Bull. Natn. Sci. Mus., Tokyo, Ser. C, 20 (3), pp. 89–108, September 22, 1994

Betulaceae from the Paleogene of Hokkaido, Japan

By

Toshimasa TANAI

23–546 Dialand, Kannami-cho, Shizuoka Pref. 419–01
(Communicated by Teruya UYENO)

Abstract Fossils of the Betulaceae abundantly occur in the Eocene and Oligocene of Hokkaido, especially during the cooler intervals; they are represented by 5 genera (*Alnus*, *Betula*, *Carpinus*, *Corylus* and *Ostrya*) and 17 species, which include 3 new species and 1 new combination. All the taxa of this family are represented by leaves, except some of *Betula* and *Carpinus*. Their stratigraphic distribution of the Paleogene taxa of Hokkaido indicates that the differentiation of the Betulaceae into extant genera seems to have occurred during the Late Eocene to Early Oligocene.

Introduction

The Betulaceae has long history of evolution since Late Cretaceous time; this family is widely distributed in the Northern Hemisphere through the Tertiary to the Recent. Although the Betulaceae was supposed to have appeared in the Late Cretaceous, principally based on palynological record (WOLFE, 1973; MULLER, 1981), the current studies of fossil reproductive organs and leaves indicate that unequivocal differentiation into extant genera seems to have occurred during the Eocene and Oligocene (CRANE, 1989).

Fossils of the Betulaceae in East Asia are commonly described from the Neogene by various authors, with many species represented by both leaves and reproductive organs; they are documented to be closely related to the extant species. On the other hands, Paleogene fossils of this family hitherto described from East Asia were represented only by foliage, with exception of some Oliogocene specimens (UEMURA & TANAI, 1993). Although they seem to be distinguished from Neogene species, some of them need to be reinvestagated in generic assignment.

A number of taxa referred to temperate families are more commonly included during the cooler intervals of the Late Eocene to Oligocene in Hokkaido, compared with warmer interval of the Middle Eocene (TANAI, 1992b). This indicates that the temperate dicots diversified since the Late Ecoene due to cooling climate. Of the temperate families from the Paleogene of Hokkaido, the taxonomy and stratigraphic ranges of the Betulaceae are described.

The fossil specimens here studied are mainly collected by the author for many years. Oligocene specimens were partly collected by K. UEMURA of the National Science Museum, Tokyo. The author expresses his gratitude to Dr. Kazuhiko UEMURA to allow to examine his collection, and also to discuss on taxonomy of some specimens. Thank is also due to Dr. Teruya UENO, the chief of Department of Geology, the National Science Museum to provide the facilities to publish this paper.

Betulaceae from the Paleogene of Hokkaido

In the Paleogene of Hokkaido are commonly found fossils of the Betulaceae, which are represented mostly by leaves: from the Eocene coal-bearing formations of the Ishikari, Uryu and Kushiro coal fields, and the Oligocene Wakamatsuzawa Formation of Kitami region. Many taxa of the Betulaceae were described from the Eocene Ikushunbetsu Formation of Yubari by ENDO (1968), and from Eocene Harutori, Yubetsu and Shakubetsu Formations of the Kushiro coal field by the author (TANAI, 1970). Several taxa of this family were recently described from the Lower Oligocene of Kitami (UEMURA & TANAI, 1993). Combined with many well-preserved specimens from the Eocene of central Hokkaido, Paleogene specimens hitherto described ara re-examined. Thus, Paleogene species of the Betulaceae from Hokkaido are listered as follows:

Betuleae

Alnus ezoensis TANAI
Alnus hokkaidoensis TANAI
Alnus ishikariana TANAI sp. nov.
Alnus kitamiensis UEMURA and TANAI
Alnus kushiroensis TANAI
Alnus subezoensis TANAI sp. nov.
Alnus yubarica TANAI sp. nov.
Alnus sp.
Betula kitamiana UEMURA and TANAI
Betula spp. 1, 2, 3.

Coryleae

Carpinus kitamiensis UEMURA and TANAI
Carpinus kushiroensis TANAI
Carpinus shimokawarae ENDO
Corylus palaeomaximowicziana (ENDO) TANAI comb. nov.
Ostrya sp.

The stratigraphic distribution of these 17 species of Betulaecae is shown in Figure 1. It is noteworthy that the genus *Alnus* diversified since late Middle Eocene in specific level. Among the Eocene alders *A. ezoensis* and *A. subezoensis* are most abundant in number of specimens in many localities of the Kushiro and Ishikari coal fields. It is probably due to the fact that these two species are closely related to the extant water-loving alder such as *A. japonica* (THUNB.) STEUD., and that the Eocene plant-bearing formations are usually intercalated by coal beds which were formed under swamp basin.

Three species of *Betula* were described from the Ikushunbetsu Formation of

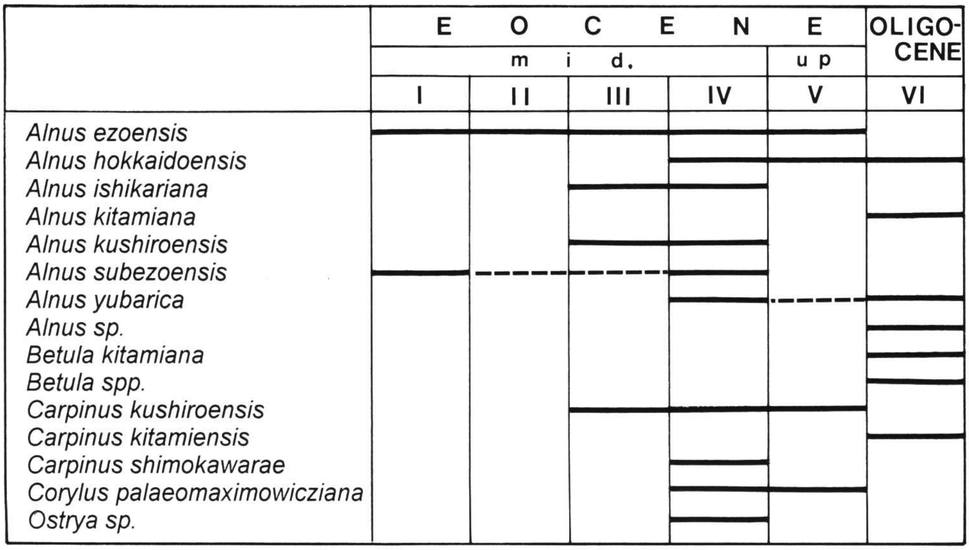


Fig. 1. Stratigraphic distribution of the Betulaceae in the Paleogene of Hokkaido. The Roman numerals (I–VI) show the Paleogene plant-bearing horizons of Hokkaido (see TANAI, 1992).

Yubari by ENDO (1968), but they show no characters of this genus. Birch is first known in the Oligocene Wakamatsuzawa Formation (UEMURA & TANAI, 1993); it was not found from the Eocene coal-bearing formations of Hokkaido in spite of extensive fossil collection. Considering common occurrence of birch specimens in the Lower Miocene coal-bearing formation of Japan (TANAI, 1961; HUZIOKA, 1964), birch seems not to have inhabited the lowland and mountain slopes of Hokkaido during the Eocene.

Coryleae is suggested to be phylogenetically older group in the Betulaceae (CRANE, 1989). The genus *Corylus* is expected to have appeared earlier in North Japan than shown in Fig. 1. The genus *Carpinus* is poorly represented in the Paleogene of Hokkaido: two species represented by leaves are from the Early Late Ecoene, and one species represented by involucre is from the Oligocene. Many species of *Carpinus* were known since the Early Miocene of Japan (TANAI, 1972), represented by both leaves and involucral nuts. The specific diversification of *Carpinus* seems to have occurred since the Early Miocene in Japan. Fossils of the genus *Ostrya* is also scarcely found in the Paleogene of Hokkaido, although they are common in the Early Miocene of Japan.

Systematic Descriptions

Terms of leaf architecture used in the description are based mostly on those of HICKEY (1979). For the occurrence of each species, the localities and stratigraphic names that are cited here, are referred to those of the previous papers (TANAI, 1981, 1989; UEMURA & TANAI, 1993).

Order Betulales

Family Betulaceae

Genus *Alnus* Mill.

Alnus ezoensis TANAI

Pl. 1, figs. 1–7; Fig. 2-Aa, b

Alnus ezoensis TANAI. 1970, p. 466, pl. 7, figs. 1, 5, 7.
Alnus palaeojaponica ENDO (non WEYLAND, 1943), 1968, p. 424, pl. 8, fig. 1.
Alnus hokkaidoensis auct. non TANAI: CHELEBAEVA, 1991 (part), p. 107, pl. 13, figs. 4, 5, text-fig. 38–3.

Type: Holotype UHMP No. 26914; Nakanosawa, Yubetsu, Akancho, Hokkaido; Yubetsu Formation (Late Eocene).

Discussion: This alder species is characterized by the following features: the oblong shape, triangular teeth (A1) with acuminate tip, 9 to 13 pairs of the craspedodromous secondary veins that are nearly straight, intercostal tertiary veins straight or slightly convex-percurrent (3 to 4 per cm), and 1 to 3 smaller teeth between the secondaries.

A single leaf described as *A. palaeojaponica* ENDO from Yubari (ENDO, 1968) is identical with *A. ezoensis*, but the epithet of "*palaeojaponica*" is the junior homonym of a German Oligocene alder species (WEYLAND, 1943). *A. palaeojaponica* WEYLAND is different from *A. ezoensis* in having smaller teeth and semi-craspedodromous secondary venation. Two leaves illustrated as *Alnus hokkaidoensis* by CHELEBAEVA (1991) from the Eocene of Kamchatka are included in *A. ezeonsis* by their leaf shape, venation and marginal features. *A. ezoensis* was first described from the Paleogene of the Kushiro coal field, and it is one of the most common dicots in the Paleogene of Central Hokkaido.

Occurrence: Ishikari coal field Nc-1, Nc-3, Yc-2, Bc-1, Ic-2, Ic-3, Ic-6, Ic-9, Ic-10, Ic-11; Kushiro coal field Kh-1, Ky-1, Ky-2, Ks-2, Ks-4.

Collections: HUMP no. 26914 (holotype), 26915 (paratype), HUMP nos. 26916, 26917; NSM–PP 10533, 10534, 10536, 10542, 10543 (hypotypes); NSM 10469 (=NSM–PP 1785), NSM–PP 10535, 10537–10541, 10543–10545.

Alnus hokkaidoensis TANAI

Pl. 5, figs. 3, 4; Pl. 6, fig. 2; Fig. 2-Da, b

Alnus hokkaidoensis TANAI, p. 467, pl. 8, figs. 2, 7; CHELEBAEVA, 1991 (part), p. 107, pl. 13, fig. 3, text-fig. 38–1.
Corylus japonica ENDO, 1968, p. 424, pl. 8, figs. 2, 3.

Type: HUMP No. 26918; Harutori coal mine, Kushiro City, Hokkaido; Harutori Formation (late Middle Eocene).

Discussion: *Alnus hokkaidoensis* has the following foliar characters: the wide ovate to suborbiculate shape (length/width ratio less than 1.2); nearly truncate to broadly cordate base that is entire-margined; acuminate teeth (D4) with glandular, sharply pointed tips; secondary veins and their branches that enter teeth centrally; 1 or 2 pairs of basal secondary veins approximately perpendicular to the midvein. Although the original specimens from the Kushiro coal field are poorly preserved in the higher order venation, some leaves of the Ishikari coal field show that 4 or 5 sided areoles (0.2–0.3 mm across) are composed of fifth order veins, and are intruded by 2 or 3 times branching veinlets.

Corylus japonica described from the Ikushunbetsu Formation of Yubari (ENDO, 1968) is identical with *A. hokkaidoensis* in all characters including areoles and veinlets, although the principal teeth have somtimes attenuate tips. As already pointed out (TANAI, 1970: p. 467), the epithet "*japonica*" for *Alnus* was occupied in the extant alder species, *A. japonica* (THUNB.) STEUD.

Occurrence: Kushiro coal field Kh-1, Ky-2, Ky-3, Ks-1, Ks-4; Ishikari coal field Ic-9, Ic-11; Wakamatsuzawa, Kitami City.

Collections: HUMP 26918 (holotype), 26919 (paratype), 26920; NSM–PP 10559, 10560, NSM 10470(=NSM–PP 1786) (hypotypes).

Alnus ishikariana TANAI, sp. nov.

Pl. 3, fig. 2; pl. 4, figs. 4–6; Fig. 2-Ea. b

Type: Holotype NSM–PP 10565: Reisuizan, Yubari, Hokkaido; Ikushunbetsu Formation (late Middle Eocene).

Diagnosis: Leaves narrow oblong to narrow elliptic in general outline, acute at both base and apex, 7 to 16 cm (estimated) long and 2.5 to 6.6 cm (estimated) wide; margin doubly serrate with glandular tipped teeth; principal teeth in which secondary veins end large, acute; except the upper margin of blade, one or two smaller teeth existing between pricipal teeth; the principal and smaller teeth accompanied with one or two minute subsidiary teeth on basal side; one minute teeth sometimes present on apical side of principal teeth; petiole missing. Venation pinnate: midvein medium in thickness, straight; secondary veins about 15 pairs, opposite to subopposite; diverging at 50° to 55°, nearly straight, parallel each other, entering principal teeth centrally, giving off basally one or two external branches which enter smaller intersecondary teeth; intercostal tertiary veins percurrent, flexuous or branched, somewhat irregularly spaced, 4 to 6 per cm; marginal tertiary veins entering minute teeth or camptodromous; quaternary and quinternary veins forming polygonal areoles that are 0.7 to 1 mm across; freely ending veinlets more than three times branching.

Discussion: The doubly serrate margin, acute glandular tipped teeth, flexuous intersecondary tertiary veins with irregular course, well-developed sinal knots of vein and more than three times branching veinlets are feutures of many extant alders. However, no extant leaf is closely similar to these fossil leaves.

Leaves of *Alnus rubra* BONG, living in western North America resemble the fossil leaves in having lobulate and doubly serrate margin and broadly cuneate base, but

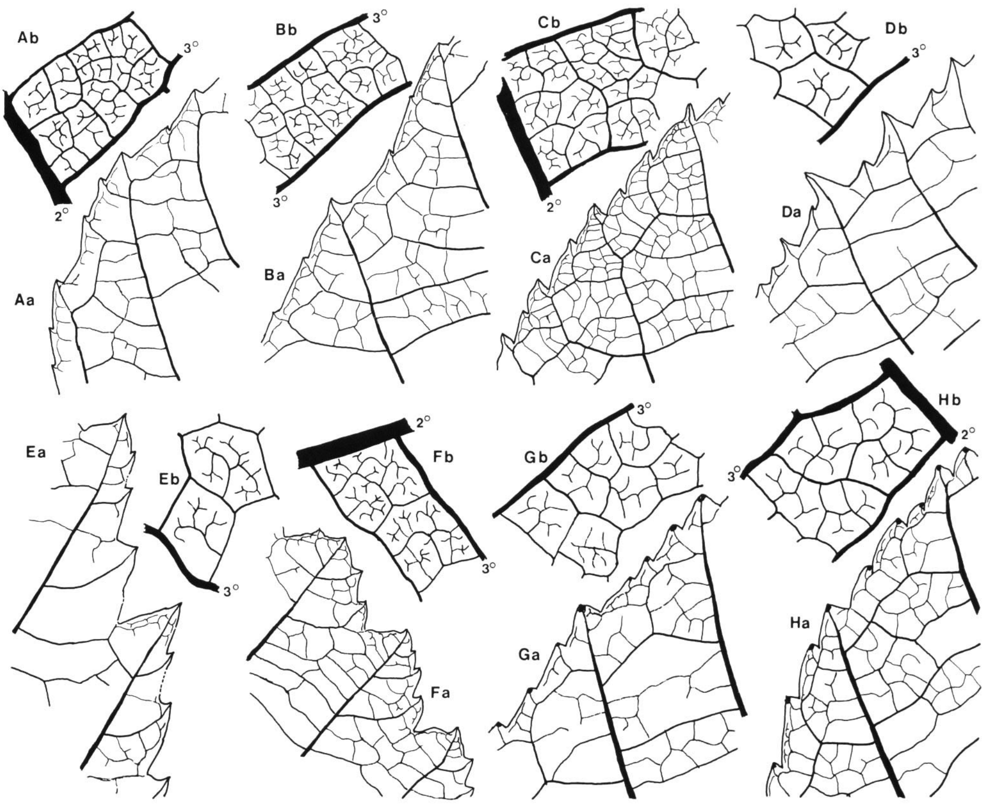


Fig. 2. The marginal venation features and areoles of Paleogene *Alnus* leaves and their related extant species. 2° and 3° in each figure indicate the secondary and tertiary veins, respectively. Aa, b, *Alnus ezoensis* TANAI, NSM–PP 10536 (pl. 1, fig. 4), Aa ×2.5, Ab ×12.5; Ba, b, *Alnus subezoensis* TANAI, NSM–PP 10549 (pl. 2, fig. 3), Ba ×2.5, Bb ×12.5; Ca, b. *Alnus traveculosa* HAND.–MAZZ., NSM Paleobot. Ref. Coll. T-559, Ca ×4, Cb ×12.5; Da, b, *Alnus hokkaidoensis* TANAI, NSM–PP 1786 (pl. 6, fig. 2), Da ×2.5, Db ×12.5; Ea, b, *Alnus ishikariana* TANAI, NSM–PP 10565 (pl. 4, fig. 4), Ea ×2.5, Eb ×12.5; Fa, b, *Alnus rubra* BONG., NSM Paleobot. Ref. Coll. T-1832, Fa ×2.5, Fb ×12.5; Ga, b, *Alnus yubarica* TANAI, NSM–PP 10568 a (pl. 3, fig. 3), Ga ×4, Gb ×12.5; Ha, b, *Alnus serrulatoides* CALL., NSM Paleobot. Ref. Coll. T-731, Ha ×4, Hb ×12.5.

differ in less secondary veins and usually ovate shape. *A. hirsuta* Turcz. of East Asia may be also related to *A. ishikariana* in marginal character, although quite different in leaf shape.

Occurrence: Ishikari coal field Ic-3, Ic-9.

Collection: NSM–PP 10565 (holotype); NSM–PP 10567, 10567 (hypotypes).

Alnus kitamiensis UEMURA et TANAI

Alnus kitamiensis UEMURA and TANAI, 1993, p. 21, figs. 1–13, 16.

Occurrence: Wakamatsuzawa and Minamigaoka, Kitami City.

Collection: NSM–PP 10500 (holotype), NSM–PP 10501–10503 (paratypes); NSM–PP 10504–10508, 105518–10532.

Alnus kushiroensis TANAI

Pl. 4, fig. 2; pl. 5, figs. 1, 2; Fig. 3-Aa, b

Alnus kushiroensis TANAI, 1970 (part), p. 468, pl. 8, fig. 1; CHELEBAEVA, 1991 (part), p. 107, pl. 11, fig. 14, text-fig. 38–2.

Corylus fosteri auct. non WARD: ENDO, 1968 (part), pl. 22, fig. 9.

Type: Holotype HUMP no. 26921; Harutori coal mine, Kushiro City, Hokkaido; Harutori Formation (late Middle Eocene).

Discussion: This species is similar to *Alnus hokkaidoensis* in some features, but it is distinguishable in the following characters: typically wide oblong to ovate shape (length/width ratio 1.45 to 1.7), and the secondary veins and marginal tertiary veins branching exmedially from the secondaries that are sometimes semicraspedodromous. Among the extant alders *A. japonica* (THUNB.) STEUD., *A. fauriei* LEV., *A. cordata* DESF. and *A. subcordata* C. A. MEY. have leaves of semicraspedodromous secondary veins. It is noteworthy that *A. kushiroens* is closely related not to East Asian extant species but to West Asian *A. subcordata*.

Of two original specimens from the Kushiro coal field, a specimen (TANAI, 1970: pl. 9, fig. 5) is excluded from *Alnus*, and is transferred to *Carpinus kushiroensis* in marginal features. A single specimen illustrated as *Corylus fosteri* WARD from Yubari by ENDO (1968) is referred to *A. kushiroensis* in marginal and venation characters, and represents a small leaf. *A. kushiroensis* is rather an uncommon alder in the Paleogene of Hokkaido.

Occurrence: Kushiro coal field Kh-1, Ky-3; Ishikari coal field Bc-1, Ic-9, Ic-11.

Collections: HUMP no. 26921 (holotype), 26923; NSM 10542 (=NSM–PP 1858), NSM–PP 10561–10563 (hypotypes); NSM–PP 10564.

Alnus subezoensis TANAI, sp. nov.

Pl. 2, figs. 1–6; pl. 3, fig. 1; pl. 4, fig. 3; Fig. 2-Ba, b

Type: Holotype, NSM–PP 10547; Reisuizan, Yubari City, Hokkaido; Ikushunbetu Formation (late Middle Ecoene).

Diagnosis: Leaves narrow ovate to elliptic in shape, 8.3 to 12 cm (estimated) long and 3.5 to 5.3 cm wide, length/width ratio 2.26 to 2.38; apex attenuate; base obtuse to rounded; margin finely serrate with minute, sharp teeth that are irregularly spaced, teeth 4 to 6 per sencondary vein; teeth apex showing glandular-like thickening; petiole thick, 1.1 to 2.2 cm long. Venation pinnate; midvein stout, straight; secondary veins rather slender, 11 to 12 in pairs, opposite to subopposite, diverging at angles of 40° to 50° on the middle and upper parts of the blade, and at wider angles on the basal part, gently curving upward, craspedodromous or semicraspedodromous; intercostal tertiary veins distinct, closely spaced (about 10 per cm), oriented obliquely to the secondary, convex-percurrent, sometimes forking at the midway; marginal tertiary veins emerging basally at acute angles from the secondary, craspedodromous or semicraspedodromous; most of secondary and marginal tertiary veins directly reaching the tooth apex along the apical side of tooth, but some of them branching just near sinus, sending one main branch to superadjacent secondary vein and the other slender branch to tooth apex; the quaternary and quinternary veins forming 4 or 5 sided areoles; the highest order venation 6th; ultimate veinlets once to twice branching.

Discussion: These leaves are closely similar to *Alnus ezoensis* in general features, and are probably a phylad of this species. However, the small, sharp teeth, closely spaced secondary veins and some semicraspedodromous secondary and marginal tertiary veins distinguish these fossil leaves from *A. ezoensis*. These features indicate that *A. subezoensis* is related to the phylad of the extant *A. japonica* and its allies, and is especially close to *A. traveculosa* HAND.-MAZZ.

Occurrence: Ishikari coal field Nc-3, Ic-3, Ic-9.

Collection: NSM–PP 10547 (holotype), 10548, 10549 (paratypes), 10549–10550 (hypotypes); NSM–PP 10551–10557.

Alnus yubarica TANAI, sp. nov.

Pl. 3, figs. 3–7; Fig. 2-Ga, b

Type: Holotype NSM–PP 10568; Dam-site, Shimizusawa, Yubari City, Hokkaido; Ikushunbetsu Formation (late Middle Eocene).

Diagnosis: Leaves wide obovate in shape, 4.2–5.4 cm long and 3.5–4 cm wide, obtuse at apex, rounded at base; margin serrate with small, deltoid, obtuse teeth; teeth typically 4 per sencondary vein, having glandular-like thickening at apex; petiole rather slender, 1.1 cm long. Venation pinnate, midvein stout, straight; secondary veins 8 in pairs, opposite to subopposite, stout except a slender basal pair, diverging at angles of 35° to 40°, broadly curving, entering the main teeth centrally; intercostal tertiary veins irregularly spaced (5 to 6 per cm), straight-percurrent, sometimes forking; the most exmedial intercostal tertiary vein convex, sending off a subtertiary branch which extends up to the superadjacent secondary vein; 4 or 5 marginal tertiary veins diverging exmedially from the basal two pairs of the secondary veins, entering teeth centrally; marginal quaternary veins from marginal convex tertiary and subtertiary veins entering teeth centrally: intercostal quaternary and higher order veins reticulate; the highest order vein sixth; areoles quadrangular to polygonal, 0.4 to 0.6 mm across; ultimate veinlets irregularly and more than 2 times branching.

Discussion: These obovate leaves are closely related to the extant *Alnus serrulatoides* CALL. in the following features: obtuse teeth, secondary veins entering teeth centrally, marginal quaternary veins from most exmedial convex tertiary entering subsidiary teeth, and irregularly branching veinlets. *Alnus yubarica* also resembles the extant *A. matsumurae* CALL. in shape and venation features; leaves of *A. matsumurae*, however, have usually larger teeth and emarginate apex. An extant alder of North America, *A. maritima* (MARSH.) NUTT., is somewhat similar to *A. yubarica* in general outline; but in *A. maritima* the marginal tertiary veins that typically emerge from secondary veins, enter subsidiary teeth with a few exceptions.

Occurrence: Ishikari coal field Ic-9, Ic-11; Wakamatsuzawa, Kitami City.

Collection: NSM–PP 10568 (holotype), 10569 (paratype).

Alnus sp.

Alnus sp., UEMURA and TANAI, 1993. Mem. Natn. Sci. Mus. Tokyo, (26): 22, fig. 18, 26.

Discussion: This incomplete specimen from Wakamatsuzawa is similar to an Eocene alder, *Alnus ishikariensis*, in foliar shape and marginal features, although less in the secondary veins. This Oligocene fossil may represent a descendant of *A. ishikariensis*.

Occurrence: Wakamatsuzawa, Kitami City.

Collection: NSM–PP 10514.

Genus *Betula* L.

Betula kitamiana UEMURA et TANAI

Betula kitamiana UEMURA and TANAI, 1993, p. 22, figs. 14, 15, 17, 19, 20.

Occurrence: Wakamatsuzawa and Minamigaoka, Kitami City.

Collection: NSM–PP 10510 (holotype), 10109 (paratype).

Genus *Carpinus* L.

Carpinus kitamiensis UEMURA et TANAI

Carpinus kitamiensis UEMURA and TANAI, 1993, p. 26, figs. 21a, b.

Occurrence: Wakamatsuzawa, Kitami, Hokkaido.

Collection: NSM–PP 10516 (holotype).

Carpinus kushiroensis TANAI

Pl. 4, fig. 1; pl. 6, fig. 6

Carpinus kushiroensis TANAI, 1970, p. 469, pl. 9, figs. 2, 4, 6–8.

Betula brongniarti auct. non, ETTINGSHAUSEN: ENDO, 1968 (part), p. 423, pl. 7, fig. 1 (only).
Alnus kushiroensis TANAI, 1970 (part), p. 468, pl. 9, fig. 5 (only).

Type: Holotype HUMP no. 26924; Nakanosawa, Yubetsu coal mine, Akan-cho, Hokkaido; Yubetsu Formation (Late Eocene).

Discussion: Leaves of this species are characterized by the following features: cordate base; doubly serrate margin with apiculate teeth; regularly spaced, craspedodromous secondary veins that upturn suddenly within teeth (D4); closely spaced (10 to 12 per cm), thin tertiary veins that are single or bifurcate. These features indicate that *Carpinus kushiroensis* is related to some of the extant *Carpinus* such as *C. cordata* BL. of Japan, although less in the secondary veins and rather obtuse teeth. This Eocene hornbeam may be a progenitor of *C. subcordata* NATHORST, which is commonly known in the Neogene of East Asia.

No fossil bract comparable to *C. kushiroensis* is yet found in the Paleogene of Hokkaido, although some undescribed bracts of this genus were collected by M. KOBAYASHI from the Yubari Formation of the Heiwa coal mine, Yubari.

Occurrence: Kushiro coal field Kh-1, Ky-2, Ks-2, Ks-3, Ks-4; Ishikari coal field Yc-2, Ic-8, Ic-9, Ic-11; Rumoe coal field Ur-1.

Collections: HUMP no. 25921 (holotype), no. 25923; NSM–PP 10570, 10571 a (hypotypes); NSM 10465 (=NSM–PP 1781), NSM–PP 10572–10574.

Carpinus shimokawarae ENDO

pl. 6, fig. 1

Carpinus shimokawarai ENDO, 1968, p. 425, pl. 9, figs. 1, 2.

Type: Holotype NSM 10476 (NSM–PP 1792); Middle course of the Enhorokabetsu River, Yubari City, Hokkaido; Ikushunbetsu Formation (late Miiddle Eocene).

Discussion: The original specimen is lacking in apical and basal parts of blade, and is also not preserved in quaternary and higher-order venatin. However, ENDO's assignment of this specimen to *Carpinus* is considered valid. The doubly serrate margin, acuminate teeth with long spiny tip, regularly spaced secondary veins that abruptly change course to swing apically or basally within the teeth, and thin intercostal tertiary veins (8 to 10 per cm) indicate that the specimen is referable to *Carpinus*.

Carpinus shimokawarae is closely similar to *C. fraterna* Lesq. of the Late Eocene Florissant flora of North America (LESQUEREUX, 1878; MACGINITIE, 1953), as pointed out by ENDO (1968). *Carpinus fraterna* was recently transferred to the extinct foliage genus *Paracarpinus* by MANCHESTER and CRANE (1987), because the leaves from Florissant were associated with unique fruits (the extinct genus *Asterocarpinus*), which have involucre of 4 to 7 wings radiating from the base of nutlet. However, it seems proper that Yubari leaf specimen is referred to *Carpinus*, because no fruit of *Asterocarpinus* has been yet found in the Ikushunbetsu Formation.

Occurrence: The middle course of Enhorokabetsu River, Yubari.

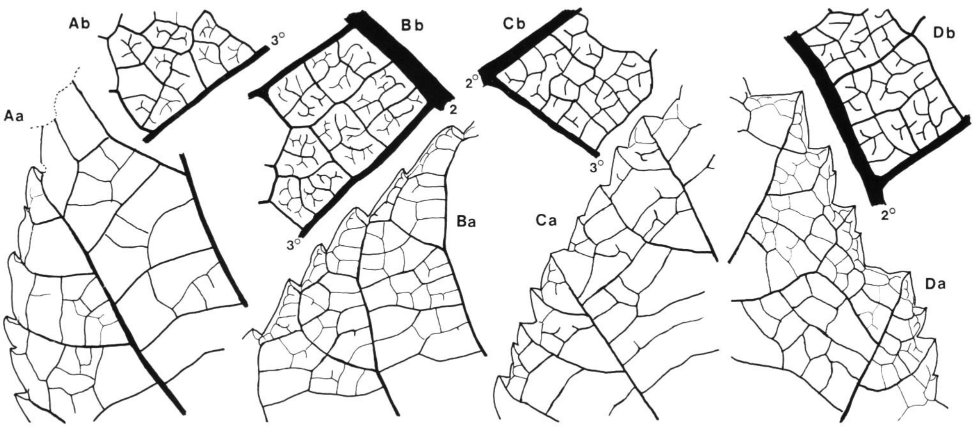


Fig. 3. The marginal venation features and areoles of Paleogene leaves of *Alnus* and *Corylus* and their related extant species. 2° and 3° in each figure indicate the secondary and tertiary veins, respectively. Aa, b, *Alnus kushiroensis* TANAI, NSM–PP 10560, Aa ×2.5, Ab ×12.5; Ba, b, *Alnus subcordata* C. A. MEY, NSM Paleobot. Ref. Coll. T-1812, Ba ×3, Bb ×12.5; Ca, b, *Corylus palaeomaximowicziana* (ENDO) TANAI, NSM 10469 (=NSM–PP 1785), Ca ×2.5, Cb ×12.5; Da, b, *Corylus chinensis* FRANCH, NSM Paleobot. Ref. Coll. T-1886, Da ×2.5, Db ×12.5.

Collection: NSM 10476 (=NSM–PP 1792) (holotype).

Genus *Corylus* L.

Corylus palaeomaximowicziana (ENDO) TANAI, comb. nov.

Pl. 6, figs. 3–5; Fig. 3-Ca, b

Betula palaeomaximowicziana ENDO, 1968, p. 425, pl. 7, figs. 3–5.
Corylus ezoana TANAI, 1970, p. 469. pl. 8, f. 5, 6; pl. 9, f. 1, 3; pl. 12, f. 1.

Type: Holotype NSM 10467 (=NSM–PP 1783); Dam-site of Shimizusawa, Yubari City, Hokkaido; Ikushunbetsu Formation (late Middle Eocene).

Discussion: The trigonal dentate teeth (type B2 or B4) separated by angular sinus, craspedodromous secondary veins that enter principal teeth centrally, simple convex-percurrent tertiary veins (5 or 6 per cm), and none or single (very rarely once branching) veinlets within irregularly sized, rectangular areoles indicate that *Betula palaeomaximowicziana* from Yubari (ENDO, 1968) is referable to *Corylus*. In *Betula*, the secondary veins abruptly upturn near the basal side of principal teeth to enter teeth along the basal side, and the veinlets are usually once to twice branching. *Corylus ezoana* TANAI from the Kushiro coal field is unseparable from *C. palaeomaximowicziana* in venation and marginal features, although most leaves of *C. ezoana* has more deeply cordate base.

In most extant species of *Corylus*, the principal teeth are usually larger than intersecondary teeth, but in *C. palaeomaximowicziana* such compound-serrate feature on the margin is not conspicuous. *Corylus palaeomaximowicziana* is similar to the extant *C. chinensis* FRANCH. of China in foliar shape and marginal serration.

Occurrence: Ishikari coal field Ic-3, Ic-5, Ic-9, Ic-11; Kushiro coal field Kh-1, Ky-2, Ky-3, Ks-1, Ks-2, Ks-4.

Collections: NSM 10467 (NSM–PP 1783) (holotype); NSM–PP 10575, 10577 (hypotypes), 10576; HUMP nos. 26929–26933.

Genus ***Ostrya*** SCOP.

Ostrya sp.

Pl. 5, fig. 5

Discussion: The specimen has elliptic shape with acuminate apex, and regularly spaced secondary veins of 13 pairs. The secondaries are straight or slightly curving up, enter the principal teeth centrally, and give basally 2 or 3 strong abmedial branches which enter smaller teeth. The teeth are deltoid (D4), and separated by acute sinus. The intercostal tertiary veins are thin, and single to branched. In these features preserved, the specimen is assignable to *Ostrya*.

Occurrence: Ishikari coal field Ic-11.

Collection: NSM–PP 10578.

Problematic and Rejected Citation of the Betulaceae in the Paleogene of Hokkaido

Except the taxa which are mentioned in the systematic chapter, several taxa of Betulaceae were described from the Paleogene of Hokkaido by ENDO (1968). However, the following taxa are excluded from the Betulaceae.

Betula brongniarti ETTINGS., ENDO, 1968 (part). p. 423, pl. 7, fig. 2. =*Carya yubarica* TANAI.

See, TANAI (1992a).

Betula ezoensis ENDO, 1968. p. 423, pl. 5, fig. 6. =*Ulmus shimogawarae* OISHI and HUZIOKA.

The secondary veins are usually bifurcate, and end in the large acute teeth centrally. The intercostal tertiary veins originate from the opposite sides of the secondary veins, and join at the midway with some crossing. These venation features are characteristic of *Ulmus*. This specimen is referable to *U. shimogawarae* in foliar shape and marginal features.

Carpinus takaoi ENDO, 1963, p. 425, pl. 8, figs. 4, 5. =dubious specimen.

The specimen is too ill-preserved to determine whether it is an involucre or not. The reinvestigation reveals that the specimen preserves no detail venation, although

ENDO (1968) described quadrate or polygonal areolation. The fossil appears to represent a small fragment of leaf.

Corylus fosteri auct. non WARD: ENDO, 1963 (part). pl. 22, fig. 10. =*Koelreuteria* sp.

Of two specimens illustrated as *Corylus fosteri* from Yubari by ENDO (1963), this specimen show the features which are unusual in leaves of *Corylus*: the foliar shape is markedly asymmetrical; the lower margin is entire; the secondary veins are typically semicraspedodromous. These features seem to be characteritic of *Koelreuteria* (Sapindaceae).

References

CHELEBAEVA, A. I., 1991. Floristic characteristics of the Snatol and Kavarovsk horizons. *Geol. Inst. Acad. Sci. USSR Trams.*, **467**: 49–119, pl. 1–22. (In Russian.)

CRANE, P. R., 1989. Early fossil history and evolution of the Betulaceae. *Syst. Assoc. Spec. vol.* (40B): 87–116.

ENDO, S., 1968. The flora from the Eocene *Woodwardia* Formation, Ishikari coal field, Hokkaido, Japan. *Bull. Natn. Sci. Mus., Tokyo*, **11** (4): 411–449, pls. 1–26.

HICKEY, L. J., 1979. A revised classification of the architecture of dicotyledonous leaves, p. 25–38, *In*: METCALFE, C. R. and L. CHALK, eds., *Anatomy of the Dicotyledons* (2nd ed.). Oxford, Claredon Press.

HUZIOKA, 1964. The Aniai flora of Akita Prefecture and the Aniai-type floras in Honshu, Japan. *J. Min. Coll., Akita Univ.*, ser. A, **3** (4): 1–105, pls. 28–40.

LESQUEREUX, L., 1878. Contribution to the fossil flora of the western territories. II. The Tertiary flora. *Rep. U. S. Geol. Surv. Terr.*, **7**: 1–366, pls. 1–65.

MACGINITIE, H. D., 1953. Fossil plants of the Florissant Beds. *Carnegie Inst. Wash. Publ.*, **599**: 1–198, pls. 1–75.

MANCHESTER, S. R. & P. R. CRANE, 1987. A new genus of Betulaceae from the Oligocene of western North America. *Bot. Gaz.*, **148** (2): 263–273.

MULLER, J., 1981. Fossil pollen record of the extant angiosperms *Bot. Rev.*, **47**: 1–142.

TANAI, T., 1961. Neogene floral change in Japan. *J. Fac. Sci. Hokkaido Univ.*, ser. 4, **11**: 119–398, pls. 1–32.

———, 1970. The Oligocene floras from the Kushiro coal field, Hokkaido, Japan. *J. Fac. Sc., Hokkaido Univ.*, ser. 4, **14**: 383–514, pls. 3–20.

———, 1972. Tertiary history of vegetation in Japan, p. 235–255. *In*: GRAHAM, A. (ed.), *Floristics and Paleofloristics of East Asia and Eastern North America.* Amsterdam, Elsevier.

———, 1981. The revision of the so-called "*Cercidiphyllum*" leaves from the Paleogene of North Japan. *J. Fac. Sci., Hokkaido Univ.*, ser. 4, **19**: 451–484.

———, 1989. The revision of the so-called "*Alangium*" leaves from the Paleogene of Hokkaido, Japan. *Bull. Natn. Sci. Mus., Tokyo*, ser. C, **15**: 121–149.

———, 1922a. Juglandaceae from the Paleogene of Hokkaido, Japan. *Bull. Natn. Sci. Mus., Tokyo*, ser. C, **18**(1): 31–41.

———, 1992b. Tertiary vegetational history of East Asia. *Bull. Mizunami Fossil. Mus.*, (19): 125–163. (In Japanese with English abstract.)

UEMURA, K. & T. TANAI, 1993. Betulaceae leaves and fruits from the Oligocene of Kitami, Hokkaido, Japan. *Mem. Natn. Sci. Mus., Tokyo*, (26): 22–29.

WEYLAND, H., 1943. Beiträge zur Kenntnis der Rheinischen Tertiärflora IV. Vierte Ergänzungen und Berichtignugen zur Flora der Blätterkhole und Polierschiefers von Rott im Siebengebirge. *Palaeontgr.* Abt. B, **87**: 94–136. pls. 16–24.

WOLFE, J. A., 1973. Fossil forms of Amentiferae. *Brittonia*, **25**: 334–355.

Explanation of Plates

(All figures in natural size unless otherwise stated)

Plate 1

Figs. 1–5. *Alnus ezoensis* TANAI.
figs. 1, 2, 4. NSM–PP 10533, 10534, 10536 a (Ic-9); fig. 3. NSM–PP 10542 (Boring core, Enhoro, Yubari. Yubari Formation); Fig. 5. NSM–PP 10543 (Nc-1).
Fig. 6. Showing the marginal serration and venation features of fig. 4 (NSM–PP 10536). ×6.
Fig. 7. Showing the areolation and ultimate veinlets of fig. 4 (NSM–PP 10536). ×30.

Plate 2

Figs. 1–4. *Alnus subezoensis* TANAI. (Ic-9).
NSM–PP 10548 (paratype), 10547 (holotype), 10549 (paratype), 10550.
Fig. 5. Showing the marginal serration and intercostal venation features of fig. 3 (NSM–PP 10549). ×6.
Fig. 6. Showing the areolation and ultimate veinlets of fig. 3 (NSM–PP 10549). ×30.

Plate 3

Fig. 1. *Alnus subezoensis* TANAI. NSM–PP 10552 (Ic-9).
Fig. 2. *Alnus ishikariana* TANAI. NSM–PP 10567 a (Ic-3).
Figs. 3–5. *Alnus yubarica* TANAI. NSM–PP 10568 a (holotype) (Ic-9), 10559 (paratype) (Ic-11), 10568 b (Ic-9).
Fig. 6. Showing the marginal serration and venation features of fig. 3 (NSM–PP 10568). ×6.
Fig. 7. Showing the areolation and ultimate veinlets of fig. 3 (NSM–PP 10568). ×30.

Plate 4

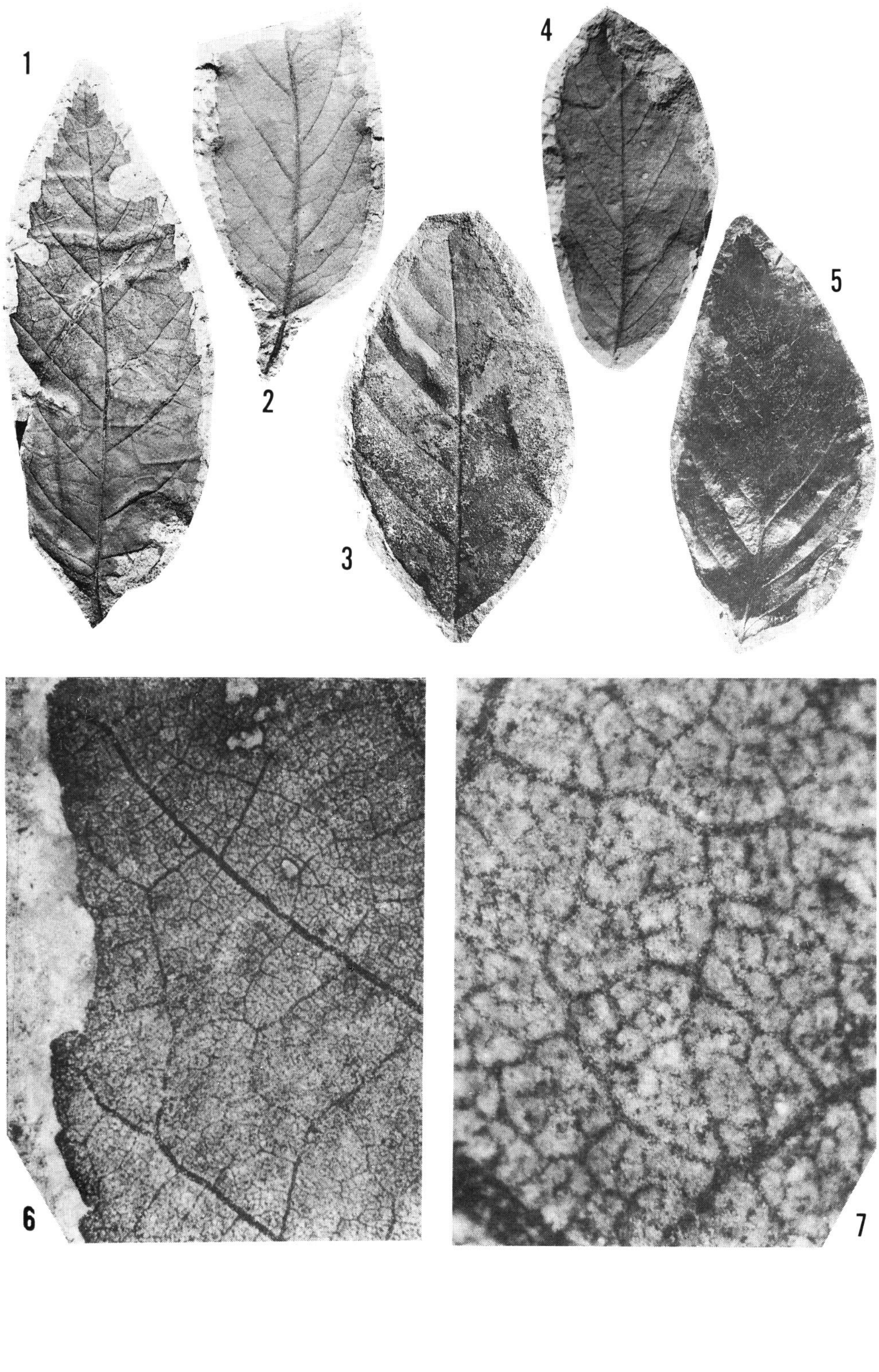
Fig. 1. *Carpinus kushiroensis* TANAI. NSM–PP 10571 a (Ic-9).
Fig. 2. *Alnus kushiroensis* TANAI. NSM–PP 10563 (Ic-11).
Fig. 3. *Alnus subezoensis* TANAI. NSM–PP 10551 (Ic-3).
Figs. 4–6. *Alnus ishikariana* TANAI. NSM–PP 10565 (Ic-9), 10566 (Ic-3), 10567 b (Ic-3).

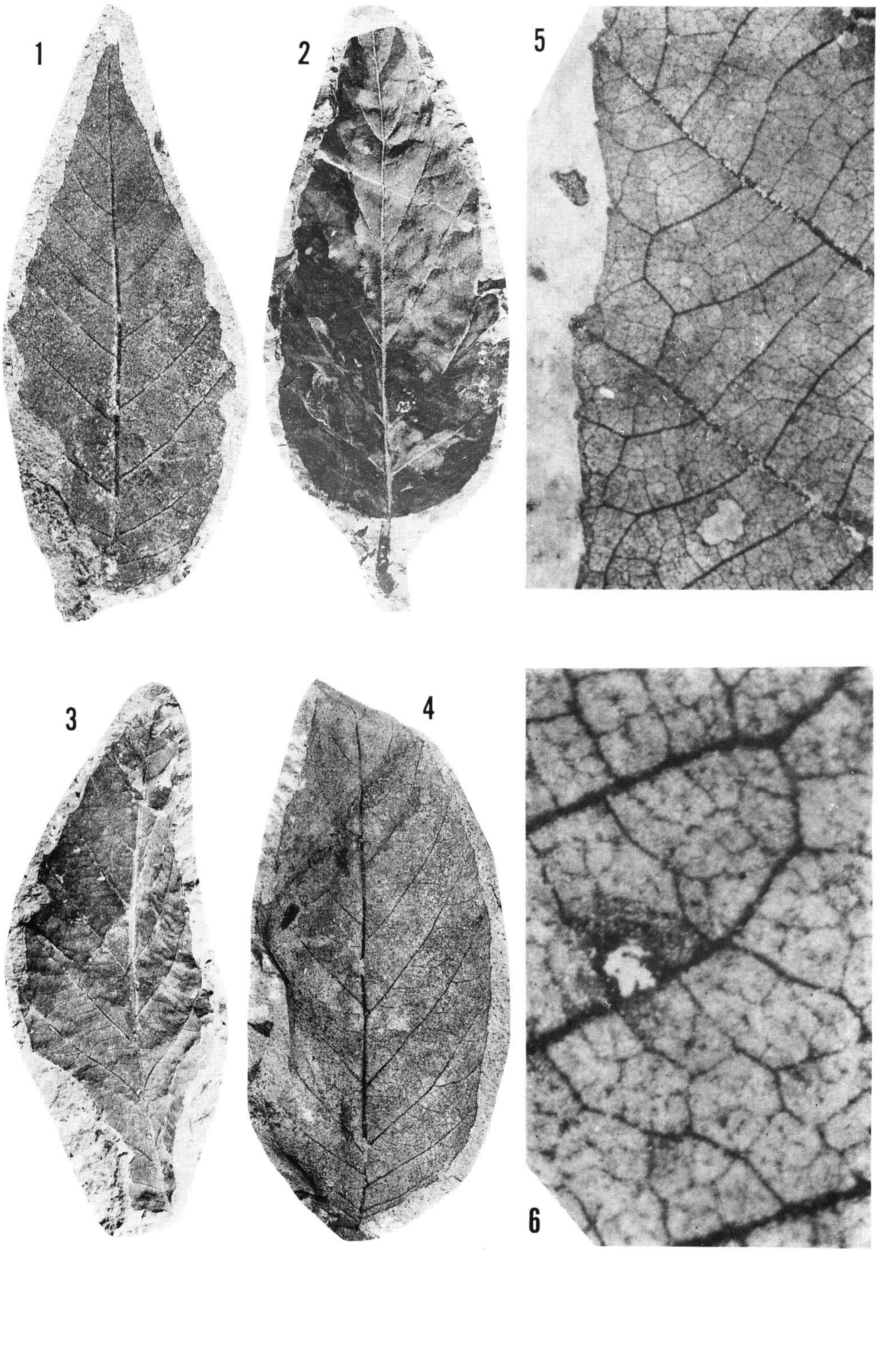
Plate 5

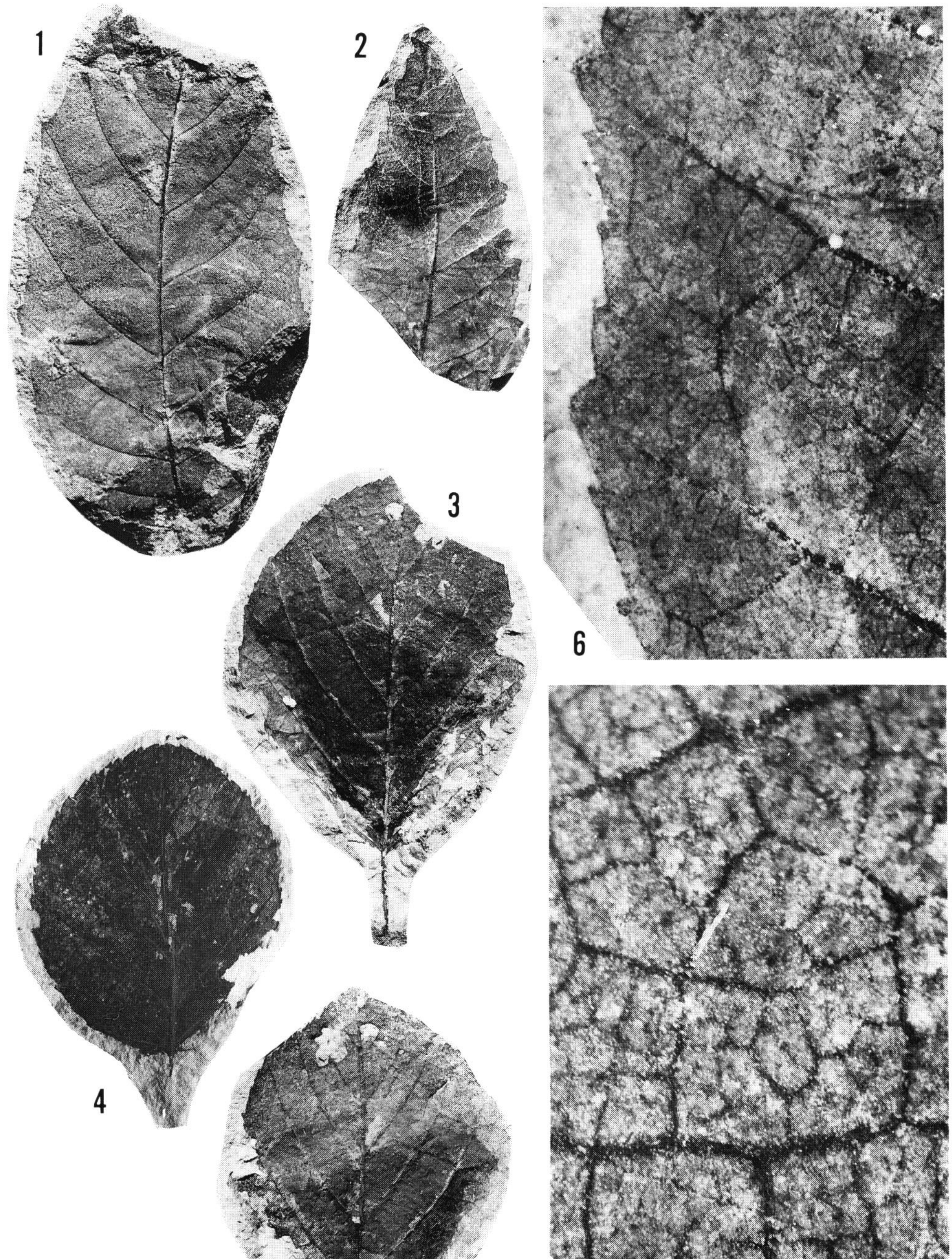
Figs. 1, 2. *Alnus kushiroensis* TANAI. NSM–PP 10562 (Ic-9), 10561 (Ic-3).
Figs. 3, 4. *Alnus hokkaidoensis* TANAI. NSM–PP 10559 (Ic-11), 10560 (Ic-9).
Fig. 5. *Ostrya* sp. NSM–PP 10578 (Ic-11).

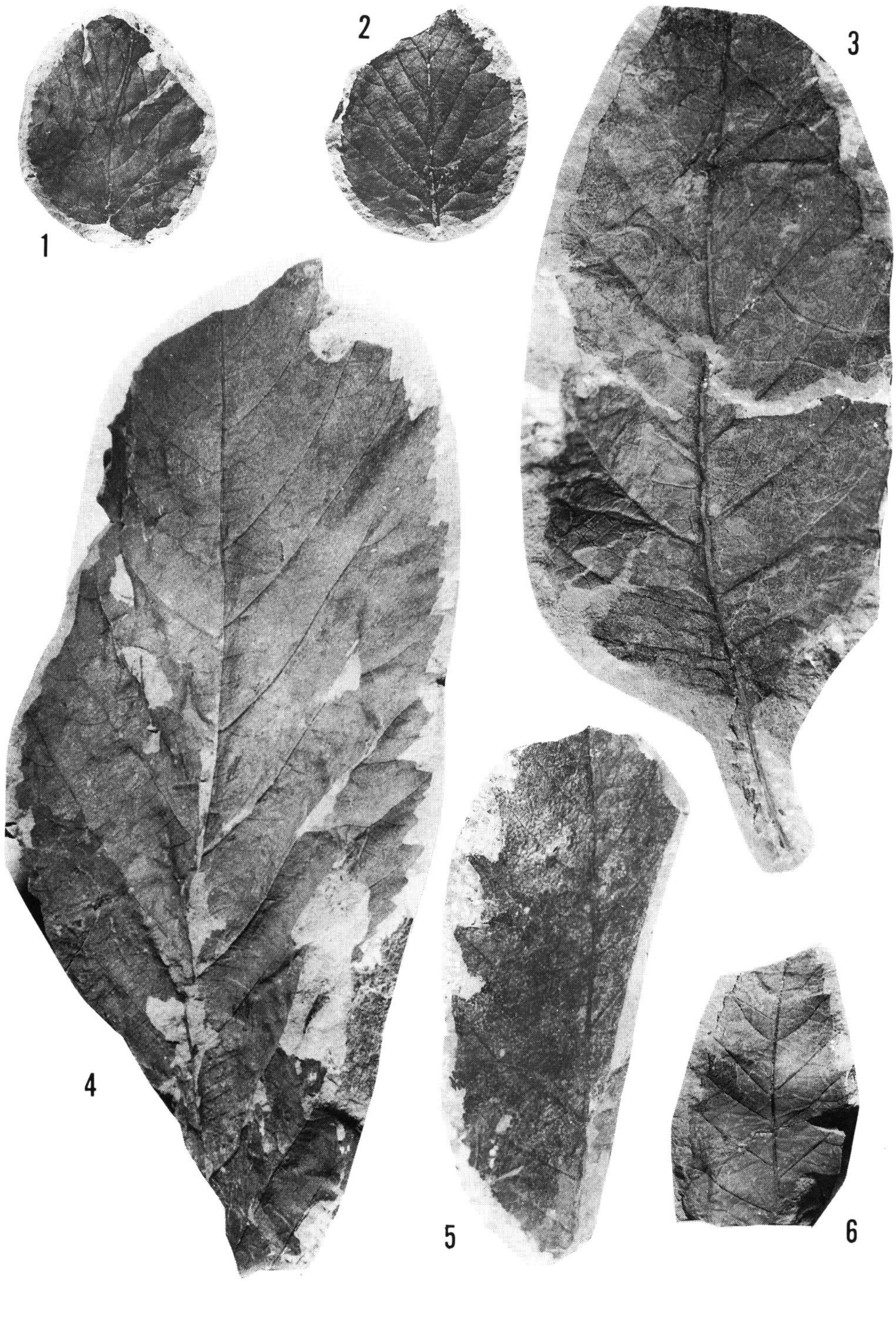
Plate 6

Fig. 1. *Carpinus shimokawarae* ENDO. NSM 10476 (=NSM–PP 1792) (holotype) (Ic-11).
Fig. 2. *Alnus hokkaidoensis* TANAI. NSM 10470 (=NSM–PP 1786) (Ic-11).
Figs. 3–5. *Corylus palaeomaximowicziana* (ENDO) TANAI. NSM–PP 10577 (Ic-5), NSM 10469 (=NSM–PP 1785) (holotype) (Ic-11), NSM–PP 10575 (Ic-9).
Fig. 6. *Carpinus kushiroensis* TANAI. NSM–PP 10573 (Ur-1).

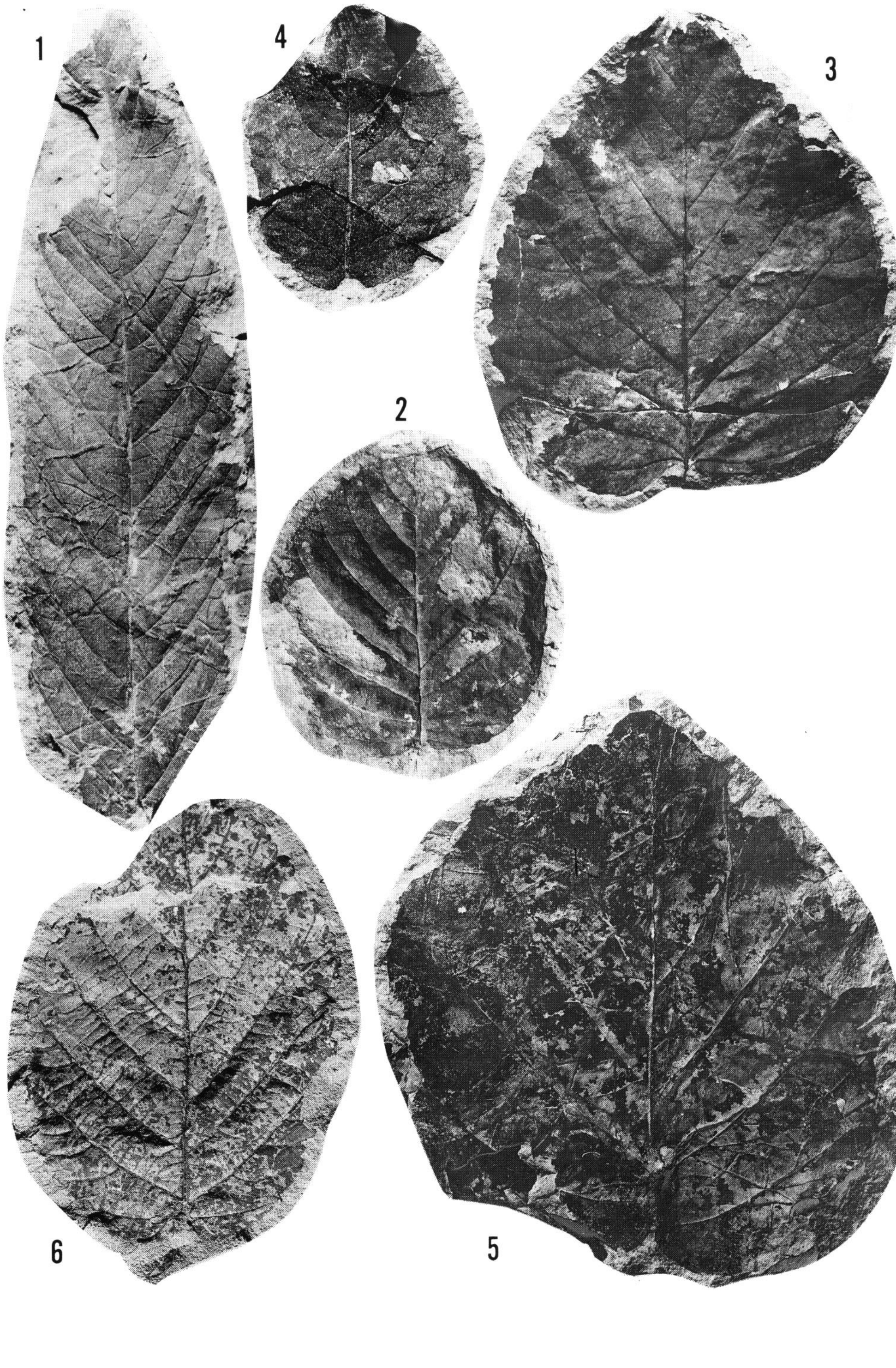

1
2
3
4
5
6
7


1
2
5
3
4
6


1
2
3
4
5
6
7


1
2
3
4
5
6


1
2
3
4
5


1
4
3
2
6
5