile cells (Table 4), only *Triplochiton* has similar parenchyma to *Wataria*, i.e., apotracheal banded of uni- or biseriate and paratracheal vasicentric 1–3-seriate sheaths (Plate III, 4). Therefore *Triplochiton* may have affinity with *Wataria* because of the similarity of axial parenchyma.

*Triplochiton* is an endemic genus in tropical Africa. There are two species, *Triplochiton scleroxylon* Schumann in western Africa (Hutchinson and Dalziel, 1958), and *Triplochiton zambesiacus* Milne-Redhead in southeastern Africa, Rhodesia (Wild, 1963). Although Schumann (1901) originally proposed *Triplochiton* as a member of a new family of the Malvales, the genus is now generally regarded as a member of the Sterculiaceae (Hutchinson, 1967; Takhtajan, 1983). Hutchinson (1967) regarded *Triplochiton* Schumann as belonging to the tribe Tarrietieae, along with *Heritiera* Aiton, *Hildegardia* Schott et Endlicher and *Mansonia* Drummond ex Prain, but Edlin (1935) regarded *Triplochiton* to belong to the tribe Mansonieae, along with *Mansonia*. In addition to the similarity in axial parenchyma, *Triplochiton* resembles *Wataria* in the following features (Table 3; Plate III, 4–6): (1) narrow latewood vessels are mostly solitary and thick-walled; (2) helical thickenings are absent on vessel walls; (3) thin-walled tyloses occur in wide vessels; and (4) tile cells are intermediate between the *Durio* and *Pterospermum* types. However, there are differences between *Wataria* and *Triplochiton* as follows (Table 3; Plate III, 4–6): (1) *Wataria* is distinctly ring porous while *Triplochiton* is semi-ring to diffuse porous; (2) *Wataria* has 2–10 cells in a parenchyma strand, while *Triplochiton* has only 2–4 cells; and (3) *Wataria* has no crystals in axial parenchyma and few crystals in the rays, while *Triplochiton* has abundant crystals in both axial and rays parenchyma. Therefore, although *Wataria* shares more characterization with *Triplochiton* than any other member of the Malvales, it is distinguishable as an extinct genus of Sterculiaceae.

### 3.3. Comparison with other fossil wood records

According to the Fossil Dicotyledonous Wood Database (Wheeler, 1991), eleven species of fossil woods where reliable tile cells were reported: *Coloxylon dechampsii* Lemoigne, 1978, *Pterospermoxylon kutchensis* Awasthi et al., 1980, *Triplochitioxylon oregonensis* Manchester, 1979 and *Chattawayia paliformis* Manchester, 1980 of the Sterculiaceae, and seven species of *Grewioxylon* of the iliaceae; *G. intertrappea* Shalloom, 1963, *G. malhurzariense* Prakash et Dayal, 1963, *G. indicum* Prakash et Dayal, 1964, *G. sp. cf. malhurzariense* Lakhanpal et al., 1976, *G. fontanesii* Vozenin-Serra, 1981, *G. neumaieri* Selmeier, 1985, and *G. ortenburgense* Selmeier, 1985. Among the above 11 species, *Coloxylon dechampsii* should be excluded, cells because Lemoigne (1978) mentioned in the original description that it has not tile cells but sheath cells. *Pterospermoxylon kutchensis* from the Pliocene of western India is quite different from *Wataria* as it is diffuse porous wood and has scanty paratracheal parenchyma and apotracheal diffuse and diffuse-in-aggregates parenchyma. All seven species of *Grewioxylon* differ from *Wataria* because they are diffuse porous woods and have indistinct and/or scanty apotracheal parenchyma. *Chattawayia paliformis* from the Middle Eocene of Oregon, USA, differs from *Wataria* as it has 4–14-seriate wide multiseriate rays, shows prominent feature of large and irregular-shaped tile cells, and lacks noticeable storied structure. *Triplochitioxylon oregonensis* from the Middle Eocene of Oregon, USA, resembles extant *Triplochiton* (Manchester, 1979). *Triplochitioxylon oregonensis* is also similar to *Wataria* as well as to *Triplochiton* in these anatomical features, e.g.: (1) distribution pattern of axial parenchyma; (2) mostly solitary and thick-walled vessels in latewood; (3) lack of helical thickenings on vessel walls; (4) thin-walled tyloses in wide vessels; and (5) intermediate tile cells (Table 3). However, *Triplochitioxylon oregonensis* differs from *Wataria* in these features: (1) diffuse porosity; (2) small number of cells in a parenchyma strand; and (3) occurrence of crystals in axial parenchyma and rays. Furthermore vessel elements and axial parenchyma strands of *Triplochitioxylon oregonensis* are much longer than in *Wataria* (Table 3). Therefore *Wataria* does not belong to *Triplochitioxylon*.

We conclude that *Wataria* is an extinct genus of the Sterculiaceae but with likely affinity with extant *Triplochiton* and fossil *Triplochitioxylon*.

### 3.4. Variation of wood structure in *Wataria*

All *Wataria* fossil woods examined are quite similar in gross anatomical features, but there is considerable variation in some quantitative characters and in a few qualitative ones (Table 2).

Tangential diameter of vessels at the beginning of annual rings is fairly stable within a species and often employed as a diagnostic characters. The mean tangential diameters of earlywood vessels of *Wataria miocenica* are 257–287  $\mu\text{m}$ , those of *W. parvipora* are 150–176  $\mu\text{m}$ , and of *W. oligocenica* are 210  $\mu\text{m}$  (Table 2). Earlywood vessel diameters are significantly larger in *Wataria miocenica* than in *W. parvipora* and *W. oligocenica* (Fig. 2). The number of layers of wide vessels in earlywood also differs *Wataria miocenica* and *W. parvipora* have 1 to 3 layers of wide vessels, while *W. oligocenica* has 3 to 5 layers (Table 2). Therefore *Wataria oligocenica* differs from *W. miocenica* in its narrower earlywood vessels and more layers of wide vessels in earlywood, as Suzuki (1976) originally described. *Wataria parvipora* differs from *W. miocenica* in its narrower earlywood vessels, and from *W. oligocenica* in fewer layers of wide vessels in earlywood (Table 2).

Height and width of multiseriate rays are variable both interspecifically and intraspecifically in extant Sterculiaceae (Chattaway, 1937). Ray height and ray width are much altered in most species during the ontogeny of the xylem cylinder (Carlquist, 1988). Ray size of *Wataria* species is highly variable (Table 2), and we did not find any diagnostic value for these characters.

Among eight specimens of *Wataria* examined, two specimens, no. 53219 of *W. miocenica* and no. 59044 of *W. parvipora*, have *Pterospermum*-type tile cells, an other six specimens are intermediate between *Durio* and *Pterospermum* types. As discussed previously, there are some extant genera and species that have two types of tile cells and/or intermediates of them. Therefore, it is not strange that there are one extreme type and intermediate one within the species of *Wataria*.

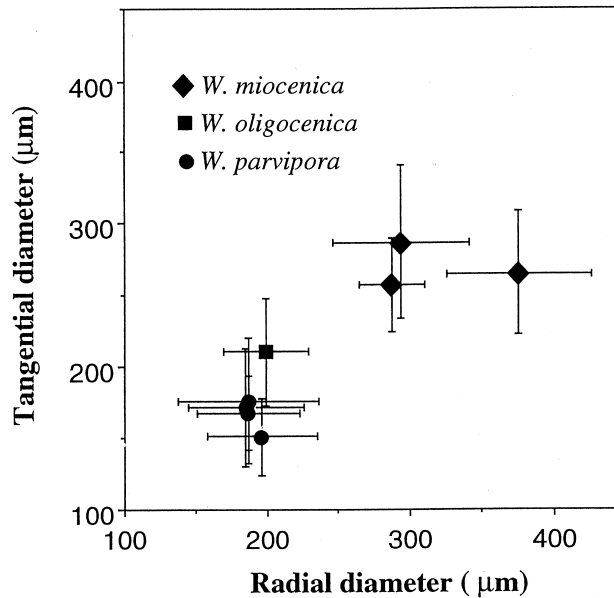


Fig. 2. Size variation of wide vessels in earlywood on *Wataria* woods, showing mean and standard deviation of diameters.

### 3.5. Fossil wood of *Reevesia*

Among ‘*Reevesia*’ fossil woods that have distinct ring porosity and tile cells, one specimen, no. 59019, appears similar to extant *Reevesia* and *Veeresia* and is not assigned to *Wataria*. This specimen has latewood vessels in clusters and helical thickenings on vessel walls (Table 2; Plate II, 2, 4). These features agree with those of extant *Reevesia* and *Veeresia* as mentioned previously. In addition, (1) no. 59019 has longer vessel elements and axial parenchyma strands than *Wataria* species, but has similar length to that of *Reevesia* and *Veeresia*, (2) the number of cells in a parenchyma strand of no. 59019, *Reevesia* and *Veeresia* is 2–4 cells, while in *Wataria* it is 2–10 cells, and (3) *Wataria* has tyloses while no. 59019 and *Reevesia* have gum-like deposits in wide vessels (Table 3).

However, no. 59019 differs from extant *Reevesia* species by being distinctly ring porous and having more layers, 2–5, of wide vessels in earlywood. *Veeresia clarkii* differs from no. 59019 as follows: (1) vessel diameter of no. 59019 decreases abruptly from earlywood to latewood while that of *V. clarkii* decreases gradually; (2) latewood vessels of no. 59019 are in clusters of 5–20, which are

distributed in ulmiform or tangential bands, while those of *V. clarkii* are in radial multiples of only 2–3 vessels; (3) no. 59019 does not have crystals in axial parenchyma or in ray cells, while *V. clarkii* has crystals abundantly in axial parenchyma and in ray cells (Table 3).

Therefore the present fossil is regarded as a member of *Reevesia*, but differs from any extant *Reevesia* and *Veeresia* species examined, and is named *Reevesia japonoxyla*. Distinct ring porosity shown in *Reevesia japonoxyla* may be regarded as a physiognomic adaptation to distinct seasonal change in the Miocene age (Suzuki and Watari, 1994). Although there are many fossil pollen records of *Reevesia* or its allies from Paleocene to Pliocene of Europe (Bertoldi et al., 1994), this is the first reliable report of fossil wood of *Reevesia*.

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