

Fagaceous Leaves from the Paleogene of Hokkaido, Japan

By

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23–546 Dialand, Kannami-cho, Shizuoka, 419–01

(Communicated by Akira KATO)

Abstract Fossils of the Fagaceae are uncommon in the Eocene of Hokkaido, although commonly known in the Oligocene. These Paleogene Fagaceae species are composed of 3 extant genera (*Castanea*, *Fagus* and *Quercus*), 1 extinct genus (*Fagopsis*), and 1 form-genus (*Dryophyllum*); 11 identified taxa of this family include 8 new species. All the taxa are represented by leaf impressions, except a poorly preserved cupule of *Quercus*. The stratigraphic distribution of these Paleogene taxa of Hokkaido indicates that the genus *Fagus* and *Castanea* first appeared in the Early Oligocene, and that the genus *Quercus* appeared in the late Middle Eocene, and then markedly diversified since the Early Oligocene. Considering these occurrence together with fossil record of other regions, Paleogene history of the Fagaceae in East Asia is briefly summarized.

Introduction

The Fagaceae is one of the large dicot group consisting of trees and shrubs, with cosmopolitan distribution; it has been classified into 3 subfamilies and 7 genera by most workers (WILLIS, 1973). The genus *Nothofagus* is, however, recently supported as an independent family, Nothofagaceae, of Fagales (JONES, 1986; NIXON, 1989), which was first proposed by KUPRIANOVA (1962, 1965) on the basis of pollen features. The Fagaceae *sensu stricto*, excluding *Nothofagus*, is widely distributed in the Northern Hemisphere, partly extending in northernmost South America.

The early history of Fagaceae *s. str.* is not yet thoroughly clarified until today, although it was recently reviewed or discussed by some workers (JONES, 1986; CREPET & NIXON, 1989; CREPET, 1989). It is partly due to the fact that few reliable fossils of this family such as reproductive organs are known in the Cretaceous and even in the Lower Tertiary. Fagaceous leaves of the pre-Tertiary and Paleocene are dubious and lack definite characteristics of Fagaceae *s. str.* (WOLFE, 1973). Current studies reveal that unequivocal fossils of Fagaceae *s. str.* are known since the Late Eocene and Oligocene (WOLFE, 1973; MANCHESTER & CRANE, 1983; JONES, 1986; CREPET, 1989; KVAČEK & WALTHER, 1989a). The origin of Fagaceae *s. str.* is suggested to be traced back to the Late Cretaceous, if fagaceous woods (WHEELER *et al.*, 1987; SUZUKI & OHBA, 1991) and *Castanea*-

type pollen (CHMURA, 1973; MULLER, 1981) from the Upper Cretaceous are accepted.

Fagaceous leaves were described from the Paleogene of East Asia by various authors, but most of them need to be re-examined in leaf architecture. Paleogene terrestrial deposits are well distributed in Hokkaido, accompanied with many fossil leaves (TANAI, 1992). The purpose of this paper is to discuss the early fossil record of Fagaceae *s. str.* in Hokkaido, and to consider some of the implications.

Paleogene Fossils of the Fagaceae from Hokkaido

The Paleogene plant-bearing deposits are widely distributed in Hokkaido, except in the southwestern region; they are typically developed in the Ishikari coal field of the central region, and are called the Ishikari Group. In the other two coal fields of central region are also developed the Uryu and Kabato Groups coeval to the Middle or Upper Ishikari Group. In the eastern region there are the Kushiro and Rikubetsu coal fields, where the coal-bearing deposits coeval to the Upper Ishikari Group (the Urahoro and Rikubetsu Groups) are developed. These Paleogene plant-bearing deposits are stratigraphically classified into 5 horizons (I–V), ranging from Middle Eocene to Latest Eocene in age (TANAI, 1990, 1992). Although the Oligocene deposits are mostly of marine origin in Hokkaido, the Lower Oligocene terrestrial deposits (the Wakamatsuzawa Formation) are distributed only in Kitami district of northeastern region; this formation represents the VI plant-bearing horizon.

The fossils referable to the Fagaceae are uncommon in the Eocene formations in spite of extensive collection through long years. On the other hand, the Oligocene deposits of Kitami commonly contain the Fagaceae fossils. Although most of these Paleogene specimens are represented only by leaf impressions, the investigation of detailed leaf architecture made possible to refer fossils to the Fagaceae.

Table 1. The systematic list of the Fagaceae from the Paleogene of Hokkaido.

Fagoideae	<i>Fagus uemurae</i> TANAI sp. nov. “ <i>Fagus</i> ” <i>kitamiensis</i> TANAI sp. nov.
Querceoideae	<i>Quercus ezoana</i> TANAI sp. nov. <i>Quercus ishikariensis</i> TANAI sp. nov. <i>Quercus kitamiana</i> TANAI sp. nov. <i>Quercus sichotensis</i> ABLAEV and KIROVOI <i>Quercus ussuriensis</i> KRYSHTOFOVICH <i>Quercus</i> sp.
Castaneoideae	<i>Castanea fujiiyamae</i> TANAI sp. nov.
Unknown subfamily	<i>Fagopsis nipponica</i> TANAI sp. nov. <i>Dryophyllum noborikawense</i> TANAI sp. nov.

The subfamilial classification of the extant Fagaceae has been debated (e.g., JONES, 1986, Table 1; NIXON, 1989). I follow here the taxonomic treatment adopted by many workers, in which Fagaceae *s. str.* is classified into 3 subfamilies, Fagoideae, Quercoideae and Castaneoideae (e.g., FORMAN, 1966; WILLIS, 1973). Paleogene taxa of the Fagaceae *s. str.* from Hokkaido consist of 5 genera and 11 species (Table 1).

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).

Family Fagaceae

Genus *Castanea* MILL.

Castanea fujiyamae TANAI sp. nov.

Pl. 4, figs. 4, 5; Fig. 1-Aa, b.

Type: Holotype NSM-PP 10600; Wakamatsuzawa, Kitami City, Hokkaido; Wakamatuzawa Formation (Early Oligocene).

Etymology: This species is named after Dr. Ienori FUJIYAMA, who collected the holotype specimen.

Description: Leaves oblong in shape, acute at apex, broadly rounded, slightly cordate; 9.8 to 20 (estimated) cm long, 4.8 to 10.5 cm wide, length/width ratio 1.9 to 2.5; margin slightly revolute toward undersurface, dentate with long acuminate tip; sinus broadly rounded; petiole long, somewhat incomplete but more than 1.5 cm long as preserved. Venation pinnate; midvein thick, straight below; secondary veins medium in thickness, about 20 pairs or more, opposite to subopposite, diverging at 60° to 70° on the lower and middle parts of blade and at 40° to 50° on the upper part, craspedodromous; tertiary veins percurrent, slightly convex to straight, sometimes branched, 5 to 6 per cm; quaternary veins mostly parallel or perpendicular to the intercostal tertiary veins, forming rectangular networks; the highest order veins 6th; areoles four- or five-sided, typically 0.5 mm across; ultimate veinlets once to twice branching.

Discussion: The oblong shape, absence of the fimbrial vein on the margin and dentate teeth with long acuminate tip are the features of some leaves of the genus *Castanea*. Of the extant chestnut species of the world, the fossil leaves resemble leaves of *C. mollissima* BL. of China and *C. dentata* (MARSH.) BORKH. of eastern North America; especially, they are closely similar to the former in

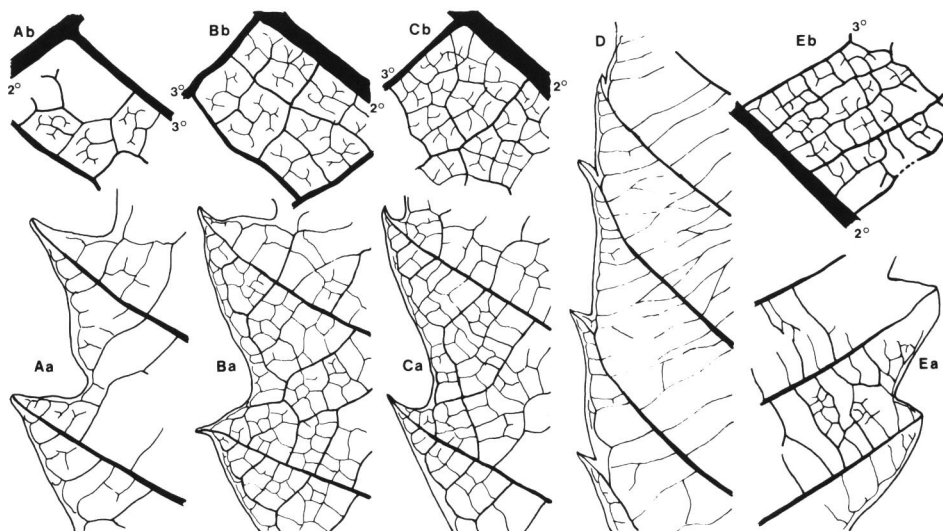


Fig. 1. The venation features of marginal area and areoles of Paleogene Fagaceae leaves (*Castanea*, *Dryophyllum* and *Fagopsis*), and their related extant species. 2° and 3° in each figure indicate the secondary and tertiary veins, respectively. Aa, b, *Castanea fujiiyamae* TANAI, holotype NSM-PP 10600 (pl. 4, fig. 4), Aa $\times 2.5$, Ab $\times 12.5$. Ba, b, *Castanea dentata* (MARSH.) BORKH., NSM Paleobot. Ref. Coll. T-1058, Ba $\times 2.5$, Bb $\times 12.5$. Ca, b, *Castanea mollissima* BL., NSM Paleobot. Ref. Coll. T-1059, Ca $\times 2.5$, Cb $\times 12.5$. D, *Dryophyllum noborikawense* TANAI, NSM-PP 10591 (pl. 3, fig. 3), $\times 2.5$. Ea, b, *Fagopsis nipponica* TANAI, NSM-PP 10580b (pl. 6, fig. 2), Ea $\times 6$, Eb $\times 12.5$.

having oblong shape, rounded base, long petiole and spaces of the intercostal tertiary veins, although *C. mollissima* has longer spiny-tipped teeth and none or single veinlet. The fossils are also similar to *C. dentata* in having large dentate teeth and once to twice branching veinlets. Thus, *C. fujiiyamae* has the combination features of the extant *C. mollissima* and *C. dentata*. It is noteworthy that leaves of the extant chestnuts are grouped into two types in the features of ultimate veinlets: in the one type (*C. dentata* and *C. sativa*) the veinlets ramify usually once to twice, while in the other type (*C. crenata*, *C. mollissima*, *C. pumila* and *C. seguinii*) they are typically none or single.

Castanea fujiiyamae superficially resembles *C. miomollissima* HU & CHANEY which is commonly known from the late Early Miocene of Japan and China. However, leaves hitherto referred to *C. miomollissima* by many authors appear to have been confused with *Quercus*. Although the holotype specimen of *C. miomollissima* from the Shanwang flora (HU & CHANEY, 1938; pl. 3, fig 7) was lost, it seems different from *C. fujiiyamae* in having smaller teeth with long spiny tip.

Occurrence: Wakamatsuzawa and Minamigaoka, Kitami City, Hokkaido.

Collection: NSM-PP 10600 (holotype); NSM-PP 10601–10606.

Genus *Dryophyllum* DEBEY ex SAPORTA

Discussion: The genus *Dryophyllum* has been widely used for the fossil Fagaceae-like leaves by many workers. The application of this name and its familial affinity have been recently discussed, along with designation of the nomenclatural type (ILJINSKAYA in TAKHTAJAN, 1982; JONES *et al.*, 1988; JONES & DILCHER, 1988; KVAČEK & WALTHER, 1989a, b). JONES, MANCHESTER and DILCHER (1988) adopting a specimen of *D. subcretaceum* Saporta as the lectotype, claimed that this fossil genus is juglandaceous rather than fagaceous. On the other hand, KVAČEK and WALTHER (1989b), designating *D. palaeocastanea* as the lectotype, described that this species indicates thoroughly the original diagnosis characteristic of the genus *Dryophyllum* ex SAPORTA (1868).

Based on leaf anatomical examination and co-occurred reproductive organs from Central Europe and eastern North America, some of leaves once described as *Dryophyllum* were transferred to new extinct genera of the Fagaceae by the above-noted authors such as KVAČEK and WALTHER, and JONES *et al.* Fossil leaves of Hokkaido here studied are represented only by impressions, and are impossible to be compared with the newly established genera by anatomical features. Thus, the fagaceous leaves that are unreferable to the extant genus are applied to *Dryophyllum*, followed the opinions of KVAČEK and WALTHER (1989b).

Dryophyllum noborikawense TANAI sp. nov.

Pl. 3, fig. 3; Pl. 5, figs. 4, 5; Fig. 1-D.

Type: Holotype NSM-PP 10590, paratypes 10591, 10592; Honcho, Yubari City, Hokkaido; Noborikawa Formation (Middle Eocene).

Etymology: The epithet refers to the Noborikawa Formation, in which this fossil typically yields.

Description: Leaves lanceolate to oblanceolate in shape, acute to slightly acuminate at apex, cuneate at base, 8.5 to 15 cm (estimated) 2.5 to 3.4 cm wide; margin serrate except entire basal margin; teeth acute, small, 1 per secondary vein; sinus acute; petiole missing; texture thick. Venation pinnate; midvein moderately thick, straight, with a single ridge on lower half part; secondary veins 12 to 15 in pairs, opposite to subalternate, diverging from midvein at about 60°, gently curving up, semicraspedodromous except in basal portion of blade where the secondaries are camptodromous to form marginal loops; secondary veins of upper and middle portions of leaf typically bifurcate just before teeth, a basal

branch entering tooth centrally, an apical branch arising up along margin to form prominent loop with marginal tertiary vein; intersecondary veins sometimes present in lower part of leaf (but 1 in each intercostal space); intercostal tertiary veins typically simple and rarely branched, percurrent, closely spaced (6 to 7 per cm); the higher order venation poorly preserved; fimbrial vein absent.

Discussion: The simple-serrate margin, small regularly spaced teeth, typically semicraspedodromous secondary veins except in basal portion of leaf, and closely-spaced percurrent tertiary veins are the features that are found in many leaves of subgenera *Cyclobalanopsis*, *Quercus* and *Erythrobalanus* of the genus *Quercus*. However, the absence of fimbrial vein excludes the fossil leaves from subgenera of *Erythrobalanus* and *Quercus*. The fossil leaves are closely similar to several extant species of *Cyclobalanopsis*, but they are unseparable from some leaves of the genera *Castanopsis* and *Lithocarpus* by the venation and marginal serration features that are shown in the fossils. Thus, the fossil leaves described here, are now referred to the form genus *Dryophyllum*. However, it is noteworthy that the intersecondary vein is usually uncommon in most leaves of the Fagaceae.

Occurrence: Ishikari coal field Nc-1, Nc-3.

Collection: NSM-PP 10590 (Holotype), 10591, 10592 (paratypes); NSM-PP 10593–10599.

Genus *Fagopsis* HOLLICK

Fagopsis nipponica TANAI sp. nov.

Pl. 5, figs. 1, 2; Pl. 6, figs. 1, 2. 5. 6; Fig. 1-Ea, b.

Quercus rectinervis auct. non BORSUK, SYCHEVA, 1977, p. 30, pl. 18, figs. 5, 6.

Quercus groenlandica auct. non HEER, ILJINSKAYA in TAKHTJAN, 1992 (part), p. 99, pl. 60, figs. 7.

Type: Holotype, NSM-PP 10579; the upper course of Subetu River, Tsukigata-cho, Hokkaido; Kabato Formation (late Middle Eocene). Paratypes, NSM-PP 10580a, b; Reisui-zan, Yubari, Hokkaido; Ikushunbetsu Formation (late Middle Eocene).

Etymology: The epithet refers to “Nippon”, which is the Japanese designation for “Japan”.

Description: Leaves narrow obovate to elliptic in general shape, revolute at the margin with thickening, 6 to 8.6 cm long (estimated) and 3.5 to 5.3 cm wide; base slightly to markedly asymmetric, obtuse; apex acute; margin serrate with large, acute teeth that are always simple, separated by broadly-opened sinus, uniformly arranged, non-glandular; both sides of teeth nearly straight or slightly convex (A1 to B2); apical side of teeth generally perpendicular to the midvein, about three times longer than the basal side; petiole thick but incomplete, more than 1 cm long. Venation pinnate, simple craspedodromous; midvein stout,

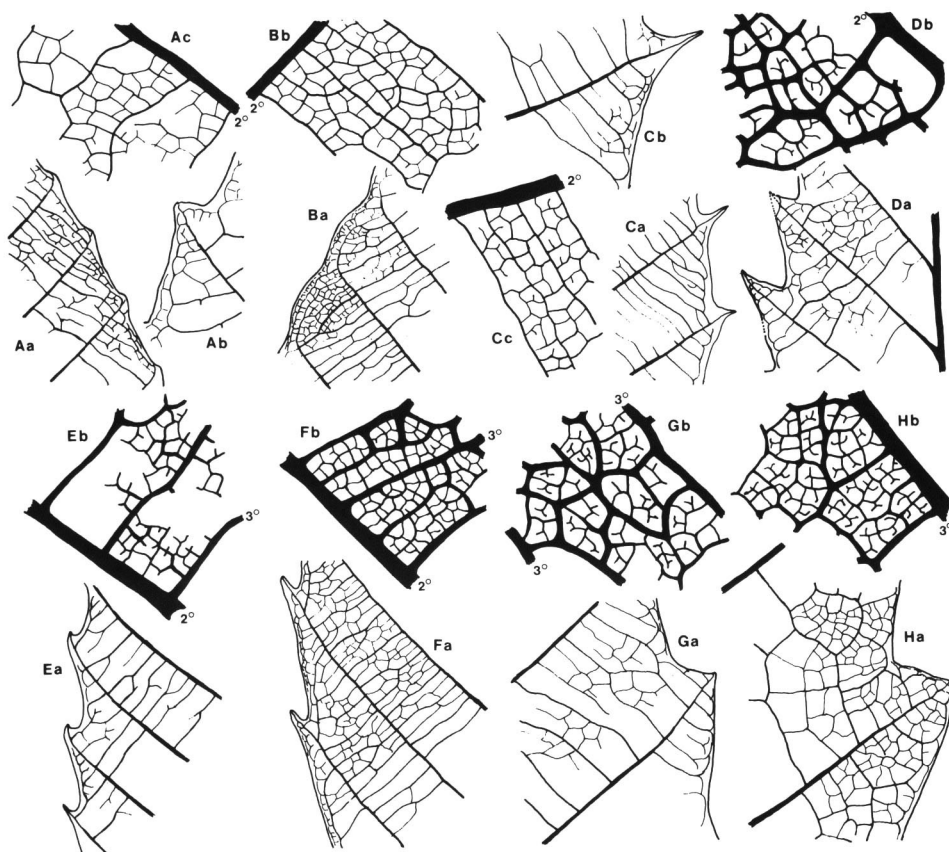


Fig. 2. The venation features of marginal area and areoles of Paleogene Fagaceae leaves (*Fagus* and *Quercus*), and their related extant species. 2° and 3° in each figure indicate the secondary and tertiary veins, respectively. Aa-c, *Fagus uemurae* TANAI, NSM-PP 10608 (pl. 1, fig. 4), Aa $\times 2.5$, Ab $\times 5$, Ac $\times 12.5$. Ba, b, *Fagus japonica* MAXIM., NSM Paleobot. Ref. Coll. T-22, Ba $\times 2.5$, Bb $\times 12.5$. Ca-c, "*Fagus*" *kitamiensis* TANAI, NSM-PP 10615 (pl. 2, fig. 3), Ca $\times 2.5$, Cb $\times 5$, Cc $\times 12.5$. Da, b, *Quercus ishikariensis* TANAI, NSM-PP 10585 (pl. 3, fig. 1), Da $\times 2.5$, Db $\times 12.5$. Ea, b, *Quercus ezoana* TANAI, NSM-PP 10634 (pl. 4, fig. 2), Ea $\times 2.5$, Eb $\times 12.5$. Fa, b, *Quercus lamellosa* SMITH, NSM Paleobot. Ref. Coll. T-2467, Fa $\times 2.5$, Fb $\times 12.5$. Ga, b, *Quercus kitamiana* TANAI, NSM-PP 10636 (pl. 5, fig. 3), Ga $\times 2.5$, Gb $\times 12.5$. Ha, b, *Quercus griffithii* HOOK f. & THOMAS., NSM Paleobot. Ref. Coll. T-2462, Ha $\times 2.5$, Hb $\times 12.5$.

straight; secondary veins thick, 25 to 27 pairs, opposite to subopposite, evenly spaced and nearly parallel each other, entering tooth apex centrally; diverging angles of the secondaries 50° to 55° in most leaves, though considerably different at the both sides of midvein in leaves having markedly asymmetric base (50° to 55° on the one side and 75° to 80° on the other side); tertiary veins very thin,

compared with thick secondary veins, closely spaced (10 to 15 per cm), irregularly and weakly percurrent, nearly perpendicular or somewhat oblique to the secondaries, sometimes branching; quaternary veins transverse to secondary veins, forming four- or five-sided areoles (0.2 to 0.3 mm across) with quaternary veins; marginal quaternary veins forming a series of irregular loops along both sides of tooth margin; ultimate veinlets ill-preserved.

Discussion: The simple craspedodromous venation, uniformly spaced and straight, unbranched secondary veins, a single prominent tooth per secondary veins, and closely spaced and extremely thin tertiary veins indicate that these fossil leaves from the Eocene of Central Hokkaido are referable to the extinct genus *Fagopsis*. Three species of *Fagopsis* are known from the Paleocene to the Eocene of Greenland, western North America, and North England (Isle of Mull): *F. longifolia* (LESQ.) HOLLICK, *F. groenlandica* and *F. undulata* (KNOWLTON) WOLFE & WEHR. Of these 3 species, *F. groenlandica* is most related to *F. nipponica* in having the shape of teeth and numerous secondary veins. *Fagopsis nipponica* has, however, usually more than 20 secondary veins, even in small lamina, while *F. groenlandica* has usually less than 20 secondaries.

Two leaves reported as *Quercus rectinervis* BORSUK from the Paleogene of Southern Sakhalin by SYCHEVA (1977) were later referred to *Q. groenlandica* by ILJINSKAYA in TAKHTAJAN, ed. (1982). However, these leaves are identical to *Fagopsis*, and is referable to *F. nipponica* in having more than 20 secondary veins.

Occurrence: Kabato coal field Ka-1; Ishikari coal field Nc-1, Ic-3, Ic-9.

Collection: NSM-PP 10579 (holotype), 10580a, b (paratypes), 10583 (hypotype); NSM-PP 10581, 10582, 10584.

Genus *Fagus* L.

Fagus uemurae TANAI sp. nov.

Pl. 1, figs. 3, 4, 6; Pl. 2, fig. 6; Fig. 2-Aa-c.

Type: Holotype NSM-PP 10607, paratypes 10608, 10609; Wakamatsuzawa, Kitami City, Hokkaido; Wakamatsuzawa Formation (Early Oligocene).

Etymology: This species is named after Dr. Kazuhiko UEMURA, who collected a number of the plant specimens from Kitami region, Hokkaido.

Description: Leaves ovate to narrow ovate in general outline, rounded at base, acute at apex, 5.6 to 6 (estimated) cm long, 2.8 to 3.2 cm wide, length/width ratio 1.8 to 2.5; margin simple serrate; teeth small with obtuse tip; petiole missing. Venation pinnate, midvein medium in thickness, straight below but somewhat sinuous at apical part; secondary veins medium in thickness, 13 to 15 pairs, diverging at angles of 40° to 50°, opposite to subopposite, nearly straight to the margin, then abruptly upturned within tooth and becoming thinner; intercostal tertiary veins thin, percurrent, nearly straight to sinuate, sometimes branched,

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	I	II	III	IV	V	VI
<i>Fagus uemurae</i>						
" <i>Fagus</i> " <i>kitamiensis</i>						
<i>Quercus ezoana</i>						
<i>Quercus ishikariensis</i>						
<i>Quercus kitamiana</i>						
<i>Quercus sichotensis</i>						
<i>Quercus ussuriensis</i>						
<i>Quercus</i> sp.						
<i>Castanea fujiyamae</i>						
<i>Fagopsis nipponica</i>						
<i>Dryophyllum noborikawense</i>						

Fig. 3. Stratigraphic distribution of the Fagaceae in the Paleogene of Hokkaido. The Roman numerals (I–VI) show the Paleogene plant-bearing horizons of Hokkaido (see, TANAI 1992).

closely spaced (12 to 14 per cm); quaternary veins reticulate; the highest order vein sixth; areoles formed by fifth and sixth order veins, mostly four- or five-sided, 0.23 to 0.3 mm across; ultimate veinlets none or single.

Discussion: These single serrate margined leaves with minute, obtuse teeth are referable to the genus *Fagus* in the following features: the midvein is sinuate in the upper part of blade; the secondary veins are nearly straight to the margin, and abruptly upturn within the teeth; and, the most abmedial tertiary vein that departs typically from the secondary vein is parallel in course to the intercostal tertiary veins.

These fossil leaves of Kitami are closely similar to *Fagus evenensis* of the Miocene of Kamchatka (CHELEBAEVA, 1980) in having toothed margin and closely spaced tertiary veins, excepting for less secondary veins. CHELEBAEVA (1980) described that *F. evenensis* has the secondary veins of 16 to 20 pairs; however, small to medium sized leaves in her illustrations (CHELEBAEVA, 1980: text-fig. 2, B-6, -7; pl. 6, fig. 5) have about 12 pairs in the secondary veins, and the other leaves illustrated have 16 to 20 pairs. So far as judged from her illustrations, leaves of *F. evenensis* are classified into two groups, and leaves having less secondary veins are better to be excluded from *F. evenensis*. It is interesting to note that *F. uemurae* is closely similar to *F. pacifica* CHANEY of the Oligocene of Oregon (CHANEY, 1927) in toothed margin, the number of secondary veins and closely spaced tertiary veins.

Fagus uemurae may be related to the extant *F. japonica* MAXIM. of Japan in

having closely spaced tertiary veins, the number of secondary veins and leaf index (TANAI, 1974), though the extant leaves are not toothed and usually undulate on the margin. This relationship is, however, unable to confirm, because no fossil bract of beech have been found in the Wakamatsuzawa Formation.

Occurrence: Wakamatsuzawa and Minamigaoka, Kitami City, Hokkaido.

Collection: NSM-PP 10607 (holotype), 10608, 10609 (paratypes), 10610–10614.

“Fagus” kitamiensis TANAI sp. nov.

Pl. 1, figs. 1, 2, 5; Pl. 2, figs. 2–4; Pl. 6, fig. 3; Fig. 2-Ca–c.

Type: Holotype NSM-PP 10615, paratypes 10616a, b, 10617; Wakamatsuzawa, Kitami City, Hokkaido; Wakamatsuzawa Formation (Early Oligocene).

Etymology: The epithet refers to Kitami City, where the Wakamatsuzawa Formation is typically distributed.

Description: Leaves elliptic to narrow ovate in shape, 7.4 to 13 cm long, 4.4 (estimated) to 6 cm wide, length/width ratio 1.97 to 2.55; margin single serrate; teeth small, acute to acuminate; apex somewhat attenuate; base obtuse to rounded; petiole medium in thickness, 0.6 to 1.8 cm long. Venation pinnate; midvein thick, straight; secondary veins medium in thickness, 18 to 21 pairs, subopposite, diverging at 45° to 55° , straight, craspedodromous, entering straightly tooth apex; intercostal tertiary veins thin, percurrent, somewhat sinuous or branched, closely spaced (10–14 per cm); most abmedial tertiary vein departing from the secondary vein typically parallel in course to the intercostal tertiary veins; quaternary veins irregularly reticulate or sometimes parallel to tertiary veins; the highest order vein 6th; 5th and 6th order veins forming areoles that are mostly five- or six-sided, and 0.18 to 0.27 mm across; ultimate veinlets none or single.

Discussion: The absence of the fimbrial vein on the margin, closely spaced, thin tertiary veins, and the typical features of the most abmedially tertiary vein indicate that these single serrate leaves are closely related to the genus *Fagus*. In actual, the fossil leaves are closely similar to the above-described *F. uemurae* in most features of venation, except marginal serration and secondary vein termination. That the secondary veins extend straightly into tooth apex, and that the teeth are acuminate with somewhat long tip, are unusual features in the extant *Fagus*. The fossil leaves also resemble superficially some extant leaves of *Quercus* (subgenus *Quercus*) in having single serrate teeth with long tip and craspedodromous secondary veins. Leaves of the subgenus *Quercus* are distinguished from the fossils in the following features: the intercostal tertiary veins are usually thicker; the most abmedial tertiary vein departing apically from the secondary vein is parallel to the margin and aparallel to the other tertiary veins; and, the fimbrial

vein is present.

In the fossil leaves here described, the most abmedial tertiary vein departing apically from the secondary vein is typically parallel to other tertiary veins as in *Fagus*, but it connects sometimes to form loops with a few marginal tertiary veins which extend basally from the superadjacent secondary vein, especially on the lower margin area. The latter marginal venation features are characteristic of *Quercus*. Thus, the fossil leaves here described are most related to the genus *Fagus*, but also they have some features characteristic of some leaves of *Quercus* (the subgenus *Quercus*). The fossils seem to represent an extinct genus of the Fagaceae, which is closely related to *Fagus*. However, the proposal for an extinct genus is reserved until the associated reproductive organs shall be found.

Occurrence: Wakamatuzawa and Minamigaoka, Kitami City, Hokkaido.

Collection: NSM-PP 10507 (holotype), 10608, 10609 (paratypes); NSM-PP 10610–10633.

Genus *Quercus* L.

Subgenus *Cyclobalanopsis* PRANTL.

Quercus ezoana TANAI sp. nov.

Pl. 4, fig. 2; Fig. 2-Ea, b.

Type: Holotype NSM-PP 10634; Wakamatsuzawa, Kitami City, Hokkaido; Wakamatsuzawa Formation (Early Oligocene).

Etymology: The epithet refers to “Ezo”, which is the old name of Hokkaido.

Description: Leaf elliptic, slightly inequilateral in shape; base cuneate, somewhat asymmetric; 8.3 cm (estimated) long and 3.2 cm wide; margin single serrate with small, sharp teeth; petiole medium in thickness, about 5 mm long as preserved. Venation pinnate; midvein thick, nearly straight; secondary veins thick, more than 15 in pairs, opposite to subopposite, diverging at 45° to 55° on one side of midvein and at 30° to 40° on the other side, nearly straight or gently curving up, entering typically along the basal side of tooth margin; intercostal tertiary veins rather thick, percurrent, straight or branched, closely spaced (11 to 12 per cm); quaternary and quinternary veins irregularly reticulate; the highest order vein 6th; areoles mostly quadrangular, formed by thick veins, 0.18 to 0.2 mm across; ultimate veinlet none or rarely single.

Discussion: The serrate margin with small, sharp teeth, thick secondary and tertiary veins, small quadrangular areoles sided by thick veins and absence of a fimbrial vein on margin indicate that this fossil leaf is referable to *Quercus* (the subgenus *Cyclobalanopsis*). That the tertiary and higher order veins are dimly impressed in this fossil, suggests tomentose undersurface of this fossil leaf.

The fossil leaf resembles those of the extant *Quercus oxyodon* MIG. and *Q. lamellosa* SMITH of central and southwestern China in having numerous secondary veins and marginal serration. These relationships are also supported by the fact that these two extant leaves are usually tomentose beneath.

Occurrence: Wakamatsuzawa, Kitami City, Hokkaido.

Collection: NSM-PP 10634 (holotype).

Subgenus *Quercus*

Quercus ishikariensis TANAI sp. nov.

Pl. 2, fig. 5; Pl. 3, fig. 1; Pl. 4, fig. 3; Fig. 2-Da, b

Quercus kushiroensis TANAI, 1970 (part), p. 471, pl. 20, fig. 2.

Type: Holotype NSM-PP 10585; Reisuizan, Yubari, Hokkaido; Ikushunbetsu Formation (late Middle Eocene).

Etymology: The epithet refers to the Ishikari coal field.

Description: Leaves narrow oblong or lanceolate, 6.5 to 14 cm long (estimated) and 1.6 to 5 cm wide; apex attenuate; base acute; margin serrate with large, triangular teeth; teeth B1 or B2, with sharply pointed tip, one per secondary veins; sinus broadly opened, with rounded bottom. Venation pinnate, simple craspedodromous; midvein thick, straight; secondary veins 11 to 13 pairs, opposite to subopposite, diverging at 40° to 50° , nearly straight, entering teeth centrally; intercostal tertiary veins irregularly percurrent, 3 to 5 per cm; marginal tertiary veins forming loops within the deltoid teeth; areoles formed by rather thick quaternary and quaternary veins, four- or five-sided, about 0.2 mm across; ultimate veinlets ill-preserved; fimbrial veins on the margin distinctly present; petiole thick, more than 1 cm (in the smaller leaves).

Discussion: The regularly spaced secondary veins that are nearly straight and craspedodromous, large triangular teeth that are separated by arcuate sinus, intercostal tertiary veins weakly percurrent or forking, marginal tertiary veins forming a series of prominent loops within the teeth are some features of *Castanea* or *Quercus*. The presence of the fimbrial vein on the margin, however, excludes the reference to *Castanea* and evergreen oak (*Cyclobalanopsis*); the fossil leaves from the Ishikari coal field are referable to *Quercus* (subgenus *Quercus*). *Quercus ishikariensis* probably belongs to the section Cerris in having the areoles that are formed by thick veins, although more than twice branching veinlets are not preserved.

A specimen of *Quercus kushiroensis* from the Eocene of the Kushiro coal field (TANAI, 1970) is included in *Q. ishikariensis* in the foliar shape, venation and marginal features, although the holotype is excluded. A single leaf described as *Castanea kamtschatica* from the Upper Eocene of Kamchatka (FOTJANOVA,

1984) is similar to *Q. ishikariensis* in general shape and marginal serration; but it needs to confirm whether or not the fimbrial vein is present.

Occurrence: Ishikari coal field Ic-9; Kushiro coal field Ks-3.

Collection: NSM-PP 10585 (holotype), 10586a, 10586b, 10587; HUMP no. 25936.

Quercus kitamiana TANAI sp. nov.

Pl. 2, fig. 1; Pl. 3, fig. 4; Pl. 5, fig. 3; Fig. 2-Ga, b.

Type: Holotype NSM-PP 10635, paratype 10636; Wakamatsuzawa, Kitami City, Hokkaido; Wakamatsuzawa Formation (Early Oligocene).

Etymology: This species referred to Kitami City, where the specimens were commonly found.

Description: Leaves narrow obovate, somewhat inequilateral, acute at both apex and base, 9.2 to 17.5 cm (estimated) long and 4.0 to 8 cm wide, 2.18 to 2.29 in length/width ratio; margin dentate except entire part of the lower one-thirds or one-fourths of blade; teeth low deltoid with bluntly pointed tip; sinus shallow, broadly rounded; thick fimbrial vein present; petiole medium in thickness, 1.0 to 1.5 cm long (in medium-sized leaves). Venation pinnate; midvein thick, nearly straight; secondary veins 15–16 in pairs, subopposite, regularly spaced, diverging at 30° to 45° in one side from midvein and at 40° to 55° in another side, nearly straight, entering teeth centrally; 3 to 5 pairs of basal secondary veins forming loops with tertiary veins along the margin; intercostal tertiary veins rather thick, 4 or 5 per cm, straight percurrent, sometimes branched, marginal tertiary veins brochidodromous within teeth; quaternary veins mostly parallel to tertiary veins; quaternary and quaternary veins making reticulate; areoles quadrangular, about 0.2 mm across; ultimate veinlets single to once or twice branching.

Discussion: The presence of a fimbrial vein, dentate margin with bluntly tipped teeth, regularly spaced secondary veins and brochidodromous tertiary veins within the teeth indicate that these leaves are referable to *Quercus* (the subgenus *Quercus*), especially to the section *Prinus*. But, that basal margin of about one-thirds of blade is entire, is uncommon feature in the extant leaves of *Prinus*, although common in those of the subgenus *Cyclobalanopsis*. The presence of fimbrial vein excludes these fossils from *Cyclobalanopsis*. Leaves of some extant species of the section *Suber* are entire on the lower half margin, as in *Quercus kingiana* CRAIB., *Q. franchetii* SKAN. and *Q. lanata* SMITH of East Asia; however, these extant leaves are quite different in having thick texture, serrate margin with small, aristate tipped teeth and smaller areoles intruded by none or single veinlet.

Among the extant species of *Prinus* the fossil leaves appear to be similar to those of the extant *Q. griffithii* HOOK. f. THOMAS of China, *Q. aliena* BL. of

Japan, and *Q. prinus* L. of eastern North America in having acute base, shallowly dentate margin, long petiole, and space of the intercostal tertiary veins, but these extant leaves are somewhat less in secondary veins and entire only on very basal margin. This relationship is, however, also supported by the features of ultimate veinlets: the above-noted 3 extant oaks have typically single to once (very rarely twice) branching as in *Q. kitamiana*, although most of other extant species of *Prinus* of East Asia and eastern North America are lacking or single in veinlets.

Several species of deciduous fossil oaks (subgenus *Quercus*) were recently described from the Lower Oligocene flora of the Kiin-Kerish Mountain, eastern Kazakhstan (ILJINSKAYA, 1991). Of these oaks, *Q. kinkerishica* closely resembles *Q. kitamiana* in general features such as foliar shape, venation, and marginal dentation, but it is distinguished in having no entire basal margin.

Occurrence: Wakamatsuzawa and Minamigaoka, Kitami City, Hokkaido.

Collection: NSM-PP 10635 (holotype), 10636 (paratype); NSM-PP 10637–10642.

Quercus sichotensis ABLAEV and GOROVoi

Quercus sichotensis ABLAEV & GOROVoi, TANAI & UEMURA, 1994, p. 352, Fig. 1–6, Fig. 5–5.

Occurrence: Wakamatsuzawa, Kitami City, Hokkaido.

Collection: NSM-PP 16358.

Quercus ussuriensis KRYSHTOFOVICH

Quercus ussuriensis KRYSHTOFOVICH, TANAI & UEMURA, 1994, p. 354, fig. 2–3, fig. 5-1–4, fig. 8-1–4.

Occurrence: Wakamatsuzawa and Minamigaoka, Kitami City, Hokkaido.

Collection: NSM-PP 16345–16349, 16335–16343a, 16350, 16352, 16353, 16355.

Quercus sp.

Pl. 3, fig. 2; Pl. 4, fig. 4

Description: Inner mould of a cupule being of shallow bowl in shape, but nearly flattened by compression, suborbiculate in face view, 2.2 cm long and 1.8 cm wide, 4 mm in height; trace of acorn scar suborbiculate, 1.5 cm long and 1.2 cm wide; cupule margin smooth, slightly incurved.

Discussion: The bowl shape and trace of acorn scar indicate that this fossil is probably a cupule of some genera of the Fagaceae. The outer surface of cupule partially remained as the carbonized matters, has no sign of concentric rings which are formed by connate scales; it appears to be covered by short, appressed

scales. The fossil is referable *Quercus*, especially to the subgenus *Quercus* excluding the section *Cerris*.

Occurrence: Hidari-ichinosawa (Left no. 1 tributary) of the Tanzan River, Ashibetsu City (Ikushunbetsu Formation).

Collection: NSM-PP 10589.

Rejected Citation of the Fagaceae in the Paleogene of Hokkaido

Except the taxa which are mentioned in the systematic chapter, the following taxa once described from the Paleogene of Hokkaido are excluded from the Fagaceae, because they lack the characteristics of this family.

Dryophyllum yubariensis ENDO (ENDO, 1968, part, p. 426, pl. 6, fig. 4. = *Dicotylophyllum* sp.

The inequilaterally elliptic shape and asymmetric base suggest that this specimen represents a leaflet. However, it is difficult to identify, because all the marginal area of blade is not preserved.

Dryophyllum yubariensis ENDO (1968, part, p. 426, pl. 14, fig. 3) = Rosaceae ? genus indet.

This specimen (holotype) is poorly preserved in the margin; it appears to be doubly serrate on the margin, having trigonal principal teeth associated with 3–4 subsidiary teeth in which the marginal tertiary veins end. These marginal characters may indicate that this specimen is a leaflet of the Rosaceae such as *Rubus* or *Sorbaria*.

Fagus antipofi ABICH (ENDO, 1968, pl. 22, figs. 1–3) = dubious specimens.

ENDO (1968) illustrated a leaf, a cupule and a seed of *Fagus* from the Ishikari coal field without any description and discussion. The re-examination reveals that the doubly serrate margin and arcuate secondary veins exclude this leaf specimen from *Fagus*, and that the seed-like impression is too dubious to be identified. The specimen illustrated as a cupule is not housed in the museum.

Quercus kushiroensis TANAI (TANAI, 1970, part, p. 471, pl. 10, figs. 9, 10, not pl. 20, fig. 2) = *Dicotylophyllum kushiroensis* (TANAI) TANAI.

Of 3 specimens described as *Quercus kushiroensis*, 2 leaves including the holotype have usually a minute subsidiary tooth on the basal side of principal teeth. A branch emerges basally from secondary veins, and enters this subsidiary tooth. Such marginal feature is unusual in the serrate margined leaves of Fagaceae, excepting for leaves of some extant species of *Nothofagus* such as *N. alessandri* and *N. alpina*. However, the secondary veins of *Nothofagus* usually enter along the basal side of main teeth (TANAI, 1986).

Although the fossil leaves superficially resemble several extant leaves of *Quercus* (*Cyclobalanopsis*), the marginal features exclude these fossil leaves from *Quercus*. They may represent leaves of a supposed extinct Fagaceae, but the

ill-preservation does not allow to study the detailed venation characters. It is noteworthy that *Phyllites kryshstofovichii* (KLIMOVA) with the double serrate margined leaves closely similar to the Kushiro specimens is known from the Oligocene of Primorye (ILJINSKAYA & ABLAEV in TAKHTAJAN, ed., 1982). If these fossils of Hokkaido and Primorye belong to Fagaceae, it may be significant that the extant *Fagus* and *Quercus* rarely have unusual leaves which have a subsidiary tooth between the principal teeth.

Discussion of Stratigraphic and Phytogeographic Implications of Paleogene Fagaceae in East Asia

Fagoideae

The evolutionary history of the genus *Fagus* during the Tertiary has been discussed by various authors; for instance, it was recently summarized by JONES (1986) and KVAČEK and WALTHER (1991, 1992). Neogene fossils of this genus are commonly known from East Asia; they are not always difficult to be identified, even in phylogenetic relationships with the extant species, because they are represented by leaves, associated with cupules or seeds. On the one hand, Paleogene specimens hitherto referred to *Fagus* in East Asia are represented mostly by leaves, and some of them seem to be unreliable in generic assignment.

Fossils referred to *Fagus* were described under various names from the Upper Eocene of Hokkaido, Sakhalin, Kamchatka and Northeast China; *Fagus* ? *feroniae* UNGER (FLORIN, 1922) and *F. chinensis* LI (Acad. Sin., ed., 1978) from the Fushun coal field, *F. paucinervis* Borsuk from the Agnevo coal mine of Sakhalin (BORSUK, 1956), and *F. napanensis* FOTJANOVA (FOTJANOVA in TAKHTAJAN, ed., 1982; CHELEBAEVA, 1991) and *F. septembris* CHELEBAEVA (CHELEBAEVA, 1991) from the Kovanchinsk Formation of Kamchatka. All of these fossils are represented only by leaf impressions; they are poor in preservation. Of these Eocene leaves, the specimens of *Fagus* ? *feroniae* are certainly excluded from *Fagus* because of having double serrate margin with minute, glandular teeth (in 1974 I could examine the Fushun specimens housed in the Natural History Museum of Stockholm). I have not yet obtained access to the other Eocene leaves described as beech. Although they may be superficially similar to some extant beech leaves, the details available in the figures of these species do not allow to refer to *Fagus* with certainty.

ENDO (1968) illustrated a leaf, a cupule, and a seed as *Fagus antipofi* from the Eocene of the Ishikari coal field without any description and discussion. As already discussed in early pages, all these specimens are too dubious to be identified to *Fagus*. No reliable specimen referable to *Fagus* has been found in the Eocene of Hokkaido.

Fagus uemurae here described from the Early Oligocene Wakamatsuzawa

Formation is the earliest unequivocal record of *Fagus* in Hokkaido. Another species from the same formation, "*Fagus*" *kitamiensis*, is somewhat uncertain to be referable to this genus, because it has some unusual features of the extant beech leaves. This species probably represents an extinct genus of Fagoideae.

The oldest record of unequivocal fossil *Fagus* in Japan is known from the Kobe Group of western Honshu. The Kobe Group is of Early Oligocene in age, but it is somewhat older than the Wakamatsuzawa Formation, considering radiometric dating together with the floristic composition (TANAI, 1992; TANAI & UEMURA, 1994). In the Kobe flora are included many leaves and some cupules, which were illustrated as *F. stuxbergii* (NATHORST) TANAI (HORI, 1987). Although these specimens need to be re-examined in specific taxonomy, they are doubtlessly referable to *Fagus*. However, the Kobe leaves are distinctly distinguished from the Kitami species in having less secondary veins and more widely spaced tertiary veins.

It is noteworthy that many leaves of *Fagus* were commonly known from the *Engelhardia*-bearing formations of North Korea and southern Primorye, which were concluded to be of Early Oligocene age (TANAI, 1992; TANAI & UEMURA, 1994). These leaves were described under various names: they are *F. koraica* HUZIOKA, *F. protologipetiolata* HUZIOKA and *F. uotanii* HUZIOKA in North Korea (HUZIOKA, 1951, 1972), while most leaves from Primorye, excepting for *F. longipetiolata*, were referred to Miocene species such as *F. hankaica* T. ALEXEENKO and *F. stuxbergii* (NATH.) TANAI (ABLAEV, 1978, 1987; ABLAEV *et al.*, 1993). Although these Oligocene leaves need to be specifically re-examined, most of them seem to be likely beech leaves.

Fagus irvajamensis CHELEBAEVA was known from the Lower Oligocene of Kamchatka, based on many leaves (CHELEBAEVA, 1980); judging from the illustrations indicated by her, a few specimens seem to be likely beech leaves, but most of the specimens seem to be equivocal, especially in features of the most abmedial tertiary vein. This Kamchatka species may contain some other taxa of the Fagaceae such as *Quercus* or *Castanea*.

So far as known from the bibliographic survey, the fossil record of *Fagus* can be traced back to the Middle Eocene in East Asia. However, the unequivocal fossils of this genus are known from the Early Oligocene and onward in Japan, North Korea, Primorye and northern Kamchatka. On the one hand, unequivocal oldest fossils of *Fagus* in the interior regions of East Asia were known from the Late Oligocene: leaves as *Fagus antipofi* Heer from Ashutas, eastern Kazakhstan (KRYSOTOVICH, ed., 1956) and cupules as *F. cf. longipetiolata* SEEM. (DOROFEEV in TAKHATAJAN, ed., 1982) from Kozyulino near Tomsk. Thus, the fossil record indicates that the genus *Fagus* first appeared along the Pacific marginal areas of the Asian continent since the Early Oligocene. The oldest unequivocal occurrence of fossil *Fagus* in the Early Oligocene is also consistent

with that of Central Europe (KVAČEK & WALTHER, 1989a, 1991) and North America (JONES, 1986).

Quercoidae

The trigonobalanoid fossils are not yet known in East Asia, although they are known from the Eocene to the Pliocene in Central Europe (MAI, 1970; KVAČEK & WALTHER, 1989a) and from the Oligocene in North America (CREPET, 1989; NIXON & CREPET, 1989). On the other hand, the fossils of *Quercus* are well known from the Eocene and onward in East Asia, especially abundant with many evergreen and deciduous species in the Miocene.

The fossils referred to *Quercus* are rather few in number of species and specimens in the Eocene. The earliest unequivocal fossil of *Quercus* is known from the Middle Eocene Ube flora of western Japan (HUZIOKA & TAKAHASHI, 1970); it is *Quercus* (*Cyclobalanopsis naitoi*) which is represented by leaves and some depressed acorns. The next older fossils are *Q. ishikariensis* and *Quercus* sp. (cupule) from the late Middle Eocene of Hokkaido; the former species probably belong to the section Cerris. Several species of *Quercus* were described from the Eocene of Northeast China (Acad. Sin., ed., 1978), Sakhalin (BORSUK, 1956; SYCHEVA, 1977) and North Kamchatka (FOTJANOVA, 1984); most of these fossils are represented by poorly preserved leaves, and need to be re-examined in more detailed leaf architecture. It is noteworthy that a Kamchatka species, *Q. bozhedomovii* (FOTJANOVA, 1984), has dentate margined leaf which is similar to leaves of the section Albae or Prinus.

Oak species are markedly diverse in the Early Oligocene of Hokkaido (Fig. 3), represented by various leaf forms which are shallowly or deeply lobed, serrate and dentate on margin. Most of these oaks belong to the sections Cerris and Albae/Prinus of the subgenus *Quercus*, and one species of the subgenus *Cyclobalanopsis* is also included. Such specific diversity of *Quercus* is also known in the Early Oligocene Kiin-Kerish flora of eastern Kazakhstan (ILJINSKAYA, 1991; AKHMETJEV, 1991), and in the Oligocene Jiggu flora of Southwest China (Acad. Sin., ed., 1978). The Early Oligocene floras of northeastern Korea (the Kogeoweong and Kungshim floras) and southern Primorye (Rettikhovka and Kraskino floras) that were recently re-evaluated in age (TANAI, 1992; TANAI & UEMURA, 1994), contain also diverse oak fossils, most of whose species are common with those of Oligocene floras of Hokkaido. Thus, the radiation of the genus *Quercus* seems to have occurred widely in East Asia since the Early Oligocene.

Castaneoideae

The fossil leaves referred to Castaneoideae were described from the Paleogene of Japan, Sakhalin, Kamchatka, southern Primorye, Southwest China and

northeastern Kazakhstan. Of these fossils, leaves referred to *Castanopsis* and *Lithocarpus* (or *Pasania*) are known from the Middle Eocene Ube flora of West Japan (HUZIOKA & TAKAHASHI, 1970), the Late Eocene Svatol flora of Kamchatka (CHELEBAEVA, 1991), the Oligocene Jiggu flora of China (Acad. Sin., ed., 1978), and the Early Oligocene Rettikhovka flora of Primorye (KLIMOVA, 1976). Some of these Paleogene leaves may need to be further reinvestigated in generic assignment, because it is sometimes difficult to distinguish *Castanea*/*Lithocarpus*/*Pasania* from *Quercus* (especially, *Cyclobalanopsis*) and some other genera only by superficial features of leaves, and even by cuticular characters (JONES, 1986).

Fossil leaves of *Castanea* are also difficult to separate from those of some deciduous oaks such as the section *Cerris* only by gross characters. *Castanea fujiyamae* here described from northeastern Hokkaido is an unequivocal record of this genus in the Early Oligocene. Leaves of *Castanea* were from the Oligocene of North Korea and Kazakhstan: *C. tanaii* from Kogeonweong and Kungshim (HUZIOKA, 1972), *C. antipovii* from Ashutas (KRYSHTOFOVICH, ed., 1956), and *C. protocrenata* and *C. zasanica* from Kiin-Kerish (ILJINSKAJA, 1991). These leaves are likely to be chestnut, but they need to be examined in leaf architecture.

Eocene fossils of *Castanea* are few in East Asia; they are described from Sakhalin and Kamchatka. *Castanea longifolia* from Aleksandrovsk of Sakhalin (BORSUK, 1956) may be *Quercus*, because it has usually long petiole (about 2 cm long) as similar as in the extant *Q. acutissima* and *Q. variabilis*. Fossil leaves of *Castanea* from the Late Eocene of North Kamchatka (FOTJANOVA, 1984) have not definite characters referable to this genus.

Distribution of the Genus *Fagopsis*

Among the Eocene Fagaceae of Hokkaido, the genus *Fagopsis* is most interesting for the phytogeographic history of this family. Based on leaves, pistillate inflorescences, *in situ* pollen and fructscences from western North America, *Fagopsis* was supposed an extinct genus of the Fagaceae (WOLFE, 1973, 1977; MANCHESTER & CRANE, 1983; WOLFE & WEHR, 1987). On the one hand, CREPET (1989) suggested that this extinct genus may be representative of a sister group to Fagaceae or even a more distantly related taxon.

Fagopsis is known principally from the Paleocene of Arctic region, although its fossils were first described as *Quercus groenlandica*: Greenland (HEER, 1868; KOCH, 1963; WOLFE, 1977), Spitsbergen (BUDANTSEV, 1983), northern England (Isle of Mull) (GARDNER, 1887; BOULTER & KVAČEK, 1989), and Alaska (HOLLIICK, 1936; WOLFE, 1977). Only southernmost distribution is known in the Fort Union Formation of Wyoming (BROWN, 1962; WOLFE, 1977). The descendants of Paleocene *Fagopsis* were known in the Middle and Late Eocene around the Rocky Mountain region in southwestern Canada and the United

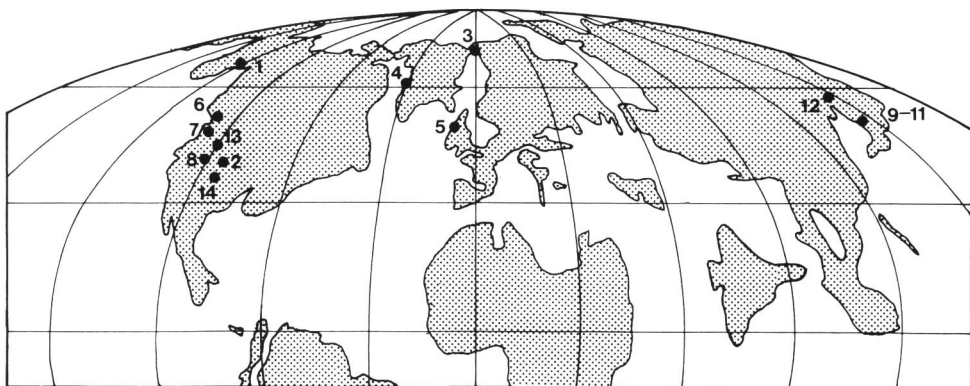


Fig. 4. The fossil occurrence of *Fagopsis* in the Northern Hemisphere. Paleocene: 1, Eska Creek, Matanuska Valley, Alaska (WOLFE, 1977). 2, Ethete and Winchester, Wyoming (WOLFE, 1977). 3, Barntsburg, Spitzbergen (described as *Quercus groenlandica* by BUDANTSEV, 1983). 4, Atanikerdluk and Agatdalen Valley, West Greenland (WOLFE, 1977). 5, Isle of Mull, Scotland (BOULTER & KVAČEK, 1989). Middle Eocene: 6, Stamp Lake, British Columbia (WOLFE & WEHR, 1987). 7, Republic, Washington (WOLFE & WEHR, 1987). 8, Elk Creek, Yellowstone Nat'l Park, Wyoming (WOLFE & WEHR, 1987). 9, Sannosawa, Bibai, Hokkaido. 10, Reisuizan, Yubari, Hokkaido. 11, Tsukigata, Hokkaido. 12, The River Kama, South Sakhalin (described as *Quercus rectinervis* by SYCHEVA, 1977). Late Eocene: 13, Ruby River, Montana (BECKER, 1961). 14, Florissant, Colorado (MACGINITIE, 1953). The paleocontinental map (Middle Eocene) after SMITH *et al.* (1994).

States (Fig. 4). In East Asia leaves of *Fagopsis* were confirmed from the Middle and late Middle Eocene of Hokkaido and late Middle Eocene of Sakhalin, although no reproductive organs have not yet been found.

The now available record shows that *Fagopsis* seems to have migrated to East Asia from North America via the Beringia during the Eocene. In spite of extensive investigation by many workers, *Fagopsis* has never been described from the Paleogene of southern England and central Europe. It is probably due to the fact that these regions were occupied by the tropical forest during the Paleocene and Eocene, and that *Fagopsis* could not enter these regions. It is noteworthy that such phytogeographic distribution of *Fagopsis* is consistent with the fact that fossil record of *Metasequoia* during the Tertiary is lacking in southern England and central Europe.

Conclusion

Paleogene fossils of Fagaceae in Hokkaido reveals a pattern in the sequence of appearance and diversification of fagaceous taxa, although most of the fossils are represented by leaves. Considering them together with Paleogene record of

other regions of East Asia, the early history of Fagaceae is envisaged.

All the Eocene fossils referred to *Fagus* lack the definite characters of this genus. *Fagus* appeared first in the Early Oligocene of Hokkaido, western Honshu, Northeast Korea, Southern Primorye and Kamchatka, and then the luxuriant beech forest prevailed in these regions during the Lower Miocene. The first appearance of *Fagus* in the Oligocene is also confirmed in central Europe and western North America. This fact may imply that the diversification from the ancestral taxon to the extant *Fagus* occurred nearly simultaneously during the Early Oligocene in the Northern Hemisphere.

The earliest unequivocal record of *Quercus* is from the Middle Eocene of West Japan. Eocene fossils of this genus are known from Hokkaido, Sakhalin, Kamchatka and North China, but they are poor in species. *Quercus* became more diverse with various species since the Early Oligocene in East Asia, from the Pacific coast region to the interior region such as eastern Kazakhstan. This specific radiation occurred not only in the temperate forests of the middle latitudes but in the Notophyllous forest of the lower latitudes, as indicated by the Oligocene Jiggu flora of Southwest China.

The early history of Castaneoid is yet uncertain, although many Cataneoid fossils were reported from the Paleogene in many regions of East Asia. It is due to the fact that most of Castaneoid fossils are taxonomically dubious. The unequivocal leaves of *Castanea* are known from the Early Oligocene of Hokkaido and eastern Kazakhstan. Castaneoid was suggested to be an older group within Fagaceae (NIXON, 1989); more reliable fossils such as reproductive organs are hoped to be found in the Paleogene of East Asia.

Acknowledgements

For preparing a part of the manuscript, I have benefited by discussion with Professor Jack A. WOLFE (University of Arizona, Tucson) on taxonomy of Paleogene "beech" leaves. I am indebted to Dr. Kazuhiko UEMURA (National Science Museum, Tokyo) for the permission to examine his collection from Kitami region. Dr. Akira KATO, the chief of Department of Geology, National Science Museum, generously provided the facilities to publish this paper.

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Explanation of Plates

(All figures in natural size unless otherwise stated)

Plate 1

- Figs. 1, 2. "*Fagus*" *kitamiensis* TANAI. Paratypes NSM-PP 10616a, 10617. (Wakamatsuzawa, Kitami).
 Figs. 3, 4. *Fagus uemurae* TANAI. fig. 3: holotype NSM-PP 10607; fig. 4: paratype NSM-PP 10608. (Wakamatsuzawa, Kitami).
 Fig. 5. Showing the marginal serration and tertiary venation features of "*Fagus*" *kitamiensis* (hypotype NSM-PP 10615). $\times 8$
 Fig. 6. Showing the marginal serration and tertiary venation features of *Fagus uemurae* (paratype NSM-PP 10608). $\times 8$

Plate 2

- Fig. 1. *Quercus kitamiana* TANAI. Holotype NSM-PP 10635. (Wakamatsuzawa, Kitami).
 Figs. 2, 3. "*Fagus*" *kitamiensis* TANAI. fig. 2: hypotype NSM-PP 10618; fig. 3: holotype NSM-PP 10615. (Wakamatsuzawa, Kitami).
 Fig. 4. Showing the tertiary venation features and areoles of "*Fagus*" *kitamiensis* (holotype NSM-PP 10615). $\times 25$
 Fig. 5. *Quercus ishikariensis* TANAI. Hypotype NSM-PP 10586a. (Reisui-zan, Yubari).
 Fig. 6. *Fagus uemurae* TANAI. Paratype NSM-PP 10609. (Wakamatsuzawa, Kitami).

Plate 3

- Fig. 1. *Quercus ishikariensis* TANAI. Holotype NSM-PP 10585. (Reisui-zan, Yubari).
 Fig. 2. *Quercus* sp. (Enlargment of plate 4, fig. 1). $\times 1.4$
 Fig. 3. *Dryophyllum noborikawense* TANAI. Paratype NSM-PP 10591. (Yubari-Honcho, Yubari).
 Fig. 4. *Quercus kitamiana* TANAI. Paratype NSM-PP 10636. (Wakamatsuzawa, Kitami).

Plate 4

- Fig. 1. *Quercus* sp. NSM-PP 10589. (Tanzan-gawa, Ashibetsu)
 Fig. 2. *Quercus ezoana* TANAI. Holotype NSM-PP 10634. (Wakamatsuzawa, Kitami).
 Fig. 3. *Quercus ishikariensis* TANAI. Hypotype NSM-PP 10586b.
 Figs. 4, 5. *Castanea fujiiyamae* TANAI. Holotype NSM-PP 10600. (Wakamatsuzawa, Kitami). fig. 4: the counterpart of fig. 5.

Plate 5

- Fig. 1. *Fagopsis nipponica* TANAI. Hypotype NSM-PP 10583. (Sannosawa, Bibai).
 Fig. 2. *Fagopsis nipponica* TANAI. Paratype NSM-PP 10580a. (Reisui-zan, Yubari).
 Fig. 3. *Quercus kitamiana* TANAI. the counterpart of Pl. 3, fig. 4 (NSM-PP 10636).
 Figs. 4, 5. *Dryophyllum noborikawense* TANAI. fig. 4: Paratype NSM-PP 10592; fig. 5: holotype NSM-PP 10590. (Yubari-Honcho, Yubari).

Plate 6

- Fig. 1. *Fagopsis nipponica* TANAI. Holotype NSM-PP 10579. (Subetsu-gawa, Tsukigata).
 Fig. 2. *Fagopsis nipponica* TANAI. Paratype NSM-PP 10580b. (Reisui-zan, Yubari).
 Fig. 3. "*Fagus*" *kitamiensis* TANAI. Hypotype NSM-PP 10619. (Wakamatsuzawa, Kitami).
 Fig. 4. Showing the areoles of *Quercus ishikariensis* (holotype NSM-PP 10585). $\times 25$
 Fig. 5. Showing the tertiary venation features of *Fagopsis nipponica* (paratype NSM-PP 10580b). $\times 6$
 Fig. 6. Showing the marginal dentation of *Fagopsis nipponica* (paratype NSM-PP 10580b). $\times 15$

Plate 1

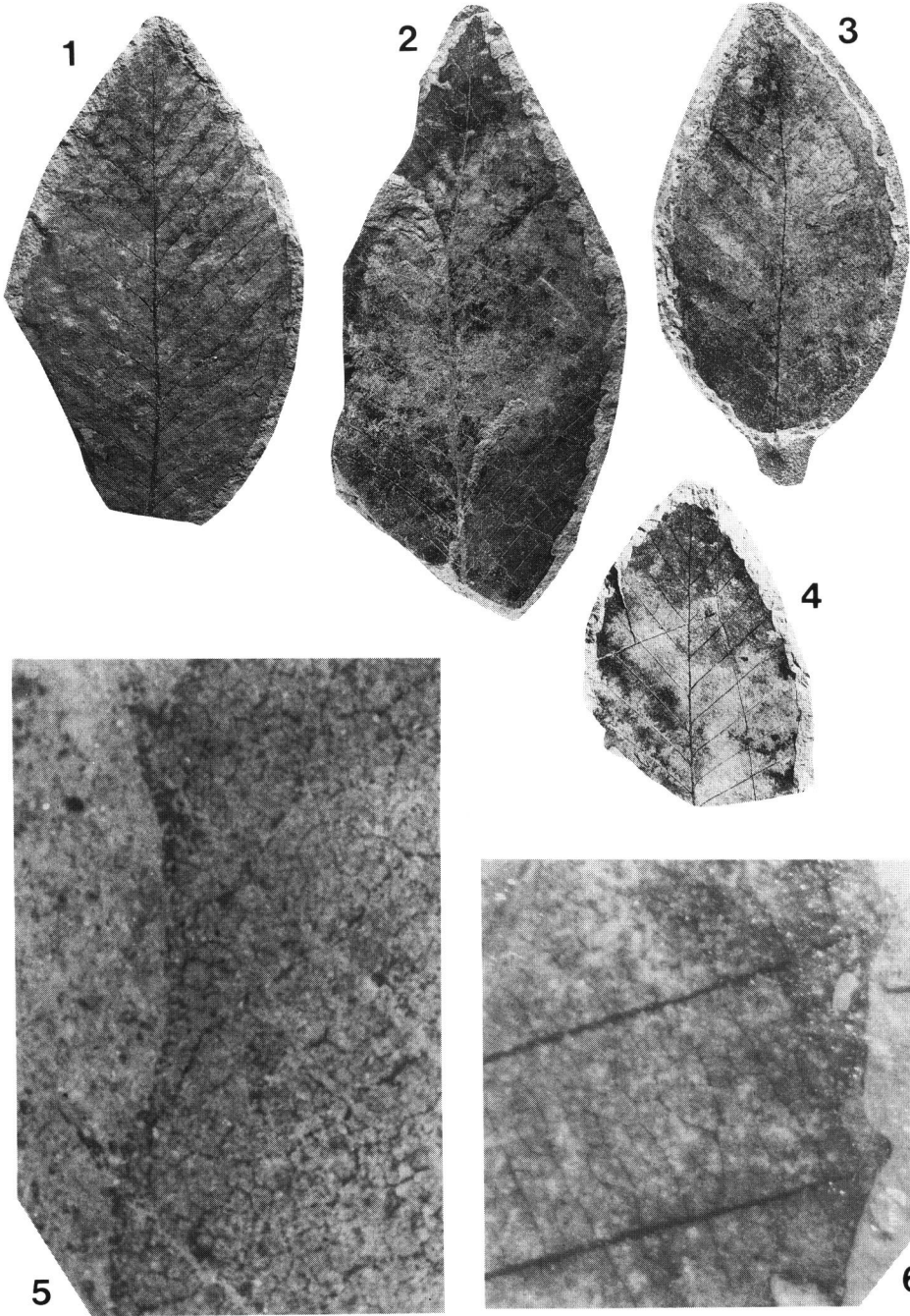


Plate 2

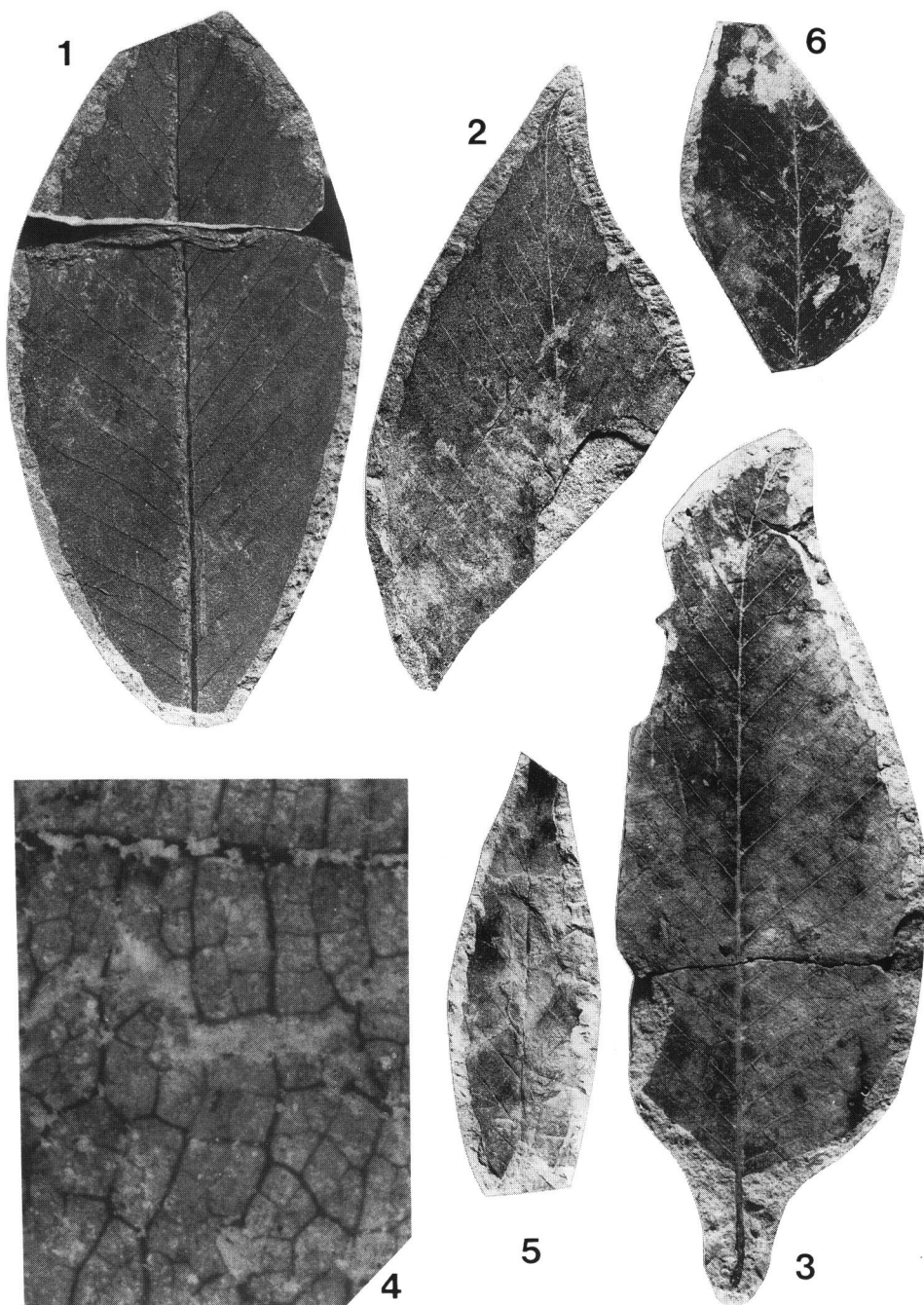


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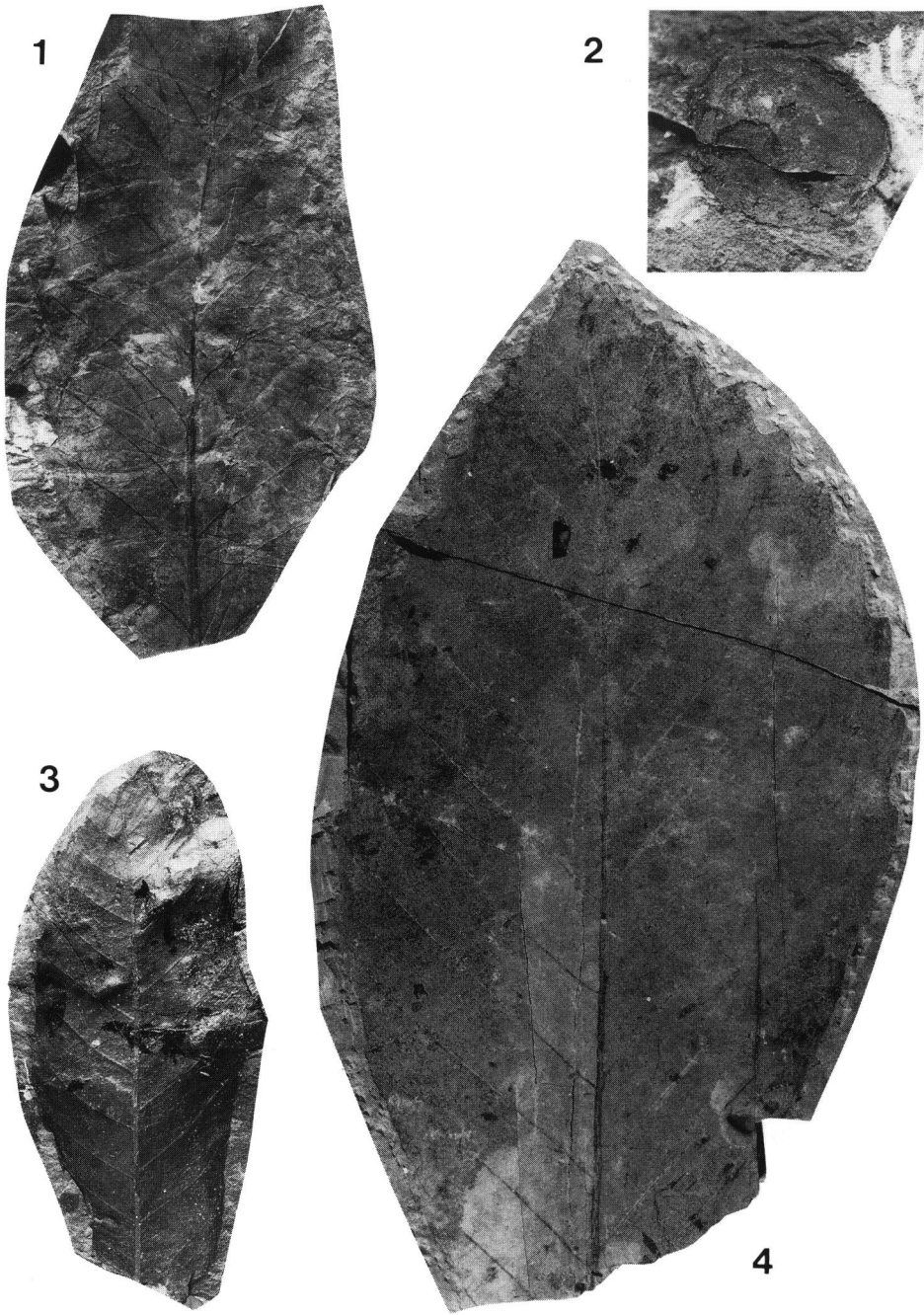


Plate 4



Plate 5

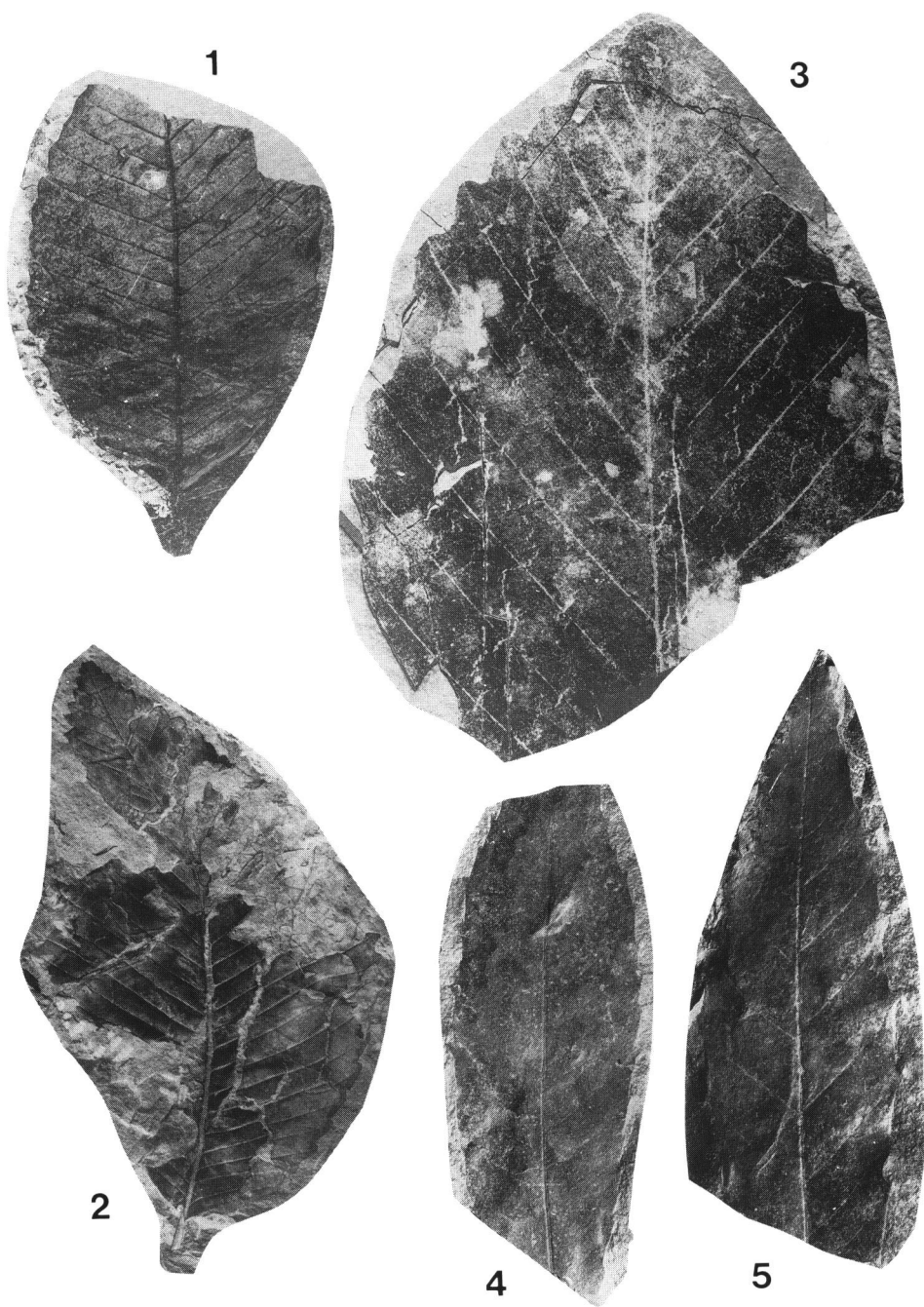


Plate 6

