

# Fossil Wood of *Keteleerioxylon kamtschatkiense* sp. nov. (Pinaceae) from the Cretaceous of the Northwestern Kamchatka Peninsula

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**Abstract**—A new species, *Keteleerioxylon kamtschatkiense*, is described from the Cretaceous of the northwestern Kamchatka Peninsula on the basis of wood anatomy. Fossil wood showing anatomical characters of the modern genus *Keteleeria* is described from the Cretaceous of the Russian Far East for the first time.

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**Key words:** fossil wood, Pinaceae, Cretaceous, Kamchatka Peninsula.

## INTRODUCTION

Fossil woods showing the anatomy of modern *Keteleeria* have been described from the Lower Cretaceous of Franz Josef Land (*Keteleerioxylon arcticum* Shilk.; Shilkina, 1960) and the Kirovsk Region (*K. fokini* Shilk.; Shilkina, 1986), the Oligocene–lower Middle Miocene of Primorye (*K. primoryense* Blokh.; Blokhina and Klimova, 2000a, 2000b), the Lower Miocene of Japan (*Keteleeria mabetiensis* (Watari) Watari; Watari, 1941, 1956), and the Pliocene of Primorye (*Keteleeria zhilini* Blokh. et O. V. Bondarenko; Blokhina and Bondarenko, 2005).

As a rule, *Keteleeria* occurs quite rarely in fossil floras, and this is the case in the Russian Far East. Imprints of leaves, cone scales, winged seeds, and wood remains of *Keteleeria* were found from the Oligocene–early Middle Miocene deposits in the basins of the Maksimovka and Amgu rivers, Primorye Region (Rybalko et al., 1980; *Resolutions ...*, 1994; Blokhina and Klimova, 2000a, 2000b). *Keteleeria* was also found on the eastern slopes of Sikhote-Alin, in the Late Oligocene and Miocene floras of Demby Bay and the basins of the Botchi and Kema rivers; unfortunately, these records are mostly palynological (Akhmetiev, 1973, 1974, 1988; Rybalko et al., 1980). Thus, no macrofossils of *Keteleeria* were found in the Late Miocene flora of the Botchi River (Khabarovsk Region), although its pollen was recorded in the palynological spectra (Akhmetiev, 1973). Pollen grains of *Keteleeria* are also present in the palynological assemblages of the Early Eocene of the northern Verkhoyansk Region, Late Eocene of the Omolon and Kolyma rivers and the Indigirka–Zyranka

Depression (Fradkina et al., 1996), Oligocene of the Rechnoi Peninsula (southern Primorye; Mamontova, 1977b), the Oligocene–Late Miocene of the Amur–Zeya Depression (Mamontova, 1977a, 1979), and the Middle Miocene of Nagaev Bay (Chelebaeva et al., 1979). It is possible that *Keteleeria*, other conifers (*Abies*, *Picea*, *Pinus*, *Larix*, *Tsuga*, and *Thuja*), and some deciduous trees, were components of mixed forests on mountain slopes.

In the Pacific Region, imprints of cones, seed scales, and winged seeds of *Keteleeria ezoana* Tanai and seed imprints of *K. robusta* Miki were described from the Middle Miocene of Japan (Tanai, 1961). In the United States, fossil leaves of *Keteleeria* were recorded from the Miocene of Idaho and Washington, and cones and cone scales were found in the Miocene deposits of Oregon (Medlyn and Tidwell, 1979).

The modern genus *Keteleeria* Carrière includes three species: *K. fortunei* (Andr. Murray) Carrière, *K. davidiana* (Bertrand) Beissner, and *K. evelyniana* Masters. *K. fortunei* differs markedly from the other two species, and *K. evelyniana* may be considered as a subspecies of *K. davidiana* (Farjon, 1989). In contrast to the past geological epochs, *Keteleeria* today has a very limited range, occurring in central, southern, and southeastern China and northern Vietnam. *K. davidiana* also occurs in Taiwan, and *K. evelyniana* in northern Laos. *Keteleeria* is confined to humid, moderately warm (to subtropical) areas with relatively low mountains: (200)700–1000(1400) m above sea level. *K. evelyniana* occasionally grows under nearly tropical condi-

tions and reaches mountain habitats up to 2700(3000) m above sea level (Farjon, 1989; *Flora of China*, 1999).

## MATERIALS AND METHODS

The wood remains under description, *Keteleerioxylon kamtschatkiense* sp. nov., were found in 1999 on the eastern coast of Penzhina Bay (northwestern Kamchatka Peninsula) during the collaborative field trip between the Far East Geological Institute (FEGI) and the University of Tokyo (Japan).

Specimens IBSS, nos. 23/1-1 and 23/4-1 were collected along the Malyi Unnavayam River (Talovka River basin) from marine terrigenous deposits of the Kedrovka Formation dated Albian or Late Albian (Avdeiko, 1968; Paraketsov et al., 1974). The formation is composed of siltstones with horizons of calcareous concretions (with petrified wood), interbeds of sandstones and mudstones with minor amounts of coal; the base of the formation is formed by gravelstones and conglomerates. These deposits contain ammonoids *Neogastropylites*, *Grantzicerias*, *Marshallites*, *Anagaudryceras*, and *Inoceramus*; plant remains include petrified wood and solitary leaf imprints of *Nilssonia*(?) type.

Specimen IBSS, no. 23/5-1 was collected on the left bank of the lower course of the Talovka River, from the deposits of Penzhina Formation, which are dated to the Turonian–Coniacian (Paraketsov et al., 1974). The formation is composed of sandstones, conglomerates, siltstones, mudstones, and coals. The deposits contain remains of ammonoids and *Inoceramus*; fossil plants are represented exclusively by petrified wood.

The specimens of fossil wood are very dense, mineralized, dark gray to almost black, with dimensions  $7 \times 4 \times 7$  cm (IBSS, no. 23/1-1),  $2 \times 3 \times 5$  cm (IBSS, no. 23/4-1), and  $3 \times 4 \times 6$  cm (IBSS, no. 23/5-1). Growth rings are 1.5–3.9(4.2) mm wide and readily distinguishable to the naked eye. Specimen IBSS, no. 23/4-1 has a pith and twenty growth rings. The wood remains are fragments of trunks or large branches. We used conventional petrographic techniques for preparing thin sections of dense mineralized wood (Gammerman et al., 1946). In view of the heterogeneous wood anatomy, entailed by diverse functions of the tissue, the anatomical sections were made in mutually perpendicular planes (transverse, radial, and tangential), at least three thin transparent sections per wood specimen. The sections were studied microscopically and photomicrographs of anatomical structures were taken with Mikmed biological light microscopes (LOMO).

## MATERIAL

The remains of fossil wood are housed in the Institute of Biology and Soil Science, Far Eastern Division, Russian Academy of Sciences, collection IBSS, no. 23.

## SYSTEMATIC PALEOBOTANY

### Genus *Keteleerioxylon* Shilkina, 1960

*Keteleerioxylon kamtschatkiense* Blokhina et M. Afonin sp. nov.

Plate 9, figs. 1–16

**E t y m o l o g y.** From the Kamchatka Peninsula.

**H o l o t y p e.** IBSS, no. 23/1-1, fossil wood; north-western Kamchatka Peninsula, eastern coast of the Penzhina Bay, Malyi Unnavayam River (Talovka River basin); Kedrovka Formation, Albian or Upper Albian (Pl. 9, figs. 1–16).

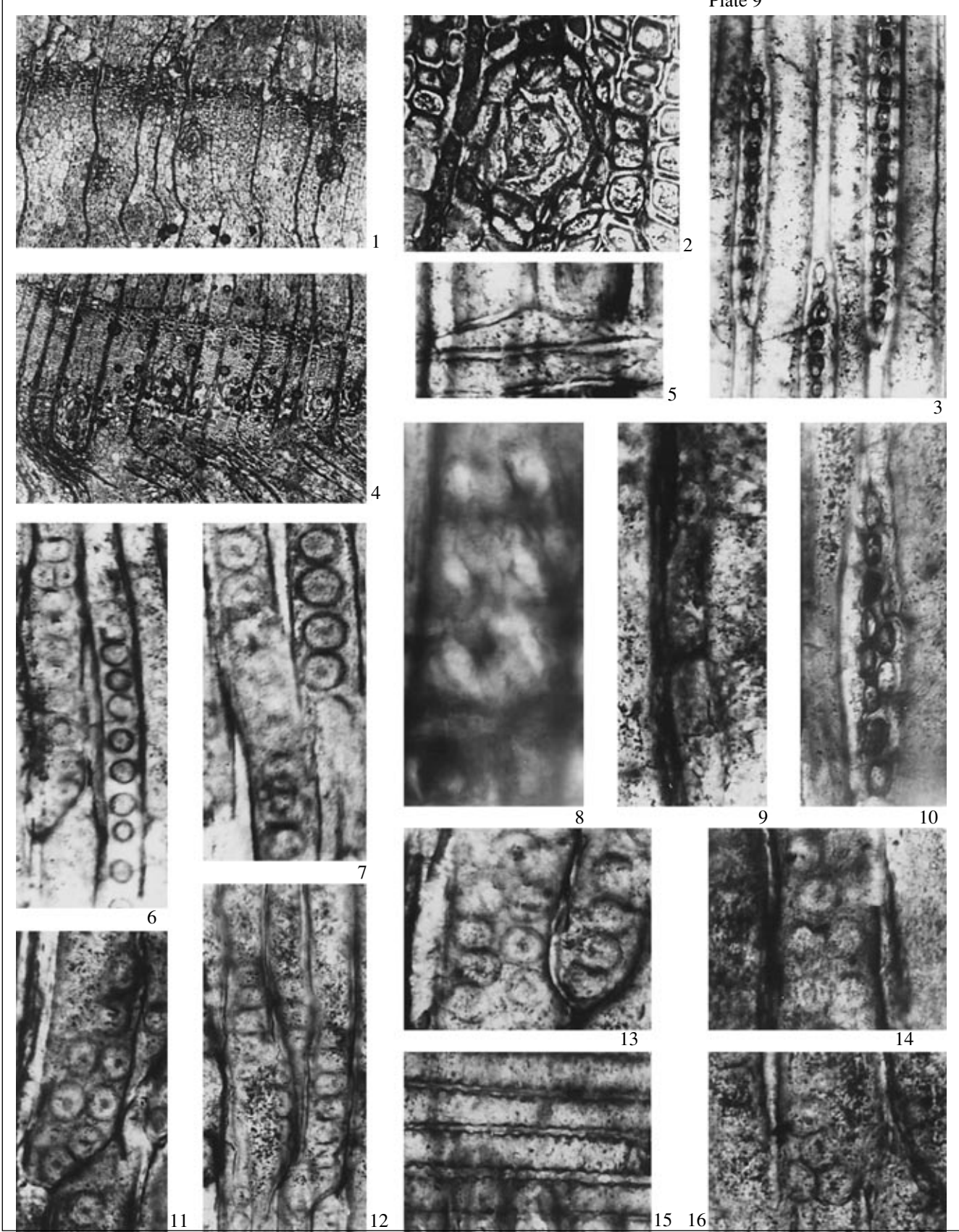
**D i a g n o s i s.** Growth rings distinct. Pits on radial walls of tracheids uniseriate, rarely with one to six layers of biseriate pits. Uniseriate pits circular or slightly elliptical, (12)18–24(27)  $\mu$ m in diameter; biseriate pits circular, 15–18  $\mu$ m in diameter. Uniseriate pits scattered or crowded along tracheid length; biseriate pits opposite or, occasionally, mixed, in the latter case alternate pits occur in stellate clusters of three pits. Pits on tangential walls of tracheids are uniseriate, 8–9  $\mu$ m in diameter. Transverse walls of axial parenchyma cells smooth. Rays 1–30(46) cells high; uniseriate, sometimes with one to three layers of biseriate cells. Rays with marginal cells resembling ray tracheids. Pits of cupressoid-taxodioid type, 1–3(5) per cross-field, 5  $\mu$ m in diameter. Resin canals vertical only, normal, surrounded by ring of six to ten thick-walled epithelial cells. Horizontal resin canals absent.

**D e s c r i p t i o n.** The wood consists of tracheids, ray and axial parenchyma, and epithelial cells of resin canals.

The growth rings are distinct, 1.8–3.9(4.2) mm wide, with readily distinct and relatively straight boundaries, although the growth rings are often crushed (Pl. 9, fig. 1). The early/late wood transition is gradual, but distinct (it is sharp in some growth rings in specimen IBSS, no. 23/4-1). As a rule, late wood occupies an insignificant portion of a growth ring; however, in specimen IBSS, no. 23/4-1 it occasionally reaches one-third of the growth ring, and in specimen IBSS, no. 23/5-1 often up to half of the growth ring. In transverse section, the early wood tracheids are large, thin-walled, with broad lumens, rectangular, and radially elongated. The late wood tracheids are thick-walled, radially compressed, and with nearly slitlike lumens near the growth ring margin. In radial section, ends of tracheids are usually pointed, but tracheids with truncate ends also occur.

Pits on the radial walls of early wood tracheids are mostly uniseriate, although one to six rows of biseriate pits occur quite often. Uniseriate pits are circular or, more rarely, elliptical, horizontally slightly compressed, with an included aperture (circular or elliptical, respectively). The circular pits are 18–25  $\mu$ m in diameter, and the elliptical pits measure (12)18  $\times$  24(27)  $\mu$ m. Pits are scattered or in a close arrangement along the length of the tracheid (Pl. 9, figs. 6, 7), more rarely, crowded (Pl. 9, figs. 12, 13). All these types may occur on the same wall of a tracheid. Biseriate pits are

Plate 9



usually located on the ends of tracheids. Pits are circular, 15–18  $\mu\text{m}$  in diameter, opposite (occupy up to six layers along the length of the tracheid) or, occasionally, in a mixed arrangement (alternate and opposite pits occur on the same tracheid wall). In mixed arrangement, alternate pits form stellate clusters of three pits each with a zigzag contact (Pl. 9, fig. 16). Opposite pits are situated close to the horizontal and vertical contact lines (Pl. 9, fig. 13) and in pairs close to the vertical contact line (Pl. 9, figs. 11, 14). Crassulae are absent between both biseriate and uniseriate pits, also it is probable that they were not found because of the poor state of preservation of the material. Pits on the radial walls of late wood tracheids are small, only uniseriate, circular or, more rarely, slightly elliptical, and are significantly remote from each other. On the tangential walls of the tracheids, pits are not numerous, uniseriate, circular, approximately 8–9  $\mu\text{m}$  in diameter. Unfortunately, due to the inadequate preservation of the material, we were unable to photograph the pits. Axial (wood) parenchyma was observed in a tangential section: it is quite scant, the transverse walls of its cells are smooth (Pl. 9, fig. 9).

Rays are numerous, 1–30(46) cells in height, uniseriate (Pl. 9, fig. 3), occasionally with one to three layers of biseriate cells (Pl. 9, fig. 10). The horizontal and tangential walls of the rays are pitted, but the horizontal walls are thickened and, in places, solid and emarginate for considerable distances (Pl. 9, fig. 15). Median ray cells are elliptical and elongated along the ray, or, more rarely, rounded; marginal cells are rounded-triangular and approximately of the same sizes as the median cells. True ray tracheids are absent, but, in places, marginal cells resembling ray tracheids were observed (Pl. 9, fig. 5).

There are 1–3(5) pits (5  $\mu\text{m}$  in diameter) of a supposed cupressoid-taxodioid type per cross-field. The pits are arranged in a single horizontal row in the case of two or three pits per cross-field and in a diffuse arrangement in the case of four or five pits (Pl. 9, fig. 8).

Only vertical resin canals are observed (Pl. 9, figs. 1, 2). Normal resin canals are solitary or, occasionally, form pairs; specimen IBSS, no. 23/4-1 contains resin canals in the second and subsequent growth ring. Canals are circular and oval, radially elongated, 100–200  $\mu\text{m}$  in diameter (50–100  $\mu\text{m}$  in specimen IBSS, no. 23/5-1), lined with six to ten thick-walled epithelial cells, and

situated in the early wood (in specimen IBSS, no. 23/4-1, resin canals also occur at the boundaries between growth rings and in the late wood). Some growth rings contain traumatic vertical resin canals arranged in long tangential rows in the late wood (Pl. 9, fig. 4).

**Comparison.** The fossil wood under study differs from the wood of all modern species of *Keteleeria* in having significantly larger pits on the radial walls of tracheids, higher rays, and in lacking crassulae. In addition, it differs from *K. davidiana* and *K. fortunei* in having fewer pits per cross-field, and from *K. evelyniana* and *K. fortunei* in having a greater number of epithelial cells lining resin canals. In contrast to the wood of *K. davidiana*, biseriate regions in uniseriate rays are shorter in the fossil wood, pits on cross-fields are smaller, and there are no triseriate or tetraseriate pits on tracheid walls. Unlike *K. evelyniana*, pits on the tangential walls of tracheids are larger, and the number of pits per cross-field is greater; unlike *K. fortunei*, pits on the tangential walls of tracheids are smaller (Table 1).

The wood under description is different from *Keteleerioxylon fokinii* from the lower Lower Cretaceous of the Kirovsk Region (Shilkina, 1986) in having a greater number of pits per cross-field and in the presence of normal vertical resin canals in both late and early wood (Table 2).

*K. kamtschatkiense* differs from *K. arcticum* from the Lower Cretaceous of Franz Josef Land (Shilkina, 1960) in the much higher rays without triseriate layers, the presence of marginal ray cells of the ray tracheid type, and in the absence of crassulae (Table 2).

It is worth noting that the anatomical descriptions of the mentioned Cretaceous woods do not provide information about the size of pits on tracheid walls and cross-fields, the number of epithelial cells lining resin canals, the presence of marginal ray cells of the ray tracheid type in *K. fokinii*, and about the length of biseriate regions in uniseriate rays in *K. arcticum*. Thus, we are not able to accomplish a more detailed comparison.

The wood studied is different from *K. primoryense* from the Oligocene–Miocene of Primorye (Blokina and Klimova, 2000a, 2000b) in having larger pits on the radial walls of tracheids, slightly higher uniseriate rays with much shorter biseriate regions, and in lacking crassulae. In addition, *K. primoryense* is characterized by exclusively opposite biseriate pits (Table 2).

#### Explanation of Plate 9

**Figs. 1–16.** *Keteleerioxylon kamtschatkiense* sp. nov. holotype IBSS, no. 23/1-1: (1) growth ring, transverse section,  $\times 35$ ; (2) vertical resin canal, transverse section,  $\times 206$ ; (3) uniseriate rays, tangential section,  $\times 206$ ; (4) tangential row of traumatic resin canals, transverse section,  $\times 35$ ; (5) marginal ray cell of the ray tracheid type, radial section,  $\times 330$ ; (6, 7) uniseriate pits on tracheid walls in diffuse and close arrangement, radial section; (6)  $\times 206$ ; (7)  $\times 330$ ; (8) pits on cross-fields, radial section,  $\times 825$ ; (9) axial parenchyma, tangential section,  $\times 330$ ; (10) uniseriate ray with a biseriate region, tangential section,  $\times 330$ ; (11, 14) biseriate pits in opposite arrangement, radial section,  $\times 330$ ; (12) uniseriate pits on tracheid walls in close arrangement, radial section,  $\times 206$ ; (13) pits on tracheid walls, uniseriate pits are in a close arrangement and biseriate pits in an opposite arrangement, radial section,  $\times 330$ ; (15) horizontal walls of rays, radial section,  $\times 330$ ; (16) pits on tracheid walls forming a stellate group, radial section,  $\times 330$ ; northwestern Kamchatka Peninsula, eastern coast of the Penzhina Bay, Malyi Unnavayam River (Talovka River basin); Kedrovka Formation, Albian or Upper Albian.

**Table 1.** Comparison of anatomical characters of fossil wood of *Keteleerioxylon kamtschatkiense* Blokhina et M. Afonin sp. nov. and woods of modern *Keteleeria* species

Anatomical characters	<i>Keteleerioxylon kamtschatkiense</i> Blokh. et M. Afonin sp. nov.	<i>Keteleeria davidiana</i> (Bertr.) Beissner (Bailey, 1933; Budkevich, 1961; Greguss, 1963; Chavchavadze, 1975)	<i>Keteleeria evelyniana</i> Masters (Budkevich, 1961)	<i>Keteleeria fortunei</i> (Andr. Murray) Carr. (Yatsenko- Khmelevskii, 1954; Budkevich, 1961; Greguss, 1963)
Pits on radial walls of tracheids:				
uniseriate	++	+	+	+
biseriate	+	+	+	+
triseriate	-	+–	-	-
tetraseriate	-	+–	-	-
diameter of pits, µm	(12)18–24(27)	(10)12–15(16)	15–21	12–15(16)
Diameter of pits on tangential walls of tracheids, µm	8–9	6–8(9)	6–7	6–8(10)
Crassulae	-	+	+	?
Uniseriate rays:				
height (in cells)	1–30(46)	1–30(34)	1–30	1–40
number of biseriate layers	1–3	1–8	+–	+
number of triseriate layers	-	-	-	-
marginal ray cells of the ray tracheid type	+	+	+	+
Transverse walls of axial parenchyma:				
smooth	+	?	?	?
knotty	-	+	?	+
Number of epithelial cells in vertical resin canals	6–10	6–7(8–11)	6	6–8
Pitting on cross-fields:				
number of pits	1–3(5)	1–3(6)	1–4	1–4(6)
diameter of pits, µm	5	(4)5–8(12)	?	4–6
type of pitting:				
cupressoid	+	-	-	-
taxodioid	+	++	+	+
piceoid	-	+	?	?
pinoid	-	+	-	-

Note: a character is present (+), absent (-), prevailing (++), uncommon (+–), no data (?).

In distinction to *Keteleeria mabetiensis* from the Lower Miocene of Japan (Watari, 1941, 1956), the wood under description has higher rays and is devoid of crassulae. Furthermore, the anatomical description of the Japanese species lacks the information about the size of pits on tracheid walls and cross-fields, the number of epithelial cells lining resin canals, and the position of resin canals within the growth ring (Table 2).

The Cretaceous wood under study differs from *K. zhilini* from the Pliocene of Primorye (Blokhina and Bondarenko, 2005) in having larger pits on tracheid walls and small pits on cross-fields, high rays, numer-

ous epithelial cells lining resin canals, and only smooth transverse walls of axial parenchyma cells (Table 2).

**Remarks.** The combination of such characteristics of wood anatomy as the presence of vertical (and only vertical) normal resin canals with thick-walled epithelial cells, axial parenchyma, and large marginal cells of rays resembling ray tracheids and the absence of true ray tracheids is characteristic of the modern genus *Keteleeria*.

The presence of vertical (and only vertical) normal resin canals having thick-walled epithelial cells and the total absence of horizontal resin canals is a unique char-

**Table 2.** Comparison of anatomical characters of fossil wood of *Keteleerioxylon kamtschatkiense* Blokhina et M. Afonin sp. nov. and woods of closely related fossil species

Anatomical characters	<i>Keteleerioxylon kamtschatkiense</i> Blokh. et M. Afonin sp. nov.	<i>Keteleerioxylon fokinii</i> Shilk. (Shilkina, 1986)	<i>Keteleerioxylon arcticum</i> Shilk. (Shilkina, 1960)	<i>Protopiceoxylon amurense</i> Du, 1982	<i>Keteleerioxylon primoryense</i> Blokh. (Blokhina and Klimova, 2000; Blokhina, Klimova, 2000)	<i>Keteleeria mabetsensis</i> (Watari, 1941, 1956)	<i>Keteleeria zhilini</i> Blokh. et O.V. Bondarenko (Blokhina and Bondarenko, 2005)
Pits on radial walls of tracheids:							
uniseriate	++	+	+	+	+	+	+
biseriate	+	+	+	+	+	+	+–
triseriate	–	–	–	–	–	+–	–
tetraseriate	–	–	–	–	–	–	–
diameter of pits, µm	(12)18–24(27)	?	?	?	12–18	?	(10)12–18(24)
Diameter of pits on tangential walls of tracheids, µm	8–9	–	+–	?	+–	+	4.5–6
Crassulae	–	–	+	+	+	+	+–
Uniseriate rays:							
height (in cells)	1–30(46)	1–30	1–24	1–45	1–40	1–36	1–25
number of biseriate layers	1–3	+–	+–	+	1–4(10)	1–4	1–3(4)
number of triseriate layers	–	–	1	–	–	–	–
marginal ray cells of the ray tracheid type	+	?	–	?	+	+	+
Transverse walls of axial parenchyma:							
smooth	+	+	+	–	+	?	+
knotty (number of knots)	–	–	–	–	–	+	2–3
Number of epithelial cells in vertical resin canals	6–10	?	?	10	(5)6–8(10)	?	(5)6–7(8)
Pitting on cross-fields:							
number of pits	1–3(5)	1–2(3)	1–3(4)	?	1–3(5)	1–4(5)	1–4(5)
diameter of pits, µm	5	?	?	?	6–7.5	?	6–9
type of pitting:							
cupressoid	+	+	–	–	–	–	–
taxodioid	+	–	+	+	+	+	+
piceoid	–	–	–	–	–	+–	–
pinoid-simple	–	–	–	+	–	–	–

Note: a character is present (+), absent (–), prevailing (++) , uncommon (+–), no data (?).

acter of the wood of *Keteleeria*, unknown in any other modern conifer (Yatsenko-Khmelevskii, 1954; Shilkina, 1960; Budkevich, 1961; Chavchavadze, 1979; Lin and Liang, 2000). However, resin canals do not necessarily occur in each of the growth rings. They may be lacking or limited to traumatic resin canals near the pith (Kanehira, 1921; Bailey, 1933). The first resin canals appear in the third to sixth growth rings. Their epithelial cells soon become lignified and are hardly distinguishable from nearby tracheids and parenchyma cells, which do not always form a continuous lining of the resin canal, and the numbers of epithelial and parenchyma cells greatly vary even in mature wood (Chavchavadze, 1975, 1979). In addition to normal resin canals, traumatic vertical resin canals also occur in the wood of *Keteleeria*. Chavchavadze (1979) believed that the considerable rarity of resin canals in the wood of *Keteleeria* and their relatively unusual morphology apparently led some scientists to conclude that resin canals were absent in the wood of *Keteleeria* or that only traumatic resin canals occurred. Consequently, the considerable rarity of normal vertical resin canals hampers the determination of fossil woods having the anatomical characteristics of *Keteleeria*.

Solely vertical resin canals may also occur in the wood of some members of the Taxodiaceae and Cupressaceae, and in *Abies* Mill. and *Tsuga* Carr. (Pinaceae). However, these canals are traumatic: they often form tangentially orientated rows of varying length usually along the growth ring in late wood. In these rows, the canals are usually arranged in groups of two to four (or more), i.e., there is no ray or layer of tracheids between the canals. The canals are usually short in vertical direction. In transverse section, they are relatively large, with irregular outlines, without parenchyma cells, and without typical epithelial cells that form a continuous lining around a resin canal.

One more characteristic feature of the wood of *Keteleeria* is the absence of true ray tracheids. Budkevich (1961) called attention to marginal ray cells that occur in the wood of *Keteleeria*, which are larger than the median, have a slightly greater number of pits on the radial walls and undulate slightly convex external walls. Greguss (1955) considered such cells as a transitional form toward true ray tracheids. Such marginal cells are occasionally observed in the wood of *Abies* and *Pseudolarix* Gord. According to Budkevich (1961), they reach their maximum development in the wood of *Pseudolarix*. However, normal resin canals are absent in the wood of both genera (in *Abies*, only traumatic vertical resin canals occur).

A characteristic feature of the wood anatomy of *Keteleeria* is also the presence of axial parenchyma, although, according to Yatsenko-Khmelevskii (1954), Budkevich (1961), and Chavchavadze (1975, 1979), it is relatively scanty.

In terms of wood anatomy, individual species of *Keteleeria* are difficult to differentiate. However, their

wood anatomy has not been adequately studied, and the published descriptions are very incomplete. In accordance with the paleoxylotomical practice of designation of fossil wood remains, Shilkina (1960) proposed the generic name *Keteleerioxylon* for fossil woods with the anatomical characteristics of the modern genus *Keteleeria*. The studied wood should be assigned to this genus. Nevertheless, since its anatomical characteristics do not fully coincide with any published species of this genus, we describe it as a new species of the form genus *Keteleerioxylon*, *K. kamtschatkiense* sp. nov.

Shilkina and Yatsenko-Khmelevskii (1980) believed that a mixed type of pitting on the radial walls of tracheids is very typical of Mesozoic fossil woods: a combination of araucarioid and abietoid pits. Pits in Valanginian *K. fokinii* are biseriate araucarioid and abietoid in a close arrangement. In *K. arcticum* from slightly younger Lower Cretaceous deposits, biseriate pits are only abietoid and in a close arrangement; and *K. kamtschatkiense* (Albian and Upper Cretaceous) is characterized by abietoid pits in a close arrangement. Therefore, *K. kamtschatkiense* is possibly a more evolutionary advanced species than *K. fokinii* and *K. arcticum* in the arrangement of pits on the radial walls of tracheids. Triseriate pits in not completely opposite arrangement and groups of four pits (vestiges of alternate arrangement) are occasionally observed in the modern species *Keteleeria davidiana* (Bailey, 1933; Budkevich, 1961).

In the course of evolution the number of pits on cross-fields increased from three or four in Early Cretaceous *Keteleerioxylon fokinii* and *K. arcticum* to five in younger *K. kamtschatkiense*, *K. primoryense*, *Keteleeria mabetiensis*, and *K. zhilinii*, and to six in the modern *Keteleeria* species.

Other fossil woods with vertical (and only vertical) normal resin canals are also known. They were described from the Upper Jurassic–Lower Cretaceous deposits as *Pinoxylon* Knowlton emend. Read or *Protopiceoxylon* Gothan (cited after Watari, 1941; Medlyn and Tidwell, 1979): *P. edwardsi* Stopes, *P. johnseni* (Schroeter) Edwards, *P. arcticum* Seward, *P. dacotense* (Knowlton) Vogellehner, *P. resiniferous* Medlyn et Tidwell, and *P. canadense* Medlyn et Tidwell (Medlyn and Tidwell, 1979). All these species, except for *P. resiniferous*, have axial parenchyma. Marginal ray cells of the ray tracheid type occur in *P. arcticum* and *P. resiniferous*; ray tracheids are recorded in *P. dacotense*. Abundant biseriate and triseriate abietoid pits and biseriate araucarioid pits in a close arrangement are present on tracheid walls of *P. dacotense*; and only araucarioid pits in *P. johnseni* and *P. canadense* (Medlyn and Tidwell, 1979). The above-listed fossil woods belong to the group of ancient conifers Protopinaceae, some members of which are unequivocally related to modern Pinaceae (Watari, 1941; Yatsenko-Khmelevskii, 1954; Medlyn and Tidwell, 1979). There is a distinct possibility that some of them belong to remote ancestors of

*Keteleeria*. The fossil wood *Protopiceoxylon amurense* Du from the Cretaceous and Danian deposits of the Heilongjiang Province, China, is an example (Du, 1982; Wang et al., 1997).

**Material.** IBSS, nos. 23/1-1 (holotype), 23/4-1, and 23/5-1; three specimens in total.

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