DICOTYLEDONOUS FOSSIL WOOD FLORA AND
EARLY EVOLUTION OF WOOD CHARACTERS IN THE CRETACEOUS
OF HOKKAIDO, JAPAN

by

Ken'ichi Takahashi[1] & Mitsuo Suzuki[2]

SUMMARY

Fossil woods are abundant in the Cretaceous Yezo Group in Hokkaido, Japan, in strata of Albian to Santonian ages. From 144 dicotyledonous samples, fourteen species representing 10 genera were identified: *Castanoradix cretacea* gen. et sp. nov., *C. biseriata* gen. et sp. nov., *Frutecoxylon yubariense* gen. et sp. nov., *Hamamelidoxylon obiraense* sp. nov., *Icacinoxylon kokubunii* sp. nov., *I. nishidae* sp. nov., *Magnoliaceoxylon hokkaidoense* sp. nov., *Nishidaxylon jezoense* gen. et sp. nov., *Paraphyllanthoxylon cenomaniana* sp. nov., *P. obiraense* sp. nov., *Plataninium jezoensis* sp. nov., *P. ogasawarae* sp. nov., *Sabiaceoxylon jezoense* gen. et sp. nov. and *Ulminium kokubunii* sp. nov. All 14 species are new and four of the 10 genera are new. Five genera (*Icacinoxylon, Magnoliaceoxylon, Paraphyllanthoxylon, Plataninium* and *Ulminium*) already are known from the Cretaceous and Tertiary, one (*Hamamelidoxylon*) previously is known only from the Tertiary. The species distribution by age is: Albian: one species; Cenomanian: four species in four genera; Turonian: ten species in eight genera; Coniacian: six species in five genera; Santonian: eight species in seven genera. The two specimens of *Icacinoxylon kokubunii* from the Albian are the oldest records of dicotyledonous woods in Japan.

Key words: Fossil wood, dicotyledons, Cretaceous, wood evolution, paleobotany, Hokkaido, Japan.

INTRODUCTION

Presence of vessel elements is one of the characters of dicotyledons that differentiate them from most gymnosperms. Bailey and his collaborators studied wood evolution and concluded that vessel elements evolved from primitive long and narrow elements with scalariform perforation plates to short and wide ones with simple perforation plates, while many other wood anatomical characters evolved in concert (Bailey & Tupper 1918; Bailey 1954). Many wood anatomists and plant phylogenists accept the general Baileyan trends of wood evolution (Carlquist 1988; Wheeler & Baas 1991, 1993). Since the trend indicates wood structural evolution from gymnosperms to dicotyledons, it

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would be expected that the earliest woody dicotyledons would have the most primitive vessel elements with scalariform perforation plates, and wood with simple perforation plates would appear later. Furthermore, based on the trend, tracheids of vesselless dicotyledons such as occur in *Tetracentron*, *Trochodendron*, Winteraceae, have been regarded as the most primitive conducting tissues among dicotyledons. However, some morphological and molecular phylogenetic studies of vascular plants reveal that those vesselless dicotyledons are not situated at the most primitive position among dicotyledons (Young 1981; Hufford & Crane 1989; Chase et al. 1993). Suzuki et al. (1991) reexamined the fossil woods described as vesselless dicotyledons from the Jurassic, Cretaceous, and Tertiary and concluded the oldest wood of vesselless dicotyledon is *Tetracentronites* described by Page (1970) from the Maastrichtian (the youngest stage of the Cretaceous) of California. Later, Poole and Francis (2000) described the vesselless dicotyledonous wood *Winteroxylon jamesrossi* from the Santonian–Campanian (Upper Cretaceous) of Antarctica. The known vesselless dicotyledon fossil woods are younger than vessel-bearing fossil woods. The latest molecular phylogenetic analyses reveals that one of the vesselless dicotyledons, *Amborella*, is the sister group of all other angiosperms, while other vesselless dicotyledons are intermingled among vessel-bearing dicotyledons (Qiu et al. 1999; Zanis et al. 2002). Therefore, it is still obscure whether vessels were evolved from tracheids of vesselless dicotyledons or the first dicotyledons were already provided with vessels and the vesselless dicotyledons were a result of reduction.

The lowermost horizon that undoubtedly bears angiosperm fossils is the Lower Cretaceous (e. g., Hickey & Doyle 1977). Serlin (1982) reported a dicotyledonous wood associated with fern fronds and coniferous branches from the Albian of Texas. Thayn et al. (1983, 1985) reported two dicotyledonous woods from the Lower Cretaceous (probably Albian) of Utah. These are the oldest records of dicotyledonous wood.
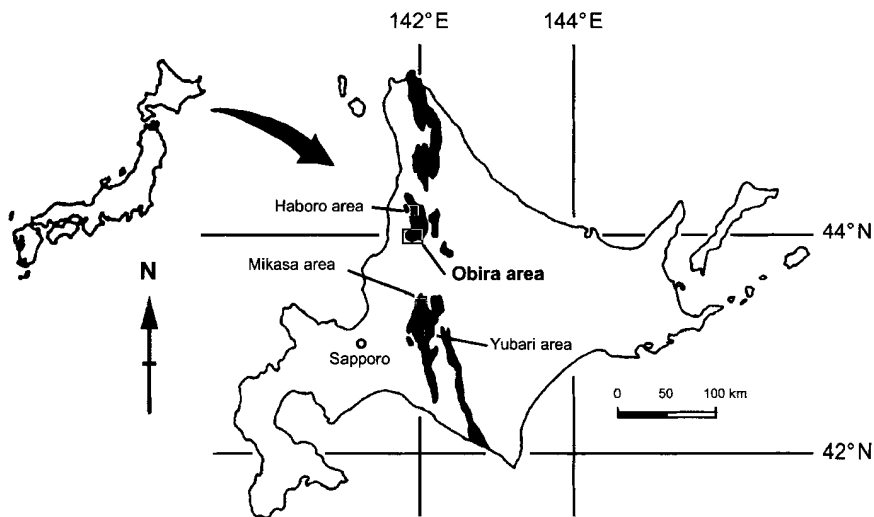

Fig. 1. Map showing the distribution of the Cretaceous Yezo Group and locations of the sampling areas.

In Japan, although Lower Cretaceous sediments bearing many fossil plants are widespread, no angiosperms have ever been found in those sediments (e. g., Nishida & Nishida 1983; Kimura 1987). In Hokkaido, sediments from the early Cretaceous (Aptian) to the end of the Cretaceous (Maastrichtian) are widely distributed (Fig. 1) and bear many fossils, including wood. The first study of angiosperm fossils from the Cretaceous in Japan was by Stopes and Fujii in 1910 (Nishida 1991). They described *Jugloxylon hamanoanum, Populocaulis jezoensis, Fagoxylon hokkaidense* and *Sabiocaulis sakuraii*, but they did not give details on the specific geological horizon in which they were found. Subsequently, Shimakura (1937) described *Dryoxylon* cfr. *jezoense* (= *Populocaulis jezoensis* Stopes & Fujii), *Aptiana?* sp. and *Casuaroxylon japonicum*, also from the Upper Cretaceous of Hokkaido. Sediments of the Cretaceous Yezo Group, ranging from the Aptian to the Santonian, bear many fossil woods. The ages of those woods are established by accompanying marine fossils. Therefore, these fossil woods are invaluable resources for clarifying wood anatomy of early dicotyledons and the evolution of wood characters.

MATERIALS AND METHODS

The Cretaceous Yezo Group (Fig. 1) is widely distributed in Hokkaido, the northernmost part of Japan, and is composed of marine sediments from shallow to moderate depth in which fossil mollusks and fossil plants are abundant. Based on many studies of ammonites and *Inoceramus* (Bivalvia), the biostratigraphy has been established in detail (e. g., Matsumoto et al. 1976; Matsumoto 1977). Deposits of the Yezo Group are dated as Aptian to Santonian. The Yezo Group is lithostratigraphically divided into lower, middle and upper strata. Fossil woods described in this paper were collected from the middle and upper strata of the Yezo Group. Most of the woods were collected in the Obira (Tappu) area (Fig. 1, roughly 44° N 142° E) where beautifully preserved fossils were especially abundant. In the Obira area, the middle part of the Yezo Group (from the Albian to Turonian) is subdivided into 15 members designated as Ma (= middle-a) to Mo (= middle-o) in an alphabetical sequence; the upper part (from the Turonian to Santonian) is subdivided into 12 members designated as Ua (= upper-a) to Ul (= upper-l) (Tanaka 1963; Maeda 1987). All the members yield fossil woods, but dicotyledons are absent or very rare in the lowermost members (Fig. 2).
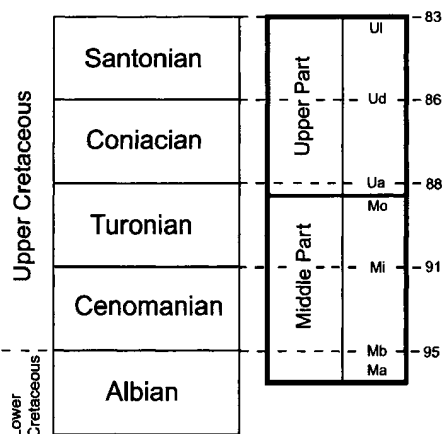
Fig. 2. Geological age of the Cretaceous Yezo Group in the Obira area. Numerals indicate million years BP.

Table 1. Geological occurrence of identified species with their anatomical characters.

Species	growth ring	vessel perfor.	interv. pitting	axial par.	ray width	type	Alb	Cen	Tur	Con	San
									stages		
Icacinoxylon kokubunii	–	sca	op-sca	d-a	wide	hetero	+	+	+	+	+
Plataninium jezoensis	(+)	sca	op	d-a	wide	homo		+	+		
Hamamelidoxylon obiraense	+	sca	op-sca	d	narrow	hetero		+	+	+	+
Paraphyllanthoxylon cenomaniana	–	smp	alt	s	narrow	hetero		+	+	+	
Icacinoxylon nishidae	–	sca	op	d	wide	hetero			+	+	+
Magnoliaceoxylon hokkaidoense	–	sca	op-sca	d	narrow	hetero			+	+	+
Frutecoxylon yubariense	–	sca	op-sca	d	wide	homo			+		
Ulminium kokubunii	+	sca & smp	alt	v	narrow	homo			+	+	+
Castanoradix cretacea	–	smp	alt	s	uniseriate	hetero			+		
Castanoradix biseriata	–	smp	alt	v	narrow	homo			+		
Sabiaceoxylon jezoense	–	sca & smp	alt	?	narrow	hetero				+	
Plataninium ogasawarae	(+)	sca	op	d	wide	homo					+
Nishidaxylon jezoense	–	sca	–	d-a	wide	homo					+
Paraphyllanthoxylon obiraense	–	smp	alt	s	narrow	hetero					+

vessel perfor. = vessel perforation plate; sca = scalariform, smp = simple.

interv. pitting = intervessel pitting; op = opposite, sca = scalariform, alt = alternate.

axial par. = axial parenchyma; d = diffuse, d-a = diffuse-in-aggregates, s = scanty paratracheal, v = vasicentric.

ray: hetero = heterocellular, homo = homocellular.

stages: Alb = Albian, Cen = Cenomanian, Tur = Turonian, Con = Coniacian, San = Santonian

More than 400 specimens from the Obira area and other areas of Hokkaido were collected by us or were donated by several scientists and many amateur collectors. Most specimens are calcareous, but some are silicified. Microscopic preparations were made by the peel method (Joy et al. 1956) using 2% hydrochloric acid solution for the calcareous ones, and 23% hydrofluoric acid solution for the silicified ones. Ground thin sections were also made from some specimens. All the specimens and the preparations are kept in the Botanical Garden, Faculty of Science, Tohoku University (TUSw).

RESULTS

Among more than 400 fossil wood specimens, 144 dicotyledonous woods were found. Their ages are Albian, Cenomanian, Turonian, Coniacian and Santonian. Fourteen species representing ten genera are recognized (Table 1). Figure 3 gives a key for their identification.

A Perforation plates exclusively scalariform
  B Maximum ray width more than 10 cells
    C Rays composed of procumbent and upright cells .... *Icacinoxylon*
    C Rays composed of procumbent cells only
      D Vessels solitary and in multiples .... *Plataninium*
      D Vessels exclusively solitary .... *Nishidaxylon*
  B Maximum ray width less than 10 cells
    C' Rays composed of procumbent and upright cells
      D' Rays usually narrow (less than 3 cells) and high .... *Hamamelidoxylon*
      D' Rays a little wide (up to 4 cells) and low .... *Magnoliaceoxylon*
    C' Rays composed of upright cells only .... *Frutecoxylon*

A Perforation plates simple and scalariform
  B' Axial parenchyma abundant vasicentric .... *Ulminium*
  B' Axial parenchyma scarce .... *Sabiaceoxylon*

A Perforation plates exclusively simple
  B" Rays moderately wide .... *Paraphyllanthoxylon*
  B" Rays exclusively or mostly uniseriate .... *Castanoradix*

Fig. 3. Key to 10 genera of Cretaceous dicotyledonous wood from Hokkaido.

TAXONOMICAL DESCRIPTIONS

CASTANORADIX Ken. Takahashi & M. Suzuki, gen. nov. (Fagaceae?)

Generic diagnosis:
  Wood diffuse-porous.
  Vessels few; predominantly solitary and sometimes in radial pairs; round in outline; medium to large in diameter; perforation plates exclusively simple; intervessel pits polygonal, crowded alternate; vessel-ray pits large, simple, variously shaped.

Vasicentric tracheids abundant.

Rays exclusively uniseriate; heterocellular.

Derivation of generic name: Similarity to root wood of *Castanea* (Fagaceae).

Type species: *Castanoradix cretacea* Ken. Takahashi & M. Suzuki.

1. ***Castanoradix cretacea*** Ken. Takahashi & M. Suzuki, gen. et sp. nov. (Fig. 4–10)

Description:

Growth rings absent; primary xylem at centre of wood; no pith tissue.

Wood diffuse-porous.

Vessels few, 12–18 (mean 15) per square mm; solitary (71%) and in radial or tangential pairs, and rarely in radial multiples of 3; round in outline; 80–240 (mean 168) × 85–265 (mean 189) μm in tangential × radial diameter; 70–750 (mean 569) μm in vessel element length; perforation plates exclusively simple; intervessel pits polygonal (7 μm in diameter), crowded alternate; vessel-ray pits large (12 μm in diameter), simple, variously shaped.

Imperforate tracheary elements fibers with no pits and vasicentric tracheids; vasicentric tracheids abundant.

Axial parenchyma scanty, paratracheal, no crystalliferous elements observed.

Rays almost uniseriate; 240 μm–2.4 mm high; heterocellular; procumbent cells 50 × 15 μm in radial length × height; upright cells 30 × 45 μm in radial length × height; no crystalliferous elements observed.

Derivation of species name: Wood from the Cretaceous.

Holotype: OG 94021 (2.5 cm in diameter) is assumed to be root wood due to the absence of pith.

Locality: 66-rinpan-sawa, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Member Ml–Mo, Middle part of the Yezo Group; Turonian.

Collector: Yutaka Ogasawara.

This species is based on a single specimen.

2. ***Castanoradix biseriata*** Ken. Takahashi & M. Suzuki, gen. et sp. nov. (Fig. 11–14)

Description:

Growth rings absent.

Wood diffuse-porous.

Vessels moderately few, 17–24 (mean 20) per square mm; mostly solitary (93%) and rarely in radial pairs; round to oval in cross section; 40–85 (mean 68) × 70–130 (mean104) μm in tangential × radial diameter; 390–660 (mean 495) μm in vessel element length; perforation plates exclusively simple; intervessel pits alternate, round to elliptical (5 μm in diameter); vessel-ray pits simple, variously shaped (10 μm in diameter).

Imperforate tracheary elements fiber-tracheids with small bordered pits.

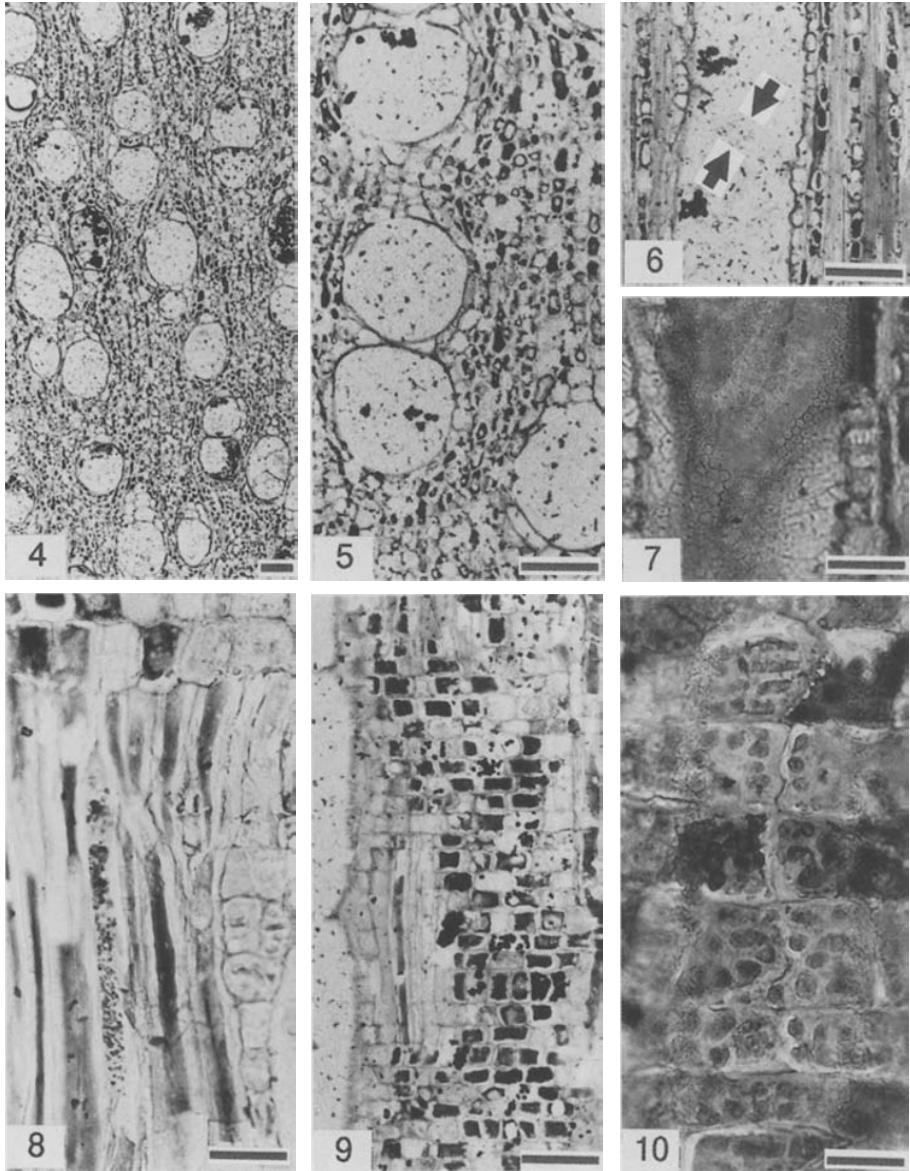Axial parenchyma vasicentric, no crystalliferous elements observed.

Fig. 4–10. *Castanoradix cretacea* gen. et sp. nov. (TUSw-OG 94021, holotype) – 4: TS, diffuse-porous wood. – 5: TS, solitary vessels. – 6: TLS, uniseriate rays and vessel with simple perforation plate (between arrows). – 7: TLS, minute alternate intervessel pits. – 8: RLS, vasicentric tracheids. – 9: RLS, heterocellular ray. – 10: RLS, vessel-ray pits of variable size and shape. — Scale bars = 100 μm in Fig. 4, 5, 6 & 9; 50 μm in Fig. 7 & 8; 25 μm in Fig. 10.
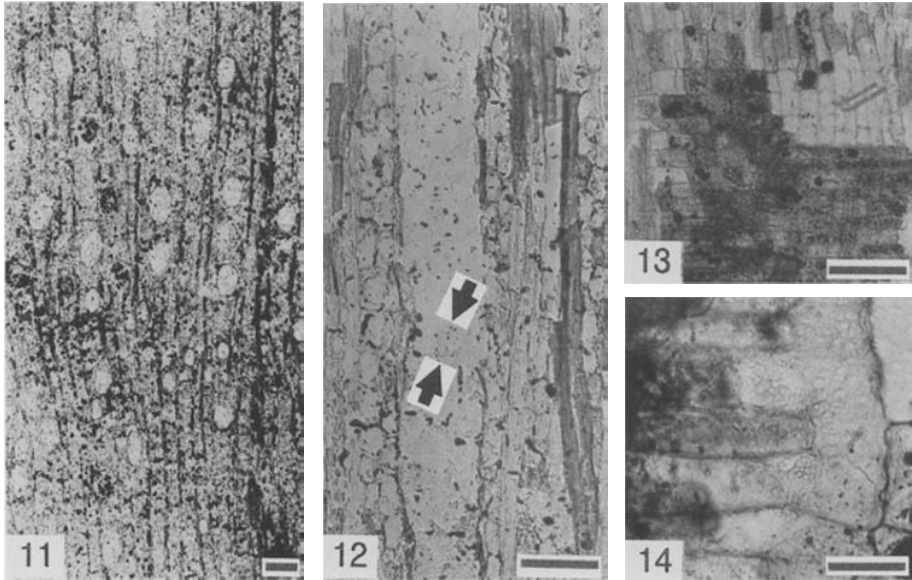
Fig. 11–14. *Castanoradix biseriata* gen. et sp. nov. (TUSw-SZ 95011, holotype) – 11: TS, diffuse-porous wood. – 12: TLS, biseriate rays and vessel with simple perforation plates (between arrows). – 13: RLS, heterocellular ray. – 14: RLS, vessel-ray pits. — Scale bars = 100 μm in Fig. 11 & 13; 50 μm in Fig. 12; 25 μm in Fig. 14.

Rays predominantly uniseriate, and sometimes biseriate (35 μm wide); 240 μm–1.3 mm high; nearly homocellular, occasionally with 1 to 2 marginal rows of upright or square cells; procumbent cells 40 × 25 μm in radial length × height; upright cells 30 × 50 μm in radial length × height; no crystalliferous elements observed.

Derivation of species name: Wood with biseriate rays.

Holotype: SZ 95011 (2 × 3.5 cm in transverse diameter) is a piece of a wood of which the original diameter is estimated to be 4 cm.

Locality: San-no-sawa, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Member Ml–Mo, Middle part of the Yezo Group; Turonian.

Collector: Ken'ichi Saiki et al.

Other specimens: Turonian: IW 95021, TK 95315; age unknown: YK 96011.

Affinity — The specimens of *Castanoradix* are similar in anatomy to root wood of *Castanea*, except that vessels of *Castanoradix* are more frequently in multiples than those of *Castanea*, and intervessel pits of *Castanoradix* are not the same as those of *Castanea*. Radial multiples are not a feature of the Fagaceae, so *Castanoradix* cannot be assigned with certainty to the Fagaceae.

We recognized two types of *Castanoradix, C. cretacea* has wider vessels and narrower (uniseriate only) rays than *C. biseriata*. The former is undoubtedly root wood as it has no pith. Because stem wood of *Castanea* is ring-porous, an interesting question

is if the stem of *Castanoradix* was ring-porous. *Castanoradix biseriata* is possibly a stem of *C. cretacea*. However, all specimens of *C. biseriata* are fragmented so it is impossible to confirm whether or not they have pith.

Stopes and Fujii (1910) described *Jugloxylon hamanoanum* from the Upper Cretaceous of Hokkaido. The species is characterized by 1) round vessels of 60–120 µm in diameter which are solitary or in radial multiples of 2–4, 2) sparse and evenly distributed vessels, and 3) rays that are mostly uniseriate or sometimes biseriate. The two species of *Castanoradix* are similar to *Jugloxylon hamanoanum,* but the vessel diameter of *C. cretacea* is much larger, whereas that of *C. biseriata* is nearly identical to that of *J. hamanoanum.* It is therefore possible that *C. biseriata* is of the same wood type as *J. hamanoanum.* However, Stopes and Fujii did not describe many anatomical characters, such as perforation plates or ray types, so further comparison is difficult.

There are two Cretaceous woods that resemble Fagaceae. Wheeler et al. (1987) described *Paraquercinium cretaceum* resembling *Quercus* and *Lithocarpus* from the Maastrichtian of southern Illinois. Unfortunately, because of the lack of some characters (e. g., vessel-ray pits), it could not be confirmed that *Paraquercinium* belonged to the Fagaceae. Suzuki and Ohba (1991) described *Quercus cretaceoxylon* from the upper stratum of the Yezo Group (Coniacian to Santonian) of Hokkaido. This species is undoubtedly in the Fagaceae, but its geological age is questionable, because the holotype specimen is a pebble found on a river floor, so there is a possibility that the specimen is Tertiary. No in situ Cretaceous woods were found nearby.

FRUTECOXYLON Ken. Takahashi & M. Suzuki, gen. nov. (family unknown)

Generic diagnosis:

Wood diffuse-porous.

Vessels small, mostly solitary, perforation plates exclusively scalariform with many bars (>50), intervessel pits alternate to scalariform.

Imperforate tracheal elements fiber-tracheids.

Axial parenchyma diffuse.

Rays abundant and occupying a large proportion of the wood (>50%), uniseriate to multiseriate, homocellular, composed of all upright cells.

3. *Frutecoxylon yubariense* Ken. Takahashi & M. Suzuki, gen. et sp. nov.
(Fig. 15–21)

Description:

Growth rings absent.

Wood diffuse-porous.

Vessels evenly distributed, mostly solitary (91%) and rarely in radial pairs, rather few, 8–21 (mean 16) per square mm; polygonal in cross section, 30–50 (mean 39) µm × 35–80 (mean 61) µm in tangential × radial diameter, thin-walled. Vessel elements 520–1040 (mean 772) µm long; perforation plates exclusively scalariform with 18–67 bars; intervessel pits opposite to scalariform, round (5 µm in diameter) or elongated
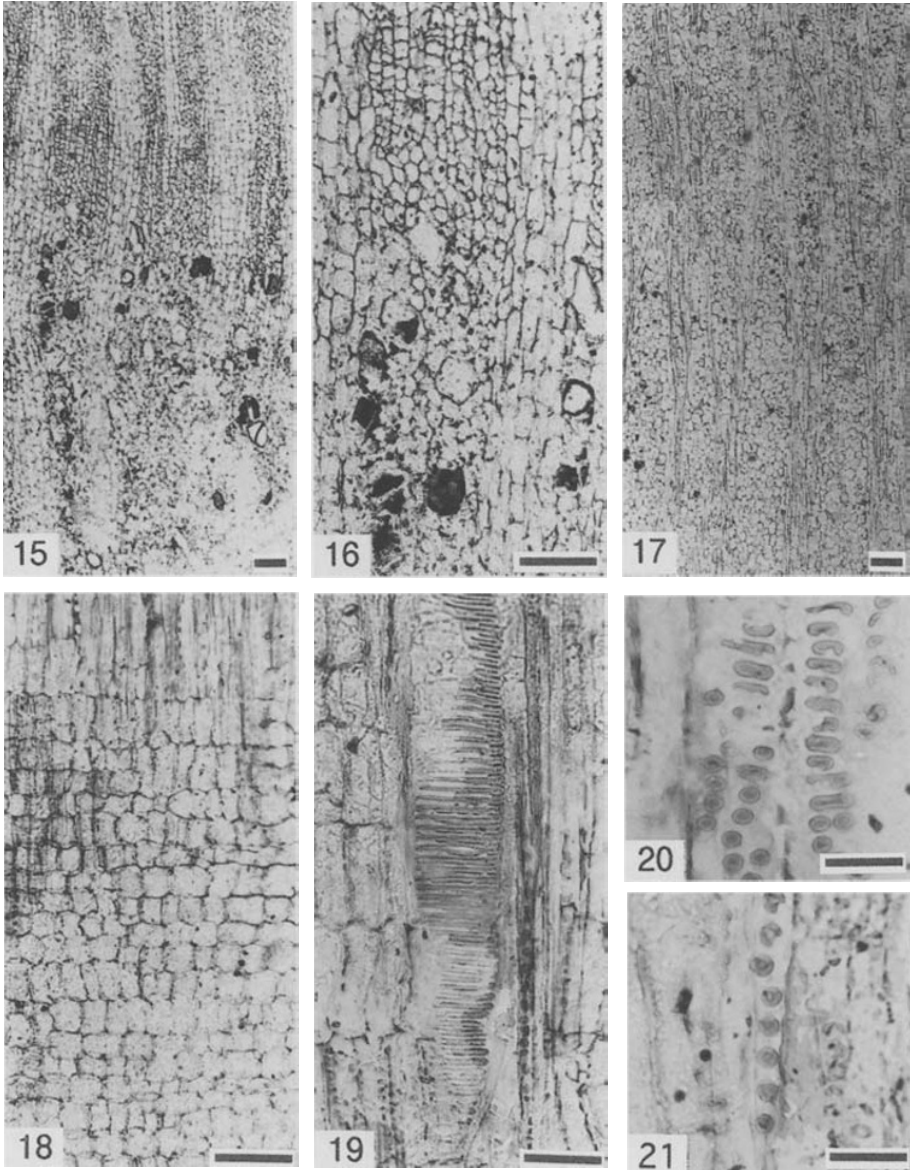
Fig. 15–21. *Frutecoxylon yubariense* gen. et sp. nov. (TUSw-TK 97243, holotype) – 15: TS, diffuse-porous wood. – 16: TS, sparse solitary vessels. – 17: TLS, abundant moderately wide rays. – 18: RLS, homocellular ray composed of upright and square cells. – 19: RLS, scalariform perforation plate with many bars. – 20: TLS, scalariform to opposite intervessel pits. – 21: RLS, fiber-tracheid with distinctly bordered pits. — Scale bars = 100 μm in Fig. 15, 16, 17 & 18; 50 μm in Fig. 19; 25 μm in Fig. 20 & 21.

horizontally (10 × 4 μm in radial × vertical diameter); spiral thickenings absent; vessel-ray pits similar to intervessel pits.

Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.

Axial parenchyma diffuse, no crystalliferous elements observed.

Rays abundant, occupying 52–65% of the total wood volume, homocellular, numerous, wide and tall, up to 10 cells (230 μm) wide and 0.4–4.4 mm high; uniseriate rays rare, multiseriate rays composed of all upright cells (mostly 25 × 40 μm in radial length × height) and sometimes very tall (70 μm in height); crystals absent.

Derivation of species name: After Yubari City, Hokkaido where the holotype was collected.

Holotype: TK 97243, 2 × 4.5 cm in transverse diameter. Estimated diameter of original sample is about 7 cm.

Locality: Shirakin-sawa, Yubari City, Hokkaido.

Horizon and age: Takinosawa Formation, Middle part of the Yezo Group; Turonian.

Collector: Ken'ichi Takahashi.

Other specimen: Turonian: IW 95011.

Affinity — The most prominent features of the present fossil are 1) evenly distributed almost solitary, narrow vessels, 2) exclusively scalariform perforation plates with numerous bars, and 3) a large volume of large homocellular rays composed of upright cells. There are many tree taxa which have conspicuously large rays, e. g., some species of *Casuarina*, *Fagus, Platanus* and *Quercus*, as well as *Icacinoxylon* and *Plataninium*, fossil genera. Shrubs and vines often have conspicuously large rays. Large rays of the above mentioned tree species generally do not constitute a large volume of wood, but in many shrubby and vine species they do. For example, ray volume reaches 30–45% of wood in *Coriaria* species (Yoda & Suzuki 1992). Although they have a large volume of large rays, most vine species have large vessels or two distinct size classes of vessels (e. g., *Vitis*, *Clematis*).

There are several shrubby species that have small vessels with the perforation plates having numerous bars and a large amount of ray volume, e. g., *Aucuba* and *Helwingia* (Cornaceae), *Ribes* and *Hydrangea* (Saxifragaceae), shrubby species of *Ilex* (Aquifoliaceae). Among them, rays of *Ribes*, *Hydrangea* and *Ilex* are distinctly heterocellular with multiseriate parts composed of procumbent cells, while cells in multiseriate parts of rays in *Aucuba* and *Helwingia* are square or upright cells with large longitudinal and tangential lengths and a small radial length. In ray cellular composition, the present fossil resembles *Aucuba* and/or *Helwingia*. Nevertheless, it is not appropriate to conclude a direct affinity of *Frutecoxylon* to those genera of the Cornaceae, because only relatively little information about the wood anatomy of shrubby plants is available for comparison. Therefore we describe the present fossil under a new form genus *Frutecoxylon*, which means wood of a shrub, since we cannot find a direct affinity to an extant or fossil species already described. As the estimated stem diameter of the studied specimen is about 7 cm, the original plant might be a large shrub (or small tree) up to several meters tall.

HAMAMELIDOXYLON Lignier 1907 (Hamamelidaceae)

4. ***Hamamelidoxylon obiraense*** Ken. Takahashi & M. Suzuki, sp. nov. (Fig. 22–25)

Description:

Growth rings distinct, marked by differences in vessel size.

Wood diffuse-porous.

Vessels very numerous, 83–120 (mean 100) per square mm; predominantly solitary (70%) and in radial or rarely in tangential pairs; round, somewhat angular in cross section; 40–65 (mean 52) × 40–105 (mean 60) μm in tangential × radial diameter; 640–1200 (mean 951) μm in vessel element length; perforation plates exclusively scalariform with 22–56 bars; intervessel pits opposite to scalariform, elliptical, horizontally elongated, 15 × 2.5 μm in radial × vertical diameter; vessel-ray pits similar to intervessel pits.

Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.

Axial parenchyma diffuse, no crystalliferous elements observed.

Rays mostly (93%) uniseriate and rarely biseriate; 350 μm–2.1 mm high; markedly heterocellular with 1–4 marginal rows of upright or square cells; procumbent cells 90 × 15 μm in radial length × height; upright cells 30 × 50 μm in radial length × height; no crystalliferous elements observed.

Derivation of species name: After Obira-cho, Rumoi County, Hokkaido where the holotype was collected.
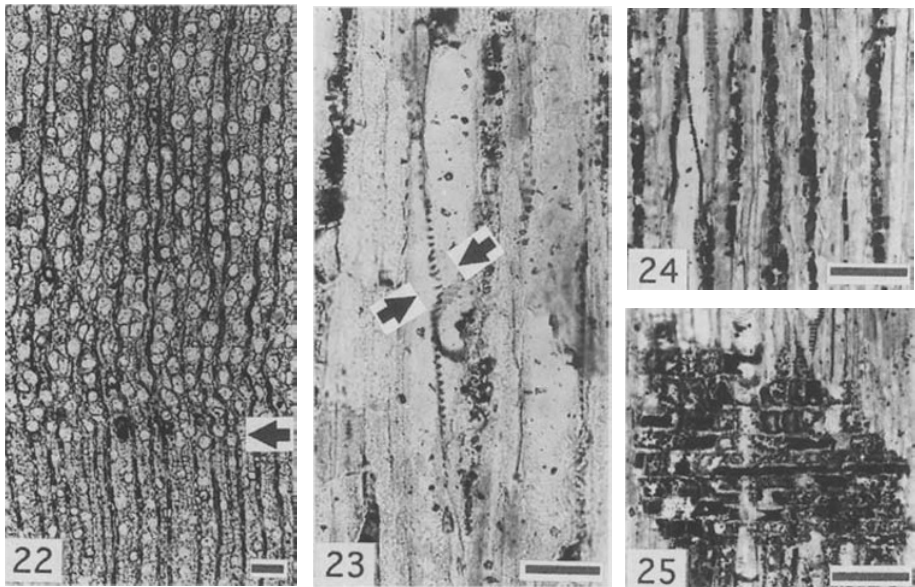

Fig. 22–25. *Hamamelidoxylon obiraense* sp. nov. (TUSw-OG 97021, holotype) – 22: TS, diffuse-porous wood, growth ring (arrow showing boundary), and high vessel frequency. – 23: TLS, scalariform perforation plate (between arrows) with numerous bars. – 24: TLS, uniseriate rays and vessels with scalariform perforation plates. – 25: RLS, markedly heterocellular ray. — Scale bars = 100 μm in Fig. 22, 24 & 25; 50 μm in Fig. 23.

Holotype: OG 97021 (8 × 10 cm in diameter) is a stem wood.

Locality: Obirashibe River, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Unknown, probably Coniacian to Santonian.

Collector: Yutaka Ogasawara.

Other specimens: Cenomanian: CR 96031, CR 96061, KR 95021; Turonian: CR 96201, MT 95011, OG 94023, TK 95041, UM 95021, UM 95022; Coniacian: TK 97264; Santonian: KK 96021, TK 95131; age unknown: KK 94011, KM 95032.

Affinity — The evenly distributed narrow solitary vessels with scalariform perforation plates, high vessel frequency, apotracheal parenchyma and very narrow markedly heterocellular rays of the present fossils suggest affinity to Hamamelidaceae. In this family, the wood anatomy of many genera is quite similar, so it is difficult to recognize each genus by wood structure except for certain genera which provided peculiar anatomical characters. We suggest that fossil woods only assignable to the Hamamelidaceae belong in the genus *Hamamelidoxylon*.

Hamamelidoxylon uniseriatum (Wheeler & Manchester 2002) is very similar to *H. obiraense* in some characters (e. g., vessel frequency, vessel diameter, pits, ray width). However, *Hamamelidoxylon uniseriatum* has fibers without pits, while *H. obiraense* has fiber-tracheids with distinctly bordered pits.

Grambast-Fessard (1969) described *Hamamelidoxylon castellanense* from the Miocene of the Alps. *H. castellanense* has vessels with scalariform perforation plates with a few (number unknown) bars and multiseriate rays up to three cells wide, while *H. obiraense* has vessels with scalariform perforation plates with numerous bars (more than 50) and has only uniseriate and biseriate rays. In these wood characters, *H. castellanense* differs from *H. obiraense*.

Hamamelidoxylon rhenanum from the Miocene of Germany (Van den Burgh 1973) has smaller vessels (30–50 in diameter) and scalariform perforation plates with fewer bars (20–25) than those of *H. obiraense*. Moreover, *H. rhenanum* has both apotracheal and paratracheal parenchyma. Therefore, the present fossils are described as a new species, *H. obiraense*.

ICACINOXYLON Shilkina 1956 (family unknown)

5. *Icacinoxylon kokubunii* Ken. Takahashi & M. Suzuki, sp. nov. (Fig. 26–29)

Description:

Growth rings absent.

Wood diffuse-porous.

Vessels very few, 4–9 (mean 6) per square mm; mostly solitary (92%) and rarely in radial pairs; round, somewhat angular in cross section; 70–130 (mean 93) × 70–145 (mean 112) μm in tangential × radial diameter; 580–1040 (mean 821) μm in vessel element length; perforation plates exclusively scalariform with 5–35 bars; intervessel pits opposite to scalariform, elliptical, horizontally elongated, 6 × 3 μm in radial × vertical diameter; vessel-ray pits similar to intervessel pits.

Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.
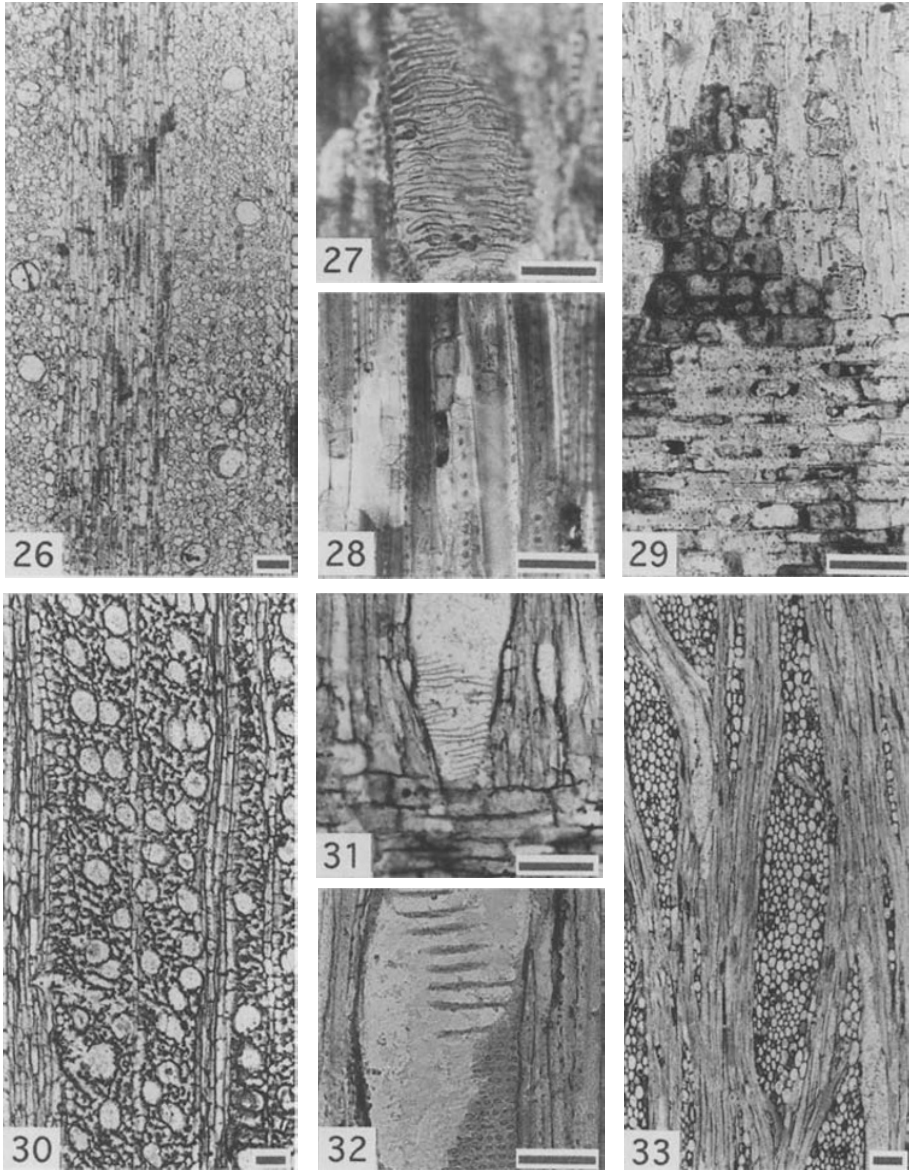
Fig. 26–29. *Icacinoxylon kokubunii* sp. nov. (TUSw-KK 94291, holotype) – 26: TS, diffuse-porous wood and low vessel frequency. – 27: RLS, scalariform perforation plate. – 28: RLS, fiber-tracheids with distinctly bordered pits. – 29: RLS, markedly heterocellular ray. — Fig. 30 – 33. *Icacinoxylon nishidae* sp. nov. (TUSw-NS 96011, holotype) – 30: TS, diffuse-porous wood. – 31: RLS, heterocellular ray. – 32: RLS, scalariform perforation plate and opposite intervessel pits. – 33: TLS, wide and narrow rays. — Scale bars = 100 μm in Fig. 26, 29, 30, 31 & 33; 50 μm in Fig. 27, 28 & 32.

Axial parenchyma abundant, diffuse-in-aggregates, no crystalliferous elements observed.

Rays uniseriate and multiseriate; uniseriate rays abundant (44%) and low; multiseriate rays large, up to 35 cells (630 μm) wide and 14.4 mm high; multiseriate rays markedly heterocellular with 1–6 marginal uniseriate rows; uniseriate rays and uniseriate marginal rows of multiseriate rays composed of upright cells, 40 × 65 μm in radial length × height; body of multiseriate rays composed of procumbent cells, 90 × 25 μm in radial length × height; no crystalliferous elements observed.

Derivation of species name: After Hiroji Kokubun, who collected the holotype.

Holotype: KK 94291 (6 × 10 cm in transverse diameter) is about half of a trunk of which the original diameter is estimated to be more than 10 cm.

Locality: 66-rinpan-sawa, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Member Ml–Mo, Middle part of the Yezo Group; Turonian.

Collector: Hiroji Kokubun.

Other specimens: Albian: TK 98081, TK 98101; Cenomanian: AD 97011; Turonian: IW 95012, SZ 95021, TK 97241; Coniacian: KK 94181, TK 97261, TK 97262; Santonian: OG 94044, TK 95211; age unknown: HS 98011, KE 97011, TK 97331, TK 97332.

6. *Icacinoxylon nishidae* Ken. Takahashi & M. Suzuki, sp. nov. (Fig. 30–33)

Description:

Growth rings absent.

Wood diffuse-porous.

Vessels moderately few, 16–28 (mean 21) per square mm; predominantly solitary (60%) and in radial multiples of 2, rarely of 3; round, somewhat angular in cross section; 65–130 (mean 92) × 75–135 (mean 99) μm in tangential × radial diameter; 550–1150 (mean 850) μm in vessel element length; perforation plates exclusively scalariform with 7–26 bars; intervessel pits opposite, elliptical, horizontally elongated, 8 × 3 μm in radial × vertical diameter; vessel-ray pits similar to intervessel pits.

Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.

Axial parenchyma abundant, diffuse, no crystalliferous elements observed.

Rays uniseriate and multiseriate; uniseriate rays abundant (33%) and low; multiseriate rays moderately large, up to 17 cells (445 μm) wide and 5.8 mm high; multiseriate rays markedly heterocellular with 1–4 marginal uniseriate rows; uniseriate rays and uniseriate marginal rows of multiseriate ones composed of upright cells, 40 × 60 μm in radial length × height; multiseriate cores composed of procumbent cells, 95 × 30 μm in radial length × height; no crystalliferous elements observed.

Derivation of species name: After the late Prof. Makoto Nishida, who collected the holotype.

Holotype: NS 96011 (5 × 5 cm in transverse diameter) is a fragment of a large trunk of which the original diameter is estimated at more than 15 cm.

Locality: Obirashibe River, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Unknown, probably Coniacian to Santonian.

Collector: Makoto Nishida.

Other specimens: Turonian: TK 95451; Coniacian: TK 95141; Santonian: KK 96081, KM 97011, KM 97012, OG 94041.

Affinity — Because of their solitary vessels with exclusively scalariform perforation plates, abundant apotracheal parenchyma, large markedly heterocellular rays and abundant uniseriate rays, the two species described in the present paper are assigned to the genus *Icacinoxylon* Shilkina (1956).

There are two other Cretaceous species of *Icacinoxylon* (Thayn et al. 1985; Wheeler et al. 1987). *Icacinoxylon pittiense* resembles *I. nishidae*, but has abundant tyloses. *Icacinoxylon kokubunii* has much wider rays than those of the two species previously described (Table 2).

Icacinoxylon citronelloides Shilkina (Shilkina 1956), the type species of the genus, is different from the two Japanese species as it has growth rings and smaller vessels (less than 50 μm in tangential diameter); therefore it is distinguishable from the two species from Japan. Greguss (1969) discussed 25 taxa of *Icacinoxylon* from the Oligocene and Miocene of Hungary; however, only eight taxa were assigned species names. All differ from the two Japanese species in presence/absence of growth rings, vessel frequency, vessel diameter, presence/absence of tyloses, type of ray or ray width.

Petrescu (1978) described five species of *Icacinoxylon* from the Oligocene of Rumania. All have more numerous and smaller vessels than the Japanese species.

Shimakura (1937) described *Casuaroxylon japonicum* from the Upper Cretaceous (Coniacian–Maastrichtian) of Hokkaido. This species is characterized by conspicuous rays that he called 'compound rays'. In the present paper, taxa with conspicuous rays are *Icacinoxylon*, *Plataninium* and *Nishidaxylon*. Shimakura described *Casuaroxylon japonicum* with simple and rarely scalariform (?) perforation plates. So *Casuaroxylon japonicum* has no relation with the aforementioned taxa.

MAGNOLIACEOXYLON Wheeler, Scott & Barghoorn 1977 (Magnoliaceae)

7. *Magnoliaceoxylon hokkaidoense* Ken. Takahashi & M. Suzuki, sp. nov.
   (Fig. 34–36)

Description:

   Growth rings absent.

   Wood diffuse-porous.

   Vessels few, 11–25 (mean 16) per square mm; mostly solitary (87%) and sometimes in radial or tangential pairs; round to oval, somewhat angular in cross section; 20–60 (mean 45) × 30–90 (mean 63) μm in tangential × radial diameter; 440–890 (mean 661) μm in vessel element length; perforation plates exclusively scalariform with 12–47 bars; intervessel pits opposite to scalariform, elliptical, elongated horizontally (30 × 2 μm in radial × vertical diameter), vessel-ray pits scalariform.

   Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.

   Axial parenchyma diffuse and rarely scanty paratracheal, no crystalliferous elements observed.

Table 2. Comparison of the Cretaceous *Icacinoxylon* species.

Species:	*I. pittiense*	*I. alternipunctata*	*I. kokubunii*	*I. nishidae*
Reference	Thayn et al. 1985	Wheeler et al. 1987	this study	this study
Geological time	Albian	Maastrichtian	Albian, Cenomanian, Turonian, Coniacian & Santonian	Turonian, Coniacian & Santonian
Locality	Utah, USA	Illinois, USA	Hokkaido, Japan	Hokkaido, Japan
V/MM	24	8–17	6	21
MTD (μm)	90	163	92	92
Bars	4–30	12–27	5–35	7–26
Intervessel pits	opposite to scalariform	alternate	opposite to scalariform	opposite to scalariform
Tyloses	present, abundant	absent	absent	absent
Imperforate tracheary elements	fiber-tracheids with bordered pits	septate fibers	fiber-tracheids with bordered pits	fiber-tracheids with bordered pits
MSRW	up to 12	up to 10	up to 35	up to 17

V/MM = vessels per sq. mm; MTD = mean tangential diameter; MSRW = multiseriate ray width.
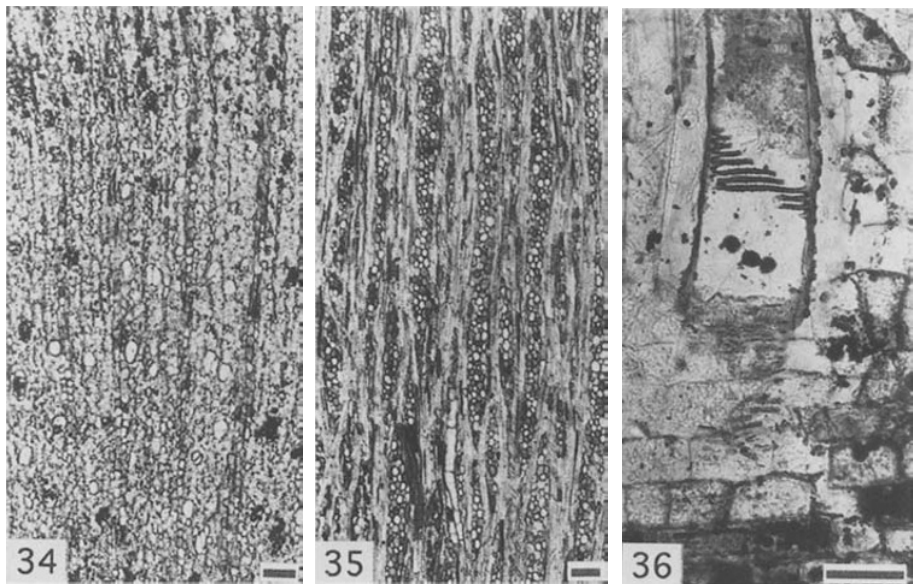

Fig. 34–36. *Magnoliaceoxylon hokkaidoense* sp. nov. (TUSw-KK 94182, holotype) – 34: TS, diffuse-porous wood. – 35: TLS, low narrow rays. – 36: RLS, scalariform perforation plate and markedly heterocellular ray. — Scale bars = 100 μm in Fig. 34 & 35; 50 μm in Fig. 36.

Rays up to 4 cells (90 μm) wide; 140 μm–1.4 mm high; markedly heterocellular with 1–4 marginal rows of upright or square cells; procumbent cells 45 × 25 μm in radial length × height; upright cells 35 × 45 μm in radial length × height; uniseriate rays rare; crystalliferous elements almost absent (KK 94182, KK 95021, KK 98041), and rarely present (KK 94261).

Derivation of species name: After Hokkaido where the woods of this species were collected.
Holotype: KK 94182 (2.5 × 3 cm in transverse diameter) is a small piece of a wood of which the original diameter is estimated at 5 cm.
Locality: Obirashibe River, Obira-cho, Rumoi County, Hokkaido.
Horizon and age: Member Ub, Upper part of the Yezo Group; Coniacian.
Collector: Hiroji Kokubun.
Other specimens: Turonian: KK 94261; Santonian: KK 95021, KK 98041.
The holotype has a small diameter; however, one specimen (KK 94261) is a fragment of a mature wood of more than 30 cm in diameter.

Affinity — Because of its small solitary and paired vessels with scalariform perforation plates with numerous bars, scanty apotracheal parenchyma and low narrow and markedly heterocellular rays, the species described here belongs to the Magnoliaceae. As it cannot be assigned to any extant genus of the family, it is assigned to the genus *Magnoliaceoxylon*.
Wheeler et al. (1977) established *Magnoliaceoxylon* based on a specimen from the Eocene of Yellowstone National Park. *Magnoliaceoxylon wetmorei*, the type species of the genus, has larger vessels (75 μm in mean tangential diameter) with fewer bars (up to 26) than *M. hokkaidoense*.
Page (1970) described *Magnolioxylon panochensis* (= *Magnoliaceoxylon panochensis* (Page) Wheeler et al.) from the Maastrichtian of California. *Magnoliaceoxylon panochensis* is characterized by: 1) small (80 μm in mean tangential diameter) solitary vessels with scalariform perforation plates and opposite-transitional intervessel pits; 2) diffuse parenchyma; 3) low, narrow (up to 4 cells wide) rays. *Magnoliaceoxylon panochensis* has larger vessels with scalariform perforation plates with fewer (up to 20) bars than *M. hokkaidoense*. Moreover, *M. panochensis* has numerous homocellular rays, while *M. hokkaidoense* has exclusively heterocellular rays.
Shimakura (1937) described *Aptiana*? sp. from the Upper Cretaceous (Coniacian–Maastrichtian) of Hokkaido. It is branch wood with the characters: 1) diffuse-porous wood with distinct growth rings and numerous (60 per square mm) narrow (20–90 μm) vessels, 2) exclusively scalariform perforation plates with 20–30 or more bars, and 3) distinctly heterogeneous rays 1–7 cells wide. Although his fossil may be similar in some vessel and ray characters, *Aptiana*? sp. is apparently different from our fossil as it has more abundant vessels, which are more frequently in multiples.

NISHIDAXYLON Ken. Takahashi & M. Suzuki, gen. nov. (family unknown)

Generic diagnosis:
    Wood diffuse-porous.

Vessels sparse; exclusively solitary; small to medium in diameter; perforation plates exclusively scalariform; vessel-ray pits alternate to opposite, oval to elliptical, horizontally elongated.

Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.

Axial parenchyma diffuse and scanty paratracheal.

Rays of two distinct sizes, mostly narrow and sometimes conspicuously large; nearly homocellular composed of procumbent cells.

Derivation of generic name: After the late Prof. Makoto Nishida, who was a pioneer of the Cretaceous fossil wood study in Japan.

Type species: *Nishidaxylon jezoense* Ken. Takahashi & M. Suzuki.

8. ***Nishidaxylon jezoense*** Ken. Takahashi & M. Suzuki, gen. et sp. nov. (Fig. 37–42)

Description:

Growth rings absent.

Wood diffuse-porous.

Vessels few, 10–13 (mean 12) per square mm; exclusively solitary (100%); round to oval in cross section; 40–140 (mean 92) × 65–180 (mean 136) μm in tangential × radial diameter; 570–1060 (mean 796) μm in vessel element length; perforation plates exclusively scalariform with 7–20 bars; vessel-ray pits alternate to opposite, oval to elliptical, horizontally elongated, 6 μm in diameter.

Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.

Axial parenchyma abundant, diffuse and scanty paratracheal; no crystalliferous elements observed.

Rays of two distinct sizes, mostly (88%) narrow, 1–7 cells wide and 220 μm–1.6 mm high, and sometimes conspicuously large, 13–66 cells (340 μm–1.4 mm) wide and 5770 μm–23.4 mm high; almost homocellular composed of procumbent cells (120 × 25 μm in radial length × height), occasionally with one marginal row of upright or square cells (30 × 40 or 30 × 30 μm in radial length × height); no crystalliferous elements observed.

Derivation of species name: After Yezo, the old name of Hokkaido.

Holotype: KK 98141 (4 × 5.5 cm in transverse diameter) is a fragment of a large trunk of which the original diameter is estimated to be more than 10 cm.

Locality: Araki-sawa, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Member Uf–Uk, Upper part of the Yezo Group; Santonian.

Collector: Hiroji Kokubun.

Other specimen: Age unknown: II 96011.

Affinity — A combination of exclusively (100%) solitary vessels and rays of two distinct sizes (low narrow ones and high broad ones) occurs in some species of *Casuarina* (Casuarinaceae) and in some species of Fagaceae. *Casuarina* and the Fagaceae have simple perforation plates, while *Nishidaxylon jezoense* has vessels with exclusively scalariform perforation plates. We could not find any other wood among extant species, which closely resembles the present fossil.
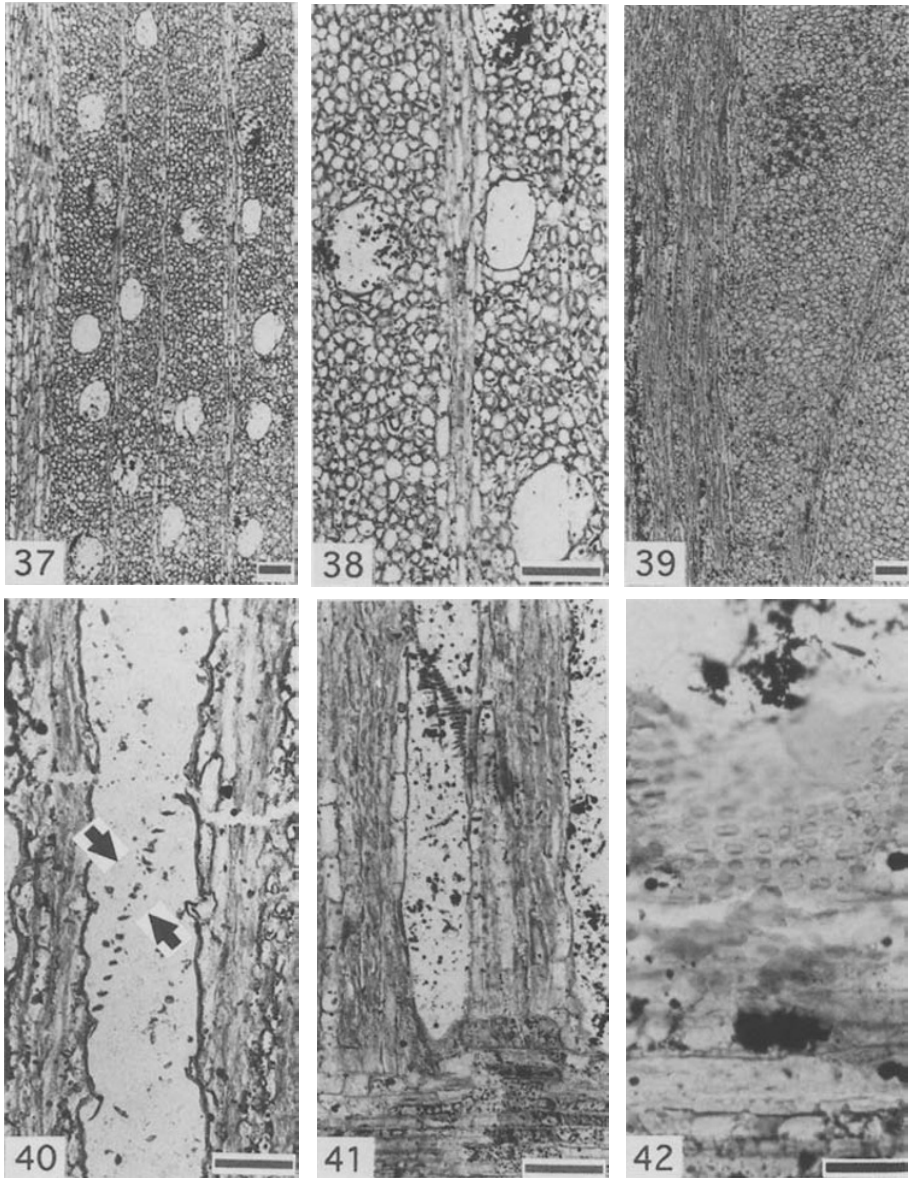
Fig. 37–42. *Nishidaxylon jezoense* gen. et sp. nov. (TUSw-KK 98141, holotype) – 37: TS, diffuse-porous wood. – 38: TS, solitary vessels and apotracheal and paratracheal parenchyma. – 39: TLS, conspicuous wide ray and narrow rays. – 40: TLS, scalariform perforation plate (between arrows). – 41: RLS, almost homocellular ray. – 42: RLS, opposite to alternate vessel-ray pits. — Scale bars = 100 μm in Fig. 37, 38, 39 & 41; 50 μm in Fig. 40; 25 μm in Fig. 42.

Stopes and Fujii (1910) described *Fagoxylon hokkaidense* from the Upper Cretaceous of Hokkaido. *Fagoxylon hokkaidense* is characterized by 1) almost solitary numerous vessels (0.06–0.1 mm in diameter), 2) vessels showing 'scalariform thickening' and 3) conspicuous rays up to 20 cells wide. If the 'scalariform thickening' of vessels means scalariform perforation plates with many bars, the wood may be assignable to *Icacinoxylon*, *Plataninium* or *Nishidaxylon* (Fig. 3). They described *F. hokkaidense* as having radially elongated ray cells (procumbent cells), so it may be of the same wood type as *Nishidaxylon*, although *N. jezoense* has much wider rays. Stopes and Fujii named their fossil *Fagoxylon* because they considered it to be similar to the extant *Fagus* of the Fagaceae.

PARAPHYLLANTHOXYLON Bailey 1924 (family unknown)

9. *Paraphyllanthoxylon cenomaniana* Ken. Takahashi & M. Suzuki, sp. nov.
   (Fig. 43–46)

Description:
   Growth rings absent.
   Wood diffuse-porous.
   Vessels very few to few, 6–16 (mean 11) per square mm; solitary (46%) and in radial multiples of 2–5; round in cross section; 80–240 (mean 174) × 90–310 (mean 201) μm in tangential × radial diameter; tyloses abundant, obscuring vessel element length; perforation plates exclusively simple; intervessel pits alternate, large (13 × 8 μm in radial × vertical diameter), horizontally elongated; vessel-ray pits simple, large, round to elliptical, horizontally or vertically elongated (20 × 9 μm or 8 × 24 μm in radial × vertical diameter).
   Imperforate tracheary elements septate fibers, without pits.
   Axial parenchyma scanty, paratracheal, no crystalliferous elements observed.
   Rays up to 5 cells (140 μm) wide; 0.32–20.5 mm high; heterocellular; procumbent cells 50 × 20 μm in radial length × height; upright cells 30 × 45 μm in radial length × height; uniseriate rays rare; no crystalliferous elements observed.

   Derivation of species name: After Cenomanian, the age from which the holotype was yielded.
   Holotype: TK 97191 (1 × 4 cm in transverse diameter) is a piece of a trunk of which the original diameter is estimated to be more than 10 cm.
   Locality: Shinonome-sawa, Obira-cho, Rumoi County, Hokkaido.
   Horizon and age: Member Mf, Middle part of the Yezo Group; Cenomanian.
   Collector: Ken'ichi Takahashi.
   Other specimens: Turonian: TK 97164; Coniacian: TK 97265.

10. *Paraphyllanthoxylon obiraense* Ken. Takahashi & M. Suzuki, sp. nov.
   (Fig. 47–51)

Description:
   Growth rings absent.
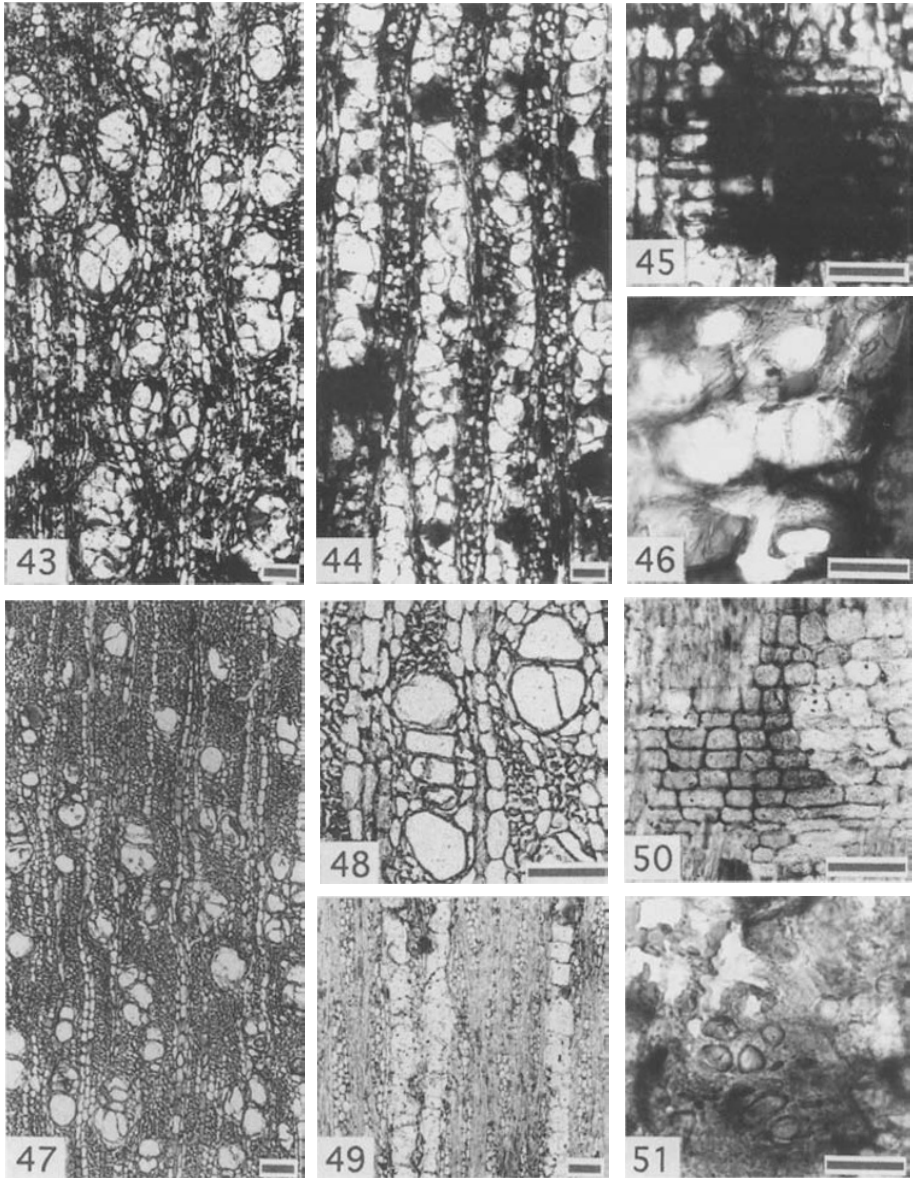
Fig. 43–46. *Paraphyllanthoxylon cenomaniana* sp. nov. (TUSw-TK 97191, holotype) – 43: TS, diffuse-porous wood. – 44: TLS, vessels filled by tyloses and moderately wide rays. – 45: RLS, heterocellular ray. – 46: RLS, large vessel-ray pits. — Fig. 47–51. *Paraphyllanthoxylon obiraense* sp. nov. (TUSw-TK 98141, holotype) – 47: TS, diffuse-porous wood. – 48: TS, vessels solitary and in radial multiples and paratracheal parenchyma. – 49: TLS, vessels filled by tyloses and 3–4-seriate rays. – 50: RLS, heterocellular ray. – 51: RLS, vessel-ray pits. — Scale bars = 100 μm in Fig. 43, 44, 45, 47, 48, 49 & 50; 25 μm in Fig. 46 & 51.

Wood diffuse-porous.

Vessels common, 22–36 (mean 27) per square mm; solitary (52%) and in radial multiples of 2–5; round in cross section; 65–130 (mean 93) × 70–140 (mean 96) μm in tangential × radial diameter; 230–370 (mean 298) μm in vessel element length; tyloses abundant; perforation plates exclusively simple; intervessel pits alternate, round to oval (10 × 7 μm in radial × vertical diameter), horizontally elongated; vessel-ray pits simple, large, round to oval (12 μm in diameter), horizontally or vertically elongated.

Imperforate tracheary elements fibers with no pits, septa not observed (N.B.: but absence of septa is likely due to poor preservation).

Axial parenchyma moderately abundant, vasicentric, no crystalliferous elements observed.

Rays up to 3 cells (60 μm) wide; 240 μm–1.1 mm high; heterocellular; procumbent cells 70 × 25 μm in radial length × height; upright cells 25 × 50 μm in radial length × height; uniseriate rays rare; no crystalliferous elements observed.

Derivation of species name: After Obira-cho, Rumoi County, Hokkaido from which the specimen was collected.

Holotype: TK 98141 (3.5 × 5 cm in transverse diameter) is a piece of a trunk of which the original diameter is estimated to be more than 10 cm.

Locality: Araki-sawa, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Member Uf–Uk, Upper part of the Yezo Group; Santonian.

Collector: Ken'ichi Takahashi.

This species is established and based on a single specimen.

Affinity — Because of vessels with exclusively simple perforation plates and large vessel-ray pits, abundant tyloses, scanty paratracheal parenchyma and narrow hetero-cellular rays, the two species described above are assigned to the genus *Paraphyllanthoxylon*. Eight species of *Paraphyllanthoxylon* have been described from the Cretaceous of North America and Africa (Bailey 1924; Spackman 1948; Mädel 1962; Cahoon 1972; Thayn et al. 1983; Wheeler et al. 1987; Herendeen 1991a; Wheeler et al. 1995) (Table 3).

Paraphyllanthoxylon arizonense Bailey (1924), *P. idahoense* Spackman (1948) and *P. alabamense* Cahoon (1972) are very similar to *P. cenomaniana*. However, *P. cenomaniana* is distinguishable from *P. arizonense* by the shape of vessel-ray pits, and is distinguishable from *P. idahoense* and *P. alabamense* by the vessel diameter.

Paraphyllanthoxylon anasazi Wheeler, McClammer & LaPasha (1995) closely resembles *P. obiraense*. However, vessels of *P. anasazi* are in radial multiples of 2 or 3, while those of *P. obiraense* are in radial multiples of up to 5. Moreover, axial parenchyma of *P. obiraense* is more abundant than that of *P. anasazi*.

Jugloxylon hamaoanum (Stopes & Fujii 1910) from the Upper Cretaceous of Hokkaido has vessels of medium size (60–120 μm) and narrow rays (1 to 2 cells wide). Perforation plate type was not mentioned. Although there is some possibility that *J. hamaoanum* is of the same wood type, this cannot be established because Stopes and Fujii did not give information on perforation type and ray cellular composition.

Table 3. Comparison of the Cretaceous *Paraphyllanthoxylon* species.

Species	Reference	Geological time	Locality	V/MM	Vessel multiples	MTD (μm)	Tyloses	VRP	MSRW
P. arizonense	Bailey 1924	Cenomanian	Arizona, USA	6	up to 4	175	bubble-like	mostly round	up to 7
P. idahoense	Spackman 1948	Lower Cretaceous?	Idaho, USA	?	up to 4	100	bubble-like	oval	up to 4
P. capense	Mädel 1962	Upper Cretaceous	South Africa	39	up to 6	76	bubble-like	oval	up to 5
P. alabamense	Cahoon 1972	Cenomanian	Alabama, USA	12	up to 7	105	bubble-like	round to oval	up to 5
P. utahense	Thayn et al. 1983	Albian	Utah, USA	12	up to 5	93	segmenting vessel	round to elliptical	up to 5
P. illinoisense	Wheeler et al. 1987	Maastrichtian	Illinois, USA	13–27	up to 8	118	segmenting vessel	oval to elliptical	up to 6
P. marylandense	Herendeen 1991	Cenomanian	Maryland, USA	35–60	up to 5	81	segmenting vessel	round to elliptical	up to 4
P. amasazi	Wheeler et al. 1995	Maastrichtian	New Mexico, USA	20–25	up to 3	84	segmenting vessel	mostly round	up to 3
P. cenomaniana	this study	Cenomanian, Turonian & Coniacian	Hokkaido, Japan	11	up to 5	174	bubble-like	round to elliptical	up to 5
P. obiraense	this study	Santonian	Hokkaido, Japan	27	up to 5	93	segmenting vessel	round to oval	up to 3

V/MM = vessels per sq. mm; MTD = mean tangential diameter; VRP = vessel-ray pits; MSRW = multiseriate ray width.

Table 4. Comparison of the Cretaceous *Plataninium* species.

Species	Reference	Geological time	Locality	Growth rings	V/MM	MTD (μm)	Bars	Ray type	MSRW
P. platanoides	Page 1968	Maastrichtian	California, USA	absent	?	60–70	4–22	homocellular, some-times heterocellular	up to 15
P. californicum	Page 1968	Maastrichtian	California, USA	absent	?	?	up to 30	homocellular, some-times heterocellular	up to 15–25
P. piercei	Wheeler et al. 1995	Maastrichtian	New Mexico, USA	absent	64	48	6–9	homocellular, some-times heterocellular	15–25
P. jezoensis	this study	Cenomanian & Turonian	Hokkaido, Japan	present, indistinct	51	83	9–29	homocellular	up to 30
P. ogasawarae	this study	Santonian	Hokkaido, Japan	present, indistinct	59	63	6–37	homocellular	up to 27

V/MM = vessels per sq. mm; MTD = mean tangential diameter; MSRW = multiseriate ray width.

PLATANINIUM Unger emend. Brett 1972 (Platanaceae?)

11. *Plataninium jezoensis* Ken. Takahashi & M. Suzuki, sp. nov. (Fig. 52–55)

Description:

Growth rings indistinct, delineated by radially flattened fiber-tracheids and a slight difference of vessel diameter between latewood and earlywood.

Wood diffuse-porous.

Vessels numerous, 45–57 (mean 50.6) per square mm; solitary (76%) and in radial or tangential pairs; round to oval in cross section; 65–115 (mean 83) × 80–145 (mean 103) μm in tangential × radial diameter; 500–1150 (mean 802) μm in vessel element length; perforation plates exclusively scalariform with 9–29 bars; intervessel pits opposite, almost round, 3 μm in diameter; vessel-ray pits similar to intervessel pits.

Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.

Axial parenchyma very abundant, diffuse-in-aggregates, no crystalliferous elements observed.

Rays rarely uniseriate (6%), mostly multiseriate; uniseriate rays low; multiseriate rays large, up to 30 cells (555 μm) wide and 6.3 mm high; homocellular composed of all procumbent cells, 110 × 30 μm in radial length × height; no crystalliferous elements observed.

Derivation of species name: After Yezo, old name of Hokkaido from which the specimens were yielded.

Holotype: CR 96041 (4 × 5 cm in transverse diameter) is a fragment of a large trunk of which the original diameter is estimated at more than 20 cm.

Locality: Kabano-sawa, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Member Mf, Middle part of the Yezo Group; Cenomanian.

Collector: Mitsuo Suzuki et al.

Other specimens: Cenomanian: CR 96161; Turonian: TK 95091.

12. *Plataninium ogasawarae* Ken. Takahashi & M. Suzuki, sp. nov. (Fig. 56–59)

Description:

Growth rings indistinct, delineated by differences in vessel diameter between earlywood and latewood, and layers of radially flattened fiber-tracheids in latewood.

Wood diffuse-porous.

Vessels numerous, 52–64 (mean 59) per square mm; solitary (65%) and in radial or tangential pairs, rarely in radial multiples of 3; round, somewhat angular in cross section; 45–85 (mean 63) × 50–90 (mean 65.5) μm in tangential × radial diameter; 330–1020 (mean 720.3) μm in vessel element length; perforation plates exclusively scalariform with 6–37 bars; intervessel pits opposite, elliptical, horizontally elongated, 15 × 3 μm in radial × vertical diameter; vessel-ray pits similar to intervessel pits.

Imperforate tracheary elements fiber-tracheids with distinctly bordered pits.

Axial parenchyma moderately abundant, diffuse, no crystalliferous elements observed.

Rays rarely uniseriate (7%) and mostly multiseriate; uniseriate rays low; multiseriate
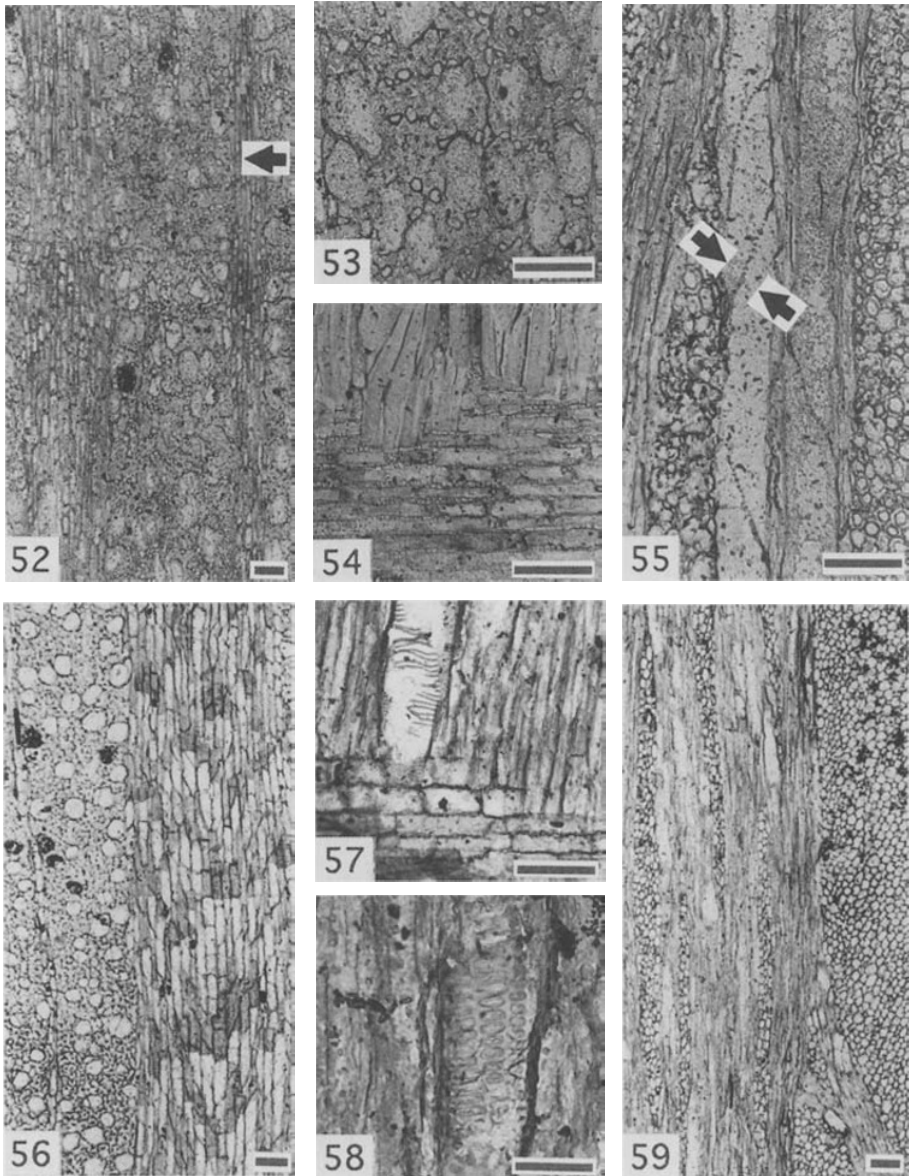
Fig. 52–55. *Plataninium jezoensis* sp. nov. (TUSw-CR 96041, holotype) – 52: TS, diffuse-porous wood and indistinct growth ring (arrow showing boundary). – 53: TS, vessels solitary or in radial or in tangential multiples and diffuse-in-aggregates parenchyma. – 54: RLS, homocellular ray. – 55: TLS, scalariform perforation plates (between arrows). — Fig. 56–59. *Plataninium ogasawarae* sp. nov. (TUSw-OG 96111, holotype) – 56: TS, diffuse-porous wood. – 57: RLS, homocellular ray. – 58: TLS, opposite intervessel pits. – 59: wide and narrow rays. — Scale bars = 100 μm in Fig. 52, 53, 54, 55, 56, 57 & 59; 50 μm in Fig. 58.

rays large, up to 27 cells (505 μm) wide and 10 mm high; homocellular composed of all procumbent cells, 100 × 30 μm in radial length × height; no crystals observed.

Derivation of species name: After Yutaka Ogasawara, who collected the holotype.

Holotype: OG 96111 (2 × 3 cm in transverse diameter) is a small piece of a wood of which the original diameter is estimated at 6 cm.

Locality: Obirashibe River, Obira-cho, Rumoi County, Hokkaido.

Horizon and age: Unknown, probably Coniacian to Santonian.

Collector: Yutaka Ogasawara.

Other specimens: Santonian: KK 95351, SK 95011.

Affinity — Small solitary vessels with scalariform perforation plates, apotracheal parenchyma, wide homocellular rays composed of procumbent cells and scanty uniseriate rays suggest affinities with the fossil genus *Plataninium* of the Platanaceae. The anatomy of *Plataninium* is similar to that of *Platanus*, but *Plataninium* differs from *Platanus* in its wider rays, and absence of simple perforation plates in some *Plataninium* species.

The genus *Plataninium* was established by Unger (1842), and Brett (1972) emended it as follows: 1) the wood is diffuse or graded porous, 2) vessels are 20–150 per square mm, 3) vessels are mostly solitary, sometimes in tangential multiples, 4) the tangential diameter of vessels is rarely more than 100 μm, 5) perforation plates are mostly scalariform, rarely simple in larger vessels in earlywood, 6) imperforate tracheary elements are fiber-tracheids with bordered pits, 7) axial parenchyma is abundant and diffuse-in-aggregates, 8) rays are commonly 5–15 cells wide and more or less homocellular, and 9) uniseriate rays are rare. Page (1968) extended the anatomical range of the genus, so that woods with vessels having both exclusively scalariform or scalariform-simple perforation plates were included. All of the Cretaceous *Plataninium* species described to date have vessels with exclusively scalariform perforation plates.

Süss and Müller-Stoll (1977) emended *Plataninium* noting Unger's original diagnosis. They assigned *Platanus*-like woods with a spiral thickening to *Plataninium*, and other woods to *Platanoxylon*. However, all the Cretaceous *Platanus*-like woods which were previously described were named *Plataninium*; moreover, *Plataninium* is prior to *Platanoxylon*. So, in the present paper, we assign the *Platanus*-like woods from the Cretaceous of Hokkaido to *Plataninium*.

Three species of *Plataninium* have previously been described from the Cretaceous (Page 1968; Wheeler et al. 1995) (Table 4). The three species of North America have no growth rings, both homocellular and heterocellular rays, while Japanese species have indistinct growth rings and exclusively homocellular rays.

There were also several species of *Plataninium* from the Paleogene. *Plataninium decipiens* (Brett 1972) from the Eocene of England has fewer vessels and narrower rays than the species from the Yezo Group. Moreover, crystals are commonly present in ray cells of *P. decipiens*. *Plataninium bretti* (Crawley 1989) from the Paleocene of Scotland has much smaller vessels (35 μm in mean tangential diameter) and narrower rays (up to 14 cells wide). *Plataninium haydenii* Felix emend. Wheeler, Scott & Barghoorn (Wheeler et al. 1977; Scott & Wheeler 1982) from the Eocene of North America has more distinct growth rings and more vessels (number not shown) than

the species from the Yezo Group. Moreover, *P. haydenii* has both homocellular and heterocellular rays. In comparison to the Cretaceous species, the Paleogene ones are distinguished by more distinct growth rings and more frequent vessel multiples.

SABIACEOXYLON Ken. Takahashi & M. Suzuki, gen. nov. (Sabiaceae?)

Generic diagnosis:
  Wood diffuse-porous.
  Vessels numerous; predominantly in radial multiples of 2 to 3, occasionally solitary; polygonal in cross section; very small in diameter; perforation plates simple and scalariform with few bars; intervessel pits crowded alternate, large, polygonal; vessel-ray pits large, round to oval, horizontally elongated.
  Imperforate tracheary elements libriform fibers with no pits.
  Rays narrow; heterocellular.

  Derivation of generic name: Similarity to wood of Sabiaceae.
  Type species: *Sabiaceoxylon jezoense* Ken. Takahashi & M. Suzuki.

13. *Sabiaceoxylon jezoense* Ken. Takahashi & M. Suzuki, gen. et sp. nov.
    (Fig. 60–67)

Description:
  Growth rings absent.
  Wood diffuse-porous.
  Vessels extremely numerous, 95–188 (mean 138) per square mm; solitary (29%) and in radial multiples of 2 to 3; polygonal in cross section; 20–50 (mean 32) × 25–55 (mean 35) μm in tangential × radial diameter; walls rather thick (about 3 μm); 200–530 (mean 383) μm in vessel element length; perforation plates mostly simple and sometimes scalariform with less than 10 bars; intervessel pits crowded alternate, large (8 μm in diameter), polygonal; vessel-ray pits large, round to oval, horizontally elongated (10 × 5 μm in radial × vertical diameter).
  Imperforate tracheary elements libriform fibers with no pits.
  Axial parenchyma sparse, apotracheal, no crystalliferous elements observed.
  Rays up to 3 cells (55 μm) wide; 170 μm–4.1 mm high; heterocellular; procumbent cells 40 × 20 μm in radial × vertical lengths and upright cells 20 × 50 μm in radial × vertical lengths; uniseriate rays abundant; no crystalliferous elements observed.

  Derivation of species name: After Yezo, the old name of Hokkaido.
  Holotype: KK 94183 (0.8 × 1 cm in transverse diameter) is a stem wood.
  Locality: Obirashibe River, Obira-cho, Rumoi County, Hokkaido.
  Horizon and age: Member Ub, Upper part of the Yezo Group; Coniacian.
  Collector: Hiroji Kokubun.
  The genus and the species are established based on a single specimen.

Affinity — Woods with both simple and scalariform perforation plates, alternate intervessel pits and rather thick vessel walls occur in the Sabiaceae (Metcalfe & Chalk
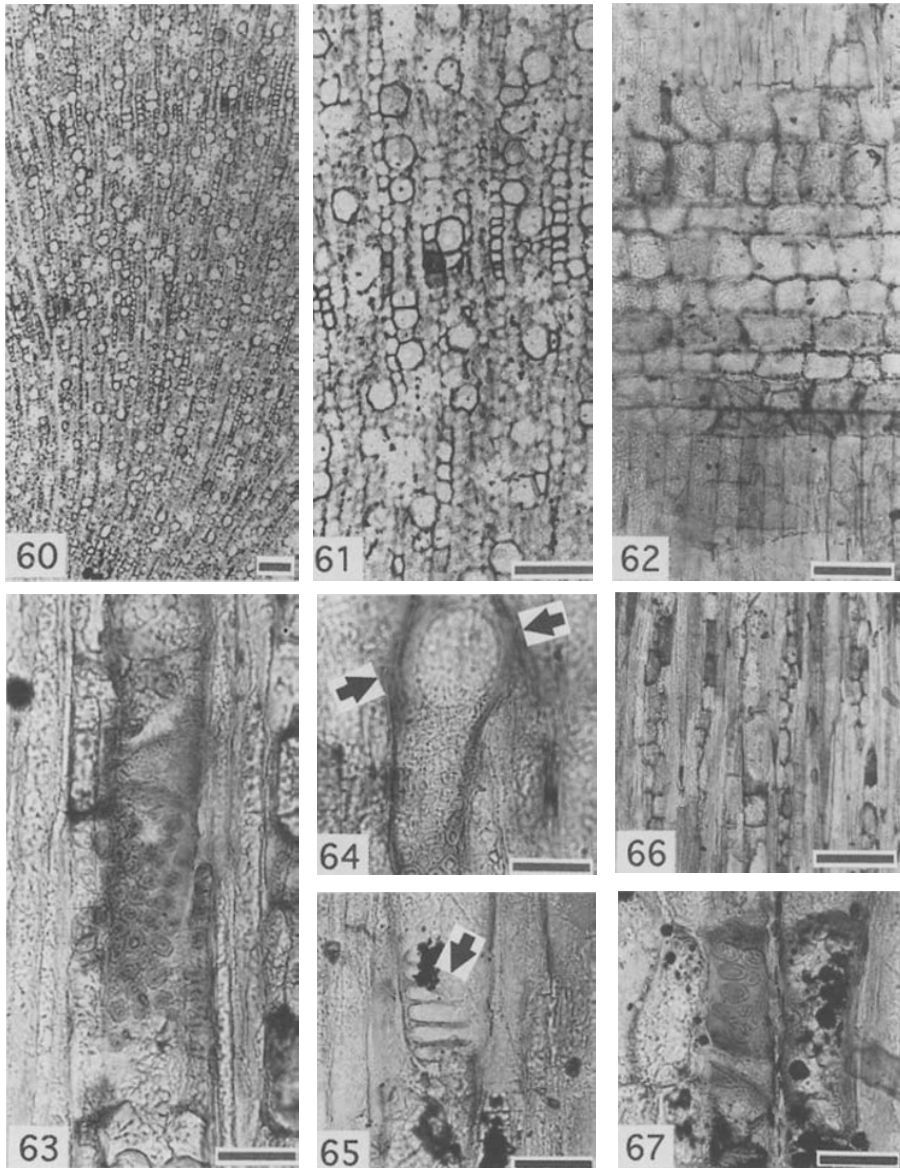
Fig. 60–67. *Sabiaceoxylon jezoense* gen. et sp. nov. (TUSw-KK 94183, holotype) – 60: TS, diffuse-porous wood and high vessel frequency. – 61: TS, vessels solitary and in radial multiples. – 62: RLS, heterocellular ray. – 63: TLS, alternate intervessel pits. – 64: RLS, simple perforation plate (between arrows). – 65: RLS, scalariform perforation plate (arrow). – 66: TLS, narrow rays. – 67: RLS, large vessel-ray pits. — Scale bars = 100 μm in Fig. 60, 61 & 66; 50 μm in Fig. 62; 25 μm in Fig. 63, 64, 65 & 67.

1950). Vessels often in radial multiples and the simultaneous occurrence of simple and scalariform perforation plates are known in *Meliosma* and *Ophiocaryon* of the Sabiaceae. Rays are heterocellular and narrower in *Ophiocaryon* (less than 4 cells wide) than in *Sabia* (up to 20 cells wide). Axial parenchyma is vasicentric in *Meliosma* and *Ophiocaryon,* but sparse or absent in *Sabia*. Therefore, the present fossil has anatomical characters that occur in the Sabiaceae and, consequently, the fossil is described under the new generic name *Sabiaceoxylon.*

There is only one report of fossil wood comparable to the Sabiaceae. Watari (1949) reported silicified woods of *Meliosma oldhami* from the Miocene of Japan. It is similar to the living species *Meliosma oldhami.*

Shimakura (1937) reported *Dryoxylon* cfr. *jezoense* from the Upper Cretaceous (Coniacian–Santonian) of Hokkaido. It is similar to the present fossil in vessel characters (vessel distribution, diameter, radial multiples), ray characters (type, width) and others, but differs in having spiral thickenings in the vessels and the absence of scalariform perforation plates. He compared his fossil to *Populocaulis jezoensis* (Stopes & Fujii 1910). *Populocaulis jezoensis* is a diffuse-porous wood characterized by uniseriate rays, but Stopes and Fujii (1910) did not describe important anatomical features such as perforation plates, intervessel pits, cell shape of rays etc. Therefore, it is difficult to compare it to the present fossil. We conclude that there is no Cretaceous fossil wood comparable with the present one.

Stopes and Fujii (1910) also reported a twig with pith as *Sabiocaulis sakuraii*. Because it has a very small amount of secondary xylem, their diagnosis is mainly based on primary tissue structure and lacks a description of the wood structure.

ULMINIUM Unger emend. Felix 1883 (Lauraceae)

14. *Ulminium kokubunii* Ken. Takahashi & M. Suzuki, sp. nov. (Fig. 68–72)

Description:

Growth rings very distinct, marked by difference of vessel size between earlywood and latewood and radially flattened fibers in the latewood.

Wood semi-ring-porous.

Vessels common, 24–32 (mean 26) per square mm; round in cross section; solitary (49%) and in radial multiples of 2 to 4; 45–115 (mean 78) × 55–125 (mean 94) μm in tangential × radial diameter; 310–500 (mean 390) μm in vessel element length; perforation plates mostly simple and sometimes scalariform with less than 10 bars; intervessel pits crowded alternate; polygonal, 6 μm in diameter; vessel-ray pits alternate, simple and round.

Imperforate tracheary elements septate fibers with no pits.

Axial parenchyma abundant, vasicentric, composed of large cells (20 × 30 μm in cross section) including swollen ones similar to oil cells; no crystalliferous elements observed.

Rays up to 3 cells (40 μm) wide; 90–580 μm high; generally homocellular, occasionally with one marginal row of upright or square cells; procumbent cells 50 × 25 μm
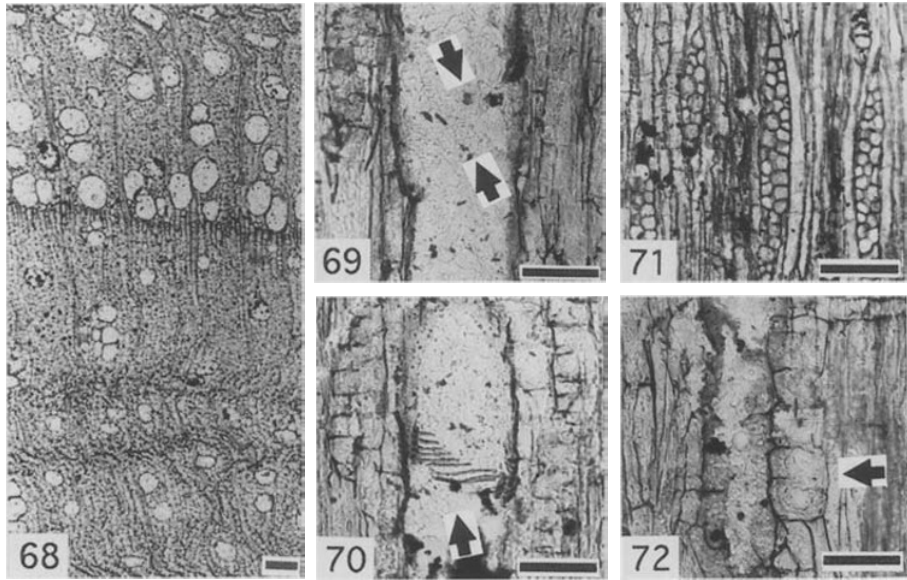
Fig. 68–72. *Ulminium kokubunii* sp. nov. (TUSw-KK 95511, holotype) – 68: TS, semi-ring-porous wood. – 69: TLS, simple perforation plate (between arrows). – 70: RLS, scalariform perforation plate (arrow). – 71: TLS, low narrow rays. – 72: RLS, vasicentric parenchyma and swollen parenchyma cells (arrow). – Scale bars = 100 μm in Fig. 68 & 71; 50 μm in Fig. 69, 70 & 72.

in radial × vertical lengths and upright cells 20 × 40 μm in radial × vertical lengths; uniseriate ones abundant; no crystalliferous elements observed.

Derivation of species name: After Hiroji Kokubun, who collected the holotype.
Holotype: KK 95511 (1.2 × 1.5 cm in diameter) is a stem wood.
Locality: Gakko-no-sawa, Obira-cho, Rumoi County, Hokkaido.
Horizon and age: Member Uf–Uk, Upper part of the Yezo Group; Santonian.
Collector: Hiroji Kokubun.
Other specimens: Turonian: KM 97041; Coniacian: KK 94184; Santonian: KK 95512; age unknown: NS 96021.

Affinity — Distinct growth rings, vessels in radial multiples, simple and scalariform perforation plates, crowded alternate intervessel pits, vasicentric parenchyma, idioblasts resembling oil cells, and narrow rays in the present fossils indicate an affinity to the genus *Ulminium*.

Ulminium was established by Unger (1842) based on a fossil wood from the Tertiary of the Czech Republic, and he considered the fossil as anatomically similar to *Ulmus* of the Ulmaceae. The original description of *Ulminium diluviale*, the type species of the genus, was brief. Later, Felix (1883) found many characters of the Lauraceae in the holotype specimen of *Ulminium*, so *Ulminium* was referred to the Lauraceae.

There are six species of *Ulminium* described from the Cretaceous (2 species) and Paleogene (4 species) (Page 1967; Wheeler et al. 1977; Scott & Wheeler 1982; Crawley 1989) (Table 5). Except for *U. porosum*, these species differ from *U. kokubunii* by their heterocellular rays. Furthermore, *U. porosum, U. parenchymatosum, U. elliotti* and *U. pattersonensis* have only simple perforation plates. Therefore, *U. kokubunii* is distinguishable from all *Ulminiun* species already known.

Sassafrasoxylon gottwaldii, attributed to the Lauraceae, was described by Poole et al. (2000) from the Maastrichtian of Antarctica. It has ring-porous wood and mostly solitary vessels.

Table 5. Comparison of the *Ulminium* species.

Species:	*U. porosum*	*U. parenchymatosum*	*U. scalariforme*	*U. elliotti*	*U. pattersonensis*	*U. mulleri*	*U. kokubunii*
Reference	Wheeler et al. 1977	Wheeler et al. 1977	Scott & Wheeler 1982	Crawley 1989	Page 1967	Page 1967	this study
Geological time	Eocene	Eocene	Eocene	Paleocene	Maastrichtian	Maastrichtian	Turonian
Locality	Yellowstone National Park, USA	Yellowstone National Park, USA	Oregon, USA	England	California, USA	California, USA	Hokkaido, Japan
Growth rings	indistinct	indistinct	indistinct	distinct	indistinct	absent	distinct
Vessel arrangement	diffuse-porous	diffuse-porous	diffuse-porous	diffuse-porous	diffuse-porous	diffuse-porous	semi-ring-porous
Vessel multiples	up to 5	mostly solitary	up to 3	mostly solitary	up to 5	mostly solitary	up to 4
MTD (μm)	92	92	70	135–147	106	103	78
Perforation plates	simple	simple	simple & scalariform	simple	simple	simple	simple & scalariform
VRP	round to oval, or irregular	large, horizontally elongate	large, horizontally elongate	alternate, round to elliptical	large, horizontally elongate	?	alternate, round
Ray type	heterocellular	homocellular	homocellular	heterocellular	heterocellular	heterocellular	homocellular
MSRW	up to 5	up to 4	up to 3	up to 7	up to 3	up to 4	up to 3
Oil or mucilage cells	present	present	present	present	absent	present	present

MTD = mean tangential diameter; VRP = vessel-ray pits; MSRW = multiseriate ray width.

DISCUSSION

In this paper, 14 new species representing 10 genera were described from the Cretaceous, ages ranging from the Albian to Santonian of the Yezo Group (Table 1). There is no fossil that we could identify to an already described species. Five genera (*Icacinoxylon*; *Plataninium*; *Magnoliaceoxylon*; *Ulminium*; *Paraphyllanthoxylon*) are already known from the Cretaceous of other regions of the world (e. g. North America, Europe, Africa), one genus, *Hamamelidoxylon*, from the Tertiary, and four genera, *Frutecoxylon*, *Nishidaxylon*, *Sabiaceoxylon* and *Castanoradix*, are new. The fact that all species and the four genera are new reflects the absence of previous studies about dicotyledonous fossil wood from the Cretaceous in Japan.

There are only two pioneer works on the Cretaceous dicotyledonous wood in Japan: Stopes & Fujii (1910) and Shimakura (1937). Stopes and Fujii described *Jugloxylon hamanoanum*, *Populocaulis jezoensis*, *Fagoxylon hokkaidense* and *Sabiocaulis sakuraii*. It is difficult to compare these fossil woods and our fossil woods because Stopes and Fujii's descriptions are so brief. Shimakura (1937) also described *Aptiana?* sp. and *Casuaroxylon japonicum* from the Upper Cretaceous of Hokkaido. These two species probably represent taxa different from those described here. This indicates that there was a more diverse woody flora than previously known in the Cretaceous of Hokkaido.

Evolution of wood anatomical characters

Geological ages of the fossil woods described in this paper range from 83 Ma (million years ago) to at least 95 Ma (Fig. 2).

Growth rings

Among the dicotyledonous woods described in the present paper, growth rings are absent in most specimens, and are restricted to three genera: *Plataninium, Hamamelidoxylon* and *Ulminium* (Table 1). Growth rings of *Plataninium jezoensis* and *P. ogasawarae* woods are indistinct, whereas most *Hamamelidoxylon obiraense* specimens have relatively distinct growth rings. *Ulminium kokubunii* woods have distinct growth rings, and one specimen (KK 95511, holotype) is semi-ring-porous. This is the only non-diffuse-porous representative among the 144 fossil woods examined.

Wheeler and Baas (1991, 1993) found that distinct growth rings occur in a much lower percentage of Cretaceous dicotyledonous woods than in Tertiary or Recent woody flora. They suggested they indicate less seasonal environments. Poole (2000) suggested that this phenomenon might reflect the higher temperature in the Cretaceous than the later periods.

Twenty-one taxa of conifers have been described from the Cretaceous of Hokkaido (Stopes & Fujii 1910; Shimakura 1937; Ogura 1944; Nishida 1974; Nishida & Nishida 1984, 1985; Nishida et al. 1995). Of these, presence or absence of growth rings was described for 19 taxa; 15 taxa have distinct growth rings, three have indistinct ones, and only one lacks them. We examined about 400 Cretaceous wood specimens, 144 were dicotyledons. Most of the remaining conifers had distinct growth rings (data not shown). Therefore, we suggest there were seasonal climates in the Cretaceous of Hokkaido that

resulted in the formation of distinct growth rings in the majority of conifers, and the absence of growth rings in the majority of dicotyledonous woods indicates that distinct growth rings in dicotyledons had not yet evolved. However, Poole (1999) suggested that the presence / absence of growth rings is most likely to be the result of spatial separation. She assumed that conifers grew in areas with high mountains, edaphic drought or inundation. Further investigation of both the coniferous and dicotyledonous wood from the Yezo Group is needed.

Vessels

The oldest vessel-bearing Japanese fossil wood is *Icacinoxylon kokubunii* from the Albian, which is the same stage of previous reports from the United States (Serlin 1982; Thayn et al. 1983, 1985). Although the origin of Angiosperms is considered to be in the Jurassic (Poole & Francis 2000), there are no reliable evidences of dicotyledonous woods in that age. Our study confirms that vessel-bearing woods had evolved and were widely distributed in Asia and North America in the early Cretaceous.

Perforations — Wheeler and Baas (1991, 1993) pointed out that exclusively scalariform perforation plates are more frequent and exclusively simple perforation plates are less common in late Cretaceous woods compared with Tertiary woods. This condition in the older Cretaceous is also found in the present study. Eight of the 14 species have exclusively scalariform perforation plates (species of *Frutecoxylon, Hamamelidoxylon, Icacinoxylon, Magnoliaceoxylon, Nishidaxylon* and *Plataninium*), four species have only simple perforation plates (species of *Castanoradix* and *Paraphyllanthoxylon*), while two species have both (species of *Sabiaceoxylon* and *Ulminium*) (Table 1). Although the oldest wood (*Icacinoxylon kokubunii* in the Albian) has exclusively scalariform perforation plates, *Paraphyllanthoxylon cenomaniana*, with exclusively simple ones, appeared in the Cenomanian of Japan. Thayn et al. (1983, 1985) reported *Paraphyllanthoxylon* (simple) and *Icacinoxylon* (scalariform) from the same stratum of the Lower Cretaceous. These results suggest two possible ideas. If the simple perforation plates were derived from the scalariform ones, the simple ones evolved during very early stages of vessel evolution among dicotyledons. Another is that the simple perforation plates and scalariform perforation plates evolved from tracheids independently. The simultaneous presence of simple and scalariform perforation plates within one wood in some dicotyledons (e. g. Lauraceae) may argue against the latter idea. Further studies on older dicotyledonous wood will be required for verification of these ideas.

Vessel size and arrangement — Most of the specimens described in the present paper have narrow vessels (less than 100 μm mean tangential diameter). *Paraphyllanthoxylon cenomaniana* and *Castanoradix cretacea* have wider vessels (about 170 μm mean tangential diameter), both species with exclusively simple perforation plates.

Vessel grouping — Among the 14 species described herein, one species has exclusively solitary pores (*Nishidaxylon jezoense*), two species have mostly solitary pores (more than 80% solitary pores) (*Icacinoxylon kokubunii* and *Magnoliaceoxylon hokkaidoense*), one species has pores predominantly in multiples (*Sabiaceoxylon jezoense*), and the remaining nine species are intermediate. Although Wheeler and Baas (1991, 1993) reported that woods with exclusively solitary pores are more frequent in the

Cretaceous than in the Tertiary and Recent, the results of the present paper do not support that observation. It may be due to the fact that most of their data were for the latest Cretaceous.

Intervessel pits — In the Hokkaido woods, opposite and/or scalariform intervessel pitting is recognized from the Albian onward, and alternate pitting appears soon after in the Cenomanian (Table 6). The Baileyan trends suggest scalariform and opposite pits precede alternate pits, but there is no significant difference between the ages of

Table 6. Occurrence of wood anatomical characters by geological age.

Wood anatomical characters		Stage				
		Alb	Cen	Tur	Con	San
Growth rings distinct			+	+	+	+
Vessels	predominantly solitary	+	+	+	+	+
	solitary & in multiples		+	+	+	+
	mostly multiples		+	+	+	+
diameter	< 50 μm			+	+	+
	50–150 μm	+	+	+	+	+
	> 150 μm		+	+	+	
element length	> 800 μm	+	+	+	+	+
	< 500 μm			+	+	+
perforation	scalariform only	+	+	+	+	+
	simple only		+	+	+	+
	scalariform & simple			+	+	+
intervessel pit	scalariform	+	+	+	+	+
	opposite only		+	+		+
	alternate only		+	+	+	+
Imperforate tracheary elements						
fiber-tracheids		+	+	+	+	+
libriform fibers	non-septate		+	+	+	+
	septate			+	+	+
vasicentric tracheids				+		
Axial parenchyma						
	diffuse		+	+	+	+
	diffuse-in-aggregates	+	+	+	+	+
	scanty paratracheal		+	+	+	+
	vasicentric		+	+	+	+
Rays						
width	up to more than 10 cells wide	+	+	+	+	+
	up to 10 cells wide		+	+	+	+
	uniseriate only			+		
heterocellular		+	+	+	+	+
homocellular	all procumbent cells		+	+	+	+
	all upright cells			+		

Alb = Albian, Cen = Cenomanian, Tur = Turonian, Con = Coniacian, San = Santonian.

appearance of those types of intervessel pitting. Among the 14 Yezo species, three species have opposite and/or scalariform pitting, three species have opposite pitting, six species have alternate pitting, while one species lacks intervessel pitting because of its exclusively solitary pores. Wheeler and Baas (1991) found a tendency toward more frequent opposite and/or scalariform pitting and less frequent alternate pitting in Cretaceous woods than in Tertiary and Recent woods. The present study found a rather high frequency of alternate intervessel pitting, but still lower than present-day incidences.

Spiral thickenings — Spiral thickenings of vessel walls were not found in any fossil woods in the present study. This agrees with previous studies on Cretaceous woods (Wheeler & Baas 1991). Of course we cannot exclude the possibility that the spiral thickenings were not observed because of poor preservation in fossil woods. But the fact that no fossil woods reported from the Cretaceous strata have spiral thickenings is supported by our findings. The absence of this character in Cretaceous wood may suggest its advanced or derivative origin among wood characters.

Axial parenchyma

Kribs (1937) proposed the idea that axial parenchyma distribution parallels the vessel element evolution described by Bailey and Tupper (1918). We observed four axial parenchyma patterns, i.e., diffuse, diffuse-in-aggregates, scanty paratracheal and vasicentric (Table 6). In Kribs's model, diffuse and diffuse-in-aggregate patterns are more primitive and scanty paratracheal and vasicentric patterns are more advanced. Highly specialized parenchyma patterns (e.g., aliform, confluent and others) are not seen in any Yezo woods. These results may support Kribs's idea as indicated by Wheeler and Baas (1991).

Rays

Ray types — Kribs (1935) classified rays of dicotyledons, and proposed an idea of ray evolution in accordance with that of vessel element evolution proposed by Bailey and Tupper (1918). In Kribs's view, heterocellular rays with procumbent body cells and many marginal rows of upright and/or square cells (Kribs's heterogeneous type I) are the most primitive; homocellular rays composed of procumbent cells only (Kribs's homogeneous type II & III) is the most advanced. The oldest wood in the present paper (*Icacinoxylon kokubunii* from the Albian) has markedly heterocellular rays assigned to Kribs's heterogeneous type I (Table 6). So-called primitive rays are more abundant in woods from the early half of the Yezo Group and more advanced rays are present in woods from the later half. Therefore, the tendency from heterogeneous rays to homogeneous ones may roughly be recognized as Wheeler and Baas (1991) indicated more frequent heterocellular rays and less frequent homocellular rays in the Cretaceous in comparison with ones in the Tertiary and Recent.

Fossil wood floras from the Cretaceous of Japan

We examined 54 wood samples obtained from strata of the Aptian and Albian in Hokkaido (Table 7). We could find only two specimens of *Icacinoxylon kokubunii,* which is the species most widely found in the geological ages of the present study (Table 1), while all of the remaining 52 specimens are coniferous woods. Despite their small size (both

Table 7. Frequency of dicots among fossil wood specimens from the Cretaceous of Hokkaido. (Samples with uncertain age excluded.)

Age	No. of samples	No. (%) of dicot samples	No. of dicot species
Albian	54	2 (4%)	1
Cenomanian	33	7 (21%)	4
Turonian	119	62 (52%)	10
Coniacian	34	13 (38%)	7
Santonian	69	33 (48%)	8
Total	309	117 (38%)	14

about 1 cm in diameter), the two specimens from the Albian are important because they are the earliest dicotyledonous fossils in Japan. *Icacinoxylon* is also one of the earliest fossil dicotyledonous woods in the world (Thayn et al. 1983). As stated in the introduction of the present paper, the most reliably reported earliest dicotyledonous woods were from the Albian (*Aplectotremas halistichum* Serlin 1982; *Paraphyllanthoxylon utahense* Thayn et al. 1983; *Icacinoxylon pittiense* Thayn et al. 1985).

From the Cenomanian, we examined 33 woods and found seven dicotyledonous woods (Table 7) assigned to *Icacinoxylon kokubunii, Plataninium jezoensis, Hamamelidoxylon obiraense* and *Paraphyllanthoxylon cenomaniana* (Table 1). The first three species have scalariform perforation plates, and the last has exclusively simple ones. *Paraphyllanthoxylon* is the earliest taxon found in Japan with simple perforation plates. *Plataninium* and *Hamamelidoxylon* are members of the Platanaceae and Hamamelidaceae respectively. These two are the earliest taxa that have possible affinities to Recent families.

From the Turonian, 62 dicotyledonous woods were identified from 119 specimens (Table 7). Among the 10 species recognized, six species are new: *Castanoradix cretacea, C. biseriata, Frutecoxylon yubariense, Icacinoxylon nishidae, Magnoliaceoxylon hokkaidoense* and *Ulminium kokubuni* (Table 1). We suggest that Lauraceae were in Japan by the Turonian, based on the occurrence of *Ulminium*.

From the Coniacian, 13 dicotyledonous woods, representing seven species, were found among 34 specimens (Table 7). One species (*Sabiaceoxylon jezoense*) is new (Table 1). It has fairly advanced characters.

From the Santonian, 33 dicotyledonous woods, representing eight species, were found among 69 wood specimens (Table 7). Three species are new: *Nishidaxylon jezoense, Paraphyllanthoxylon obiraense*, and *Plataninium ogasawarae* (Table 1).

Dicotyledonous woods were diversified already in Japan by the Turonian age (mid-Cretaceous) with 10 species of eight genera (Table 1). In North America, many dicotyledonous woods from the Maastrichtian (the uppermost Cretaceous) show considerable diversity in structural characters (Page 1967, 1968, 1970, 1979, 1980, 1981; Wheeler et al. 1987, 1995; Wheeler & Lehman 2000). However, studies on dicotyledonous fossil woods from ages earlier than the Maastrichtian are few (e. g., Herendeen 1991a, b; Thayn et al. 1983, 1985). The present study extends our knowledge of wood structural diversity among the early dicotyledons in the mid-Cretaceous in the northern hemisphere.

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