

Revision of the early Pleistocene Minoshirotori flora in the plant fossil collection of the National Museum of Nature and Science, Tokyo

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Abstract In 1980, several of the original specimens of the Minoshirotori flora from the inland basin of Gujo City, middle west of Gifu Prefecture, central Japan, were donated to the National Museum of Nature and Science, Tokyo. This collection, together with other collections in the museum, was taxonomically revised in the present study in order to determine the altitudinal distribution of extant and extinct species during that time period, and to gain an insight on the ecological requirements of the extinct Neogene elements known in this flora. Thirty-eight taxa belonging to 27 genera and 15 families were identified, 23 of which are new taxa that have not been previously recorded in this flora. Most components of the flora are deciduous and typical of the modern lower *Fagus* zone in cooler temperate climates. The assemblage resembles the vegetation surrounding the fossil localities in the inland region at altitudes over 500 m. Although the Minoshirotori flora has modern traits, it also contains some Neogene elements. One of these is *Cunninghamia konishii* Hayata, which is native to the middle and high mountain regions of Taiwan under a warmer temperate climate. On the basis of its composition and recent K-Ar dating of the overlying strata, the age of the flora is suggested to be early Pleistocene. Thus, this taxon was revealed to have survived under cooler temperate conditions, at least during the early Pleistocene in the inland region of central Japan.

Key words: *Fagus* zone, altitudinal distribution, *Cunninghamia konishii* Hayata, early Pleistocene, central Japan

Introduction

A late Cenozoic plant megafossil assemblage from the upper reaches of the Nagaragawa River in Gujo City, in the western center of Gifu Prefecture, central Japan, was first described and named as the “Minoshirotori flora” by Matsuo (1968). He reported 30 angiosperm and conifer taxa, four of which were aquatic. Their presence and the lithology of the plant-bearing strata indicate formerly lacustrine conditions in an inland hilly region at an altitude of approximately 700 m. The flora mainly consisted of extant species typical of the modern *Fagus* zone. One extinct aquatic plant species, namely *Trapa mamillifera* Miki, was identified and was believed to be characteristic of the Pliocene epoch (Miki, 1952). Therefore, Matsuo (1968)

suggested that the flora belonged to the late Pliocene age.

Although there are several Pliocene–Pleistocene fossil assemblages in central Japan, most of those recorded to date have been collected from the strata accumulated in lowland and marine environments (Momohara, 2016). The Minoshirotori flora is significant in that it provides details of the altitudinal distributions of both extant and extinct species and indicates their differential responses to changes in climate and habitat.

During the course of my study on *Cunninghamia* species in Japan, I have realized that this taxon is included in the Minoshirotori flora (Yabe and Yamakawa, 2017). Therefore, it is necessary to recheck the floral composition of this locality and its relationship to other Minoshirotori ele-

ments, which indicate considerably cooler climatic conditions than those characterizing the modern habitat of *Cunninghamia* species. However, the locality bearing *Cunninghamia* specimens (Kaibutsu) has been abandoned and no longer yields any fossils (Yabe, personal observation in 2014).

In the present study, the author revisited the original specimens from the Minoshirotori flora donated in 1980 to the National Museum of Nature and Science, Tokyo, by Matsuo. Moreover, other collections preserved in the museum have been examined and many of the species identified by Matsuo (1968) have been revised. An updated age assignment is proposed based on the floral composition and radiometric ages recently determined for the overlying strata. Climatic conditions indicated by the flora and the possible habitat of locally extinct species, and their differences in inland hill and near-sea lowland areas, are briefly discussed.

Physical conditions and modern vegetation

Climate conditions and modern vegetation

Minoshirotori (north of Gujo) is a hilly region with an elevation range of approximately 400–700 m (Fig. 1). It is surrounded by high volcanic mountains to the north, east, and west. The climate near the fossil site (Nagataki: altitude approximately 430 m, Japan Meteorological Agency: <http://www.data.jma.go.jp>) is distinctly cool-temperate with mean annual, coldest month mean, and warmest month mean temperatures of 11.4, -0.3 , and 22.9°C , respectively, and a mean annual precipitation of approximately 3,000 mm. The potential vegetation of the area corresponds to the *Fagus* zone, which consists exclusively of deciduous angiosperms dominated by *Fagus crenata* Blume and *Quercus mongolica* subsp. *crispula* (Blume) Menitsky (Japan Environment Agency, 1982a, b). The vegetation below the *Fagus* zone is more prominent toward the south at lower altitudes and is dominated by evergreen dicots, such as *Quercus* (*Cyclobalanopsis*) spp. and lauraceous species.

Geological Setting

Fossil plants were embedded in white diatomaceous mudstone at Kaibutsu and Atagi or in buff-colored tuffaceous and sandy mudstone at Hokuno, Chujo, and Nishibora in the Atagi Formation. This formation overlies pre-Cretaceous basements. On its eastern border, it is covered by both older and younger Eboshi-Washigadake volcanic rocks (Wakita, 1984; Tanase *et al.*, 2007). To the north, it is covered by Dainichigadake volcanic rock (Matsuo, 1968) (Fig. 2).

The origin of the Atagi Formation is considered to be at least partially lacustrine. The four localities covered by this formation are collectively referred to as “Minoshirotori-ko” (Lake Minoshirotori) (Matsuo, 1968) (Fig. 1). Matsuo inferred that the lake developed at an elevation of approximately 700 m owing to the activity of the Eboshi-Washigadake volcano. Similar deposits have been observed in Kaibutsu (Locality 5, Fig. 1) located 11.5 km southeast of Atagi, where thin white diatomite is intercalated with tuff, tuffaceous sandstone, and mudstone (Kondo and Kubo, 1959; Wakita, 1984). The lacustrine deposits are of freshwater origin and contain freshwater diatoms (Kondo and Kubo, 1959; Tanaka *et al.*, 2011) and some aquatic plants (Matsuo, 1968).

The age of the Atagi Formation had been assumed to be late Pliocene, as it contains *Trapa mammillifera* Miki, which is considered to be characteristic of that period (Miki, 1952). Takahashi and Shimono (1980), however, proposed that the Atagi Formation is, in fact, considerably younger than the Pliocene because its palynoflora lacks typical Neogene elements, such as *Carya*, *Nyssa*, and *Liquidambar*. Moreover, the assemblage lacks the pollen grains of *Metasequoia*. Therefore, it was correlated with the “*Fagus* phytozone” known in the upper part of the Osaka Group (late-early to middle Pleistocene: Tai, 1973). The overlying Dainichigadake and Eboshi-Washigadake volcanic rocks have been subjected to K-Ar dating (Higashino *et al.*, 1984; Shimizu *et al.*, 1988; Tanase *et al.*, 2007), which indicated that the age ranges of the older and

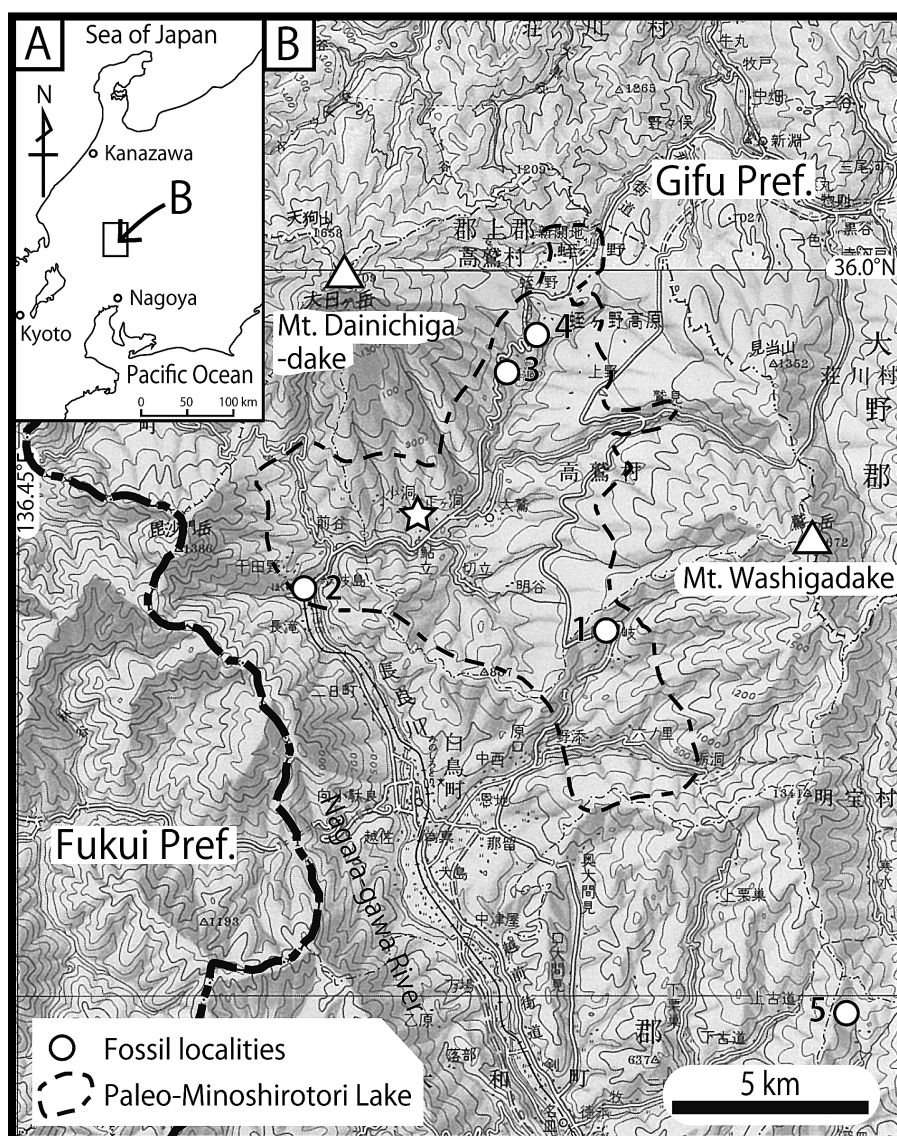


Fig. 1. Localities of the Minoshirotori flora, adapted to 1:20,000-scale regional maps “Gifu” and “Kanazawa” published by the Geospatial Information Authority in Japan (GSI). 1, Atagi; 2, Hokuno; 3, Chujo; 4, Nishibora; 5, Kaibutsu. Star, area investigated by Takahashi and Shimono (1980) for phytoplankton and pollen grains. The area of “Minoshirotori-ko” (encircled by a dotted line) was slightly modified from Matsuo (1968).

younger Eboshi-Washigadake volcanic rocks are 1.21 ± 0.04 – 1.15 ± 0.04 Ma and 1.15 ± 0.03 – 1.07 ± 0.06 Ma, respectively (Tanase *et al.*, 2007). The Dainichigadake volcanic rocks are slightly younger than those at Eboshi-Washigadake (1.034 ± 0.028 – 0.96 ± 0.10 Ma; Higashino *et al.*, 1984; Shimizu *et al.*, 1988). Therefore, the Atagi Formation is approximately 1.2 Ma old

(late-early Pleistocene) or older.

Materials and methods

Approximately 240 specimens were examined in total. Most of these were collected in 1963 and 1964 from five localities at an elevation of 600–800 m in Gujo City, middle west of Gifu Prefec-

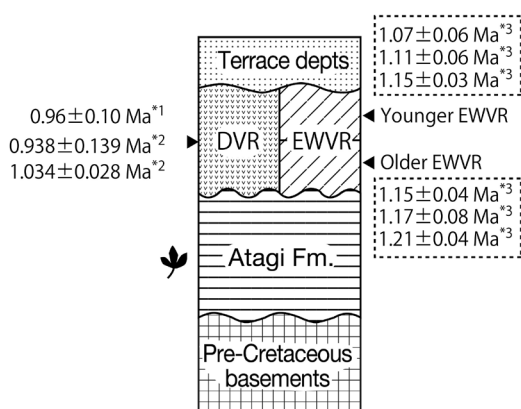


Fig. 2. Schematic stratigraphic section of the Cenozoic deposits in the Gujo area. Solid triangles: age based on K-Ar dating. *1, Higashino *et al.* (1984); *2, Shimizu *et al.* (1988); *3, Tanase *et al.* (2007). Fm., Formation; DVR, Dainichigadake volcanic rock; EWVR, Eboshi-Washigadake volcanic rock; depts, deposits.

ture (Fig. 1) by Dr. Hidekuni Matsuo and his students (Matsuo, 1968). In 1980, a part of his collection was donated to the paleobotany section of the National Science Museum (NSM PP), Tokyo. A smaller collection from Atagi, one of the five localities studied by Matsuo, was assembled by Dr. Ienori Fujiyama in 1978. The specimens were cleaned and prepared as necessary. Their macromorphology, venation patterns, and cuticular features were examined. Cuticles were treated with Schultz's solution (Kerp and Krings, 1999), followed by diluted sodium hydroxide until they were cleared. They were rinsed with deionized water and mounted in glycerine jelly or gum chloral. The depository abbreviations used for the specimens are as follows: paleobotanical collections of the National Museum of Nature and Science: NSM PP, and Department of Geology, College of Liberal Arts, Kanazawa University: DGLAKZ.

Results

Table 1 shows a revised list of the Minoshirotori flora. Thirty-eight taxa belonging to 27 genera and 15 families were identified, 23 of which

are new to this floral collection. They consist mainly of deciduous woody dicots, along with three evergreen conifer species and three aquatic plants. Among the specimens identified to the species level, only *Trapa mamillifera* is extinct. *Cunninghamia konishii* Hayata had become extinct in the Japanese Islands by approximately 0.5 Ma (Momohara, 2011), but it is an extant indigenous species in Taiwan at elevations of 1,300–2,000 m (Zheng, 1983).

The floral compositions of the individual localities are shown in Table 2. Atagi, the most productive, has 17 taxa. Hokuno and Kaibutsu have 14 and 12 taxa, respectively, followed by Chujo and Nishibora with 10 and five taxa, respectively. Approximately two-thirds of the taxa were recorded in only one locality. Although many of these taxa are represented by only a few specimens, some were represented by more than three, and others occurred in very large numbers: these include *Cryptomeria japonica* D. Don, *Cunninghamia konishii* Hayata, *Potamogeton* spp. 1 & 2, *Trapa mamillifera* Miki, and *Trapa* sp. The following species were distributed over three localities: *Betula* sp. cf. *B. grossa* Siebold *et* Zucc., *Tilia* sp. cf. *T. japonica* (Miq.) Shimonk., and *Quercus* sp. cf. *Q. mongolica* Fisch. ex Turcz. Those found at two localities were *Cercidiphyllum* sp., *Betula* sp. cf. *B. maximowicziana* Regel, *Carpinus* sp. cf. *C. cordata* Blume, *Carpinus* sp. cf. *C. japonica* Blume, *C. laxiflora* (Siebold *et* Zucc.) Blume, *C. tschonoskii* Maxim., *Corylus* sp., *Fagus* sp. cf. *F. crenata* Blume, *F. japonica* Maxim., *Quercus* sp. cf. *Q. serrata* Thunb., *Trapa* sp., *Ulmus* sp. cf. *U. davidiana* Planch., and *Fraxinus* sp.

The Atagi, Hokuno, and Chujo localities had many species in common. Nevertheless, two beech species present at Atagi and Hokuno were absent from Chujo. Most of their constituent species are typical of the modern *Fagus* zone, which flourishes in cooler temperate climates. The Kaibutsu locality had isolated leafy shoots of *Cryptomeria japonica* and *Cunninghamia konishii*, together with isolated leaves of *Sorbus* sp., *Acer* sp. cf. *A. pycnanthum* K. Koch, and *Phyllites* sp. Leaves of

Table 1. Systematic list of the Minoshiratori Flora.

Gymnospermae	<i>Quercus</i> sp. cf. <i>Q. mongolica</i> Fisch. ex Turcz.
Family Cupressaceae	<i>Quercus</i> sp. cf. <i>Q. serrata</i> Thunb.
<i>Cryptomeria japonica</i> D.Don	Family Trapaceae
<i>Cunninghamia konishii</i> Hayata*	<i>Trapa mammillifera</i> Miki
<i>Thujopsis</i> sp. cf. <i>T. dolabrata</i> (Thunb. ex L.f.) Siebold et Zucc.	<i>Trapa</i> sp.*
Angiospermae	Family Rosaceae
Family Magnoliaceae	<i>Rosa</i> sp.*
<i>Magnolia</i> sp.*	<i>Sorbus</i> sp.*
Family Potamogetonaceae	Family Ulmaceae
<i>Potamogeton</i> sp. 1*	<i>Ulmus</i> sp. cf. <i>U. davidiana</i> Planch.*
<i>Potamogeton</i> sp. 2*	<i>Zelkova</i> sp. cf. <i>Z. serrata</i> (Thunb.) Makino*
Family Cercidiphyllaceae	Family Malvaceae
<i>Cercidiphyllum</i> sp.*	<i>Tilia</i> sp. cf. <i>T. japonica</i> (Miq.) Shimonk.
Family Salicaceae	Family Sapindaceae
<i>Populus?</i> sp.*	<i>Acer</i> sp. cf. <i>A. pictum</i> Thunb.
<i>Salix</i> sp.*	<i>Acer</i> sp. cf. <i>A. pycnanthum</i> K.Koch*
Family Betulaceae	<i>Acer</i> sp. cf. <i>A. rufinerve</i> Siebold et Zucc.
<i>Betula</i> sp. cf. <i>B. grossa</i> Siebold et Zucc.*	<i>Aesculus</i> sp. cf. <i>A. turbinata</i> Blume*
<i>Betula</i> sp. cf. <i>B. maximowicziana</i> Regel	Family Hydrangeaceae
<i>Carpinus</i> sp. cf. <i>C. cordata</i> Blume	<i>Hydrangea</i> sp.*
<i>Carpinus</i> sp. cf. <i>C. japonica</i> Blume*	Family Oleaceae
<i>Carpinus laxiflora</i> (Siebold et Zucc.) Blume	<i>Fraxinus</i> sp.*
<i>Carpinus tschonoskii</i> Maxim.	Family Caprifoliaceae
<i>Corylus</i> sp.	<i>Viburnum</i> sp.
Family Fagaceae	Angiospermae <i>incertae cedis</i>
<i>Castanea</i> sp.*	<i>Phyllites</i> sp.*
<i>Fagus</i> sp. cf. <i>F. crenata</i> Blume	<i>Carpolithes</i> sp. 1*
<i>Fagus japonica</i> Maxim.*	<i>Carpolithes</i> sp. 2*

38 taxa (15 families, 27 genera, including two fossil-genera)

Species with asterisk indicate new to this flora or renamed by the present study.

Potamogeton sp. 1 show mass occurrence, whereas the fruits of *Trapa* sp. were dispersed in massive diatomaceous mudstone. Some of the Kaibutsu species are characteristic of wet valley forests (*Cryptomeria japonica*, *Cunninghamia konishii*, and *Acer* sp. cf. *A. pycnanthum*) and ponds (*Potamogeton* sp. 1 and *Trapa* sp.), whereas the Nishibora locality contained aquatic plants (*Potamogeton* sp. 2 and *Trapa mammillifera*) and a possible riparian species (*Fraxinus* sp.).

Identification of the specimens

Remarks for the identification of each species are presented herein. Descriptive terminology for dicotyledonous leaves follows the protocols of Hickey (1973, 1979) and Ellis *et al.* (2009). Extant species nomenclature follows Iwatsuki *et al.* (1993, 1995) and Iwatsuki *et al.* (1999, 2001, 2006). Taxonomic arrangements of gymnosperms and angiosperms are based on Kramer and Green (1990) and APGIII (2009), respectively.

Family Cupressaceae

Genus *Cryptomeria* D.Don

Cryptomeria japonica D.Don

(Figs. 3-E, F; 4-B, C)

Cf. *Cryptomeria japonica* D.Don, Matsuo, 1968, p. 43, pl. 1, figs. 8, 9, 11.

Coniferous shoots with long, spirally arranged, falcate leaves are characteristic of this species. Although, Matsuo (1968) did not establish its identity, the cuticular features of the specimens (i.e., randomly oriented stomatal pits, and number of subsidiary cells) confirm their identification.

Material examined: NSM PP-14402a (Fig. 4-C), 14403a (Figs. 3-F, 4-B, C), 14404a (Fig. 3-E), 14405, 14406, loc. Kaibutsu.

Table 2. Occurrence of Minoshirotori species at each locality.

Species	Atagi	Hokuno	Chujo	Nishibora	Kaibutsu
<i>Cryptomeria japonica</i> D.Don					○
<i>Cunninghamia konishii</i> Hayata					○
<i>Thujopsis</i> sp. cf. <i>T. dolabrata</i> (Thunb. ex L.f.) Siebold et Zucc.			○		
<i>Magnolia</i> sp.	○				
<i>Magnolia obovata</i> Thunb.*					○*
<i>Potamogeton</i> sp. 1					○
<i>Potamogeton</i> sp. 2				○	
<i>Cercidiphyllum</i> sp.	○		○		
<i>Populus?</i> sp.		○			
<i>Salix</i> sp.	○				
<i>Betula</i> sp. cf. <i>B. grossa</i> Siebold et Zucc.	○	○			○*
<i>Betula</i> sp. cf. <i>B. maximowicziana</i> Regel	○		○		
<i>Carpinus</i> sp. cf. <i>C. cordata</i> Blume	○	○			
<i>Carpinus</i> sp. cf. <i>C. japonica</i> Blume		○			○
<i>Carpinus laxiflora</i> (Siebold et Zucc.) Blume		○			○
<i>Carpinus tschonoskii</i> Maxim.		○*	○		
<i>Corylus</i> sp.	○	○*			
<i>Castanea</i> sp.	○				
<i>Fagus</i> sp. cf. <i>F. crenata</i> Blume	○	○			
<i>Fagus japonica</i> Maxim.	○	○			
<i>Quercus</i> sp. <i>Q. mongolica</i> Fisch. ex Turcz.	○	○	○		
<i>Quercus</i> sp. cf. <i>Q. serrata</i> Thunb.	○	○*			
<i>Trapa mamillifera</i> Miki				○	
<i>Trapa</i> sp.			○		○
<i>Rosa</i> sp.				○	
<i>Sorbus</i> sp.					○
<i>Ulmus</i> sp. cf. <i>U. davidiana</i> Planch.		○	○		
<i>Zelkova</i> sp. cf. <i>Z. serrata</i> (Thunb.) Makino			○		
<i>Tilia</i> sp. cf. <i>T. japonica</i> (Miq.) Shimok.		○	○		○
<i>Acer</i> sp. cf. <i>A. pictum</i> Thunb.	○				
<i>Acer</i> sp. cf. <i>A. pycnanthum</i> K.Koch					○
<i>Acer</i> sp. cf. <i>A. rufinerve</i> Siebold et Zucc.	○				
<i>Aesculus</i> sp. cf. <i>A. turbinata</i> Blume	○				
<i>Hydrangea</i> sp.	○				
<i>Fraxinus</i> sp.		○		○	
<i>Viburnum</i> sp.	○				
<i>Phyllites</i> sp.					○
<i>Carpolithes</i> sp. 1				○	
<i>Carpolithes</i> sp. 2			○		
Number of species in each locality	17	14	10	5	12

Asterisks indicate those species confirmed based on Matsuo's (1968) illustration.

Genus *Cunninghamia* R.Br.

Cunninghamia konishii Hayata

(Figs. 3-A–C; 4-D, E)

Taxus cuspidata Siebold et Zucc., Matsuo 1968, p. 42, pl. 1, figs. 2, 3.

Cunninghamia sp. cf. *C. konishii* Hayata, Yabe and Yamakawa, 2017, p.312, figs. 5J, 6L.

Coniferous leafy shoots identified as *Taxus cuspidata* by Matsuo (1968) clearly possess ser-

ulate leaves. The leaves of these specimens are hypostomatic or amphistomatic and have distinct stomatal bands between the midrib and the margin. The adaxial and abaxial epidermis has longitudinally arranged stomatal- and stoma-free zones. The randomly arranged stomatal pits, and typically undulating, thickened anticlinal cell walls of the normal cells in the stoma-free zones confirm that these specimens are identical to those of the genus *Cunninghamia*. All the specimens

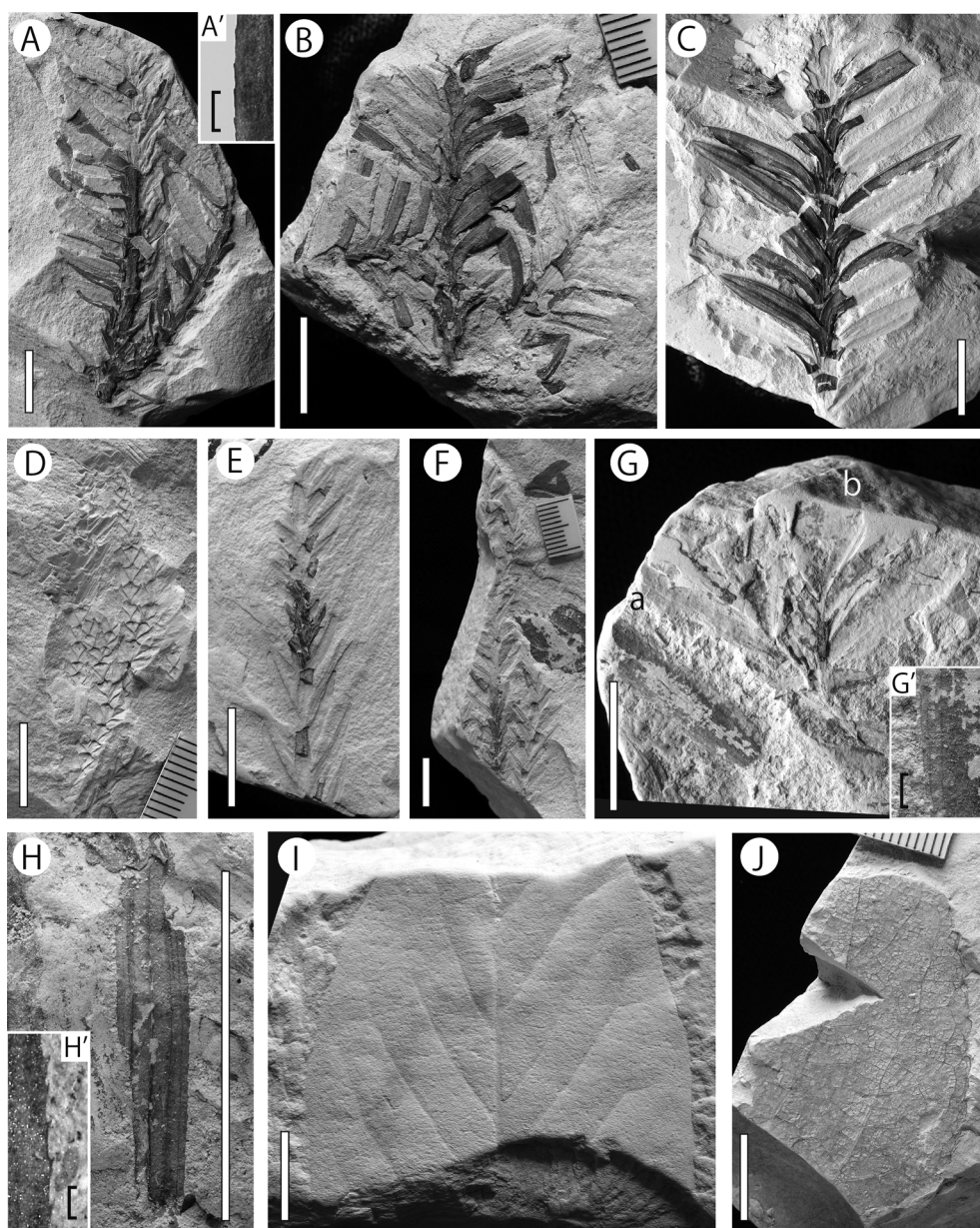


Fig. 3. A–C, *Cunninghamia konishii* Hayata, loc. Kaibutsu. A, NSM PP-14407; B, NSM PP-14408; C, NSM PP-14409. D, *Thujopsis* sp. cf. *T. dolabrata* (Thunb. ex L.f.) Siebold *et* Zucc., NSM PP-14410a, loc. Chujo. E, F, *Cryptomeria japonica* D.Don, loc. Kaibutsu. E, NSM PP-14404a; F, NSM PP-14403a. G, G', *Potamogeton* sp. 2, NSM PP-14412a, loc. Kaibutsu. a, isolated leaf; b, shoot. G', an enlargement of Ga. H, H', *Potamogeton* sp. 1, NSM PP-14413, loc. Nishibora. H', enlargement of marginal teeth. I, *Magnolia* sp., NSM PP-14411, loc. Atagi. J, *Cercidiphyllum* sp., NSM PP-14418, loc. Chujo. Scale bars in G' and H' are 1 mm and 200 μ m long, respectively. Scale bars for the other parts of the figure are 1 cm long.

examined had distinctly short falcate leaves, and were therefore identified as *C. konishii* Hayata, which is native to Taiwan.

Material examined: NSM PP-14407 (Fig. 3-A; 4-D, E), 14408 (Fig. 3-B), 14409 (Fig. 3-C), loc. Kaibutsu.

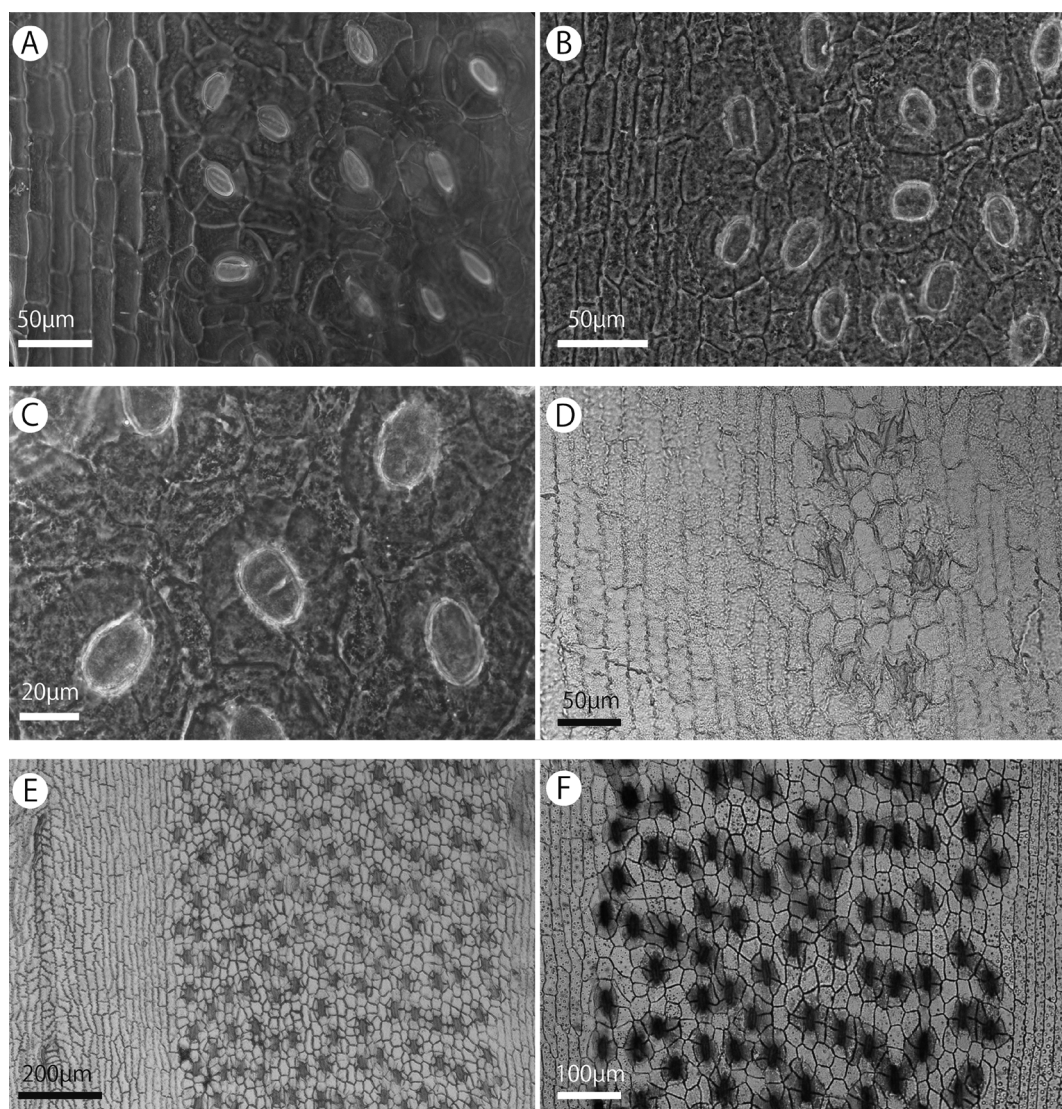


Fig. 4. Photomicrographs of the cuticles of fossil and modern materials. **A–C**, *Cryptomeria japonica* D.Don. **A**, NSM PPref-003, modern; **B**, **C**, NSM PP-14403a, fossil, loc. Kaibutsu. **D–F**, *Cunninghamia konishii* Hayata. **D**, NSM PP-14407, fossil, loc. Kaibutsu. **D**, adaxial epidermis; **E**, abaxial epidermis. **F**, lower epidermis, NSM PPref-004, modern.

Genus *Thujopsis* Siebold *et* Zucc.

Thujopsis sp. cf. *T. dolabrata* (Thunb. ex L.f.)

Siebold *et* Zucc.

(Fig. 3-D)

Cf. *Thujopsis dolabrata* Siebold *et* Zucc., Matsuo, 1968, p. 43, pl. 1, figs. 7, 10.

This cupressaceous conifer species is characterized by opposite decussate leaves. It has two

lateral leaves, which do not cover the base of the facial leaf. No cuticular data is available for this specimen. Nevertheless, on the basis of its leaf size and arrangement, it is comparable to *Thujopsis dolabrata*.

Material examined: NSM PP-14410a (Fig. 3-D), loc. Chujo.

Family Magnoliaceae

Genus *Magnolia* L.*Magnolia* sp.

(Fig. 3-I)

A single fragmentary leaf has an obovate shape, a wavy entire margin, pinnate venation, weak brochidodromous secondary veins and opposite percurrent tertiary veins oriented at obtuse to right angles from the primary vein. The intersecondary veins arising from the primary vein connect to tertiary veins in the intercostal area (magnoliarian tertiary system: Wolfe, 1973). These features are assignable to the genus *Magnolia* L. Matsuo (1968) reported a single *Magnolia obovata* Thunb. leaf from the Kaibutsu locality with a macrophyllous lamina and secondary veins diverging at obtuse to right angles from the primary vein. The present species is readily distinguishable from the specimen collected at Kaibutsu in its size and venation traits, and more closely resembles the modern *M. kobus* DC.

Material examined: NSM PP-14411 (Fig. 3-I), loc. Atagi.

Family Potamogetonaceae

Genus *Potamogeton* L.*Potamogeton* sp. 1

(Fig. 3-H, H')

Isolated leaves are linear and less than 3 mm wide. It has a thick primary vein with two parallel secondary veins on each side of the blade. The intercostal areas are connected by transverse tertiary veins. Those from the outermost secondary veins enter marginal spinose teeth. These features resemble the submerged leaves of certain *Potamogeton* species.

Material examined: NSM PP-14413 (Fig. 3-H, H'), 14414, loc. Nishibora.

Potamogeton sp. 2

(Fig. 3-G, G')

The specimen is represented by a number of isolated leaves and a single stem bearing leaves arranged in a helix. The linear leaves are characterized by entire margins, thick primary veins, and parallel secondary veins that rarely branch at acute angles. The intercostal areas are transversely connected by thin tertiary veins. These features are common to *Potamogeton* sp. 1, but the specimen differs from this species in that it has a higher number of secondary veins and an entire margin. The author has tentatively named this specimen *Potamogeton* sp. 2.

Material examined: NSM PP-14412a (Fig. 3-G, G'), 14416, 14417, loc. Kaibutsu.

Family Cercidiphyllaceae

Genus *Cercidiphyllum* Siebold et Zucc.*Cercidiphyllum* sp.

(Fig. 3-J)

Two fragmentary leaves are identical to those of the genus *Cercidiphyllum*. They have festooned brochidodromous secondary veins, round teeth, polygonal areoles, and simple- or twice-branched ultimate veinlets.

Material examined: NSM PP-14418 (Fig. 3-J), loc. Chujo; PP-14419, loc. Atagi.

Family Salicaceae

Genus *Populus* L.*Populus?* sp.

(Fig. 11-F)

Although fragmentary, the leaf has distinct features such as a relatively thick secondary pair diverging near the leaf base, which sends branches exmedially to the sinus of the marginal teeth. The leaf margin is remotely serrate with a round tip. These features are common to the

genus *Populus*. Nevertheless, the specimen lacks the intersecondary veins that are characteristic of this genus.

Material examined: NSM PP-14481 (Fig. 11-F), loc. Hokuno.

Genus *Salix* L.

Salix sp.

(Fig. 8-B, B')

A single fragmentary leaf has pinnate venation with parallel secondary veins that abruptly bend upwards near the margin. No marginal teeth were detected, but the author tentatively classified the specimen as *Salix* L. based on its secondary and intersecondary veins.

Material examined: NSM PP-14420 (Fig. 8-B, B'), loc. Atagi.

Family Betulaceae

Genus *Betula* L.

Betula sp. cf. *B. grossa* Siebold et Zucc.

(Fig. 5-F, H)

Carpinus laxiflora (Siebold et Zucc.) Blume, Matsuo, 1968, p. 45, pl. 3, fig. 7.

Viburnum? sp., Matsuo, 1968, pl. 2, fig. 4.

Several leaves have slightly inequilateral, wide-elliptic laminae with acuminate apices and shallowly cordate bases. They have duplicate serrate margins with blunt, flexuous-flexuous teeth and basally eccentric principal veins leading to them. One specimen, identified by Matsuo (1968) as "*Carpinus laxiflora* (Siebold et Zucc.) Blume" (Matsuo, 1968, pl. 3, fig. 7) was assigned to this species based on the characteristics of its teeth. The other specimen, identified as "*Viburnum?* sp.," is also identical to this species in terms of evenly spaced craspedodromous secondary veins and flexuous-flexuous teeth with blunt apices.

Material examined: NSM PP-14419, 14421 (Fig. 5-F), 14422 (Fig. 5-H), 14423, 14424, 14425, loc. Atagi; PP-14485 (= DGLAKZ13748), loc. Hokuno.

Betula sp. cf. *B. maximowicziana* Regel

(Fig. 9-A, B)

Betula maximowicziana Regel, Matsuo, 1968, p. 46, pl. 2, fig. 8.

Corylus? sp., Matsuo, 1968, pl. 2, fig. 5.

These fragmentary leaves are characterized by a relatively large leaf size, cordate bases, and dentate margins, with relatively long, flexuous-flexuous teeth with blunt apices situated on either side of the dents. One of these specimens was formerly identified as "*Corylus?* sp." (Matsuo, 1968, pl. 2, fig. 5). Nevertheless, the specimen is readily distinguishable from *Corylus* in that its ultimate veinlets branch several times. Therefore, it belongs to the tribe Betuleae rather than the Coryleae (Uemura, 1988).

Material examined: NSM PP-14426a (Fig. 9-A), 14426b, 14427 (Fig. 9-B), loc. Chujo.

Genus *Carpinus* L.

Carpinus sp. cf. *C. cordata* Blume

(Fig. 5-B)

Carpinus cordata Blume, Matsuo, 1968, p. 45, pl. 2, fig. 7.

The specimens are characterized by wide elliptic shapes, deeply cordate bases, craspedodromous secondary veins, acutely pointed flexuous-convex teeth, and principal veins entering the teeth centrally. They are distinct from *Betula grossa* in terms of tooth shape and venation, and from *Carpinus japonica* and *C. laxiflora* in terms of tooth shape, number of secondaries, size, and marginal characteristics.

Material examined: NSM PP-14428 (Fig. 5-B), NSM PP-14429, loc. Atagi.

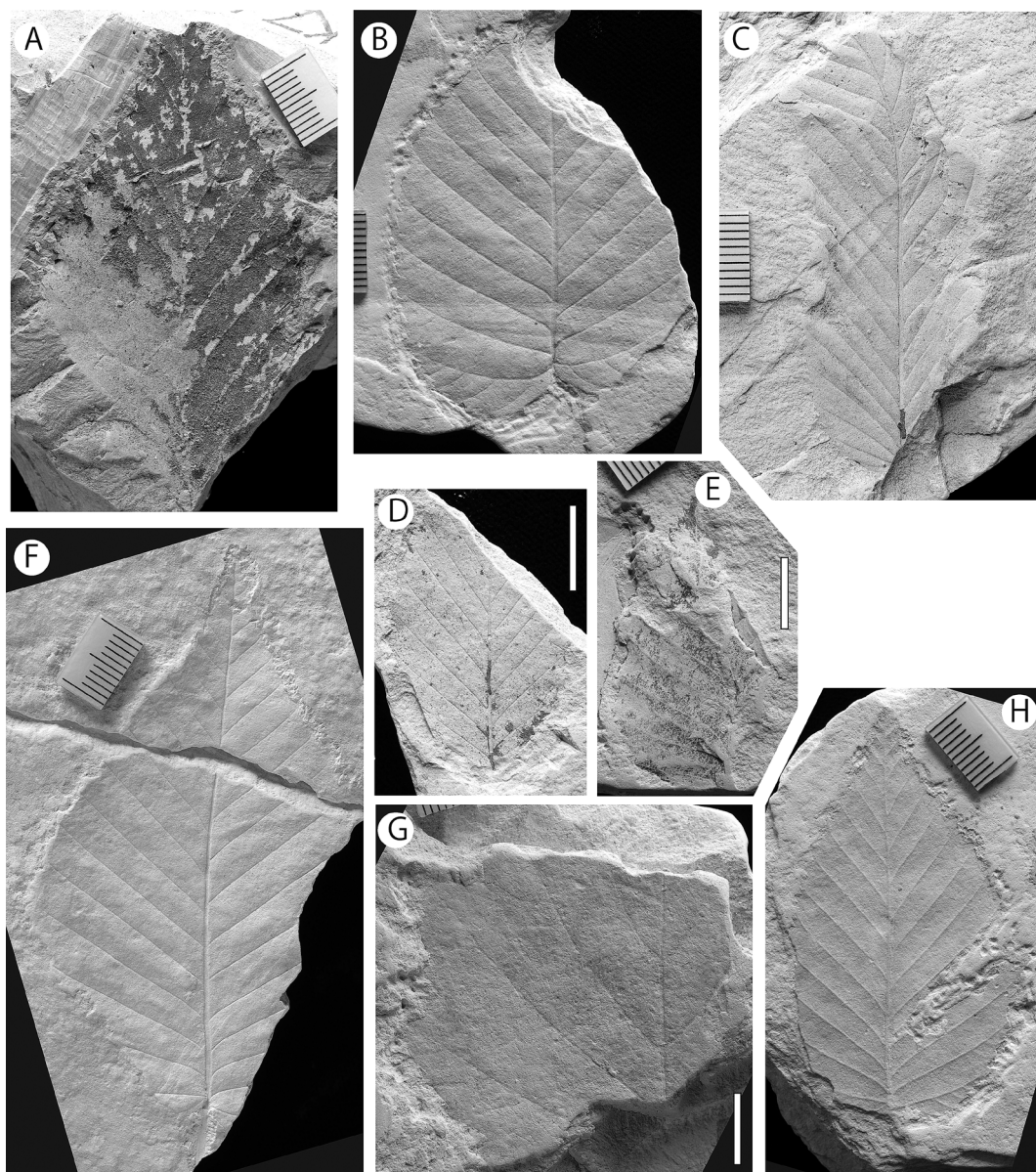


Fig. 5. **A**, *Carpinus tschonoskii* Maxim, NSM PP-14435, loc. Chujo. **B**, *Carpinus* sp. cf. *C. cordata* Blume, NSM PP-14428, loc. Atagi. **C**, *Carpinus* sp. cf. *C. japonica* Blume, NSM PP-14402b, loc. Kaibutsu. **D**, **E**, *Carpinus laxiflora* (Siebold et Zucc.) Blume, loc. Hokuno. **D**, NSM PP-14432; **E**, NSM PP-14483d. **F**, **H**, *Betula* sp. cf. *B. grossa* Siebold et Zucc, loc. Atagi. **F**, NSM PP-14421; **H**, NSM PP-14422. **G**, *Corylus* sp., NSM PP-14436b, loc. Atagi. Scale bar = 1 cm.

Carpinus sp. cf. *C. japonica* Blume
(Fig. 5-C)

The general features of these specimens resemble those of *Carpinus cordata*. Neverthe-

less, their marginal teeth are considerably smaller and more acutely pointed. The number of secondary veins is considerably higher than that of *C. cordata*. These features correspond to those of *C. japonica* Blume.

Material examined: NSM PP-13889a, 14402b (counter part of PP-13889a; Fig. 5-C), loc. Kai-butsu.

Carpinus laxiflora (Siebold *et* Zucc.) Blume

(Fig. 5-D, E)

Carpinus laxiflora (Siebold *et* Zucc.) Blume, Matsuo, 1968, p. 45, pl. 1, fig. 13 (involucre); pl. 2, figs. 2, 3; pl. 5, fig. 1.

Carpinus japonica Blume, Matsuo, 1968, pl. 5, fig. 2.

The specimens are characterized by small laminae, wide elliptic to wide ovate shapes, and relatively small, acutely pointed teeth with flexuous-convex or flexuous-flexuous shapes forming zigzag margins. They are identical to *Carpinus laxiflora*. A single involucre from Hokuno (Matsuo, 1968, pl. 1, fig. 13) probably corresponds to this species in terms of its size and lateral lobe extruding upward on one side. One specimen, identified by Matsuo (1968) as *C. japonica* (Matsuo, 1968, pl. 5, fig. 2), is identical to this species in terms of its size, tooth shape, and marginal characteristics.

Material examined: PP-14430, 14433, loc. Kai-butsu; NSM PP-14432 (Fig. 5-D), 14483d (Fig. 5-E), loc. Hokuno.

Carpinus tschonoskii Maxim.

(Fig. 5-A)

Carpinus tschonoskii Maxim., Matsuo, 1968, p. 44, pl. 1, figs. 12, 14.

This specimen is characterized by a wide elliptic leaf having an acute apex, a short acuminate tip, an acute base, craspedodromous secondaries, and comparatively large marginal teeth with central tooth venations. On the basis of these traits, it is identical to *Carpinus tschonoskii* Maxim. A single isolated leaf from Hokuno was reported by Matsuo (1968: pl. 1, fig. 12) and had similar characteristics. An associated involucre from the same locality (Matsuo, 1968, pl. 1, fig. 14) is very large (ca. 24.5 mm long) with an inequilateral triangular shape and one incurved side,

which also corresponds to this species.

Material examined: NSM PP-14435 (Fig. 5-A), loc. Chujo.

Genus *Corylus* L.

Corylus sp.

(Fig. 5-G)

A single fragmentary leaf having compound agrophytic secondaries is tentatively assigned to the genus *Corylus* L. Matsuo (1968) reported a single leaf of "Cf. *C. heterophylla*" from the Atagi Formation at Hokuno, which resembles the current specimen.

Material examined: NSM PP-14436b (Fig. 5-G), loc. Atagi.

Family Fagaceae

Genus *Castanea* Mill.

Castanea sp. cf. *C. crenata* Siebold *et* Zucc.

(Fig. 7-F)

The specimen is characterized by a single petiolate leaf with its basal half preserved. It has a slightly inequilateral base, of which one side is shallowly cordate. The secondaries are craspedodromous and enter the marginal spinose teeth. The intercostal tertiary veins are coarsely percurrent. The specimen is assigned to the genus *Castanea* Mill. based on its venation characteristics, cordate basal shape, and simple spinose marginal teeth.

Material examined: NSM PP-12233, loc. Atagi.

Genus *Fagus* L.

Fagus sp. cf. *F. crenata* Blume

(Fig. 6-A, B)

Fagus crenata Blume, Matsuo, 1968, p. 47, pl. 3, figs. 2, 4 (excluding pl. 3, figs. 1, 3, 9; pl. 4, fig. 1)

Several leaves are identical to those of this

species in that they are simple, wide ovate in form, and have short acuminate tips, wavy margins, pinnate venation, and parallel secondaries that abruptly bend upwards below the margins to connect with contiguous secondaries. Their intercostal tertiaries are relatively thick and coarsely percurrent. Among those specimens identified as this species by Matsuo (1968), DGLAKZ13770 (Matsuo, 1968, pl. 4, fig. 1) and DGLAKZ 13791 (Matsuo, 1968, pl. 3, fig. 9) are excluded here. The former is identical to *Quercus*, as it has a simple serrate margin and craspedodromous secondaries, and the latter corresponds to *F. japonica* Maxim., because it has a higher number of secondaries (≥ 10 veins).

Material examined: NSM PP-14419c (Fig. 6-B), 14437a (Fig. 6-A), 14438, 14439, 14440, 14441, loc. Atagi; PP-14434, loc. Hokuno.

Fagus japonica Maxim.

(Fig. 6-C, C', D-F)

Fagus crenata Blume, Matsuo, 1968, p. 47, pl. 3, figs. 1, 3, 9.

Carpolithes sp., Matsuo, 1968, pl. 1, fig. 6 (cupule).

Several beech leaves are identical to those of this species. They are elliptic and have shortly acute apices and as many as 10–12 secondary veins. Matsuo (1968) classified all of these specimens as *F. crenata*. Nevertheless, they are identical to each other based on the aforementioned characteristics. A single cupule with leaf-like projections on its valve surface was found in the collection (Fig. 6-C'). It is identical to those of this species with its small size and long (~18 mm) slender peduncle.

Material examined: Cupule, NSM PP-14442 (Fig. 6-C, C'), loc. Hokuno; leaves, NSM PP-14443 (Fig. 6-E), 14444 (Fig. 6-F), 14445 (Fig. 6-D), 14446, 14447, loc. Atagi.

Genus *Quercus* L.

Quercus sp. cf. *Q. mongolica* Fisch. ex Turcz.

(Fig. 7-A–E)

Quercus serrata Thunb., Matsuo, 1968, pl. 4, fig. 2.

Quercus crispula Blume, Matsuo, 1968, pl. 4, figs. 3, 4, 6, pl. 5, fig. 3.

These specimens are characterized by oblanceolate shape, a basal fourth of the lamina that is sided by straight to slightly concave margins, and shallowly cordate bases. They have very short petioles and evenly spaced, triangular teeth whose secondary veins enter centrally. They are identical in all characteristics to the genus *Quercus* and comparable to *Q. mongolica* Fisch. ex Turcz., particularly its subspecies *Q. mongolica* subsp. *crispula* (Blume) Menitsky. They are widely distributed in the cooler temperate forests of Japan and northeastern Asia.

One specimen from Chujo was identified by Matsuo (1968) as *Q. serrata* Thunb. (Matsuo, 1968, pl. 4, fig. 2). It resembles this species in terms of its very short petiole and marginal characteristics.

Material examined: NSM PP-14448 (Fig. 7-D), 14451, 14452 (Fig. 7-E), 14453 (Fig. 7-B), 14455, 14456, 14458, 14459, loc. Atagi; PP-14449 (Fig. 7-C), 14460a, 14460b, loc. Chujo; PP-14450a (Fig. 7-A), 14454, 14457, loc. Hokuno.

Quercus sp. cf. *Q. serrata* Thunb.

(Fig. 8-A)

Fagus crenata Blume, Matsuo, 1968, p. 47, pl. 4, fig. 1.

A single fragmentary leaf, formerly identified by Matsuo as *Fagus crenata* Blume, corresponds to *Quercus* species on the basis of its simple teeth, craspedodromous secondaries, and thicker venation. The specimen is comparable to *Q. serrata* in that it has a long petiole and an acutely decurrent base.

Material examined: NSM PP-14462b (Fig. 8-A), loc. Atagi.

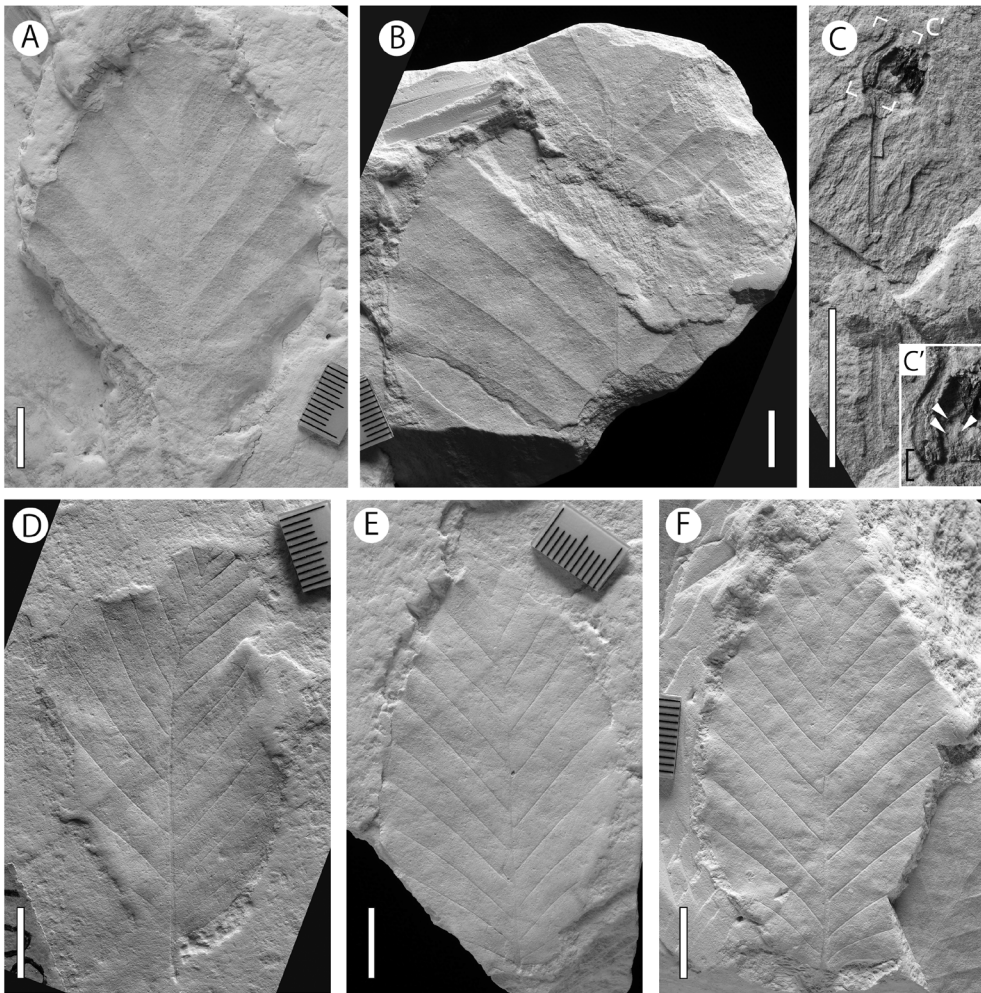


Fig. 6. A, B, *Fagus* sp. cf. *F. crenata* Blume, loc. Atagi. A, NSM PP-14437a; B, NSM PP-14419c. C–F, *Fagus japonica* Maxim. C, C', cupule, NSM PP-14442, loc. Hokuno; C', an enlargement of the cupule; D–F, leaf, loc. Atagi; D, NSM PP-14445; E, NSM PP-14443; F, NSM PP-14444. Scale bar = 1 cm. White arrowheads: leaf-like appendages on the cupule surface.

Family Trapaceae

Genus *Trapa* L.

Trapa mamillifera Miki

(Fig. 8-D, E)

Trapa mamillifera Miki, Matsuo 1968, p. 56, pl. 8, figs. 1, 5, 6.

The specimens are compressed *Trapa* fruits. The specimen in Figure 8-D is laterally compressed, whereas another (Fig. 8-E) is vertically

compressed. They are characterized by a triangular shape, with two pairs of horns at two different levels. The tubercles are located alternately to the horn. These features are characteristic of the fruits of *Trapa mamillifera* Miki (Miki, 1938, 1952). The fruit horn shape and position in this species are similar to those of the modern *T. incisa* Siebold *et* Zucc. in East Asia. It is believed to be an extinct species representing this lineage in the late Pliocene (Miki, 1952). Nevertheless, certain localities of this species have been dated as early

Pleistocene (e.g., the “Stegodon bed” in Nakayagi near Akashi, Hyogo Pref., and the “Yamaashiya” at Ashiya, Hyogo Pref., see Yamada *et al.*, 2014 for age assignments) according to the modern chronostratigraphic scheme (Cohen *et al.*, 2013, updated).

Material examined: NSM PP-14463 (Fig. 8-D), 14464a (Fig. 8-E), loc. Nishibora.

Trapa sp.

(Fig. 7-G)

A vertically compressed fruit from the Kaibutsu locality possesses two pairs of horns but no tubercles. On the basis of these traits, it is distinguished from *T. mammillifera* and is tentatively identified here as *Trapa* sp.

Material examined: NSM PP-14466 (Fig. 7-G), loc. Kaibutsu.

Family Rosaceae

Genus *Rosa* L.

Rosa sp.

(Fig. 8-F)

A single leaf (or leaflet) is characterized by a small, oblong, relatively inequilateral lamina with pinnate venation and simple marginal teeth. The leaf apex and base are convex and acutely round. All of these features correspond to those of the genus *Rosa*.

Material examined: NSM PP-14468 (Fig. 8-F), loc. Nishibora.

Genus *Sorbus* L.

Sorbus sp.

(Fig. 8-C)

The specimen is characterized by an inequilateral shape, deeply incised marginal teeth with flexuous-flexuous shape, irregularly spaced

craspedodromous secondaries, and common presence of intersecondary veins. Although fragmentary, the specimen is most likely a leaflet of a compound leaf of the genus *Sorbus*, based on its venation pattern and marginal characteristics.

Material examined: NSM PP-14469 (Fig. 8-C), loc. Kaibutsu.

Family Ulmaceae

Genus *Ulmus* L.

Ulmus sp. cf. *U. davidiana* Planch.

(Fig. 9-C)

A single specimen is characterized by an inequilateral lamina, oblong shape, deeply cordate base, and relatively thick secondaries curving upwards toward the margin. Its teeth are a flexuous-convex shape with basally eccentric principal veins. The intercostal tertiaries are close and oppositely percurrent, and the finer venations are very well developed with quadrangular meshes. These features are readily assignable to the genus *Ulmus* and comparable to *U. davidiana* var. *japonica* Rehder, which is native to Japanese montane forests.

Material examined: NSM PP-14470a (Fig. 9-C), loc. Hokuno.

Genus *Zelkova* Spach

Zelkova sp. cf. *Z. serrata* (Thunb.) Makino

(Fig. 9-E)

A single specimen from the Chujo locality is comparable to *Zelkova serrata*. It has a simple leaf with a serrate margin and large flexuous-convex teeth. Craspedodromous secondaries enter the teeth basally.

Material examined: NSM PP-14472 (Fig. 9-E), loc. Chujo.

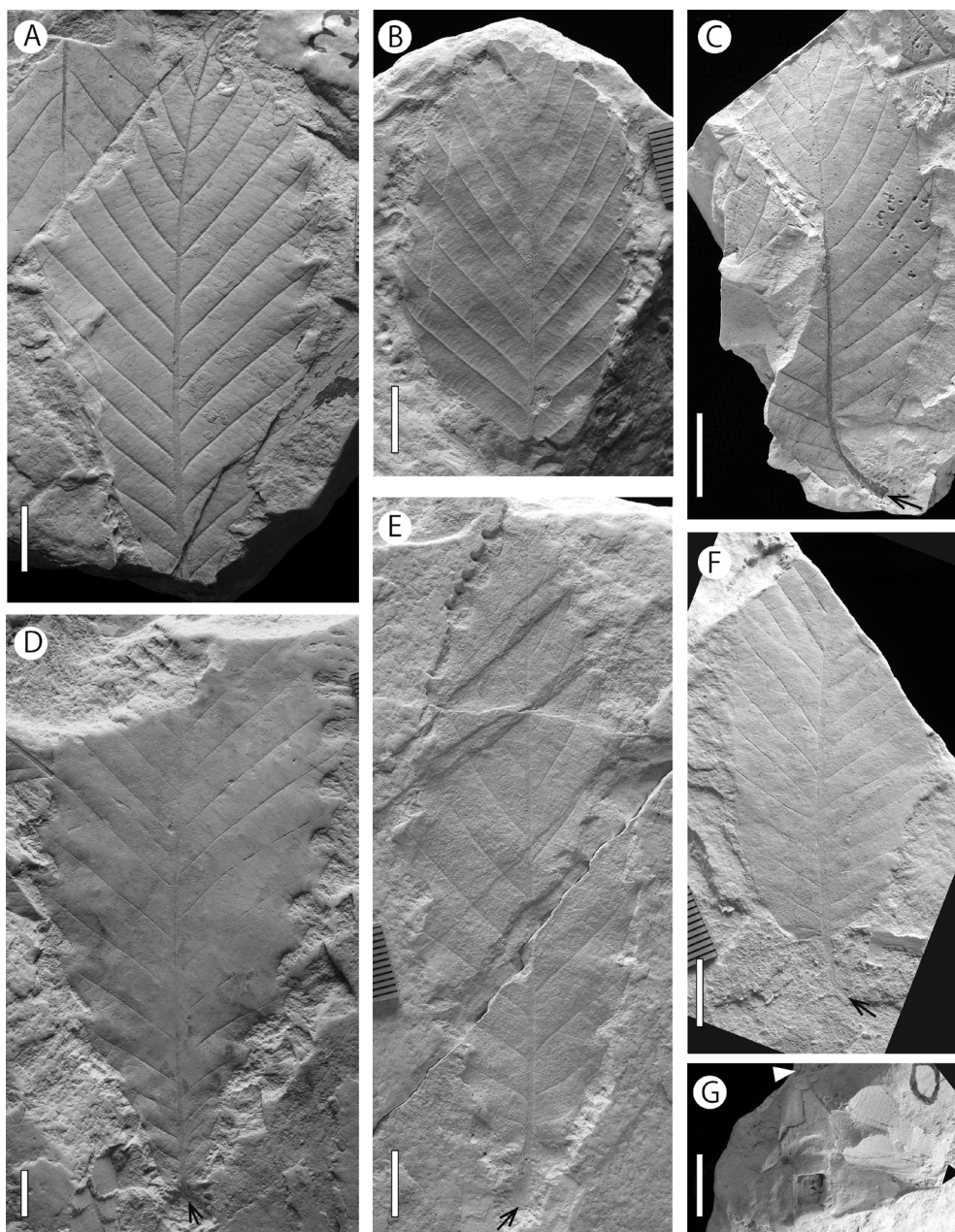


Fig. 7. A–E, *Quercus* sp. cf. *Q. mongolica* Fisch. ex Turcz. A, NSM PP-14450a, loc. Hokuno; B, NSM PP-14453, loc. Atagi; C, NSM PP-14449, loc. Chujo; D, NSM PP-14448, loc. Atagi; E, NSM PP-14452, loc. Atagi. F, *Castanea* sp. cf. *C. crenata* Siebold et Zucc., PP-12233, loc. Atagi. G, *Trapa* sp., NSM PP-14466, loc. Kai-butstu. White and black arrowheads indicate upper and lower horns of *Trapa* fruit, respectively. Bar = 1 cm. Black arrows, end of the petiole.

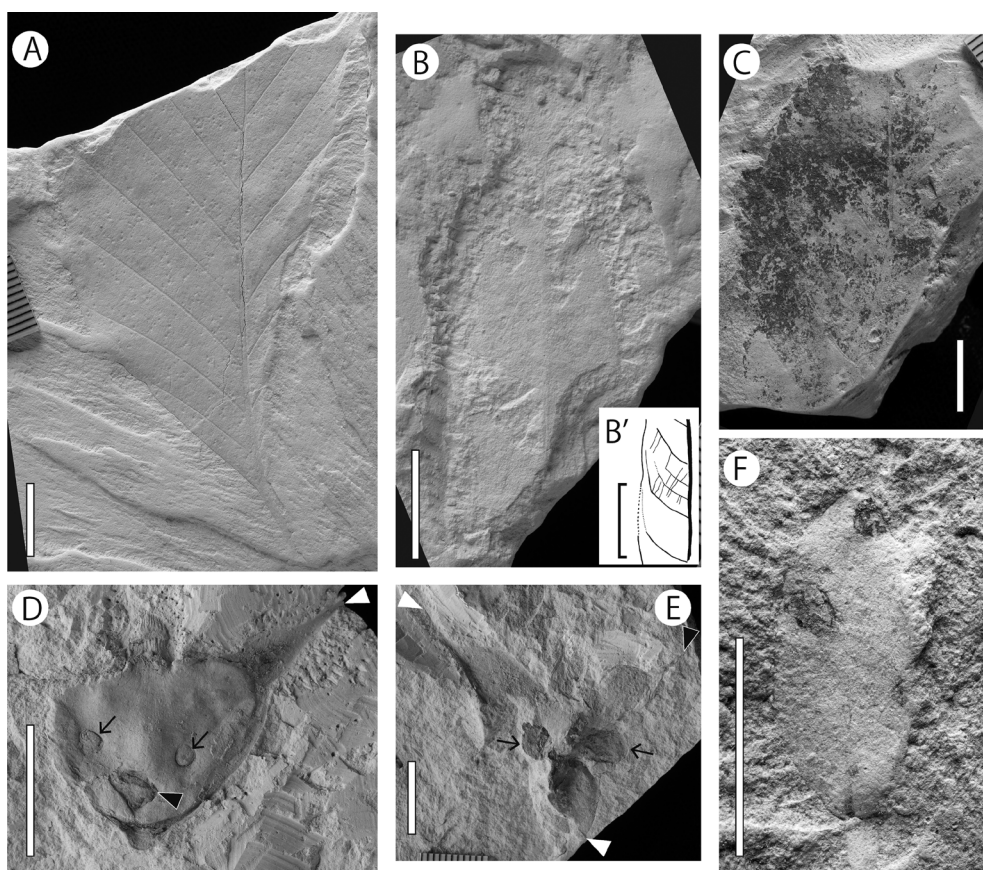


Fig. 8. **A**, *Quercus* sp. cf. *Q. serrata* Murray, NSM PP-14462b, loc. Atagi. **B**, **B'**, *Salix* sp., NSM PP-14420, loc. Atagi. **C**, *Sorbus* sp., NSM PP-14469, loc. Kaibutsu. **D**, **E**, *Trapa mamillifera* Miki, loc. Nishibora. **D**, NSM PP-14463; **E**, NSM PP-14464a. **F**, *Rosa* sp., NSM PP-14468, loc. Nishibora. Scale bar = 1 cm. White arrow-heads, upper *Trapa* fruit horns or their scar. Black arrowheads, lower *Trapa* fruit horns or their scar. Black arrows, tubercles or their scar on fruit surface.

Family Malvaceae

Genus *Tilia* L.

Tilia sp. cf. *T. japonica* (Miq.) Simonk.

(Fig. 9-F, G)

These specimens are comparable to those of *Tilia japonica* in that they have inequilateral laminae with truncate bases, basal actinodromous primary veins, semi-craspedodromous secondary veins, and duplicate serrate margins with blunt tooth apices. The tertiary veins in the intercostal area are straight and oppositely percurrent. Their angles increase exmedially against the central primary vein.

Material examined: NSM PP-14450b, 14483a (Fig. 9-F), loc. Hokuno; PP-14474 (Fig. 9-G), loc. Chujo.

Family Sapindaceae

Genus *Acer* L.

Acer sp. cf. *A. pictum* Thunb.

(Fig. 10-A)

Acer mono Maxim., Matsuo, 1968, p. 51, pl. 6, figs. 1, 4, 5.

Several specimens are characterized by shallowly five- or more-lobed leaves with entire margins. The very thin secondaries form brochido-

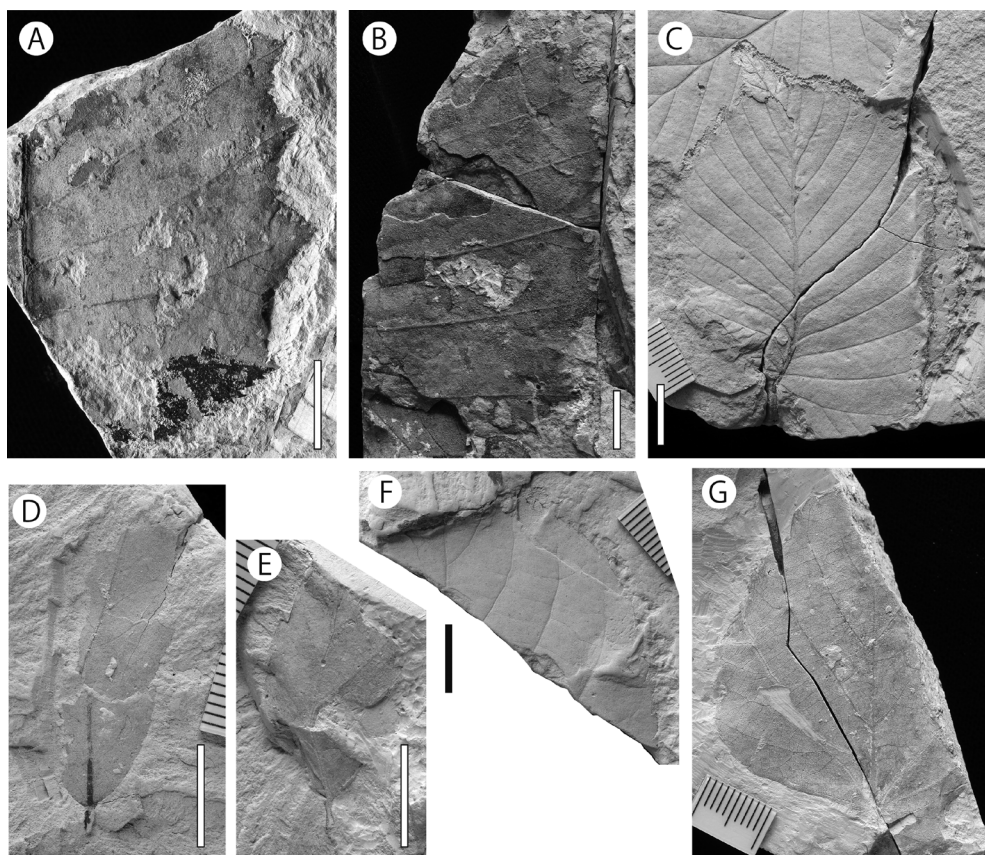


Fig. 9. **A, B**, *Betula* sp. cf. *B. maximowicziana* Regel, loc. Chujo. **A**, NSM PP-14426a; **B**, NSM PP-14427. **C**, *Ulmus* sp. cf. *U. davidiana* Planch., NSM PP-14470a, loc. Hokuno. **D**, *Fraxinus* sp., NSM PP-14464b, loc. Nishibora. **E**, *Zelkova* sp. cf. *Z. serrata* (Thunb.) Makino, NSM PP-14472, loc. Chujo. **F, G**, *Tilia* sp. cf. *T. japonica* (Miq.) Simonk. **F**, NSM PP-14483a, loc. Hokuno; **G**, NSM PP-14474, loc. Chujo. Scale bar = 1 cm.

dromous venation. The finer venation is well developed and forms small quadrangular areoles with simple or no veinlets. These features are assignable to *Acer pictum*.

Material examined: NSM PP-12234 (Fig. 10-A), 14479, loc. Atagi.

Acer sp. cf. *A. pycnanthum* K.Koch
(Fig. 10-B)

The specimen is characterized by a palmately trilobate leaf with actinodromous primaries entering the lobe tips. The secondary veins are craspedodromous and send off branches to the

marginal teeth. The intercostal areas are reticulate. The leaf margin is remotely serrate with acute teeth and fringed with a thin fimbrial vein.

The specimen is incomplete but assignable to the genus *Acer* based on its marginal serration and venation characteristics. It is comparable to *A. pycnanthum* in terms of its shape and presence of a fimbrial vein. This species is sporadically distributed in the wet valley forests of central Honshu.

Material examined: NSM PP-14478 (Fig. 10-B), loc. Kaibutsu.

Acer sp. cf. *A. rufinerve* Siebold *et* Zucc.

(Fig. 10-C)

Acer rufinerve Siebold *et* Zucc., Matsuo, 1968, p. 52, pl. 8, fig. 2.

This species was recorded by Matsuo (1968: p. 52, Pl. 8, Fig. 2). It has three basal actinodromous primaries and marginal double serration. It is further characterized by a long acuminate lobe tip. Only one fragmentary specimen in the collection is comparable to this species in terms of venation pattern.

Material examined: NSM PP-14477 (Fig. 10-C), loc. Atagi.

Genus *Aesculus* L.

Aesculus sp. cf. *A. turbinata* Blume

(Fig. 11-A)

The specimen is characterized by a slightly inequilateral lamina, possibly an obovate shape, and evenly spaced straight secondaries abruptly curving upwards near the margin to form a loop, sending off some branches toward the teeth. The leaf margin is not well preserved. Few branches from the secondary veins indicate the presence of smaller teeth on the basal flank of the larger teeth. These features are comparable with *Aesculus turbinata* Blume, which is distributed throughout the temperate forests of Japan.

Material examined: NSM PP-14480 (Fig. 11-A), loc. Atagi.

Family Hydrangeaceae

Genus *Hydrangea* Gronov.

Hydrangea sp.

(Fig. 11-B, B')

A single specimen from Atagi is characterized by its wide obovate lamina and a possibly acuminate apex. The venation is typical semi-craspedodromous. It has distinct triangular teeth, in which

tertiary veins from the marginal loop enter centrally. These features are characteristic of the genus *Hydrangea*. The specimen resembles leaves of *H. hirta* (Thunb.) Siebold *et* Zucc., but is too large for assignment to this species.

Material examined: NSM PP-14437b (Fig. 11-B), loc. Atagi.

Family Oleaceae

Genus *Fraxinus* L.

Fraxinus sp.

(Figs. 9-D; 11-C-E)

Elaeocarpus japonicus Siebold *et* Zucc., Matsuo, 1968, p. 53, pl. 6, fig. 8

Hydrangea sp.?, Matsuo, 1968, pl. 7, fig. 5.

Two specimens from the Hokuno locality are identical to those from the genus *Fraxinus* L. They are elliptic and have acuminate apices, acute bases, and remotely serrate margins with typically incurved pointed teeth having concave apical and retroflexed basal sides. The secondary veins are pinnate and semi-craspedodromous. They send off tertiary veins to the acute sinuses of the teeth. The tertiary veins in the intercostal area are thin, remotely percurrent, and obtuse to the midvein. The higher venations are finely reticulate. Another specimen from the Nishibora locality shows similar venation and marginal tooth characteristics, and is therefore identified as *Fraxinus* L.

Matsuo (1968) identified one of these specimens (DGLAKZ13735b = NSM PP-14483b) as "*Elaeocarpus japonicus*". Nevertheless, the intercostal tertiary veins of this species are considerably thicker and are nearly perpendicular to the midvein. Furthermore, the meshes of the finer venation of *E. japonicus* are large and its ultimate veinlets are admedially reticulate.

Material examined: PP-14464b (Fig. 9-D), loc. Nishibora; NSM PP-14482 (Fig. 9-C, D), 14483b (Fig. 9-E), loc. Hokuno.

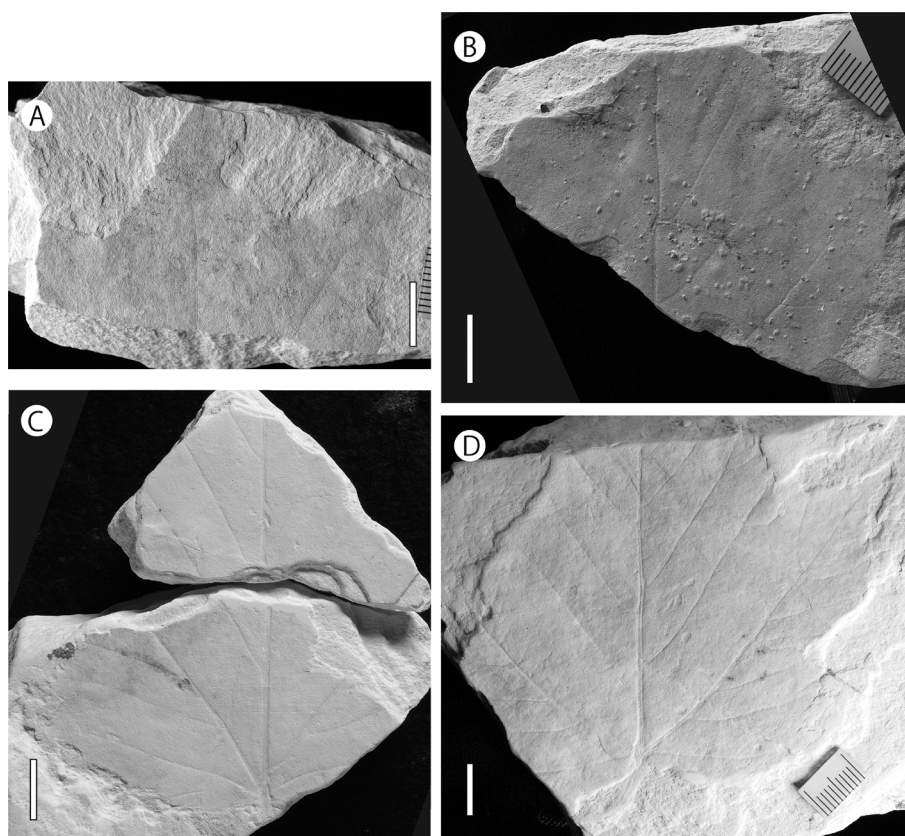


Fig. 10. **A**, *Acer* sp. cf. *A. pictum* Thunb., PP-12234, loc. Atagi. **B**, *Acer* sp. cf. *A. pycnanthum* K.Koch, NSM PP-14478, loc. Kaibutsu. **C**, **D**, *Acer* sp. cf. *A. rufinerve* Siebold *et* Zucc., loc. Atagi. **C**, NSM PP-14477; **D**, DGLAKZ13802 (Kanazawa Univ. specimen). Scale bar = 1 cm long.

Family Caprifoliaceae

Genus *Viburnum* L.

Viburnum sp.

(Fig. 12-A)

A single incomplete specimen is characterized by a shallowly cordate base, irregularly spaced, relatively thick secondaries, and opposite percurrent intercostal tertiaries arranged at obtuse angles to the midvein. The first basal secondary vein divides at least three times to send off thick subsecondaries toward the margin. The next basal secondary divides at least once. The secondary vein pattern is characteristic of this specimen. This feature and the tertiary venation are identical to those of certain *Viburnum* species, such as *V. furcatum* Blume ex Maxim.

Material examined: NSM PP-14484 (Fig. 12-A), loc. Atagi.

Angiospermae *incertae sedis*

Phyllites sp.

(Fig. 12-B, C)

A single microphyllous leaf with an entire margin is characterized by a narrow ovate to elliptic shape, a shallowly cordate base, and a possibly acute apex. Its primary vein is straight and moderately thick. There are at least seven pairs of secondary veins. The basal ones diverge from the base of the lamina. The others are slightly decurrent to the primary and curve up toward the margin. The vein spacing is irregular.

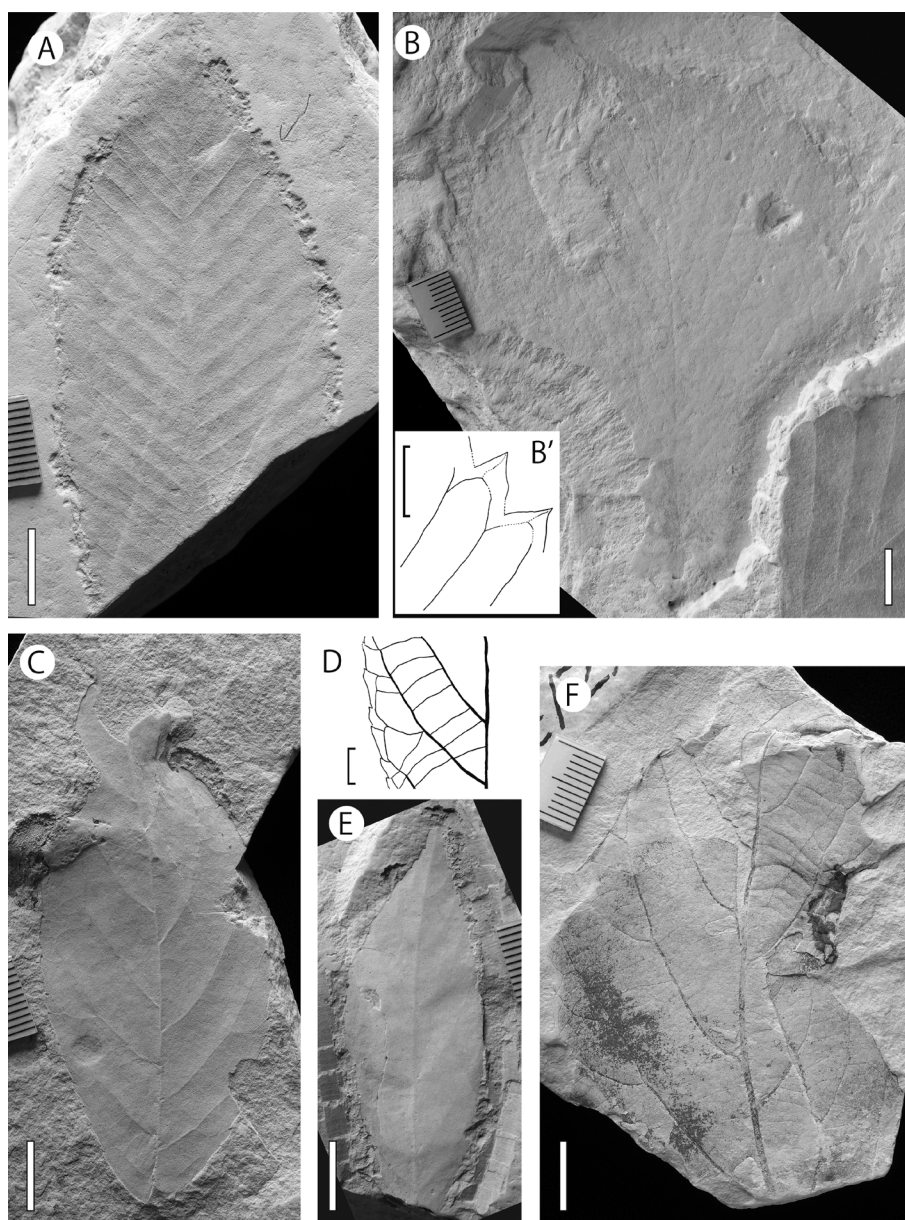


Fig. 11. A, *Aesculus* sp. cf. *A. turbinata* Blume, NSM PP-14480, loc. Atagi. B, B', *Hydrangea* sp., NSM PP-14437b, loc. Atagi. C–E, *Fraxinus* sp., loc. Hokuno. C, D, NSM PP-14482; E, NSM PP-14483b. F, *Populus?* sp., NSM PP-14481, loc. Hokuno. Scale bar = 1 cm.

No tertiary or higher venation patterns were observable.

The stomata on the abaxial cuticle are cyclocytic and randomly arranged. The epidermal walls of the guard cells are 16.6–24.4 μm long and 15.6–16.7 μm wide. The tangential cell walls of the normal cells are typically undulate.

Material examined: NSM PP-14487a (Fig. 12-B, C), loc. Kaibutsu.

Carpolithes sp. 1
(Fig. 12-D)

An isolated spindle-shaped seed, 4.3 mm long

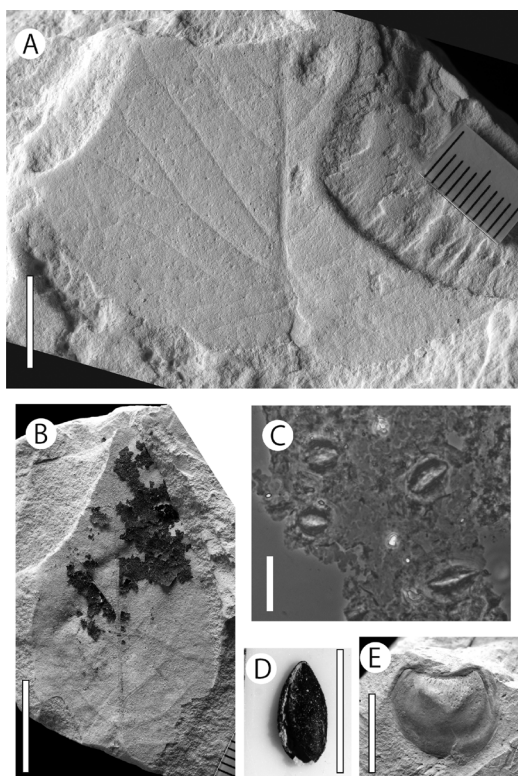


Fig. 12. A, *Viburnum* sp., NSM PP-14484, loc. Atagi. B, C, *Phyllites* sp., NSM PP-14487a, loc. Kaibutsu. C, abaxial epidermis. D, *Carpolithes* sp. 1, NSM PP-14412b, loc. Kaibutsu. E, *Carpolithes* sp. 2, NSM PP-14461, loc. Chujo. Scale bars, A, B, 1 cm; C, 20 μ m; D, E, 5 mm.

and 2.0 mm wide was newly discovered in the Matsuo collection. It occurred along with a number of leaves of *Potamogeton* species found in the Kaibutsu locality. It resembles certain Poaceae seeds but further information is required to confirm its affinity.

Material examined: NSM PP-14412b (Fig. 12-D), loc. Kaibutsu.

Carpolithes sp. 2

(Fig. 12-E)

An isolated compressed globose seed 5.6 mm long and 7.1 mm in diameter is characterized by a smooth surface with small circular dots in the upper portion.

Material examined: NSM PP-14461 (Fig. 12-E), loc. Chujo.

Discussion

Vegetation of the Minoshirotori flora

Among the constituents of the Minoshirotori flora reported here, *Fagus crenata*, *Quercus mongolica* subsp. *crispula*, *Betula grossa*, *B. maximowicziana*, *Carpinus japonica*, *C. laxiflora*, *Tilia japonica*, *Acer pictum*, and *A. rufrinerve* are considered to be components of the *Fagus* zone in this region. *F. japonica* occurs sporadically in this region (Suzuki and Miyawaki, 2001). The species often co-occurs with *F. crenata*, particularly on the lower *Fagus* zone, in the Pacific Ocean side of central and northeast Japan (Suzuki and Miyawaki, 2001; Hara, 2010). According to Hayashi (1960), *Cryptomeria japonica* and *Thujaopsis dolabrata* often coexist with beech species in the wet valley forests of this area. Therefore, the assemblages from Atagi, Hokuno, and Chujo represent those of the *Fagus* zone. In contrast, the Kaibutsu locality is characterized by *Betula* sp. cf. *B. grossa* and *Tilia* sp. cf. *T. japonica*, and does not contain beech species. Other deciduous woody dicots from this site are also distributed within the same altitudinal range (Takahashi, 1962). In addition, Kaibutsu has other species from the wet valley forest (*Cryptomeria japonica*) in the *Fagus* zone of this region and some indigenous species from lacustrine conditions (*Trapa* sp. and *Potamogeton* sp. 1). Therefore, the Kaibutsu locality may represent a lacustrine area fringed by forest with compositions similar to those of the other localities.

None of the localities of the Minoshirotori flora contain evergreen woody dicots from oak-laurel forest. Matsuo (1968) reported *Ficus faveolata* Wall. and *Diospyros kaki* Thunb. from Hokuno, both of which are distributed in considerably warmer conditions than the other identified constituents (Takahashi, 1962). However, on the basis of the pictures presented in his paper (Matsuo, 1968), the presence of these species should be ruled out because of their short, thick

petioles or petiolules. They are most likely fabaceous species. Therefore, the Minoshirotori flora may represent the lower part of the *Fagus* zone, which most closely resembles the modern vegetation around the fossil localities.

Cunninghamia konishii from Kaibutsu is the only locally extinct woody species in this assemblage. It is currently distributed within and limited to the mountain forests of Taiwan at elevations of 1,300–2,000 m under warmer temperate climate conditions (Zheng, 1983). This species has been recorded at the Pliocene–Pleistocene localities in central Japan (Momohara, 2011), and its distribution extended toward Kyushu (Hase, 1988). It often co-occurs with certain warmer climate elements in the allochthonous assemblages of shallow marine conditions (Nirei, 1968). This study indicates for the first time that *C. konishii* tolerated the cooler temperate climate in which the Minoshirotori flora grew.

Age of the Minoshirotori flora

Since the report by Matsuo (1968), the age of the Minoshirotori flora had been accepted as late Pliocene. Subsequently, however, Takahashi and Shimono (1980) proposed a new age assignment for the flora based on palynomorphs from the Atagi Formation in the Washimi area (Fig. 1). They argued that the pollen assemblage of the formation lacked typical Neogene elements, such as *Nyssa*, *Carya*, *Liquidambar*, and *Metasequoia*, while containing an abundance of *Cryptomeria* and *Fagus*. Therefore, they compared the assemblage to that of the “*Fagus* phytozone.” This phytozonation occurred after the extinction of *Metasequoia* in the upper part of the Osaka Group (Tai, 1973). This Osaka Group criterion was, however, established based on fossil records from the lowland and/or shallow marine conditions in central Japan. Therefore, the timings of the flourishing and recession of key taxa may differ from those for an inland basin like Minoshirotori.

With the exception of *Cunninghamia konishii* and *Trapa mamillifera*, nearly all components of the Minoshirotori flora are comparable to

those of the modern *Fagus* zone and resemble those surrounding the fossil sites. In addition, certain *Trapa mamillifera* localities are assigned to the lower Pleistocene. Therefore, the age of this flora is probably closer to that of the overlying volcanic rocks, which are approximately 1.2 Ma (Tanase *et al.*, 2007).

In the Osaka Group of the Kinki area, *Cunninghamia* species often co-occur with *Metasequoia glyptostroboides* and the latter species became extinct by approximately 1.0 Ma (Momohara, 2005). This difference in survival is likely attributable to differences in the ecological requirements of these two locally extinct species. Namely, *Metasequoia* might have disappeared earlier in an inland hilly region like Minoshirotori, whereas *Cunninghamia* could have inhabited an area characterized by such conditions.

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