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Plant macrofossils from the marine Ieda Group (lower middle Miocene) in northern Iwata City, Shizuoka, Central Japan

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Abstract Plant macrofossils from the lower middle Miocene Ieda Group in northern Iwata City, Shizuoka, central Japan are reported for the first time. The assemblage consists of 29 taxa, represented by a single beech species and various deciduous species from the families Fabaceae, Ulmaceae, and Sapindaceae, along with some evergreen species of Fagaceae and Lauraceae. These remains are scattered in deep sea sediments and almost exclusively consists of isolated leaf remains; no conifers and herbaceous remains are observed. Fossil occurrences and sedimentary features show characteristics of allochthonous assemblages, and it can be regarded that the composition of the assemblage was skewed through transportation processes. Nevertheless, based on a number of common species, the assemblage can be correlated to the late early–early middle Miocene Daijima-type flora, which flourished during the mid-Miocene Climatic Optimum. The assemblage also contains *Fagus stuxbergi*, *Clethra* sp., and *Myrtonium* sp., which have never been reported from the Daijima-type flora to date. The former two species are shared by late Miocene–Pliocene fossil assemblages. This is the oldest concrete fossil record of *Fagus stuxbergi* and it provides us an idea that this species appeared much earlier under warmer temperate climatic conditions.

Key words: allochthonous fossil assemblage, early middle Miocene, *Fagus stuxbergi*, mid-Miocene Climatic Optimum, plant macrofossils

Introduction

The early–middle Miocene transition is known as the warmest time period during the Neogene and is often regarded as the mid-Miocene Climatic Optimum (MMCO; Zachos *et al.*, 2001). This event and the following cooling are considered to have contributed to the floristic diversity of the Japanese Islands because of the evolution and subsequent diversification of some exotic lineages (Yamada and Yamada, 2018; Yabe and Nakagawa, 2018). However, as a consequence of marine transgression during this time period, terrestrial vegetation and climate in the Japanese Islands were scarcely recorded (*e.g.*, Shibata and Ina, 1983; Uemura, 2004; Ina *et al.*, 2008; Yabe and Nakagawa, 2018), particularly on the Pacific side of the islands.

In the southern part of the Akaishi Mountains, small Miocene sedimentary basins were formed as a consequence of tectonic subsidence during the early to middle Miocene (Kano *et al.*, 1993). The ages of these deposits are biostratigraphically well constrained (Ibaraki, 2004). It is known that they yielded an abundance of plant fossils; however, no attempt has so far been made to describe them taxonomically, probably due to the poor quality of their preservation.

In the present study, we describe plant macrofossils from the lower middle Miocene Ieda Group from northern Iwata City, Shizuoka Prefecture, central Japan. This is the first concrete evidence of terrestrial vegetation in this region. We briefly discuss its characteristics as well as its implications on the floristic changes in the Japanese Islands.

Geological setting

The study site is located northeast of Iwata City, western Shizuoka Prefecture, central Japan (Fig. 1A). The investigated lower to middle Miocene marine deposits are distributed in several fault-contacted geological blocks (Fig. 1B).

Relatively few geological and paleontological studies have been carried out in this area (Maki-

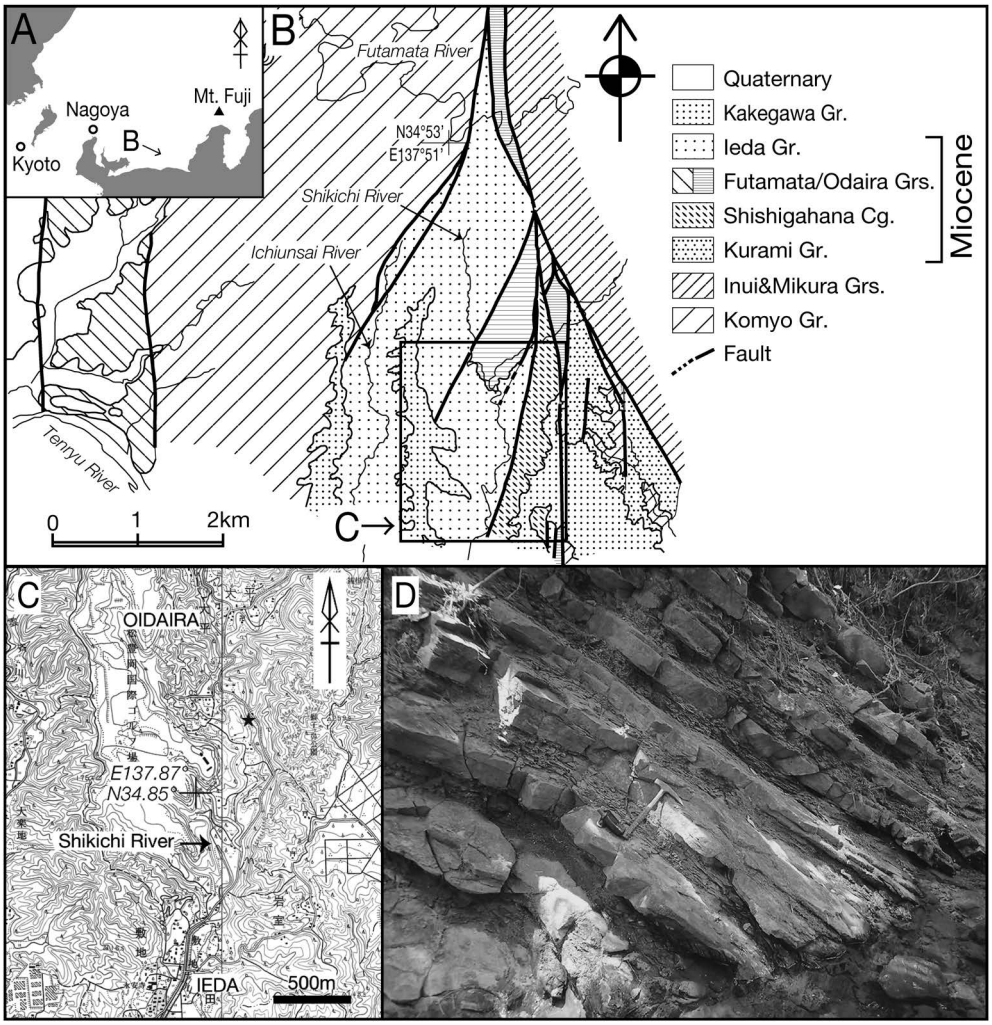

Figure 1. A. Index map of study area. B. Geologic map of northern Iwata City and adjacent areas (Kano *et al.*, 1993). C. Locality of plant macrofossils in this study, adapted to 1 : 25,000 scale topographic maps "Futamata" and "Mori" published by Geospacial Information Authority in Japan (GSI). D. One of the outcrops of the Ieda Group along Shikichi River, comprising of alternating beds of sandstone and mudstone. Hammer for scale has handle 30 cm long. Gr.: Group, Grs.: Groups, Cg.: Conglomerate.

yama, 1934; Saito and Isomi, 1954; Saito, 1963; Shibata and Kato, 1975; Yoshida, 1992; Kano *et al.*, 1993; Tanaka and Kitamura, 2008; Ibaraki and Kitamura, 2010). The Miocene deposits of the area are fault-contacted with the upper Cretaceous Komyo Group, which is one of the components of the Shimanto belt accretionary complexes. Miocene deposits in the western block are called the Futamata Group (Saito and Isomi, 1954), whereas those in the eastern block are divided into the Odaira and Ieda groups in ascending order. They are unconformably overlain by the Pliocene and Quaternary deposits or fault-contacted with the lower Miocene Shishigahara conglomerate (Kano *et al.*, 1993).

The Futamata Group represents a single depositional cycle which starts from conglomerate and changes into massive sandstone, mudstone, and conglomerate. The Odaira Group also consists of basal conglomerate, sandstone, and mudstone, and is overlain by the Ieda Group, which consists exclusively of alternating beds of sandstone and mudstone (Kano *et al.*, 1993). The middle or upper part of the Futamata and Odaira groups yield deep sea marine molluscs (Shibata and Kato, 1975), and the latter also yields deep sea fishes (Tanaka and Kitamura, 2008). The occurrence of plant macrofossils from the Ieda Group has been mentioned in previous geological studies (Makiyama, 1934; Saito and Isomi, 1954); however, the taxonomic study of this group has not been published.

The Futamata Group is correlated to the late early–early middle Miocene based on planktonic foraminifera of Blow's (1969) N8 zone (16.4–15.1 Ma) (Saito, 1963), as well as on the presence of

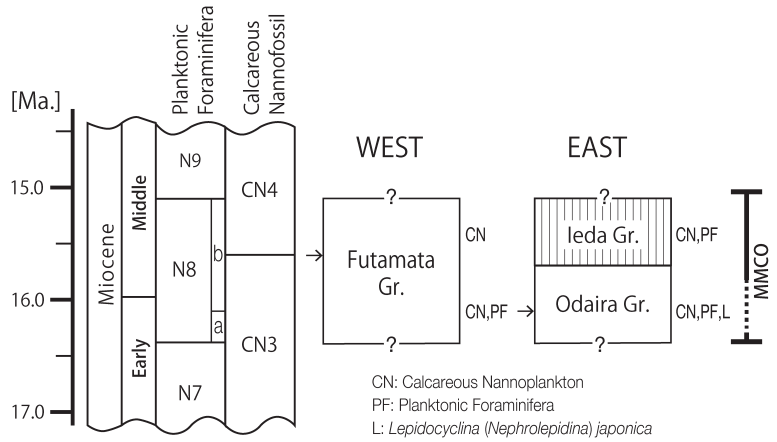

Figure 2. Stratigraphic relationship of selected Miocene groups in northern Iwata City, showing biostratigraphic correlation. Chronostratigraphic framework is followed after Gradstein *et al.* (2012). The age range of the mid-Miocene Climatic Optimum (MMCO) follows Kurihara *et al.* (2005). Dashed line indicates a cooling event called a Miocene isotope event of Miller *et al.* (1991).

CN3/CN4 boundary of calcareous nannofossil zonation (Kano *et al.*, 1993) in the middle mudstone (Fig. 2). The Odaira and overlying Ieda groups can be stratigraphically correlated to the Futamata Group by depositional sequence (Saito and Isomi, 1954). This is supported by the occurrence of calcareous nannofossils of CN3 or CN4 (Kano *et al.*, 1993) and the presence of so-called *Praeorbulina* datum (ca. 16.1 Ma; Fig. 2, arrow) in the upper mudstone (Yoshida, 1992), along with a larger benthic foraminifera, *Lepidocyclina* (*Nephrolepidina*) *japonica* (Ibaraki and Kitamura, 2008) from the Odaira Group. The Ieda Group also yields N8 zone planktonic foraminifera (Saito, 1963) and CN3 or CN4 calcareous nannofossils (Kano *et al.*, 1993). Therefore, it is most probable that the plant-bearing Ieda Group can be correlated with the latter half of the N8 zone (early middle Miocene: ca. 15.5 Ma) (Fig. 2).

Materials and methods

Plant macrofossils were collected from brown- to white-colored, medium to very coarse-grained hard sandstone in the river gravel of the Shikichi River and its tributary in the northeast part of Iwata City (Fig. 1C). The sandstone rarely contained small patches of permineralized mudstone, but no plant fossils were generally recognized in these patches. Although plant fossils were collected from float rocks, their lithological characteristics fit very well with sandstone bed in the alternating beds of sandstone and mudstone of the Ieda Group, which comprises a small cliff along the river (Fig. 1D).

Figure 3. An example of occurrence of plant macrofossils in the Ieda Group. Leaves are scattering without specific orientation. Scale equal to a 5 cm long.

Fragments of leaves and woods were abundant and concentrated in particular bedding plane, in which few identifiable leaf remains were preserved (Fig. 3). They were generally scattered without specific orientation and were sometimes curled, folded, or oblique to the bedding plane.

Only two fruit specimens were obtained in this study. Isolated alder infructescence was found in very coarse sandstone which contained abundant fragmentary leaves. A single beech nut was also found as a float in a small tributary approximately 10 m from the confluence point with Shikichi River. The specimen was also embedded in white coarse sandstone. This sandstone was partly and weakly permineralized, which may have contributed to three-dimensional preservation of this nut. Because

the upstream of this tributary is dammed, the specimen is considered to have originated from the outcrop of the Ieda Group.

In the present study, all identifiable plants are systematically described. The descriptive terminology for dicotyledonous leaves follows the protocols of Ellis *et al.* (2009) and relevant literature. The taxonomic arrangement of angiosperms is based on APG IV (2016). The specimens used in this study are stored in the National Museum of Nature and Science, Ibaraki, Japan (NSM PP).

Most plant fossils were preserved as impressions, yielding no structurally preserved material. They were studied under a Nikon SMZ745T binocular microscope equipped with Nikon DS-Fi1 digital camera. Sketches were created using Adobe Illustrator Draw (Adobe Inc., San Jose, California, USA). The specimens were photographed using a Pentax K-3II digital camera with a 35 mm Pentax-DA macro lens at low-angle illumination.

Results

A total of 29 taxa distributed in 19 genera and 11 families were recognized in this study (Table 1). Fagaceae was the largest family with six taxa, followed by Lauraceae and Fabaceae (four species each). The percentage of woody taxa with smooth leaf margins was ca. 48%. Herein, we provide a systematic paleobotany of the plant species found in

Table 1. Systematic list of the plant megafossils of the Ieda Group.

Family Lauraceae
Cinnamomophyllum sp.
Litseaphyllum sp.
Machilus nathorsti Huzioka
Machilus ugoana Huzioka
Family Altingiaceae
Liquidambar sp.
Family Fabaceae
Leguminophyllum sp. 1 (cf. *Robinia*)
Leguminophyllum sp. 2 (cf. *Cassia*)
Leguminophyllum sp. 3
cf. *Podocarpium podocarpum* (A.Braun) Herendeen
Family Ulmaceae
Ulmus longifolia Ung.
Ulmus sp.
Zelkova zelkovaefolia (Ung.) Bůžek et Kotlaba
Family Fagaceae
Fagus stuxbergi (Nath.) Tanai
Fagus sp. (nut)
Lithocarpus? sp.
Quercus (*Cyclobalanopsis*) *mandraliscae* (Gaudin) Huzioka
Quercus (*Cyclobalanopsis*) *praegilva* Kryshtofovich
Quercus sp. cf. *Q.* (*Cyclobalanopsis*) *nathorstii* Kryshtofovich
Family Juglandaceae
Juglandaceae genus et species indeterminate (*Carya* or *Platycarya*)
Family Betulaceae
Alnus sp. (infructescence)
Family Myrtaceae
Myrtonium sp.
Family Sapindaceae
Acer sp.
Sapindus sp. cf. *S. tanaii* Onoe
Family Cornaceae
Alangium sp.
Family Clethraceae
Clethra sp.
Taxon indermined
Monocotylophyllum sp.
Phyllites sp. 1 (*Acer* ?)
Phyllites sp. 2
Phyllites sp. 3
Total 29 taxa (11 families, 19 genera)

the Ieda Group.

Systematic paleobotany

Class Angiospermae

Order Laurales Juss. *ex* Bercht. *et* J.Presl

Family Lauraceae Juss.

Genus ***Cinnamomophyllum*** Kräusel *et* Weyland

Cinnamomophyllum sp.

(Fig. 4F)

Materials examined: NSM PP-12546, 12600.

Remarks: Two fragmentary leaves are recognized in our collection. They are characterized by relatively thick leaf lamina with elliptical shape, entire margin and a pair of thick basal secondaries rising slightly above the base. Secondary veins are remote, and their number is probably three. Intercostal tertiary veins are typically percurrent and oriented perpendicularly to the primary vein. All these features are recognized in some genera and species of the family Lauraceae (*e.g.*, *Cinnamomum*, *Cryptocarya*, *Ediandra*, *Neolitsea*, and *Lindera*). Because of the absence of cuticular characteristics, we tentatively identify our materials as *Cinnamomophyllum* Kräusel *et* Weyland (Kräusel and Weyland, 1954), a form genus used for lauraceous leaves with prominent supra-basal secondaries.

Genus ***Litseaphyllum*** Wolfe

Litseaphyllum sp.

(Figs. 4A, B, 9A)

Litseaphyllum sp., Uemura *et al.*, 1999, p. 9, pl. 8, fig. 11; pl. 10, figs. 4, 5.

Material examined: NSM PP-12561b

Description: A single fragmentary leaf simple; laminae basal asymmetrical; estimated length 7.5 cm, width 1.5 cm; length/width ratio ca. 5.0, narrow oblong to lorate shape; apex missing; base narrow acute, straight to slightly convex; petiolate; margin entire, fringed with a fimbrial vein; primary vein massive, straight; secondary veins moderate, at least six pairs, opposite to subopposite, angle of divergence 40–45° in the middle part, increasing basally, gently curved, abruptly curved up along the margin, weak brochidodromous, distance between two secondaries increasing distally; inter-secondaries rare, thin, short; intercostal tertiaries moderate, percurrent, normally straight, almost perpendicular to the primary vein; quaternary veins thin, irregularly percurrent.

Remarks: This narrow oblong to lorate entire leaf with pinnate venation is comparable with those of the species of the Lauraceae family by its general shape and thick primary and comparatively thin secondary veins. The specimen resembles modern *Actinodaphne* species in shape and secondary venation characteristics: divergent angle against primary vein increases basally and the basal few pairs of secondaries derived nearly perpendicular to the primary vein. However, the species can hardly be assigned to any particular genus or species without the information on fine venation and cuticular characteristics. Thus, we determine this specimen as a form-genus *Litseaphyllum*, which was proposed for plants with lauraceous leaves with pinnate venation (Wolfe, 1977). *Litseaphyllum* sp. from the middle Oligocene Kiwado Formation (Uemura *et al.*, 1999) is probably conspecific with this species.

Genus ***Machilus*** Desr.

Machilus nathorsti Huzioka

(Figs. 4C, D, 9C)

Machilus nathorsti Huzioka, 1963, p. 203, pl. 34, figs. 2, 3; Matsuo, 1963, p. 239, pl. 50, figs. 2, 4; Huzioka and Takahasi, 1970, p. 58, pl. 9, fig. 10; Uemura *et al.*, 1999, p. 9, pl. 8, figs. 9, 10.

Material examined: NSM PP-12562

Description: A single fragmentary leaf simple; lamina slightly inequilateral; estimated length 10 cm, estimated width 3 cm, probably narrow elliptical in shape; base acute, cuneate, slightly decurrent; margin entire, fringed with a thick fimbrial vein; petiole marginal, at least 1 cm long; venation pinnate; primary vein massive; secondary veins medium, at least four opposite to subopposite pairs, basal pair weak, divergent angle against primary vein 25–35°, gently curved, parallel, vein spacing irregular, weak brochidodromous; intercostal tertiaries moderate, percurrent, straight, rarely concave or convex, obtuse to nearly perpendicular to primary vein; quaternary and quintenary veins thick, orthogonal, forming quadrangular meshes; veinlets unclear.

Remarks: The specimen is characterized by possibly oblanceolate shape, smoothly curved weak

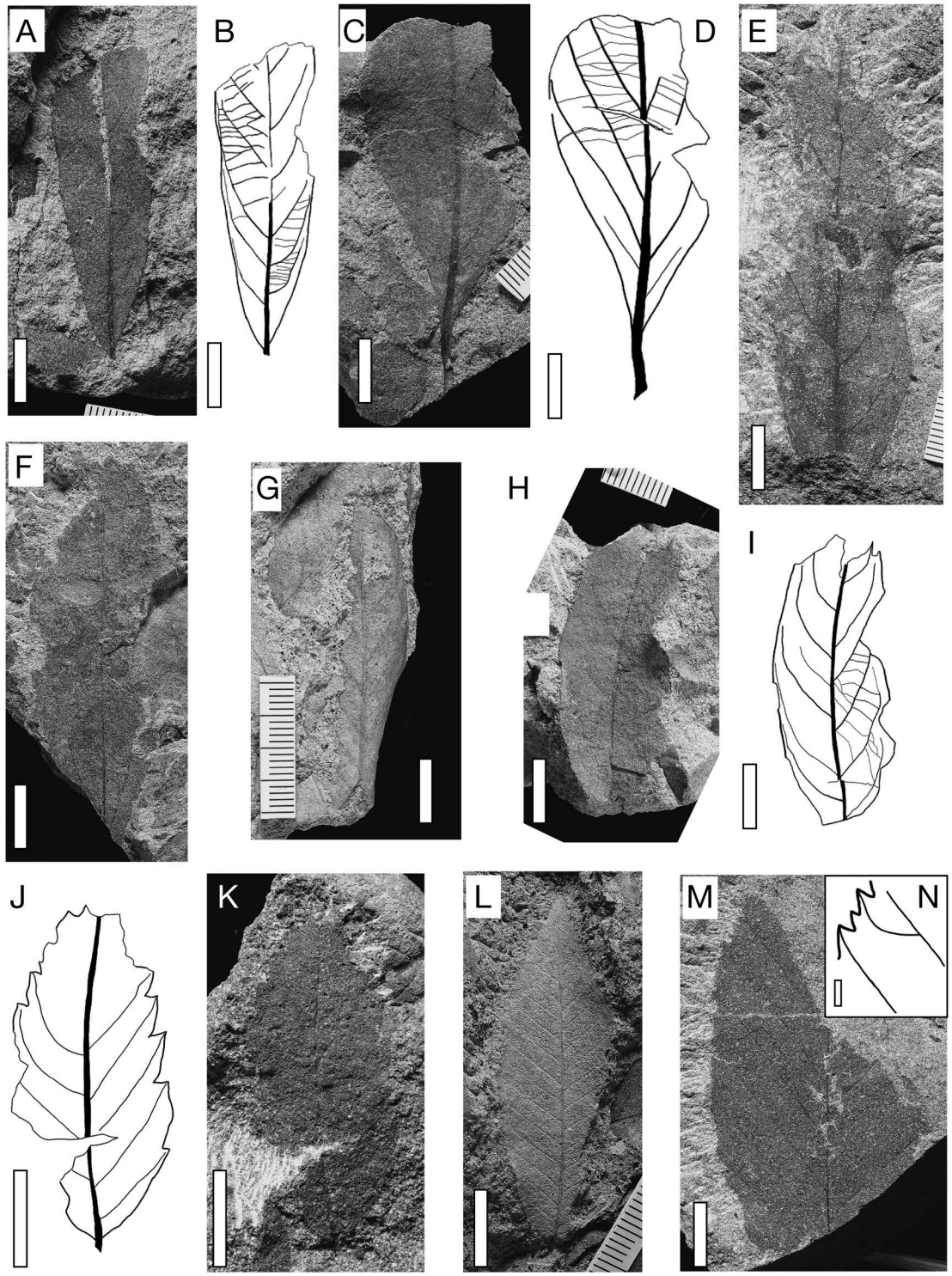

Figure 4. A. *Litseaphyllum* sp., NSM PP-12561b. B. Line drawing of A. C. *Machilus nathorsti* Huzioka, NSM PP-12562. D. Line drawing of C. E, G, H. *Machilus ugoana* Huzioka; E, NSM PP-12563; G, NSM PP-12173b; H, NSM PP-12564. F. *Cinnamomophyllum* sp., NSM PP-12456. I. Line drawing of H. J. Line drawing of K. K. *Zelkova zelkovaefolia* (Ung.) Bůžek et Kotlaba, NSM PP-12572. L. *Ulmus longifolia* Unger, NSM PP-12173a. M. *Ulmus* sp., NSM PP-12571. N. Line drawing of marginal teeth of M. Scale bar for N is equal to a 2 mm long and others to a 1 cm long.

brochidodromous secondaries, percurrent intercostal tertiaries, and well developed orthogonal meshes. All these features are comparable to those of *Machilus ugoana* Huzioka. Since its original description (Huzioka, 1963), the species has been recorded in the late-early Miocene floras in Japan. The species can be further traced back to the middle Oligocene Kiwado (Uemura *et al.*, 1999) and the middle

Eocene Ube floras (Huzioka and Takahasi, 1970) in western Honshu, Japan.

Machilus ugoana Huzioka

(Figs. 4E, G–I; 9B)

Machilus ugoana Huzioka, Tanai 1961, p. 336, pl. 22, fig. 3; Huzioka, 1963, p. 203, pl. 34, figs. 4–6, pl. 40, fig. 7; Murai, 1969, p. 60, pl. 3, fig. 4; Ishida, 1970, p. 84, pl. 13, figs. 4–6; Huzioka and Takahasi, 1973, p. 137, pl. 3, fig. 2; Onoe, 1974, p. 43, pl. 8, figs. 2, 3, 5; Ina *et al.*, 1985, p. 18, pl. 3, fig. 5; Horiuchi, 1996, p. 165, Fig. 22-6; Horiuchi and Takimoto, 2001, p. 10, pl. 1, fig. 10; Fig. 3.

Materials examined: NSM PP-12173b, 12563, 12564

Description: Several fragmentary leaves simple; laminae symmetrical to slightly asymmetrical; estimated length 6.8–9.0 cm, estimated width 2.0–2.5 cm; length/width ratio ca. 3.5, narrow elliptical shape; apex missing; base probably acute with slightly convex sides; margin entire, fringed with a fimbrial vein; venation pinnate; primary vein stout, straight or curved; secondary veins thick, at least six alternate pairs observed, divergent angle against primary vein 40–50° on middle, straight near the point of divergence, gently and abruptly curved up along the margin, weak brochidodromous; inter-secondaries rare, short, parallel to contiguous secondaries; intercostal tertiaries moderate, percurrent, straight, rarely convex, nearly perpendicular to secondaries; quaternary and quintenary veins orthogonal, forming quadrangular meshes; veinlets unclear.

Remarks: Although fragmentary, these leaves are identical to those of the genus *Machilus* in general shape, thick primary and comparatively delicate secondary veins which smoothly form series of loops, tertiary and higher order veins typically forming regular quadrangular meshes. Among several fossil *Machilus* leaves recorded in the Neogene in Japan, these leaves are assignable to *M. ugoana* Huzioka because of their narrow elliptical shape. This species is a common element in the late-early and early-middle Miocene floras in Japan.

Order Saxifragales Bercht. *et* J.Presl

Family Altingiaceae

Genus ***Liquidambar*** L.

Liquidambar sp.

(Fig. 8C)

Material examined: NSM PP-12565a

Remarks: A single fragment of palmately three-lobed leaf is comparable with that of the genus *Liquidambar* because of its glandular teeth with concave-convex shape and exmedial secondary veins forming a simple loop that sends short branches toward the teeth.

Order Fabales Bromhead

Family Fabaceae Lindl.

Genus ***Leguminophyllum*** Escalup-Bassi

Leguminophyllum sp. 1 (cf. *Robinia*)

(Fig. 5A, B)

Material examined: NSM PP-12566

Description: Leaflet lamina slightly asymmetrical; length 3.5 cm, width 2.4 cm; length/width ratio ca. 1.6–1.7, ovate to wide elliptical shape; apex acute, straight-sided, probably with round tip; base obtuse, shallowly cordate; petiolule not preserved; margin entire; venation pinnate; primary vein medium to stout, straight; secondary veins medium to thin, ＞7–8 pairs, diverging from primary vein at 50–60° in the middle part, decreasing distally, straight to gently curved, abruptly curving up to form a loop near the margin, irregularly spaced, brochidodromous; intercostal tertiaries medium, percurrent, distant, obtuse to primary vein; higher order venation not observable.

Remarks: The specimen is characterized by asymmetrical elliptical shape, acutely-round apex, and obtuse and shallowly cordate base. These features strongly suggest its affinity with fabaceous genera, particularly with the genus *Robinia*, which is native in North America. The existence of this genus in the Neogene floras of Japan was suggested for the first time by Tanai (1961) and Tanai and Suzuki (1963) who described isolated leaflets and pods from the late-early Miocene Yoshioka Formation. However, those pods were subsequently transferred to the genus *Milletia* by Ishida (1970). Generic assignment to *Robinia* is suspended here

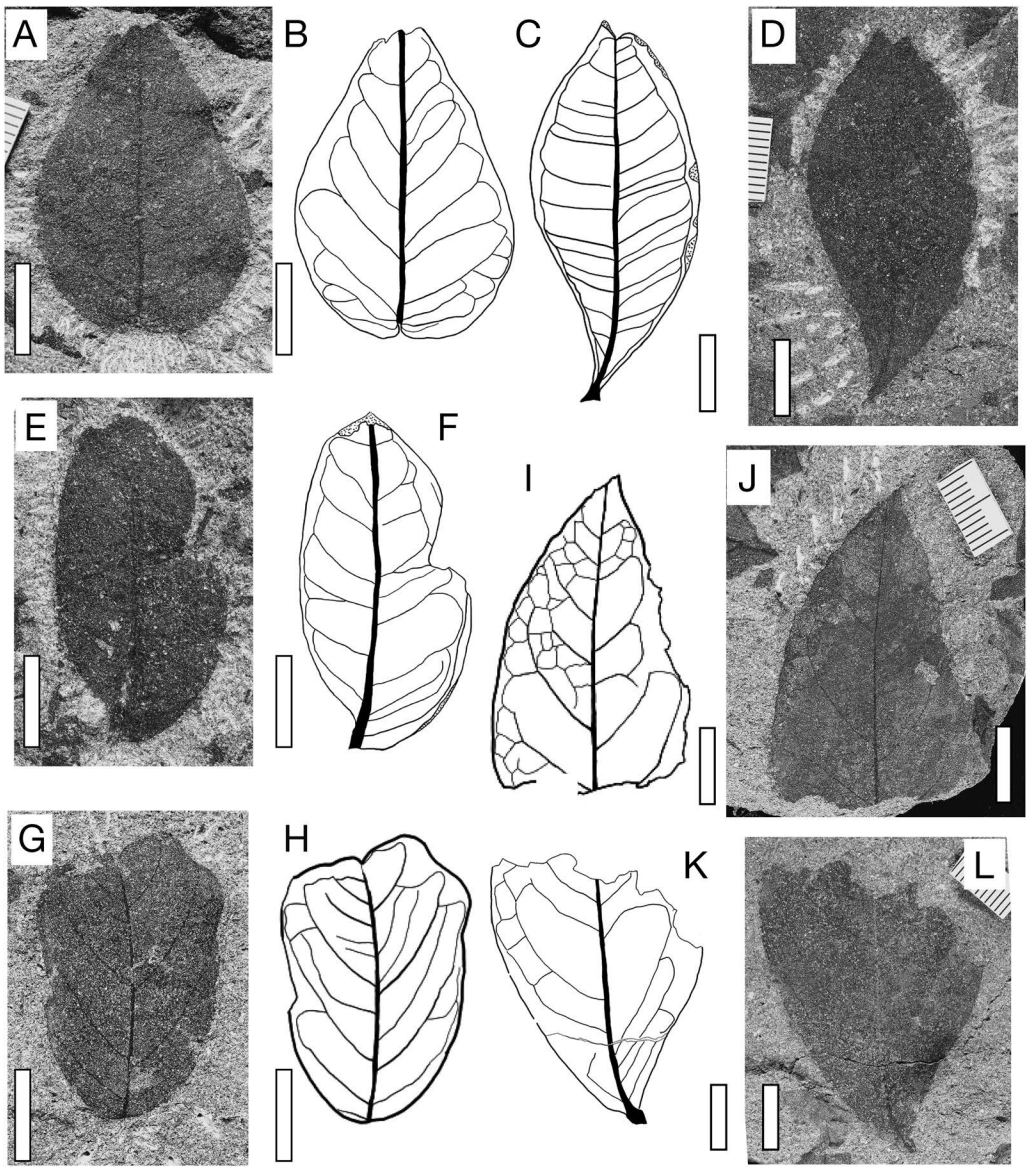

Figure 5. A. *Leguminophyllum* sp. 1, NSM PP-12566. B. Line drawing of A. C. Line drawing of D. D. *Myrtonium* sp., NSM PP-12578b. E. cf. *Podocarpium podocarpum* (A.Braun) Herendeen, NSM PP-12570. F. Line drawing of E. G. *Leguminophyllum* sp. 3, NSM PP-12569. H. Line drawing of G. I. Line drawing of J. J, L. *Leguminophyllum* sp. 2; J, NSM PP-12568a; L, NSM PP-12567. K. Line drawing of L. Scale bar is equal to a 1 cm long.

due to insufficient preservation state. The specimen is also similar to *Maackia onoei* Matsuo (Matsuo, 1963); however, it can be distinguished from *M. onoei* by its relatively thin and smooth secondaries.

Leguminophyllum sp. 2 (cf. *Cassia*)

(Figs. 5I–L)

Materials examined: NSM PP-12567, 12568a

Description: Leaflet laminae slightly asymmetrical; length 6.0–7.6 cm, width 2.8–3.3 cm; length/width ratio ca. 2.1–2.3, elliptical to narrow elliptical in shape; apex acute, probably acuminate; base acute, round; petiolule pulvinate, short; margin entire; venation pinnate; primary vein medium, slightly curved; secondary veins medium, at least nine pairs, diverging at around 60° from primary vein, curved, forming series of loops, vein spacing irregular, weak brochidodromous; intersecondaries common, strong, diverging at the same or slightly larger angle to contiguous secondaries, curved, recurved below the marginal loop to join the lower next secondary; intercostal tertiaries medium, random reticulate; higher order venation not observable.

Remarks: The specimens are readily assigned to Fabaceae family because of their asymmetrical shape, entire margin, and pulvinate petiolule. Fur-

ther, they are also characterized by thin leaf texture, presence of relatively long intersecondaries, reticulate intercostal tertiaries, and secondary veins that bend back perpendicularly to form marginal loops. These features are common to some species of the genus *Cassia* L. Fossil *Cassia* species was first described from the late-early Miocene Takaya Formation as *C. notoensis* (Ishida, 1970), which is distinguished from our specimen by its round or retuse apices. We hesitated to use its generic name, *Cassia*, because of our incomplete specimens, which is why we used the name of the fossil genus *Leguminophyllum* Escalup-Bassi (Escalup-Bassi, 1971).

Leguminophyllum sp. 3
(Fig. 5G, H)

Material examined: NSM PP-12569

Description: Leaflet slightly asymmetrical, elliptical to narrow elliptical; estimated length 4.0 cm, width 2.2 cm; length/width ratio ca. 1.8; apex missing; base wide, acute, round; petiolule not preserved; margin entire; venation pinnate; primary vein medium, slightly curved; secondary veins medium, at least nine pairs, diverging at around 60° from primary vein, curved, often bent back perpendicularly to the primary forming a loop, vein spacing irregular, brochidodromous; intersecondaries common, strong, diverging at the same or slightly lower angle to contiguous secondaries, curved, sometimes reaching the marginal loop; intercostal tertiaries medium, random reticulate; higher order venation not observable.

Remarks: The specimen is characterized by entire margined, slightly inequilateral lamina, unique course of secondaries, and the presence of long intersecondaries which reach the primary loop consisting of contiguous secondaries. This type of secondary venation can rarely be seen in some fabaceous genera and species, *e.g.*, *Cassia* or *Lespedeza*. However, we cannot compare any single genus and species with this specimen because of its poor quality of preservation. We tentatively assigned it here as *Leguminophyllum* sp. 3.

Genus ***Podocarpium*** A.Braun *et* Stizenb.
cf. *Podocarpium podocarpum* (A.Braun) Herendeen
(Fig. 5E, F)

Compare:

Podocarpium podocarpum (Braun) Herendeen, 1992, p. 731 (see synonymy).

Podogonium knorrii Braun, Hu and Chaney, 1938, p. 76, pl. 50, figs. 4, 5, 7, 10, 11; Ishida, 1970, p. 91, pl. 15, figs. 7–11; Onoe, 1974, p. 47, pl. 10, fig. 11; Ozaki, 1974, p. 14, pl. 2, fig. 12; Horiuchi and Takimoto, 2001, p. 21, pl. 6, figs. 6, 7.

Gleditsia lyelliana (Heer) Hantke, Matsushita *et al.*, 1994, p. 12, pl. 11, fig. 2.

Material examined: NSM PP-12570

Description: A single leaflet with asymmetrical lamina, elliptical in shape; estimated length 3.7 cm, width 1.9 cm; length/width ratio 1.9; apex wide-acute, probably round; base wide-acute, convex on one side, decurrent on the other side; petiolule missing; margin entire; venation pinnate; primary vein massive, curved; secondary veins medium, 6–7 alternate pairs, diverging from primary vein at 50–70°, curved, rarely branched, vein spacing irregular, brochidodromous, a single thick basal secondary extends up four-fifths of the blade along the margin; tertiary and higher order venation not observable.

Remarks: Our specimen is comparable to this species by its basal inequilateral shape, entire margin, brochidodromous secondaries, and presence of a single basal secondary vein which goes up four-fifths of the blade along the margin. Leaves and pods of this species are common in the late-early and early-middle Miocene floras in East Asia, and it was also recorded from the early Oligocene Shimokatakura flora (Matsushita *et al.*, 1994). However, our specimen is twice as big as the normal leaves recorded to date in Japan.

Order Rosales Bercht. *et* J.Presl
Family Ulmaceae Mirb.
Genus ***Ulmus*** L.
Ulmus longifolia Ung.
(Fig. 4L)

Material examined: NSM PP-12173a

Description: A single leaf simple; laminae basal asymmetrical, length 4.5 cm, width 1.6 cm; length/width ratio 2.8, narrow elliptical in shape; apex

acute, straight; base acute, shallowly cordate; petiole thick, short (ca. 2.2 mm long); margin serrate; teeth compound, rarely one smaller tooth situated on the proximal side of the large tooth; proximal side of teeth convex or flexuous, distal side convex; obtusely pointed; principal vein enters tooth basally; venation pinnate; primary vein thick, curved, tapering apically; secondary veins medium, 19 opposite pairs, diverging from primary vein at ca. 50°, straight, slightly curved near margin, regularly spaced, craspedodromous; intercostal tertiaries medium, percurrent, closely arranged, perpendicular to contiguous secondaries; higher order venation not observable.

Remarks: The specimen is identical to *Ulmus longifolia* in shape, secondary venation, and characteristic tooth shape. This species is one of the common fossil species in the late-early Miocene Daijima-type flora of Japan.

Ulmus sp.

(Fig. 4M, N)

Materials examined: NSM PP-12571, 12594b

Remarks: These fragmentary leaves were identified as *Ulmus* because of its closely arranged, relatively thick, parallel secondary veins which directly enter the larger teeth in compound serrate margin from their basal side, in addition, the shape of tooth is typically straight-convex. The specimen can be distinguished from *Ulmus longifolia* Unger in much larger primary teeth and relatively wide lamina.

Genus *Zelkova* Spach

Zelkova zelkovaefolia (Ung.) Bůžek *et* Kotlaba

(Figs. 4J, K; 9I)

Ulmus zelkovaefolia Ung., 1847, p. 94–95, pl. 24, figs. 9–12, pl. 26, fig. 7 (part)

Planera ungeri Ettingsh., 1851,

Zelkova ungeri (Ettingsh.) Kovats, 1856, p. 27–29, pl. 5, figs. 1–12, pl. 6, figs. 1–6. (see synonymy)

Zelkova zelkovaefolia (Ung.) Bůžek *et* Kotlaba in Kotlaba, 1963, p. 59–62, pl. 3, figs. 7, 8.

Material examined: NSM PP-12572

Description: A single fragmentary leaf simple; laminae symmetrical; estimated length 4.2 cm, width 2.0 cm; length/width ratio 2.1, elliptical in shape; apex missing; base acute, convex; petiole marginal, normal; margin serrate; tooth large and simple, regularly spaced; proximal flank of tooth flexuous, distal flank straight, concave, rarely convex, acutely pointed; principal vein enters tooth slightly basally; sinuses angular, acute; venation pinnate; primary vein stout, gently curved; secondary veins moderate, at least five pairs observed, subopposite, evenly-spaced, divergent angle 40 to 70° in the middle part, straight or curved, craspedodromous; intercostal tertiaries thin, percurrent or sinuous, obtuse to primary; quaternary veins medium, reticulate, forming irregular meshes.

Remarks: This simple leaf with characteristic large teeth and craspedodromous secondary venation is assignable to *Zelkova zelkovaefolia* (Ung.) Bůžek *et* Kotlaba. This is a common species throughout the Neogene of the Japanese Islands. The species has been called *Zelkova ungeri* Kovats; however, *Z. zelkovaefolia* has clear nomenclatural priority when referring to this species (Kotlaba, 1963).

Order Fagales Engl.

Family Fagaceae Dumort.

Genus ***Fagus*** L.

Fagus stuxbergi (Nath.) Tanai

(Figs. 6A–C; 9D)

Quercus stuxbergi Nath., 1883, p. 44, pl. 3, figs. 18–20, pl. 4, figs. 4–9.

Fagus palaeocrenata Okutsu 1955, p. 92, pl. 6, figs. 4–9, Tanai, 1974, p. 70, pl. 4, fig. 4, pl. 5, figs. 1, 2, 4, 6, 7.

Fagus stuxbergi (Nath.) Tanai, 1976, p. 269, pl. 1, figs. 4, 5, 8, 10 (see synonymy).

Fagus stuxbergi (Nath.) Tanai, Ozaki, 1979, p. 53, pl. 6, figs. 2–6; Uemura, 1986, p. 123, text-fig. 11, 12; Uemura, 1988, p. 119, pl. 6, figs. 7–11, Fig. 23; Horiuchi, 1996, p. 177, Fig. 32-4; Ozaki, 1991, p. 147, pl. 13, figs. 1, 3, 9c, pl. 19, figs. 4, 5; Takimoto, Horiuchi, Sugaya and Hosogai, 1998, p. 57, figs. 4-5–8; Kawase and Koike, 2004, p. 2, pl. 1, fig. 9.

Materials examined: NSM PP-12561a, 12568b, 12573, 12598a–c

Description: Laminae simple, symmetrical; length 5.1–6.0 cm, width 2.6–3.9 cm, length/width ratio 1.5–2.0, ovate to narrow ovate in shape; apex acute, straight-sided; base wide-obtuse, cuneate; petiole marginal, normal, ca. 9.0 mm long; margin serrate; tooth simple, regularly spaced; proximal flank of teeth typically concave, sometimes straight

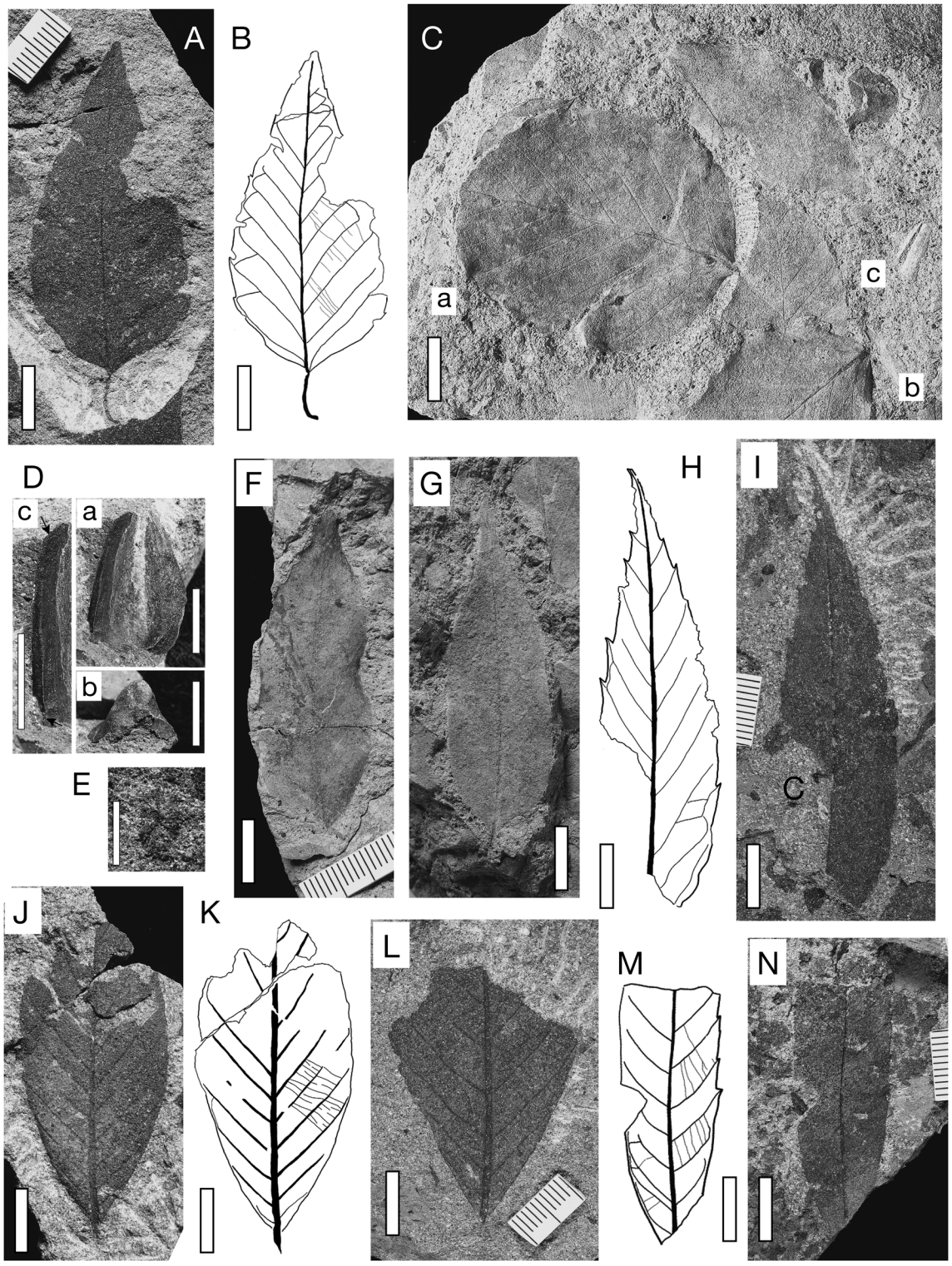

Figure 6. A, C. *Fagus stuxbergi* (Nath.) Tanai; A, NSM PP-12561a; C, NSM PP-12598a–c. B. Line drawing of A. D. *Fagus* sp., nut, NSM PP-12574; a, lateral view; b, bottom view; c, enlargement of marginal wing; arrows indicate wing attachment. E. *Alnus* sp., infructescence, NSM PP-12455. F, G, I, N. *Quercus* (*Cyclobalanopsis*) *mandraliscae* (Gaudin) Tanai; F, NSM PP-12596; G, NSM PP-12594a; I, NSM PP-12578a; N, NSM PP-12577. H. Line drawing of I. J, L. *Lithocarpus*? sp.; J, NSM PP-12575a; L, NSM PP-12576. K. Line drawing of J. M. Line drawing of N. Scale bar for D & E is equal to a 0.5 cm long and others to a 1 cm long.

or slightly convex, distal flank straight, acutely pointed; principal vein enters the tooth medially; sinuses angular, acute; venation pinnate; primary vein stout, basally straight, apically weak sinuous; secondary veins moderate, at least 11 opposite pairs, parallel, regularly spaced, diverging from primary vein at ca. 30–40° in the middle part, basal few pairs decurrent at divergence, forming loops below

Table 2. Morphological comparison of the Miocene beech species in Japan. Characters that are common to Ieda specimens are shown in bold.

	Ieda specimens: PP-12561a, 12568b, 12573, 12598a–c	*F. stuxbergi* (Nath.) Tanai, 1976	*F. antipofi* Heer, 1858	*F. intermedia* Nathorst, 1883	*F. palaeojaponica* Tanai et Onoe, 1961	*F. microcarpa* Miki, 1933
Shape	ovate to narrow ovate	**ovate**	narrow elliptic, **narrow ovate**	elliptic	elliptic	elliptic to **ovate**
Leaf index	1.5–2.0	**1.90**	2.38	**1.66**	**1.78**	**1.6–1.8**
Margin	serrate	**serrate**	serrate or undulate	undulate	undulate	undulate, **rarely serrate**
# of 2°	11	**6–13**	**11–23**	9–10	13–22	7–9
Apex	acute	**acute**	**acute**	**acute**	**acute**	short acuminate, blunt
Base	cunate	**cuneate**	cuneate round, round or shallowly cordate	cordate, round	round or shallowly cordate	round
Remarks	—	Plate 2, fig. 2 and plate 3, fig. 5 of Tanai (1974) were included	Figures 5&6 of plate 3 were transferred to *F. evenensis* (Chelebaeva, 1980)	Paleogene records were excluded.	Plate 2, fig. 2 and plate 3, fig. 5 of Tanai (1974) were excluded	—

the teeth to connect with the next upper secondary vein at wide-acute angle, semicraspedodromous; intercostal tertiaries thin, percurrent, straight, regularly and closely spaced (＞15/cm), perpendicular to adjacent secondaries; quaternaries thick, orthogonal, forming quadrangular meshes.

Remarks: These simple leaves with serrate margins and evenly spaced parallel secondary veins with semi-craspedodromous venation are readily assigned to the genus *Fagus*. Five beech species are considered valid in the Miocene to Pliocene of Japan (Tanai, 1974; Uemura, 1988), namely, *F. antipofi* Heer (mainly early Miocene), *F. intermedia* Nath. (middle to late Miocene), *F. stuxbergi* (Nath.) Tanai (late Miocene–Pliocene), *F. palaeojaponica* Tanai *et* Onoe (late Miocene–Pliocene), and *F. microcarpa* Miki (late Pliocene–Pleistocene) (Table 2). Tanai (1974) discussed that the "leaf index" (=leaf length/width ratio) is one of the important characteristics for differentiating these species. Our specimens are closest to the leaf index value of *F. stuxbergi* and secondarily to *F. microcarpa*, followed by *F. palaeojaponica* and *F. antipofi* (Table 2). All the other criteria, such as shape, number of secondaries, and marginal features strongly suggested that our specimens are identical to *F. stuxbergi.* Current record is definitely the oldest record ever known in Japan.

Fagus sp.
(Fig. 6D)

Material examined: NSM PP-12574

Description: A single nut ovoid, triquetrous; apex acute, base round with flat base; length ca. 11.0 mm, width 8.2 mm; pedunculate; margin winged over the whole length, 0.5 mm wide.

Remarks: This triquetrous ovoid nut with narrow wing at margin is identical to that of the genus *Fagus*. Fossil nuts of Miocene beech species have rarely been recorded in Japan. Marginal features of the nuts were not examined in detail in those studies (Huzioka, 1964; Huzioka and Uemura, 1973; Onoe, 1974); however, they were tentatively identified as the same species with associated leaf remains in many cases.

Miki (1933) discussed the importance of the marginal feature of nut remains in specific-level differentiation and proposed a new species, *F. microcarpa*, for those that bear marginal wings on the upper halves of the nut body (Miki, 1933). Additional specimens revealed that this species actually bears wings over the whole length of the nut body (Uemura, 1980). *F. microcarpa* resembles *F. stuxbergi* in cupula size, distribution and shape of prickles on the surface of cupula, as well as nut size (Uemura, 1980). The occurrence of *F. stuxbergi* leaves from the Ieda Group may also support this assumption; however, the feature of marginal wings of *F. stuxbergi* nuts has yet to be described. For this reason, we hesitate to assign any specific name to our specimen.

Genus *Lithocarpus* Blume
Lithocarpus? sp.
(Figs. 6J–L; 9H)

Materials examined: NSM PP-12575a, 12576

Description: Laminae symmetrical; estimated length 5.6–7.5 cm, estimated width 2.5–3.2 cm;

length/width ratio ca. 2.2–2.3, elliptical in shape; apex probably acute and short acuminate; base acute, cuneate or slightly convex; petiole marginal, thick; margin entire, slightly undulate, weakly curled, fringed with a fimbrial vein; venation pinnate; primary vein massive, straight; secondary veins thick, at least ten opposite to subopposite pairs, nearly parallel, regularly spaced, divergent angle ca. 40° in the middle part, gradually increasing toward base, admedially straight, abruptly curving up near the margin to form loops, eucamptodromous; intercostal tertiaries thick, percurrent, obtuse to primary vein, angle uniform, perpendicular to slightly oblique to secondaries; quaternaries thick, orthogonal, forming quadrangular meshes.

Remarks: Although our specimens are not well preserved in terms of finer venation and cuticular features, they are identical to the family Fagaceae because of their simple, equilateral leaf and evenly-spaced parallel secondary and tertiary veins. They are similar to some leaves of the genus *Lithocarpus* with entire margins. Fossil leaves regarded as *Lithocarpus* or *Pasania* (synonym of *Lithocarpus*) are uncommon in the Neogene floras of Japan, but common in the Paleogene floras of Japan. The leaves of our specimens are most similar to the leaves reported as *Pasania* (*Lithocarpus*) cf. *amygdalifolia* by Murai (1976) from the lower-upper Miocene Yanagisawa Formation (*sensu* Tuzino *et al.*, 2018).

Genus *Quercus* L.

Quercus (*Cyclobalanopsis*) *mandraliscae* (Gaudin) Huzioka

(Figs. 6F–I, M, N; 9E)

Quercus mandraliscae Gaudin in Gaudin and Strozzi, 1858, p. 33, pl. 2, fig. 11, Tanai, 1961, p. 310, pl. 12, figs. 4, 7; Matsuo, 1963, p. 236, pl. 49, fig. 3; Ishida, 1970, p. 76, pl. 7, figs. 1–7; Hojo, 1973, p. 26, pl. 7, figs. 7–16, 18, 20–23; Kawase and Koike, 2002, p. 2, pl. 1, figs. 12, 13.

Cyclobalanopsis mandraliscae (Gaudin) Tanai, 1953, p. 3, pl. 1, figs. 6, 7, 8, 9; Huzioka, 1954, p. 197, pl. 25, figs. 1, 2.

Quercus (*Cyclobalanopsis*) *mandraliscae* Gaudin, Huzioka, 1963, p. 197.

Materials examined: NSM PP-12577, 12578a, 12594a, 12595, 12596.

Description: Laminae simple, symmetrical, elliptical to narrow elliptical in shape; estimated length 5.0–7.2 cm, width 1.6–2.0 cm; length/width ratio 2.8–4.0; apex narrow acute, straight; base acute, convex; petiole missing; margin serrate; tooth simple, regularly spaced; proximal flank of teeth concave or straight, distal flank straight to convex, acutely pointed; principal vein enters tooth medially, rarely apically; sinuses angular, acute; venation pinnate; primary vein massive, straight to slightly sinuous, tapering apically; secondary veins moderate, at least nine, probably over ten pairs, parallel, opposite to alternate, vein spacing regular or irregular, middle acute against primary vein, gently curved, recurved near margin, rarely branched on the way, usually sending one minor secondary or tertiary along the margin, craspedodromous; intercostal tertiaries percurrent, straight, rarely convex, obtuse to primary, decreasing their angles exmedially; quaternaries thin, percurrent.

Remarks: These oak leaves are most similar to those of *Quercus mandraliscae* Gaudin, which was originally described from Sienne (Bozzone) and Val d'Arno of Toscany, Italy (Gaudin and Strozzi, 1858), because of their lanceolate leaf shape and serrate margin from near the base of the lamina. For fossil leaves in East Asia, Tanai used this name for the first time when he described fossil leaves from the middle Miocene Yeonil Flora in South Korea (Tanai, 1953). Thereafter, a number of specimens have been recorded in Japan, although attribution to this European species has never been tested in detail before. This species often co-occurs with typical ring-cup (cupula), which strongly suggests an affinity with the subgenus *Cyclobalanopsis*. On the other hand, a wide variety of oak leaves have been compared with the morphological complex *Q. drymeia* Ung. (*sensu* Denk, 2017) and are considered to belong to the section *Ilex* of subgenus *Quercus*. Detailed comparison of leaves and associated reproductive organs of these species are needed in future studies.

Quercus (*Cyclobalanopsis*) *mandraliscae* can be distinguished from *Q.* (*C.*) *praegilva* (Kryshtofovich) Huzioka from the same locality by its more lanceolate shape and long acuminate apex. The species is also distinguishable from *Q.* (*C.*) *protosalicina* Suzuki (Suzuki, 1959) from the upper Miocene Fujitoge Formation of northeast Japan, which has entire margin in the basal half of the blade. *Q.* (*C.*) *mandraliscae* has been recorded from the late-early

and early-middle Miocene of Japan and considered as one of the common species in that time period.

Quercus (*Cyclobalanopsis*) *praegilva* (Kryshtofovich) Huzioka

(Figs. 7E–H; 9G)

Quercus praegilva Kryshtofovich, 1926, p. 11, pl. 2, fig. 2; Huzioka, 1963, p. 198, pl. 31, figs. 6, 7; Matsuo, 1963, p. 237, pl. 48, fig. 1–3; Ishida, 1970, p. 78, pl. 11, figs. 1, 2 (non figs. 4, 5); Kawase and Koike, 2004, p. 2, pl. 1, fig. 6.

Quercus (*Cyclobalanopsis*) *praegilva* Kryshtofovich, Huzioka, 1963, p. 198.

Materials examined: NSM PP-12579, 12580.

Description: Two fragmentary leaves simple; laminae symmetrical; estimated length 4.3–6.0 cm, width 1.7–3.2 cm; length/width ratio 1.9–2.5, narrow obovate shape; apex narrow to middle acute, short acuminate; base missing; margin serrate on distal two-thirds; tooth simple, regularly spaced; tooth flank straight or concave, acutely pointed; principal vein enters tooth medially; sinuses angular, acute to obtuse; venation pinnate; primary vein stout, straight; secondary veins moderate to thick, more than ten opposite to subopposite pairs, straight to gently curved, abruptly curved in the marginal tooth, parallel, regularly spaced, divergent angle against primary vein 45–50° in the middle part, gently decreasing basally, craspedodromous; intercostal tertiaries thin but distinct, straight, rarely branched, oblique to contiguous secondary, narrow obtuse against primary vein, angle almost uniform; quaternary and quintenary veins thick, orthogonal, forming quadrangular meshes with adjacent tertiaries.

Remarks: These oak leaves are characterized by their narrow obovate shape, short acuminate apex, and closely and regularly spaced marginal tooth on the upper half of the blade. All these features are assignable to *Quercus* (*Cyclobalanopsis*) *praegilva* (Kryshtofovich) Huzioka, which was described from the lower to middle Miocene Tsugawa Formation of Northeast Japan (Kryshtofovich, 1926).

Quercus sp. cf. *Q.* (*Cyclobalanopsis*) *nathorstii* (Kryshtofovich) Huzioka

(Figs. 7A–D, 9F)

Compare:

Quercus nathorstii Kryshtofovich, 1926, p. 10, pl. 2, figs. 3, 4.

Materials examined: NSM PP-12565, 12581, 12582.

Description: Several fragmentary leaves simple; laminae probably symmetrical; estimated length 7.2–10 cm, estimated width 2.5–3.0 cm; length/width ratio ca. 2.9–3.3, elliptical to narrow elliptical shape; apex acute, straight with short acuminate tip; base probably acute, convex; margin of distal two-thirds serrate; tooth simple, regularly spaced; proximal flank of the tooth straight, distal flank straight or slightly concave, acutely pointed, oriented obliquely upwards; primary vein enters tooth medially or basally; sinuses rounded, acute; venation pinnate; primary vein stout, straight, tapering distally; secondary veins moderate, curved, evenly spaced, sometimes irregular, divergent angle against primary vein 40–45° in the middle part, craspedodromous; intercostal tertiaries moderate, percurrent, straight, sinuous or branched, nearly perpendicular to contiguous secondaries; quaternary and quintenary veins thick, orthogonal, forming quadrangular meshes.

Remarks: These leaves are characterized by simple remotely serrate margin on their upper half and elliptical to narrow elliptical shape. Although our leaves were fragmentary, they are comparable to *Quercus* (*Cyclobalanopsis*) *nathorstii* (Kryshtofovich) Huzioka, originally described from the early to middle Miocene Tsugawa Formation (Kryshtofovich, 1926). This species is common in the late early Miocene of Japan and has been recorded from the latest Oligocene of western Honshu (Huzioka and Takahasi, 1973).

Family Juglandaceae DC ex Perleb

Juglandaceae genus *et* species indeterminate (*Carya* or *Platycarya*)

(Fig. 7L, M)

Material examined: NSM PP-12583.

Description: A single fragmentary leaflet of pinnately compound leaf; leaflet (or leaf) asymmetrical; estimated length 6.5 cm, estimated width 2.5 cm; length/width ratio 2.6, narrow ovate in shape; apex probably acute, nearly straight; base acute and convex; petiolule (or petiole) not preserved; margin serrate; tooth compound, approximately regularly spaced; proximal flank of teeth

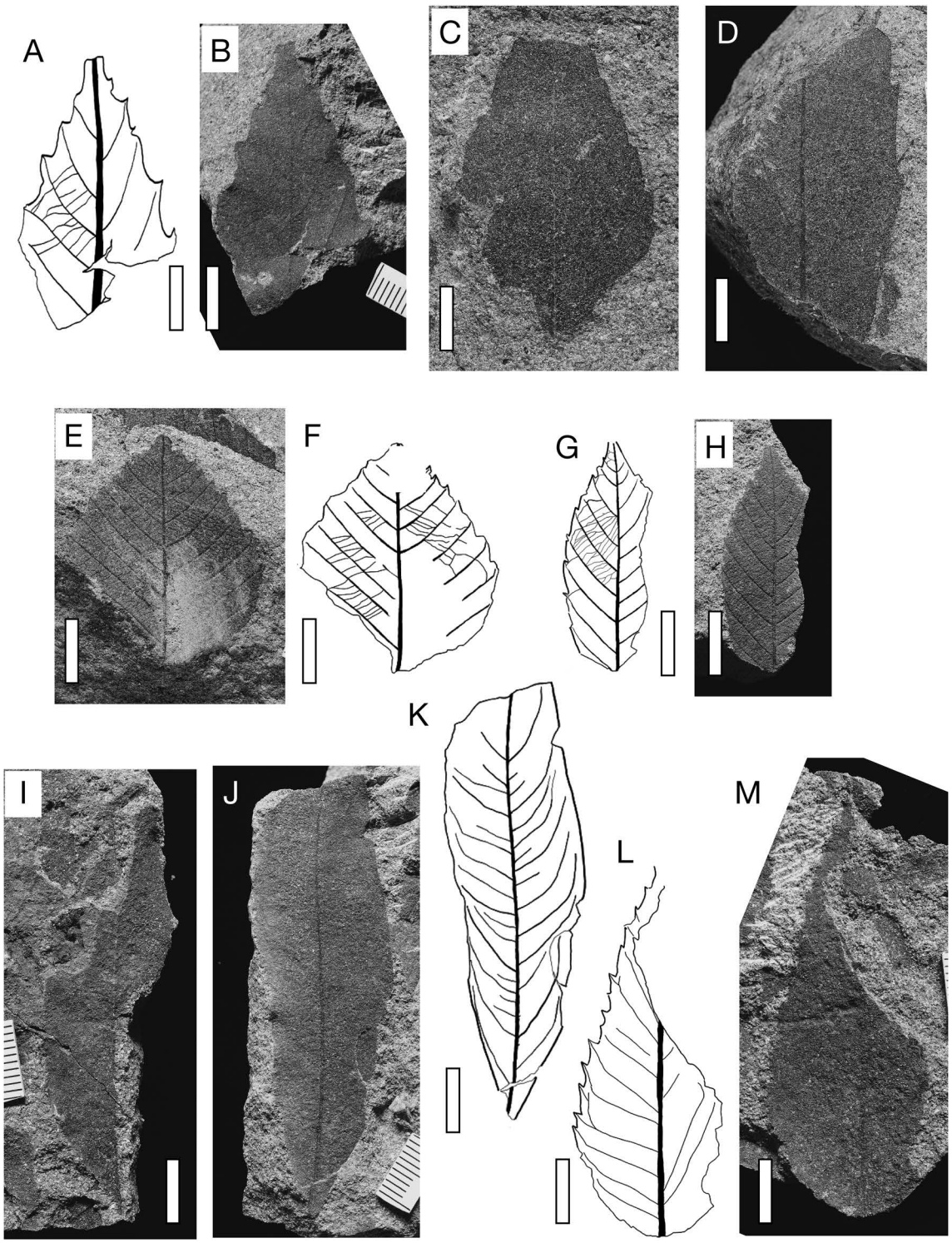

Figure 7. A. Line drawing of B. B–D. *Quercus* sp. cf. *Q.* (*Cyclobalanopsis*) *nathorstii Kryshtofovich*; B, NSM PP-12581; C, NSM PP-12565b; D, NSM PP-12582. E, H. *Quercus* (*Cyclobalanopsis*) *praegilva* (*Gaudin*) Tanai; E, NSM PP-12579; H, NSM PP-12580. F. Line drawing of E. G. Line drawing of H. I, J. *Sapindus* sp. cf. *S. tanaii* Onoe; I, NSM PP-12584; J, NSM PP-12585. K. Line drawing of J. L. Line drawing of M. M. Juglandaceae gen. *et* sp. indet., NSM PP-12583. Scale bar is equal to a 1 cm long.

concave, distal flank straight, acutely pointed; principal vein enters tooth medially or slightly basally; sinuses angular, wide-acute to obtuse; venation pinnate; primary vein stout, straight; secondary veins medium to thin, at least 12 pairs, divergent angle in the middle part ca. 50° on one side, 35° on the other side, irregularly spaced, straight, branched below tooth, sending one branch to tooth and another one forming a loop, semi-craspedodromous or craspedodromous; tertiaries thin, percurrent, straight, obtuse

to primary vein; quaternary veins medium, percurrent, straight; quintenary veins thick, reticulate, forming polygonal meshes; veinlets present.

Remarks: Our specimen was identified as a leaflet of a juglandaceous plant because of its inequilateral shape, semicraspedodromous or craspedodromous secondaries, and evenly-spaced simple teeth without any accessory features. On the basis of its secondary venation characteristics, our specimen can be compared to genus *Carya* or *Platycarya*. More well-preserved materials are needed to confirm its identification to the genus level.

Family Betulaceae Gray
Genus ***Alnus*** Mill.
Alnus sp.
(Fig. 6E)

Material examined: NSM PP-12455.

Remarks: An isolated ellipsoidal woody infructescence with helically arranged bracts was recovered. It is readily identical to the infructescence of the genus *Alnus* in its shape and characteristic structures.

Order Myrtales Juss. ex Bercht. *et* J.Presl
Family Myrtaceae Juss.
Genus ***Myrtonium*** Ettingsh.
Myrtonium sp.
(Fig. 5C, D)

Material examined: NSM PP-12578b.

Description: A single leaf simple; lamina basal asymmetrical; length 5.0 cm, width 2.4 cm; length/width ratio ca. 2.0, elliptical shape; apex acute, typically retuse; base acute, decurrent; petiole very short or sessile; margin entire; venation pinnate; primary vein very thick, expanded and curved at base; secondary or minor secondary veins numerous, irregularly spaced, divergent angle 60–90° in the middle part, sometimes recurved at divergence, straight, abruptly curved to form a pair of marginal veins, brochidodromous; rarely branched, forming irregular loops, brochidodromous or festooned brochidodromous; tertiary or higher order venation not observable.

Remarks: This specimen is characterized by asymmetrical shape, retuse apex, short petiole, and brochidodromous secondary veins that form a pair of intramarginal veins. Venation characteristics of the specimen are common in some genera and species of the family Myrtaceae. However, it is impossible to assign it to any extant genus without cuticular information (Tarran *et al.*, 2018). Therefore, we used a form genus, *Myrtonium*, which was erected for myrtaceous leaves preserved as compression/impression without cuticular information.

The specimen superficially resembles *Syzygium buxifolium* Hook *et* Arn. in overall shape and venation; the species is one of two native Myrtaceae species in the Japanese Islands, distributed in southern Kyushu and Ryukyu Islands. Fossil records of myrtaceous species are scarce in the Paleogene and Neogene of Japan and East Asia. Huzioka and Takahasi (1970) described *Syzygium chaneyi* from the middle Eocene Okinoyama Formation, although a generic assignment of this species was questioned by Tarran *et al.* (2018) because of its preservation state. Huzioka (1974) also described one fragmentary leaf with characteristic secondary venation as *Syzygium* sp. from the latest Oligocene Hitomaru Formation.

Order Sapindales Dumortier
Family Sapindaceae Juss.
Genus *Acer* L.
Acer sp.
(Figs. 8J, 9I)

Material examined: NSM PP-12175.

Remarks: A single fragmentary leaf with moderately incised three-lobed lamina is characterized by a serrate margin with acutely pointed simple teeth and craspedodromous secondaries. Areoles are well developed, and veinlets appeared to be branched several times. Based on these features, we assign it to the genus *Acer*.

Genus ***Sapindus*** L.
Sapindus sp. cf. *S. tanaii* Onoe
(Figs. 7I–K)

Compare:
Sapindus tanaii Onoe, 1974, p. 52, pl. 12, fig. 5.

Materials examined: NSM PP-12584, 12585.

Description: Leaves simple; laminae slightly

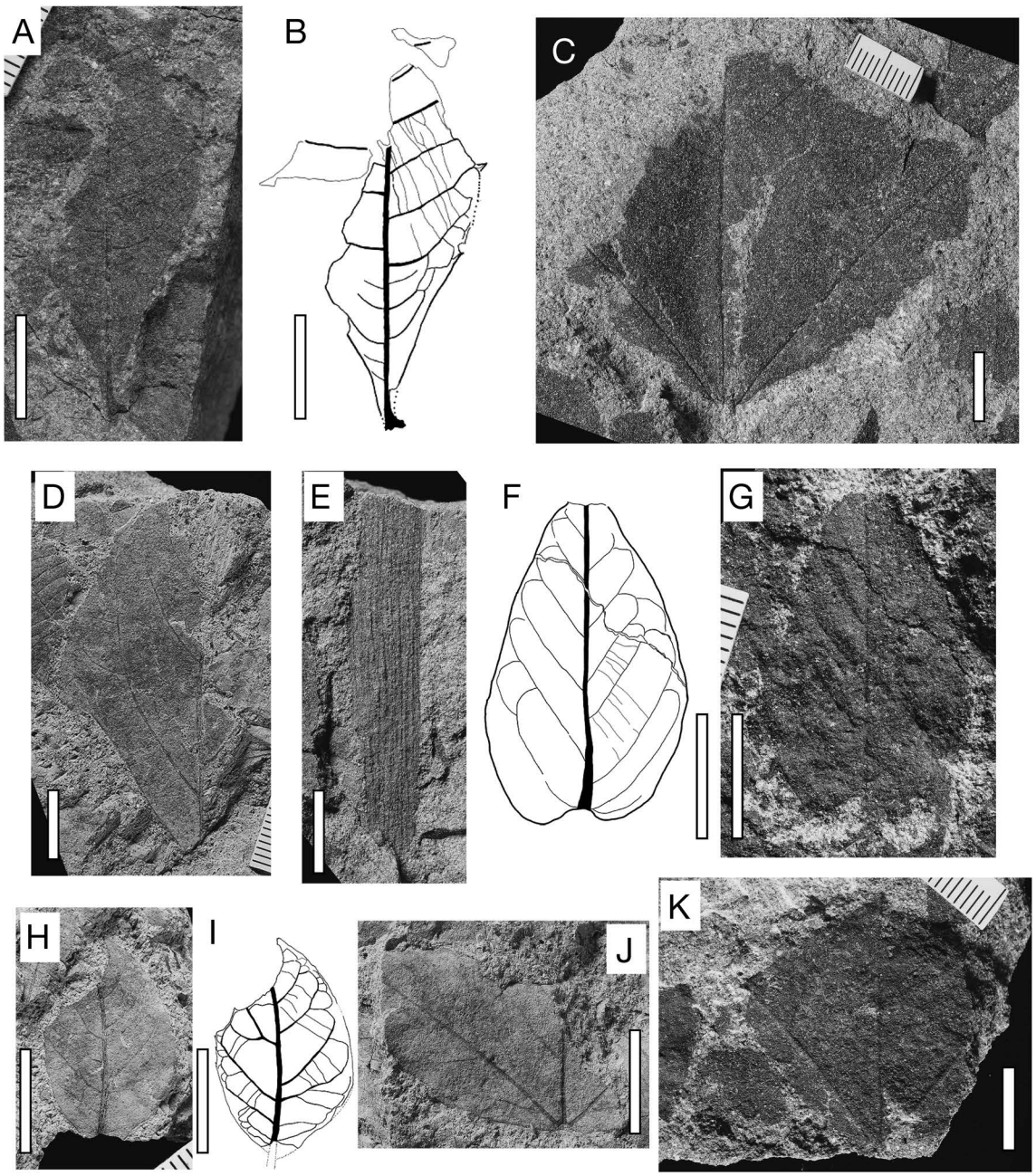

Figure 8. A. *Clethra*? sp., NSM PP-12586. B. Line drawing of A. C. *Liquidambar* sp., NSM PP-12565a. D. *Alangium* sp., NSM PP-12173c. E. *Monocotylophyllum* sp., NSM PP-12587. F. Line drawing of G. G. *Phyllites* sp. 2, NSM PP-12589. H. *Phyllites* sp. 3, NSM PP-12176. I. Line drawing of H. J. *Acer* sp., NSM PP-12175. K. *Phyllites* sp. 1 (*Acer*?), NSM PP-12588. Scale bar is equal to a 1 cm long.

asymmetrical; estimated length 8.0–9.0 cm, estimated width 2.0 cm; length/width ratio 4.0–4.5, narrow oblong in shape; petiole missing; margin entire; venation pinnate; primary vein moderate, straight to gently sinuous; secondary veins >10, opposite, divergent angle against primary vein ca. 60°, straight as much as half or two-thirds toward margin, abruptly bent-up along margin, vein spacing irregular, eucamptodromous; inter-secondaries common, 1–3, usually two between each two secondaries, diverging at the same or slightly larger angles than contiguous secondaries, extending toward the margin; tertiaries thin, straight percurrent at least on the apical fourth; higher order venation not observable.

Remarks: The specimens are characterized by narrow oblong, slightly asymmetrical leaf laminae with entire margin and eucamptodromous secondaries, and intersecondaries which run nearly parallel to contiguous secondaries. All these features are

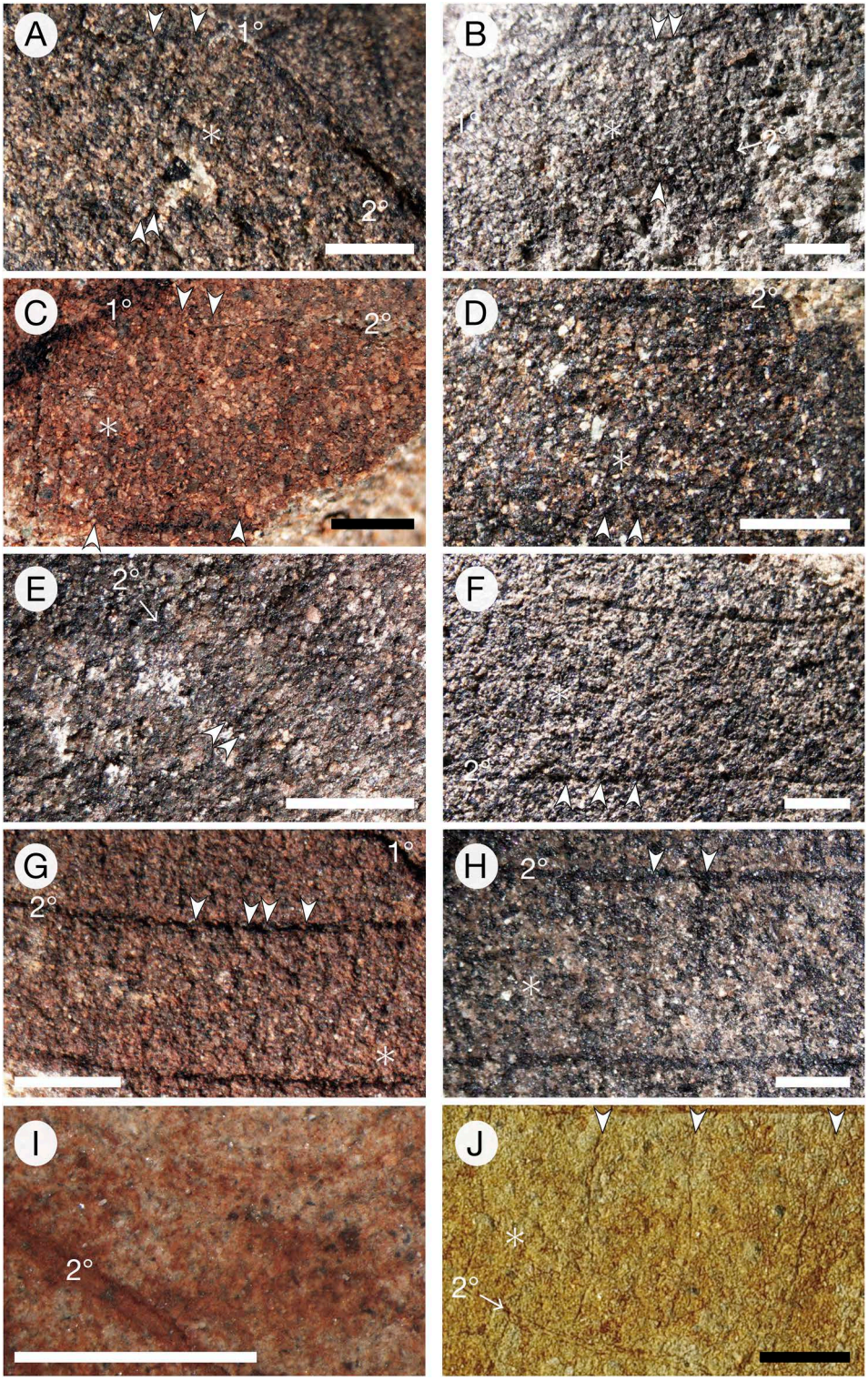

Figure 9. Photomicrographs of Ieda fossils showing fine venations. A. *Litseaphyllum* sp., NSM PP-12561b. B. *Machilus ugoana* Huzioka, NSM PP-12563. C. *Machilus nathorsti* Huzioka, NSM PP-12562. D. *Fagus stuxbergi* (Nath.) Tanai, NSM PP-12561a. E. *Quercus* (*Cyclobalanopsis*) *mandraliscae* (Gaudin) Tanai, NSM PP-12578a. F. *Quercus* sp. cf. *Q.* (*Cyclobalanopsis*) *nathorstii* Kryshtofovich, NSM PP-12582. G. *Quercus* (*Cyclobalanopsis*) *praegilva* Kryshtofovich, NSM PP-12580. H. *Lithocarpus*? sp., NSM PP-12576. I. *Acer* sp., NSM PP-12175. J. *Alangium* sp. NSM PP-12173c. Scale bar is equal to a 2 mm long. 1° & 2°: primary and secondary veins. Arrow heads indicate tertiary veins. *: position where fine venation is visible.

shared by *Sapindus tanaii* Onoe, which was originally described from the late-middle Miocene Imaichi Formation. However, we hesitate to assign it to the species level because of the absence of petioles and poor quality of preservation of higher order venation.

Order Cornales Dumort.
Family Cornaceae Bercht. *et* J.Presl
Genus ***Alangium*** Lam.
Alangium sp.
(Figs. 8D; 9J)

Material examined: NSM PP-12173c.

Remarks: A single fragmentary leaf is characterized by possibly orbicular shape, entire margin, weak brochidodromous thick secondaries, and relatively thin percurrent intercostal tertiaries. Quaternary and quintenary veins form polygonal meshes with profusely branching veinlets. These features are comparable to that of the genus *Alangium* (*Marlea*) (Tanai, 1989). The genus *Alangium* is one of the common elements of Miocene floras of Japan, although their systematic position is still the matter of debates.

Order Ericales Bercht. *et* J.Presl
Family Clethraceae Klotzsch
Genus ***Clethra*** L.
Clethra sp.
(Fig. 8A, B)

Material examined: NSM PP-12586.

Description: A single fragmentary leaf probably simple; laminae symmetrical; probably obovate shape; petiole very short, swollen; margin serrate; tooth probably compound, acutely pointed with straight sides; principal vein enters the tooth medially to slightly apically; primary vein moderate, straight; secondary veins thick, at least seven pairs, opposite to alternate, diverging from primary vein at nearly right angle near base, ca. 60° apically, straight or curved, branched near margin, sending one branch to next upper secondary to form a loop and another one toward the tooth, semicraspedodromous; intercostal tertiaries thick, straight, sinuous, rarely branched, nearly perpendicular to contiguous secondaries; higher order venation reticulate, forming large polygonal meshes.

Remarks: The specimen is characterized by obovate laminar shape with very short, swollen petiole and compound serrate margin. Detail of marginal vein configuration is also comparable with *Clethra* species: secondary and tertiary veins end in sinuses from which a branch derives toward the tooth tip. Fossil records of the genus are quite limited in Japan, even though it is common in temperate vegetation in Japan today. Nathorst (1883) described *Clethra maximowiczii* from the Pliocene Mogi flora in Nagasaki Prefecture. This species has been recorded from the late Miocene floras in Japan (Huzioka and Uemura, 1973; Tanai and Suzuki, 1965; Uemura, 1986, 1988). According to the redescription of original materials by Tanai (1976), our specimen is similar to this species in venation characteristics; however, it differs in petiole features. Another species, *C. hokiana* Ozaki, was described from the late Miocene Tochiwara Formation (Ozaki, 1980), and is characterized by elliptical lamina having evenly spaced marginal teeth and long petiole. Therefore, our specimen is distinguishable from it in all these characteristics.

Plantae *incertae sedis*
Monocotylophyllum sp.
(Fig. 8E)

Material examined: NSM PP-12587.

Remarks: A few fragments of linear leaves with parallel venation are observed. They are tentatively referred to as *Monocotylophyllum*, which is an organ genus applicable to monocot leaves with unknown affinities.

Phyllites sp. 1 (*Acer*?)
(Fig. 8K)

Material examined: NSM PP-12588.

Remarks: A single fragmentary leaf with five basal actinodromous primary veins was obtained. It can be compared with *Acer* or other genera.

Phyllites sp. 2
(Fig. 8F, G)

Material examined: NSM PP-12589.

Remarks: This fragmentary leaf or leaflet with entire margin is characterized by vein thickness and orthogonal vein configurations (from secondary to at least quaternary veins).

Phyllites sp. 3
(Fig. 8H, I)

Material examined: NSM PP-12176.

Remarks: A single fragmentary leaf or leaflet in our collection is characterized by inequilateral shape, irregularly arranged thick secondary veins, straightly percurrent intercostal tertiaries, and simple serrate margin with tiny spinose teeth.

Discussion and conclusion

Floristic characteristics of the Ieda fossil assemblage

Lithological characteristics of the lower middle Miocene Ieda Group suggested that the formation was accumulated under a deep sea depositional environment. All plant macrofossils occurred in coarse sediments and were considered to have derived through turbidity currents from terrestrial environment.

Among the 29 taxa in the assemblage, the majority has been reported from the late-early to early-middle Miocene Daijima-type flora which flourished under warmer-temperate climate (Tanai, 1961); this includes *Machilus nathorsti*, *M. ugoana*, cf. *Podocarpium podocarpum*, *Ulmus longifolia*, *Quercus* (*Cyclobalanopsis*) *mandraliscae*, *Q.* (*C.s*) *nathorstii*, *Q.* (*C.*) *praegilva*, and *Sapindus tanaii*. *Lithocarpus* is also a comparatively rare evergreen element. Diverse lauraceous, fagaceous, and fabaceous species is also a common feature of the Daijima-type flora (Tanai, 1992). On the other hand, *Fagus stuxbergi*, *Clethra* sp., and *Myrtonium* sp. have never been recorded from that type of flora.

The Daijima-type flora from terrestrial sediments generally contains various deciduous broad-leaved species as well as deciduous and evergreen conifers, including Fagaceae, Betulaceae, Ulmaceae, Fabaceae, Hamamelidaceae, Pinaceae, and Cupressaceae species. *Liquidambar miosinica* and *Comptonia naumanni* are two characteristic species of this flora (Huzioka and Uemura, 1979). In our collection, we found only one fragment of a palmately lobed leaf which is possibly identical to *Liquidambar*.

Based on our data, the Ieda assemblage is readily comparable with Daijima-type flora, but it contains some rare floral elements. The scarcity of deciduous broad-leaved species and conifers is most probably a consequence of taphonomic effects, such as sorting and skewing (e.g., Ferguson, 1985), and partially because of their preservation state, as deciduous leaves with relatively thin texture tend to be poorly preserved, making them hard to identify to the species level.

Another possibility for this scarcity can be related to climatic conditions at that time period. If the climate became warmer, the source vegetation might be more dominated by evergreen elements. Yamada and Yamada (2018) discussed the importance of climate warming during the MMCO in light of adding new elements to the vegetation of Japanese Islands. The occurrence of *Myrtonium* sp., a possible myrtaceous species, may also support this assumption.

Whichever the case, we suggest that this type of flora continued even after the transgression proceeded, and this is very well in accordance with the palynological records from Japan Sea basin (Yamanoi, 1992). Yamanoi (1992) suggested that his N2 assemblage (≈ Daijima-type flora) continued until about 12 Ma with a gradual decrease in the rate of warm elements.

The occurrence of *Fagus stuxbergi* and its implications

Beech species are one of the dominant deciduous elements in most fossil assemblages in East Asia since the early Miocene. Six species are currently recognized, namely *Fagus antipofi* Heer, *F. evenensis* Chelebaeva, *F. intermedia* Nath. (*sensu* Tanai, 1974), *F. chankaica* Pavlyutkin, *F. stuxbergi* (Nath.) Tanai, and *F. palaeojaponica* Tanai *et* Onoe. These species are readily distinguished from each other in leaf shape, venation, and marginal characteristics. Our materials from the marine Ieda Group are safely identical to *Fagus stuxbergi* in all morphological features.

This species has been recorded from the late Miocene–Pliocene floras. The oldest individual was described from the Yagii Formation in central Honshu (ca. 10 Ma, early late Miocene) (Horiuchi,

1996). Uemura (2002) suggested even earlier appearance of this species, but this has not been documented to date. Our materials from ca. 15.5 Ma are evidently the oldest records of this species in Japan, suggesting that the species coexisted with *Fagus antipofi*, an earlier Miocene species whose fossil record extends to the late middle Miocene (14–12 Ma: Komegawaki Formation: Uemura and Yasuno, 1991).

The late-middle Miocene Yagii flora represents a mixture of evergreen and deciduous hardwood species and conifers. *Fagus stuxbergi* was a quite rare element in the Yagii flora, and it was regarded as an allochthonous element being transported for a large distance (Ozaki, 1991). Currently, we cannot define the habitat of this species based only on the present study; however, this species may have inhabited areas near evergreen forests as it is one of the most dominant elements among the Ieda species.

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