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PLANT MEGAFOSSIL ASSEMBLAGE FROM THE LOWER MIOCENE ITO-O FORMATION, FUKUI PREFECTURE, CENTRAL JAPAN

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ABSTRACT

The plant megafossil assemblage of the Early Miocene Ito-o Formation in Fukui Prefecture, Central Japan was first described based on reexamination of the materials used in its original introduction, as well as those collected after that report. The plant megafossils came from lacustrine deposits and consist of 23 genera and 35 species principally represented by riparian or lakeside elements inhabited near the site of deposition. The assemblage is composed exclusively of deciduous angiosperms with two evergreen conifers and a horsetail, most of which are common to the Daijima-type flora (late Early to early Middle Miocene) of Northeast Honshu and Hokkaido. From the absence of evergreen angiosperms as well as a common occurrence of deciduous oak, *Quercus miovariabilis*, it is comparable to the modern Mixed Broad-leaved Deciduous Forest of East Asia which develops under a condition with a mean annual temperature of 10 ℃ or higher. The flora was newly dated to 21.1 ± 0.8 Ma based on the ^{40}Ar-^{39}Ar method for the intercalated andesitic lava between the two plant-bearing strata. The age is concordant to the first appearance of the species common in the Daijima-type flora in the Early Miocene floras on the Pacific side of Japan. Judging from its age as well as its composition, the Ito-o flora was regarded as a transition during the interval between the earliest Miocene Aniai-type and the late Early Miocene Daijima-type flora, and represents a period of climate warming that occurred during that interval.

Key words: Ito-o Flora, Early Miocene, Mixed Broad-leaved Deciduous Forest, Daijima-type flora, Aniai-type flora, Central Japan

矢部　淳（2008）福井県の下部中新統糸生層から産出した大型植物化石群集．福井県立恐竜博物館紀要 7：1-24.

福井県福井市に分布する下部中新統糸生層上部の，いわゆる“糸生湖成層”から産出する植物化石について，最初の報告に用いられた標本とその後採集された標本を再検討し，それらの分類学的記載を行うとともに，その組成的な特徴や同時代の植物化石群集との類似性を考察した.

２つの産地から得られた化石群集は，河川の影響のある湖の堆積物中に含まれており，河畔や堆積場付近の低地に生育したと考えられる種類が優占する．落葉広葉樹を主体に２種の常緑針葉樹と１種のトクサを含み，常緑広葉樹は含まれない．これらの特徴に加え，コナラ類の産出数が比較的多いことから，全縁葉率は低いものの，本群集は現在の東アジアに広がる落葉広葉樹混交林（Mixed Broad-leaved Deciduous Forest）に近い植生を代表するものと考えられる．

認識された 23 属 35 種のうち，24 種は前期中新世後期から中期中新世初期の台島型植物群に共通な要素で，最初期中新世の阿仁合型植物群との共通種は 14 種，このうち後者に産出が限られるものは１種のみであり，明らかに台島型植物群との共通性が高い．一方，２つの植物化石産出層準に挟まれた安山岩質溶岩の ^{40}Ar-^{39}Ar 年代は 21.1 ± 0.8 Ma となった．この年代は，太平洋側の常磐地域で台島型植物群の特徴種が初めて認められる時期によく一致する．以上のことから，糸生層の植物化石群集は，阿仁合型から台島型植物群への移行期のものであり，当時はじまった気候の温暖化を反映した群集と結論づけられる．

INTRODUCTION

Two different types of floras, termed the Aniai-type and Daijima-type floras, have been recognized in East Asia during the Early Miocene (Huzioka, 1949; Tanai, 1961, 1991, 1992). The Aniai-type flora of earliest Miocene age is characterized by various species of deciduous woody dicotyledons and deciduous and evergreen conifers, while the Daijima-type flora, ranging from late Early to early Middle Miocene, consists of a mixture of deciduous and evergreen woody dicotyledons with conifers that are closely related to those inhabited in present-day warm temperate forests (Huzioka, 1963b). These two types of floras are not defined by a presence of any single index species, but by floristic composition and physiognomy that reflects the climate

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condition which prevailed during that period (Huzioka and Uemura, 1979; Tanai, 1991). Latitudinal and altitudinal changes in floristic composition also have been recognized (Tanai and Suzuki, 1963; Tanai, 1967; Tanai and Uemura, 1988).

Floral change during the interval between the Aniai-type and the Daijima-type floras was not well understood until now because the strata that bear both of the floras are generally bounded by regional unconformity (Uemura, 1989; Kano et al., 2002). Kano and Yanagisawa (1989) suggested the relationship between the floral change and the global marine climate indicated by the oxygen isotope data, based on compiled radiometric ages of the formations that bear both the floras. However, not so many floras are well constrained by reliable radiometric ages (Uemura, 1989). Further, several floras they used in their discussion have not been described or illustrated, so the floral data itself cannot be verified in some cases (Yabe et al., 1995).

Problems also arose from the general lack of the Aniai-type flora in Southwest Japan. According to Uemura (1989) and Uemura (2001), the Aniai-type flora in Southwest Japan is represented by the following four floras: namely, the Soyama-toge (Fuji and Yoshida, 1984), Hiyoshi (Tanai, 1961; Huzioka, 1964), Ito-o (Azuma and Furuichi, 1976), and Yosa floras (Onoe, 1978). Most of them, except for the Hiyoshi Flora, have not been described systematically.

The plant megafossil assemblage of the Ito-o Formation in Fukui Prefecture, Central Japan, referred to here as the Ito-o Flora, was initially introduced by Azuma and Furuichi (1976) as of the Aniai-type flora. It was subsequently dated ca. 16 Ma, based on several fission track (Hirooka et al., 1972; Nakajima et al., 1983) and K-Ar ages of the formation (Nakajima et al., 1990). Kano and Yanagisawa (1989) regarded the Ito-o Flora as of a cooler climate interval that occurred during the time of Daijima-type flora because the age of the Ito-o Flora is as young as those of the Daijima-type flora, rather than the Aniai-type flora.

In spite of its importance in discussing the floral change and climate history during the Early Miocene, no attempts have been made to describe the Ito-o Flora systematically. In this article, the author reexamines and describes the specimens used by Azuma and Furuichi (1976) and those collected after their report (Fig. 1). Based on its composition, together with a new radiometric age of the Ito-o Flora using the ^{40}Ar-^{39}Ar method, the author suggests a transitional age and composition of the flora between the Aniai-type and Daijima-type floras, instead of a short-time climate cooling during the time of the Daijima-type flora.

GEOLOGIC OUTLINE

Neogene deposits are well exposed along the coastline of the Sea of Japan in Fukui Prefecture, Central Japan (Tsukano and Miura, 1954). They are divided, in ascending order, into the Nishitani Ryolites, the Ito-o (It-ow in Kano et al., 2007), Kunimi and Aratani formations, and the Ichinose Ryolites and the Kunimidake Volcanic Rocks (Kano et al., 2007). Plant megafossils are included in two different stratigraphic levels, namely the Ito-o and Kunimi formations. Those from the Kunimi Formation have been studied by several authors (Huzioka, 1955; Matsuo, 1956, 1975; Uemura and Yasuno, 2001),

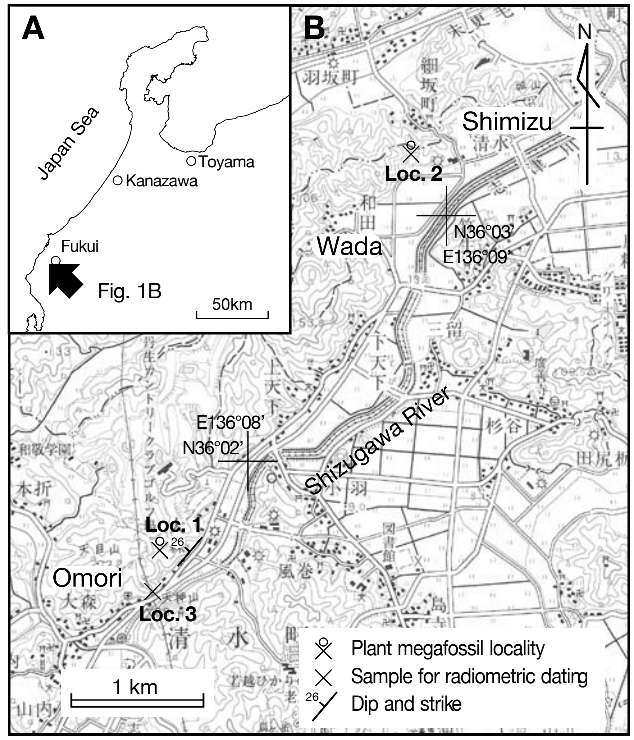

FIGURE 1. Index map of the plant megafossil locality of the Ito-o Formation. The location of a sample for ^{40}Ar-^{39}Ar analysis is also shown. Map is from 1:50,000 topographic map "Fukui" published by Geographic Survey Institute of Japan.

and are composed of a mixture of evergreen and deciduous woody dicotyledons, most of which are common to the Daijima-type Flora. Yamanoi (1992) reported pollen flora equivalent to his NP-2 assemblage and recognized an occurrence of mangrove pollen fossils from the formation. The plant megafossils from the Ito-o Formation were initially introduced by Azuma and Furuichi (1976). In contrast to the assemblage from the Kunimi Formation, the Ito-o Flora is dominated by deciduous woody dicotyledons belonging to the families of Betulaceae, Ulmaceae and Juglandaceae and it was compared with the Aniai-type flora (Azuma and Furuichi, 1976; Uemura, 1989).

The Ito-o Formation unconformably overlies the Nishitani Ryolites dated to about 22 to 27 Ma (Nakajima et al., 1983; Kano et al., 2007). The Ito-o Formation comprises terrestrial deposits consisting of basic to intermediate volcanic rocks and related clastic deposits. It is unconformably overlain by fluvial deposits of the Kunimi Formation in the western part of its distribution, while in the eastern part, it is conformably overlain by shallow-marine deposits of the same formation (Yasuno, 1979, stratigraphy is after Kano et al., 2007), which is dated to 18 to 16 Ma (Kano et al., 2007).

Megafossil evidences of the formation mainly come from fluvial and lacustrine deposits in the upper part, which is called "the Ito-o lake deposits." It yields insects (Yasuno, 1989, 1990) and fresh-water fishes (Yasuno, 1988), as well as plant megafossils (Azuma and Furuichi, 1976). Koizumi (1988) also reported an occurrence of fresh-water diatoms from the deposits.

The depositional age of the Ito-o Formation has been regarded

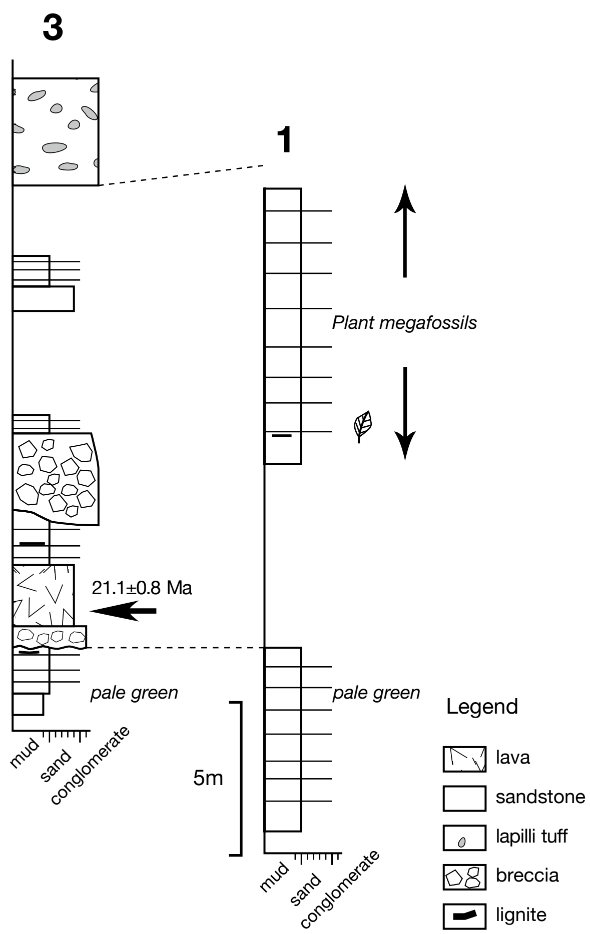

FIGURE 2. Stratigraphic columnar section at Locs. 1 and 3, showing stratigraphic levels of a sample for ^{40}Ar-^{39}Ar analysis and possible plant megafossil horizons. Two columnar sections are correlated with each other, based on the greenish mudstone at the base of each locality and the absence of lapilli tuff at the top of the Loc. 1. A leaf mark points the plant megafossil horizon collected by the author.

as 19 to 16 Ma, based on both the fission track (Hirooka et al., 1972; Nakajima et al., 1983) and K-Ar ages (whole rock, Nakajima et al., 1990). However, these ages appear young as compared with those of the overlying formations, which are more rigidly constrained by its biostratigraphy (Matsumaru et al., 1979; Nakagawa and Tahara, 1991). According to Nakajima et al. (1990), the materials used in their study for K-Ar analysis (Stage III) are slightly altered, so that the whole rock ages should be treated as minimum ones for these deposits. On the other hand, the fission track ages examined by Hirooka et al. (1972) and Nakajima et al. (1983), before the advice of I.U.G.S. (Hurford, 1990), should be treated as reference data (Nakajima et al., 1990). Very recently, Kano et al. (2007) reported two new fission track ages from the Ito-o Formation: 18.7 ± 0.4 Ma from the andesitic welled tuff near the middle of the formation; and 20.2 ± 1.3 Ma from dacitic lapilli tuff at the top. From these ages, they concluded the formation as being 18 to 20 Ma.

In the present study, the author analyzed a new ^{40}Ar-^{39}Ar age as being 21.1 ± 0.8 Ma (weighted mean plateau age) for the whole rock sample of andesitic lava that intercalates closely to the plant-bearing deposit at the upper part of the formation (Fig. 2). The age is concordant not only to the ones obtained from both the Nishitani Rhyolites and the Kunimi Formation, but also to the new fission track age obtained from the top of the formation.

MATERIALS

The materials used in this study are collections stored at the Fukui City Museum of Natural History (FCMNH) and the Fukui Prefectural Dinosaur Museum (FPDM). Parts of the collections were used by Azuma and Furuichi (1976). These collections also contain specimens collected by staff of each museum including the author, and some were collected and donated by others.

All the materials come from two localities at the upper part of the Ito-o Formation. The main locality, Demura (Loc. 1), located 9 km southwest of Fukui City, is equivalent to the one reported by Azuma and Furuichi (1976). Insects and fresh-water fishes (Yasuno, 1988, 1989, 1990), as well as fresh-water diatoms (Koizumi, 1988), have been reported from the locality. Although the exact stratigraphic horizons of each collection are not known in most cases, plant megafossils are found in white to buff-colored, finely laminated tuffaceous mudstones that are frequently intercalated with fine to coarse sandstone and rare intercalations of lignites. This facies attains less than 10 m in maximum thickness at Loc. 1 and extends laterally toward Loc. 3, where thin andesitic lava and volcanic breccia were intercalated (Fig. 2). Since there is no distinct difference in the composition of each collection, the author provisionally treated them as a single assemblage.

Most specimens in this locality are detached leaf remains preserved in mudstone or sandy mudstone in a flat-lying manner. Only some zelkova leaves are attached to their branches. They are not so well preserved but sometimes yield fine venation characters.

Loc. 2, located ca. 2 km northeast of Loc. 1, is an additional locality discovered by Dr. Y. Azuma and his colleagues approximately 30 years ago. According to Kano et al. (2007), this locality situates the northern wing of a syncline trending WNW to ESE, and stratigraphically lower than Loc. 1. Plant megafossils of the locality have been collected from white, laminated mudstone. All the specimens but nuts of *Hemitrapa* are concentrated in a relatively fine part, with leaves and leafy structures preserved in a weakly curled condition. *Hemitrapa* nuts are preserved in parallel to the bedding plain. They are not usually preserved with identical leaf remains, but with abundant fragments of leaves. These conditions might be attributed to the transportation of leaf remains and the autochthonous nature of the nuts of *Hemitrapa*.

FLORAL COMPOSITION

Plant megafossils from the two localities at slightly different stratigraphic levels are quite similar to each other in composition, although there is some difference probably caused by the difference of depositional environment and sedimentary processes (Table 1). The author treated them here as representative of the Ito-o Flora.

The Ito-o Flora comprises 23 genera and 35 species known from leaves and reproductive structures (Table 2). Of these,

TABLE 1. List and numerical representation of plant megafossils from the Ito-o Formation. Represented organs are also shown: f, fruit; l, leaf; s, seed.

Species	organ	Locality 1	Locality 2
Equisetum sp.	stem	1	
Keteleeria ezoana Tanai	l&s		7
Pseudolarix japonica Tanai	s	1	
Picea kaneharai Tanai et Onoe	s		1
Monocotylophyllum sp.	l	1	
Parrotia pristina (Ettingshausen) Stur	l		3
Hemitrapa yokoyamae (Nathorst) Miki	f		28
Gleditsia miosinensis Hu et Chaney	l	4	3
Wisteria fallax (Nathorst) Tanai et Onoe	l	1	3
Fabaceae gen. et sp. indet.	l		4
Alnus miojaponica Tanai	l	4	
Betula mioluminifera Hu et Chaney	l	4	1
Betula oobae Suzuki	l	6	3
Betula uzenensis Tanai	l	2	2
Carpinus heigunensis Huzioka	l&f	2	
Carpinus subcordata Nathorst	l	1	1
Carpinus sp. sect. *Distegocarpus* (S. et Z.) Sargent	f	2	1
Betulaceae gen. et sp. indet.	f	1	
Fagus antipofi Heer	l	1	2
Fagus sp.	f		1
Quercus miovariabilis Hu et Chaney	l		14
Juglans miochinensis (Tanai et Onoe) Suzuki	l	1	1
Pterocarya japonia (Tanai) Uemura	l	6	4
Pterocarya protostenoptera Tanai	l&f	28	1
Populus sp.	l	1	
Ulmus carpinoides Goeppert	l	26	3
Ulmus longifolia Unger	l	3	
Zelkova ungeri (Ettingshausen) Kovats	l	71	2
Rhus sp.	l	1	2
Acer palaeorufinerve Tanai et Onoe	l	2	
Acer protojaponicum Tanai et Onoe	l	1	
Acer nordenskioeldi Nathorst	l&f	2	1
Acer rotundatum Huzioka	l	3	
Styrax protojaponica Tanai	l	1	
Stewartia sp. cf. *S. submonadelpha* Tanai et Onoe	l	2	
23 genera and 33 species*		179	88

*excluding Betulaceae & Fabaceae gen. et sp. indet.

TABLE 2. Composition of the Ito-o Flora.

Division Pteridophyta
- Family Equisetaceae
  - *Equisetum* sp.

Division Gymnospermophyta
- Family Pinaceae
  - *Keteleeria ezoana* Tanai
  - *Pseudolarix japonica* Tanai et Onoe
  - *Picea kaneharai* Tanai et Onoe

Division Magnoliophyta
- Family uncertain
  - *Monocotylophyllum* sp.
- Family Hamamelidaceae
  - *Parrotia pristina* (Ettingshausen) Stur
- Family Lythraceae
  - *Hemitrapa yokoyamae* (Nathorst) Miki
- Family Fabaceae
  - *Gleditsia miosinensis* Hu et Chaney
  - *Wisteria fallax* (Nathorst) Tanai et Onoe
  - Fabaceae gen. et sp. indet.
- Family Betulaceae
  - *Alnus miojaponica* Tanai
  - *Betula mioluminifera* Hu et Chaney
  - *Betula oobae* Suzuki
  - *Betula uzenensis* Tanai
  - *Carpinus heigunensis* Huzioka
  - *Carpinus subcordata* Nathorst
  - *Carpinus* sp. sect. *Distegocarpus* (Sieb. et Zucc.) Sargent
  - Betulaceae gen. et sp. indet.
- Family Fagaceae
  - *Fagus antipofi* Heer
  - *Fagus* sp.
  - *Quercus miovariabilis* Hu et Chaney
- Family Juglandaceae
  - *Juglans miochinensis* (Tanai et Onoe) Suzuki
  - *Pterocarya japonia* (Tanai) Uemura
  - *Pterocarya protostenoptera* Tanai
- Family Salicaceae
  - *Populus* sp.
- Family Ulmaceae
  - *Ulmus carpinoides* Goeppert
  - *Ulmus longifolia* Unger
  - *Zelkova ungeri* (Ettingshausen) Kovats
- Family Anacardiaceae
  - *Rhus* sp.
- Family Sapindaceae
  - *Acer palaeorufinerve* Tanai et Onoe
  - *Acer protojaponicum* Tanai et Onoe
  - *Acer nordenskioeldi* Nathorst
  - *Acer rotundatum* Huzioka
- Family Styracaceae
  - *Styrax protojaponica* Tanai
- Family Theaceae
  - *Stewartia* sp. cf. *S. submonadelpha* Tanai et Onoe

one taxon represented by a monocotyledonous leaf remains unidentified and is treated as incertae sedis. The most diversified element in this assemblage is Betulaceae represented by eight species, followed by Sapindaceae with four species. Pinaceae, Juglandaceae, Fagaceae, Ulmaceae, and Fabaceae are also large families and comprise three species each. Regarding the number of occurrences, the dominant species are different in each site (Table 1). In Loc. 1, the most dominant are *Zelkova ungeri* and *Pterocarya protostenoptera*, followed by *Ulmus carpinoides*. The dominant species in Loc. 2 are *Hemitrapa yokoyamae*, *Quercus miovariabilis*, and *Keteleeria ezoana*. All the dicotyledons in the assemblage are assumed to be deciduous in probable abscission habit, judging from their modern equivalents as well as their leaf and vein thickness. Among 26 species of arboreal angiosperm leaves, only three yield a smooth margin (11.5%).

Most species in the assemblage are represented by single organ (Table 1), while *Keteleeria ezoana, Carpinus heigunensis, Pterocarya protostenoptera,* and *Acer nordenskioeldi* are represented by both the leaves and fruiting structures. The genera *Carpinus and Fagus* also yield both organs.

DISCUSSION

Vegetation and climatic conditions

From the lithofacies of plant-bearing strata in association with fossil occurrence (e.g., water plant), the Ito-o Flora was assumed to have been deposited under a lake environment affected by river activities. The lake was probably located near the coastal lowland because these deposits are subsequently affected by marine influences.

The most dominant elements in Loc. 1, such as *Zelkova, Ulmus*

TABLE 3. Occurrence of Ito-o species in the three types of Miocene floras in Japan. Floral data are based on the following papers: Aniai-type flora, Huzioka (1964); Daijima-type flora, Huzioka (1963a), Tanai and Suzuki (1963), Ishida (1970), Onoe (1974), Horiuchi and Takimoto (2001); Mitoku-type flora, Uemura (1988).

Floral types / Ito-o species	Aniai-type flora	Daijima-type flora	Mitoku-type flora
Keteleeria ezoana		+	(+)
Pseudolarix japonica	+	+	(+)
Picea kaneharai	(+)	+	+
Parrotia pristina		+	+
Hemitrapa yokoyamae		+	
Gleditsia miosinensis		+	+
Wisteria fallax	+	+	+
Alnus miojaponica	+	+	+
Betula mioluminifera	+	(+)	
Betula oobae		(+)	
Betula uzenensis	+	+	
Carpinus heigunensis	+	+	+
Carpinus subcordata	+	+	+
Fagus antipofi	+	+	
Quercus miovariabilis		+	
Juglans miochinensis	+		
Pterocarya japonica	(+)	(+)	+
Pterocarya protostenoptera		+	+
Ulmus carpinoides		+	
Ulmus longifolia		+	
Zelkova ungeri	+	+	+
Acer palaeorufinerve		+	
Acer protojaponicum	+	+	+
Acer nordenskioeldi		(+)	+
Acer rotundatum	+		+
Styrax protojaponica		(+)	
Number of common species	14	24	15
(%)	(53.8)	(92.3)	(57.7)

+: present, (+): present in the floras other than those mentioned above

and *Pterocarya*, are regarded as riparian or lakeside elements from the ecology of living relatives. Occurrence of these species, especially the attached zelkova leaves and co-occurrence of different organs of *Pterocarya*, also supports the closeness of their habitat area and the site of deposition. Co-occurrence of a few different organs in the other species or genera, such as *Fagus, Carpinus* and *Acer*, also implies proximity of their habitat area. Among the Ito-o species, not all, but some of the species of genus *Betula* can be derived from the vegetation at higher elevations, judging from the habitat of their modern relatives. However, all of these species occur in various collections from the same and different localities, and they co-occur with the other species probably inhabited in lowland vegetation. Thus, it is likely that the Ito-o species comprise lowland vegetation developed in coastal lowlands during that period.

All the Ito-o species, except for three evergreen conifers and one horsetail, are deciduous in the probable abscission habit, based on their living relatives and their state of preservation. Although more specimens are necessary to understand the vegetation of that period, the materials at hand strongly suggest a presence of a deciduous forest under a temperate climate regime. Taking into account the common occurrence of deciduous oak, *Quercus miovariabilis*, as well as the presence of deciduous woody dicotyledons not represented in the Mixed Northern Hardwood Forest, such as *Gleditsia*, the Ito-o Flora can be compared with the Mixed Broad-leaved Deciduous Forest in East Asia (Wolfe, 1979), which is characterized by an absence of evergreen trees and an abundance of deciduous oaks. The percentage of woody dicotyledons with an entire leaf margin as the Ito-o Flora is distinctly low (11.5%) as compared with that of the Mixed Broad-leaved Deciduous Forest (27 to 33%: Wolfe, 1979). The low percentage of entire-margined species is probably ascribed to the feature of the Ito-o Flora with an abundant association of riparian vegetation. As pointed out by Burnham et al. (2001) and Kowalski and Dilcher (2003), riparian and wetland vegetation often yield higher percentage of species with toothed leaves. According to Wolfe (1979), the Mixed Broad-leaved Deciduous Forest usually develops under conditions with a mean annual temperature of 10 ℃ or higher. In terms of the size of dicotyledonous leaves, most Ito-o species belong to the notophyll size class, indicating a relatively wet condition similar to the present-day fossil site.

Comparison with the Early Miocene floras in Central Japan

Azuma and Furuichi (1976) compared the Ito-o Flora with the Aniai-type flora because of its abundant bearing of deciduous woody dicotyledons. Re-examination of the Ito-o Flora clearly shows a presence of species that is common to or restricted to within the Daijima-type flora (Table 3). Similarity of species composition between the Ito-o and three types of Miocene floras of Japan is distinctly high in the Daijima-type flora. The Ito-o Flora also contains some species common to the Aniai-type flora and one species, *Juglans miochinensis*, is restricted in its occurrence. However, the presence of this species is also accountable for by its wide range of ecological tolerance or long distance transport.

Many Miocene floras comparable to the Daijima-type flora have been reported in Central Japan: Kunimi Flora from the Kunimi Formation that unconformably overlies the Ito-o Formation (Huzioka, 1955; Uemura and Yasuno, 2001), Notonakajima and Noroshi floras of Noto Peninsula (Ishida, 1970; Matsuo, 1963) and Inkyoyama Flora of the Mizunami Group (Ozaki, 1974). These floras include various species of evergreen woody dicotyledons belonging to Fagaceae, Lauraceae, Theaceae, etc., and are distinct from that of the Ito-o Flora described herein. Furthermore, the Ito-o Flora does not contain *Liquidambar miosinica* (Hamamelidaceae) and *Comptonia naumanni* (Myricaceae), both of which are deciduous woody dicotyledons common in the Daijima-type flora of Honshu and Hokkaido (Huzioka and Uemura, 1979; Tanai and Uemura, 1988). Thus, the Ito-o Flora cannot be readily comparable to the Daijima-type flora in floral characters.

There is still a controversy on the age of the boundary between the Aniai-type and Daijima-type floras: 22 Ma (Kano and Yanagisawa, 1989), 18-19Ma (Uemura, 1989; Yabe et al., 1995), 17.5 Ma (Suzuki, 1989). Very recently, Yabe (2007) proposed an Early Miocene floral changes in the Joban and Soma areas in Pacific side of Northeast Honshu. Based on the biostratigraphy of intercalated marine deposits and several radiometric dates, he concluded that the Daijima-type floral elements appeared from 21 Ma and increased in their occurrence as the temperature arose. The new ^{40}Ar-^{39}Ar age of ca. 21 Ma for the Ito-o Flora is concordant to that sequence.

In terms of the absence of evergreen woody dicotyledons with some species common to the Daijima-type flora, such as *Keteleeria ezoana, Parrotia pristina, Quercus miovariabilis* and *Ulmus longifolia*, the Ito-o Flora is quite similar to the Yosa Flora from the Seya Formation in Kyoto Prefecture (Onoe, 1978). Tokunaga and Onoe (1960) and Onoe (1978) considered that the Yosa Flora represented a transition during the interval between the Aniai-type and the Daijima-type floras. On the contrary, Uemura (1989) regarded the Yosa Flora to be the Aniai-type Flora located in southerly areas. The result of the present study indicates a transitional age for the Ito-o Flora between the Aniai-type and the Daijima-type floras, which probably were affected by climate warming occurred during that interval (Yabe, 2007). However, it is not denied that there was an influence of latitudinal change in floral composition. Further study is necessary on the age and composition of the Yosa Flora to understand the geographic distribution of vegetation similar to the Ito-o Flora.

CONCLUSIONS

1) A new ^{40}Ar-^{39}Ar age indicates the age of the Ito-o Flora as being ca. 21 Ma.
2) The Ito-o Flora comprises 35 species of deciduous angiosperms, evergreen conifers and a horsetail. Its composition as well as physiognomy is equivalent to the Mixed Broad-leaved Deciduous Forest that develops under a condition of MAT of 10 ℃ or higher.
3) The Ito-o Flora is more similar to the Daijima-type flora rather than the Aniai-type and probably represents a transition between both the floras in relation to a warming of the climate, which occurred during that interval.

SYSTEMATIC DESCRIPTIONS

Systematic descriptions are given for most of 35 taxa dealt with in the study. Terminology used in the descriptions of leaves or leafy structures mainly follows Hickey (1979) and the Leaf Architecture Working Group (1999). Those descriptions for the reproductive structures are based on general usage for each taxon. Taxonomic arrangement of gymnosperms adapted in this study follows Kramer and Green (1990). That for angiosperms follows the classification system of The Angiosperm Phylogeny Group (2003), which is a currently widely accepted system based on molecular study of the modern species. Abbreviations used for the depository are as follows: FPDM, Fukui Prefectural Dinosaur Museum; FCMNH-G and FCMNH-GF, Fukui City Museum of Natural History.

Order EQUISETALES Dumortier, 1829
Family EQUISETACEAE De Candolle, 1805
Genus *EQUISETUM* Linnaeus, 1753
Equisetum sp.
(Fig. 3-1c)

Discussion.—The specimen was identified as an aerial stem of *Equisetum* in its linear stem marked by three smooth keels on its surface and the presence of nodes at distances of 5.0 to 14 mm. Sheathes are not preserved, probably due to insufficient preservation.

Material.—FPDM-P-539-3 (Loc. 1).

Order PINALES Dumortier, 1829
Family PINACEAE Lindley, 1836a
Genus *KETELEERIA* Carrière, 1866
Keteleeria ezoana Tanai, 1961
(Fig. 3-5, 6, 7, 8)

Keteleeria ezoana Tanai, 1961, p. 251, pl. 1, figs. 16, 40, 41.

Description.—Winged-seed asymmetrical triangular in shape; 32.5 mm long (estimated), 11.4 mm wide (estimated); both the proximal and distal end bluntly pointed; admedial edge straight, abmedial edge curved and rounded. Seed asymmetrical triangular shape, length estimated 17 mm, width 6.2 mm. Seed wing thin, asymmetrical, attached obliquely to the upper half of the seed; 24.5 mm long, 12.0 mm wide. Leaf slightly asymmetrical, flattened, lorate in shape; 1.4 to 22.3 mm long and ca. 1.6 to 2.3 mm wide; apex rounded; base slightly convex; petiole expanded with a circular object; midrib prominent, projects beyond either surfaces; a pair of vascular bundles follows closely to the margin; margin entire, slightly revolute.

Discussion.—One detached seed was assigned to *Keteleeria ezoana* described as from the late Early Miocene Yoshioka Formation of southwestern Hokkaido (Tanai, 1961) in general characters described above. The winged-seed of *Keteleeria* resembles that of the genus *Pseudolarix*, however, it is distinguished in shape of the seed part as being triangular rather than round or obovate as in *Pseudolarix* (LePage and Basinger, 1995). The relative length of seed-wing against seed-body is also a distinct character for each genus (Wolfe and Schorn, 1990). The ratio for the present material (1.44) falls well into the range of *Keteleeria* (1.25 to 1.50).

Numerous leaves, which co-occurred with the seed, are independently comparable with the genus in petiole features and the midrib that projects beyond either surface. Although their petioles are not twisted as described by Tanai and Suzuki (1963) and later authors, the author treated them as the same species with the seed, based on their co-occurrence. This species is distinguished from *K. robusta* Miki described from the *Pinus trifolia* bed of Central Japan (Miki, 1957) in the triangular shape of the seed wing. Among three extant species of *Keteleeria* (Farjon, 1990), this species is most similar to *K. davidiana* (Bertrand) Beissner distributed in southern China and Taiwan.

Materials.—FPDM-P-483-1, 484-2, 582-5, 6 (Loc. 2).

Genus *PICEA* A. Dietrich, 1824
Picea kaneharai Tanai et Onoe, 1961
(Fig. 3-3, 4)

Picea kaneharai Tanai et Onoe, 1961, p. 17, pl. 1, fig. 9.

Description.—Seeds asymmetrical ovoid with one indentation on the proximal end of admedial edge; 6.3 mm long, 3.7 mm wide; bluntly pointed at base. Seed wing thin; asymmetrical, spatulate, widest near the distal end; attached obliquely to the upper half of the seed; 10.7 mm long, 7.7 mm wide; apex rounded.

Discussion.—*Picea kaneharai* was originally described by Tanai and Onoe (1961) based on one winged-seed from the Late Miocene Ningyo-toge Formation. It was compared with

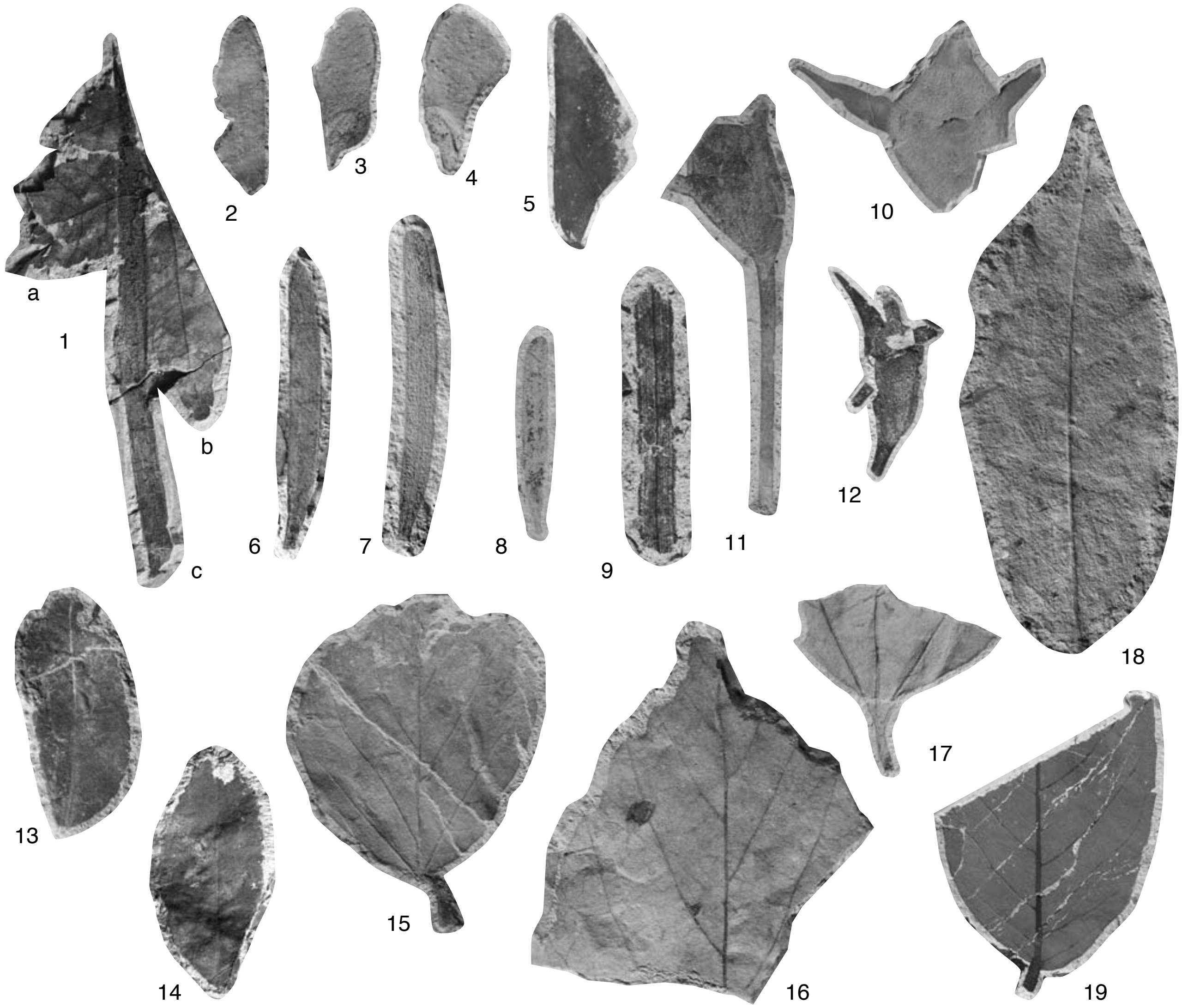

FIGURE 3. Plant megafossils from the Ito-o Formation. All figures in natural size, unless otherwise stated. **1a**, **b**. *Zelkova ungeri* (Ettingshausen) Kovats, FPDM-P-539-1, 2; **1c**. *Equisetum* sp., FPDM-P-539-3, Loc. 1. **2**. *Pseudolarix japonica* Tanai et Onoe, FCMNH-GF0517, Loc. 1. **3**, **4**. *Picea kaneharai* Tanai et Onoe (Fig. 4 is a counter part of Fig. 3), FPDM-P-474-2, x1.5, Loc. 2. **5–8**. *Keteleeria ezoana* Tanai (5: seed), Loc. 2; 5. FPDM-P-484-2; 6, FPDM-P-582-5, x2.0; 7, FPDM-P-582-6, x2.0; 8. FPDM-P-483-1, x2.0. **9**. *Monocotylophyllum* sp., FPDM-P-559, x2.5, Loc. 1. **10–12**. *Hemitrapa yokoyamae* (Nathorst) Miki, Loc. 2; 10, FPDM-P-75; 11, FPDM-P-489; 12, FPDM-P-487-2. **13**, **14**. *Gleditsia miosinensis* Hu et Chaney, x2.0, Loc. 2; 13, FPDM-P-536-1; 14, FPDM-P-536-3. **15–17**. *Parrotia pristina* (Ettingshausen) Stur, Loc. 2; 15, FPDM-P-65-1; 16, FPDM-P-495-3; 17, FPDM-P-499. **18**, **19**. *Wisteria fallax* (Nathorst) Tanai et Onoe; 18, FPDM-P-532, Loc. 1; 19, FPDM-P-594-1, Loc. 2.

the modern *P. polita* Carrière, which grows in central Honshu, Shikoku, and Kyushu in Japan at an elevation of about 1,000 m above sea level. This species has been reported from the late Early to Late Miocene floras of Japan, Korea and Sakhalin (Tanai, 1961; Tanai and Suzuki, 1965; Huzioka, 1972; Huzioka and Uemura, 1973; Fotjanova, 1988). However, those from the late Early to early Middle Miocene strata differ slightly from the type specimen in seed shape and wing width, to which the present specimen can be correlated. In this regard, further investigations for earlier Miocene records are required as to their taxonomic status in connection with those from the Late Miocene floras.

Material.—FPDM-P-474-2 (Loc. 2).

Genus *PSEUDOLARIX* Gordon, 1858

Pseudolarix japonica Tanai et Onoe, 1961
(Fig. 3-2)

Pseudolarix japonica Tanai et Onoe, 1961, p. 17, pl. 1, fig. 5

Description.—Seed orbiculate, flattened; length estimated 3.1 mm, width 2.6 mm. Seed wing thin; asymmetrical triangular in shape; probably covering the seed on one side; 24.8 mm long, 7.8 mm wide; each edge slightly convex with rounded apex.

Discussion.—The current specimen is identical to the genus *Pseudolarix* in the shape of the seed, and the wing that is attached to one side of the seed (Miki, 1957). The specimen resembles *P. japonica*, which was originally described from the Late Miocene Tatsumitoge Flora (Tanai and Onoe, 1961) and subsequently from the Early Miocene Hiyoshi and Yoshioka floras (Tanai, 1961; Tanai and Suzuki, 1963).

During a comprehensive revision of the genus *Pseudolarix*, LePage and Basinger (1995) recognized two extant species from the Eocene of Canadian Arctic, and assigned most all of the specimens ever described into them. They hesitated to make species level assignment for the materials reported by Tanai and Onoe (1961) because of the lack of bract, which is the most important character in making a positive comparison with the extant species, on the surface of the cone scale. However, the author tentatively used the name *P. japonica* in order to show the similarity to materials reported as this species.

Pseudolarix is a monotypic genus that grows in temperate to warm-temperate forests of Central China at an elevation between 100 to 1,000 m above sea level.

Material.—FCMNH-GF0517 (Loc. 1).

MONOCOTYLEDONS incertae sedis
Genus *MONOCOTYLOPHYLLUM* Reid and Chandler, in Reid et al. 1926
Monocotylophyllum sp.
(Fig. 3-9)

Description.—Leaf fragmentary, but apparently linear in shape; both the apex and base missing; over 15 mm long, ca. 2 mm wide; margin indistinct, probably entire; primary vein massive, straight; secondary (or lateral primary) veins thick, following closely to the margin, parallel to the midvein; tertiary veins between the primary and marginal secondaries moderate to thin, at least four on one side, irregularly spaced, parallel to the midvein; higher order venation not observable.

Discussion.—One fragmentary leaf is marked by thick primary and parallelodromous secondary or tertiary veins with entire margin, and comparable to a number of genera belonging to the Order Poales. However, it is impossible to assign it to any single extant genus with confidence because of the fragmentary nature of the specimen. Thus, the author applied the form-genus *Monocotylophyllum*, which was established by Reid and Chandler (in Reid et al., 1926) for the monocotyledonous leaves with unknown families.

Material.—FPDM-P-559 (Loc. 1).

Order SAXIFRAGALES Dumortier, 1829
Family HAMAMELIDACEAE R. Brown, 1818a
Genus *PARROTIA* C. Meyer, 1831
Parrotia pristina (Ettingshausen) Stur, 1867
(Figs. 3-15, 16, 17; 8-1)

Styrax pristinum Ettingshausen, 1851, p. 19, pl. 3, fig. 9.
Parrotia pristina (Ettingshausen) Stur, 1867, p. 192, pl. 5, figs. 2, 3

Description.—Leaves simple, slightly asymmetrical; laminae microphyll to notophyll, widely elliptic to elliptic in shape; apex widely acute to obtuse, acuminate in shape; base slightly asymmetrical, obtuse, convex, basal margin delineated by the lowermost secondary veins; length estimated 4.4 to 8.4 cm, width estimated 3.5 to 5.5 cm; length to width ratio 1.25 to 1.53; petiole marginal, thick basally, 6 to 8 mm long; margin entire on the basal part but toothed on the apical part; tooth distant, irregularly spaced, straight or convex on both sides, obtuse, tooth apex generally rounded with a mucronate tip; sinuses rounded; venation pinnate, usually craspedodromous; primary vein moderate, sinuous; secondary veins thick, at least five pairs, irregularly spaced, sometimes decurrent near the divergence, arising at an angle of approximately 30 degrees from the midvein on middle portion, usually more acute near the base, straight to gently curved, often outcurved near the margin, forked; tertiary veins moderate, closely (4/cm) spaced, mixture of opposite and alternate percurrent, straight to sinuous, obtuse to the midvein; marginal tertiaries arising from the basal secondaries and are abmedially brochidodromous; quaternary veins thin, relatively randomly oriented, forming medium polygonal meshes; veinlets not observable.

Discussion.—Although they are slightly ill-preserved, the present specimens are identical to *Parrotia pristina* in general shape, marginal teeth, and basally protruding secondaries, as well as thick, short petiole. This species is one of the most common species in the Daijima-type flora of Japan, and ranges at least to the Late Miocene. *Parrotia* is a monotypic genus represented by a single extant species, *P. persica* (De Candolle) C. Meyer, a deciduous shrub or small tree native to northern Iran.

Materials.—FPDM-P-65-1, 495-3, 499 (Loc. 2).

Order MYRTALES Reichenbach, 1828
Family LYTHRACEAE Saint-Hilaire, 1805
Genus *HEMITRAPA* Miki, 1941
Hemitrapa yokoyamae (Nathorst) Miki, 1953
(Fig. 3-10, 11, 12)

Trapa Yokoyamae Nathorst, 1888, p. 21, pl. 7, figs. 6-8.
Hemitrapa yokoyamae (Nathorst) Miki, 1953, p. 349, fig. 2G.

Discussion.—The detached fruits are characterized by: broadly ovate shape; brushy hairs on the apical part; four robust appendages that attain less than ovule length; long thick peduncle that suggests an absence of a dehiscence line near the fruit. These characters coincide with that of *Hemitrapa yokoyamae*, which was originally described as *Trapa* by Nathorst (1888) based on fossil fruits from the possible Middle Miocene strata in Ishikawa Prefecture. Since the first report by Nathorst (1888), this species has been described from several localities yielding the Daijima-type flora. The specimen shown in Figure 3-12 exhibits a slightly elongated shape, and in this regard it is similar to another species, *H. hokkaidoensis* (Okutsu) Miki, described from the Middle Miocene Sakipenpetsu Flora of Hokkaido (Tanai, 1971). However, the latter species usually yields long appendages that attain more than nut length, sometimes being twice as long as that length (Tanai, 1971). Thus, the author provisionally regarded it as a variation of *H. yokoyamae*.

Materials.—FPDM-P-75, 487-2, 489 (Loc. 2).

Order FABALES Bromhead, 1838
Family FABACEAE Lindley, 1836b
Genus *GLEDITSIA* Linnaeus, 1753
Gleditsia miosinensis Hu et Chaney, 1938
(Figs. 3-13, 14; 8-2; 9-7)

Gleditsia miosinensis Hu et Chaney, 1938, p. 52, pl. 26, figs. 6, 7.

Description.—Leaflet distinctly asymmetrical, microphyll, narrowly ovate to elliptic in general shape; apex wide acute, convex probably with rounded tip; base wide acute, convex on one side, straight on the other side; length ca. 1.6 cm, width ca. 0.8 cm; length to width ratio 2.0; petiolule very short; margin serrate; teeth simple, relatively regularly spaced, three teeth per centimeter on the middle of the blade, straight or convex on the apical side, convex on the basal side, vein configurations within the teeth indistinct; sinuses angular; venation pinnate, brochidodromous; primary vein stout, straight or sinuous; secondary veins thin, hair-like, at least eight pairs, irregularly spaced, divergent angle ca. 65 to 75 degrees, course straight as much as two-thirds of the distance, forked at least once, abruptly curved-up or down to form marginal loop which is enclosed by smaller loops of tertiary or higher order veins; intersecondaries common, indistinct, diverging at nearly same angles with contiguous secondaries; tertiary veins thin, indistinct, exmedially ramified; quaternary and higher order venation not observable.

Discussion.—Some specimens from the Ito-o Formation were assigned to this species in inequilateral shape, short petiolule, and inconspicuous marginal teeth, as well as in reticulodromous intercostal venations. This species was originally established by Hu and Chaney (1938) from the Middle Miocene Shanwang Flora of China and has been reported from the Miocene floras of Japan, especially from the Daijima-type flora. This species is similar to the modern *G. sinensis* Lamark of China and *G. japonica* Miquel of Japan.

Materials.—FPDM-P-477-3 (Loc. 2), 536-1, 3 (Loc. 1).

Genus *WISTERIA* Nuttall, 1818

Wisteria fallax (Nathorst) Tanai et Onoe, 1961

(Fig. 3-18, 19)

Sophora (?) *fallax* Nathorst, 1883, p. 58, pl. 10, figs. 11, 12; pl. 12, figs. 1, 2.

Wisteria fallax (Nathorst) Tanai et Onoe, 1961, p. 45, pl. 10, fig. 6; pl. 14, figs. 2-4.

Description.—Leaflets basally asymmetrical, microphyll, shape elliptic; apex acute and attenuate; base wide acute, convex; length 7.4 cm, width 2.4 cm; length to width ratio 2.6; petiolule thick with cross ridges, ca. 3.0 mm long; margin entire, undulate; venation pinnate, brochidodromous; primary vein stout, straight, curved or sinuous; secondary veins moderate, at least ten pairs, irregularly spaced, diverging from the midvein at an angle of 45 degrees on the middle portion, straight or curved, usually sinuous along the way, sometimes forked, abruptly curved near the margin to join supra-adjacent secondaries at wide acute to obtuse angles; intersecondaries common, short, nearly parallel to contiguous secondaries, tertiary veins thin, predominantly alternate percurrent, closely spaced, course straight or sinuous, obtuse to the midvein, angle decreasing exmedially; quaternary or higher order veins not observable.

Discussion.—Some leaflets are identical to *Wisteria fallax* in their thin texture, basal inequilateral elongated foliar shape, short petiolule, and entire margin, as well as in numerous secondaries forming marginal loops. This species is a common Neogene species originally described from the Pliocene Mogi Flora under the name of *Sophora* (?) *fallax* (Nathorst, 1883). This species resembles the leaflets of *Cladrastis aniensis*, but is distinguishable in general leaf form, and number and course of secondaries. This species is closely similar to the living *W. floribunda* (Willdenow) De Candolle, a common viny tree distributed in Honshu, Shikoku, Kyushu of Japan and in China.

Materials.—FPDM-P-532 (Loc. 1), 594-1 (Loc. 2).

Fabaceae gen. et sp. indet.

(Fig. 6-8, 9)

Description.—Leaf or leaflet distinctly asymmetrical, notophyll, wide ovate to suborbiculate in shape; apex missing but apparently wide acute, acuminate or straight; base obtuse, shallowly cordate on one side and convex to straight on the other side; length estimated 7.9 to 9.5 cm, width 4.7 to 6.6 cm; length to width ratio 1.43 to 1.68; petiole (or petiolule) marginal, thick with cross ridges on the surface, approximately 3.0 mm long; margin entire; venation pinnate; number of basal veins four or five; midvein thin, 0.7 mm wide at base, abruptly tapering toward the apex, course sinuous; secondary veins thick, weak brochidodromous, at least six pairs, distance between the two secondaries decreasing toward the apex, the basal pair originated from the lamina base at narrowly acute angle, admedially send off weak brochidodromous sub-secondaries at widely acute angles, gently curved, abruptly curving up near the margin; intersecondaries occasional; intercostal tertiary veins moderate, mixture of opposite and alternate percurrent, irregularly but closely spaced (5/cm), course variable, generally obtuse against the midvein, angle increasing exmedially; marginal tertiary veins curved tangentially along the margin; quaternary veins thin, orthogonal; higher order venation and veinlets not observable.

Discussion.—The materials are marked by inequilaterally foliar shapes, entire margins, and short petiole (or petiolule) with numerous tangential ridges. From these characters they are assigned to the family Fabaceae. The wide ovate to suborbiculate shape resembles the genus *Pueraria*; however, it is distinguished in its secondary venation in that those of *Pueraria* reach directly to the margin. Well-preserved materials are needed to determine them at the genus or species level.

Materials.—FPDM-P-69-3, 67 (Loc. 2).

Order FAGALES Engler, 1892

Family BETULACEAE Gray, 1821

Genus *ALNUS* Miller, 1754

Alnus miojaponica Tanai, 1961

(Figs. 4-8, 9, 10; 8-3)

Alnus miojaponica Tanai (non Tanai et Onoe, 1961), 1961, p. 280, pl. 6, fig. 8; pl. 9, fig. 5; pl. 10, fig. 10.

Description.—Laminae microphyll to notophyll, widely elliptic to ovate in shape; apex acute, short acuminate; base missing but apparently widely acute, convex; length estimated 5.3 to 8.5 cm, width estimated 2.6 to 5.4 cm; petiole not preserved; margin serrate; teeth simple or compound, irregularly spaced, straight/flexuous commonly with stick-like projections, apex usually acute, secondary vein enters large primary tooth medially, tertiary vein enters subsidiary tooth; sinuses angular, acute to obtuse; venation pinnate, craspedodromous to semi-craspedodromous; primary vein weak to moderate, usually straight in course; secondary veins thick, at least seven pairs, distance between the two secondaries irregular but usually closer on the basal part, mostly parallel to each other, relation to the midvein middle acute (40- to 50-degree angles), angle smoothly decreasing apically, course gently curved, decurrent at divergence on the basal portion, forked abmedially at acute angle to send secondary or tertiary veins toward teeth; intercostal tertiaries moderate, closely spaced (4 to 5/cm), predominantly opposite percurrent, straight or convex, rarely sinuous, generally obtuse, nearly at right angle against the midvein on the apical portion; fourth and fifth order veins moderate, orthogonal, forming medium-sized polygonal meshes; veinlets not well-preserved.

FIGURE 4. Plant megafossils from the Ito-o Formation. All figures in natural size, unless otherwise stated. **1**. *Betula mioluminifera* Hu et Chaney, FCMNH-GF0465, Loc. 1. **2**, **7**. *Betula oobae* Suzuki; 2, FPDM-P-468-2, Loc. 2; 7, FCMNH-GF0524. **3**. Betulaceae gen. et sp. indet., FPDM-P-561, x2.5, Loc. 1. **4**–**6**. *Betula uzenensis* Tanai; 4, FPDM-P-542-2, Loc. 1; 5, FPDM-P-528-1, Loc. 1; 6, FPDM-P-471-2, Loc. 2. **8**–**10**. *Alnus miojaponica* Tanai, Loc. 1; 8, FPDM-P-558; 9, FPDM-P-530; 10, FPDM-P-572-1. **11**. *Carpinus heigunensis* Huzioka, FPDM-P-529-1, x1.5, Loc. 1. **12**. *Carpinus subcordata* Nathorst, FPDM-P-527, x1.5, Loc. 1. **13**, **14**. *Carpinus* sp. sect. *Distegocarpus* (Siebold et Zuccarini) Sargent, x1.5; 13, FCMNH-G174-244, Loc. 1; 14, FPDM-P-484-1, Loc. 2.

Discussion.—*Alnus miojaponica* was established by Tanai (1961) based on one incomplete leaf from the Middle Miocene in the Nishitagawa coal field for the alder species that yields elliptic foliar shape, compound marginal serration with acutely pointed teeth, and closely spaced craspedodromous secondary veins. This species has been reported from the Early to Late

Miocene floras in Japan. According to Uemura (1988), marginal characters of this species exhibit wide range of variation from less conspicuous simple serration to distinctly compound ones. In this regard, the present materials are more similar to those reported from the Late Miocene Takamine Flora. However, they are identical to this species in secondary venation and closely spaced percurrent intercostal tertiaries. This species is distinguished from *A. arasensis* Huzioka from the Early Miocene Aniai Flora (Huzioka, 1964) in number and course of secondary veins.

Materials.—FPDM-P-530, 558, 572-1 (Loc. 1).

Genus *BETULA* Linnaeus, 1753

Betula mioluminifera Hu et Chaney, 1938

(Figs. 4-1; 8-5, 6)

Betula mioluminifera Hu et Chaney, 1938, p. 30, pl. 5, fig. 5; pl. 7, figs. 1, 2, 3; pl. 9, fig. 1 (excluding pl. 5, fig. 6).

Description.—Laminae symmetrical, notophyll, widely elliptic in shape; apex missing; base obtuse, convex above, slightly decurrent below; length estimated at 7.9 cm, width at 4.6 cm; length to width ratio probably 1.6; petiole marginal, thick basally, ca. 6.0 mm long; margin serrate; teeth compound, about eight teeth between two secondaries on middle portion, usually flexuous on the apical side, flexuous, convex or concave on the basal side, tooth apex usually attenuate with caudate tip, oriented apically, secondary or tertiary vein enters tooth medially or slightly basally; sinuses angular, acute; venation pinnate, craspedodromous; primary vein moderate, straight or weakly sinuous; secondary veins moderate, at least six pairs preserved, regularly spaced, relation to the midvein acute (35- to 40-degree angles) on middle portion, parallel to each other, course straight, forked exmedially, typically curving up near the margin, the basal one decurrent at divergence, two basal pairs forming compound agrophic venations; tertiary veins moderate, closely spaced (4 to 5/cm), predominantly opposite percurrent, straight, obtuse to the midvein; quaternary veins thick, orthogonal, forming large polygonal meshes with the quinternary veins; ultimate veinlet indistinct, probably present and branched.

Discussion.—The present material is marked by elliptic to wide-elliptic shapes, convex bases rather than cuneate, relatively distant secondaries arranged parallel to each other, and inconspicuous marginal teeth. These characters well match with those of *Betula mioluminifera* Hu et Chaney originally described from the Middle Miocene Shanwang Flora (Hu and Chaney, 1938). According to Hu and Chaney (1938), this species is most similar to the modern *B. luminifera* Winkler of China.

Materials.—FPDM-P-551-1 (Loc. 1); FCMNH-GF0465 (Loc. 1).

Betula oobae Suzuki, 1961

(Figs. 4-2, 7; 8-4)

Betula oobae Suzuki, 1961, p. 38, pl. 7, figs. 5, 6.

Description.—Lamina symmetrical, notophyll, widely ovate in shape; apex widely acute, mostly straight; base obtuse, cuneate; length estimated 6.9 to 8.8 cm, width 5.0 to 5.6 cm; length to width ratio 1.38 to 1.57; petiole marginal, expanded toward the base, 21 mm long; margin serrate; teeth compound, three to four teeth between two secondaries on middle portion, flexuous to concave on the apical side, flexuous to convex on the basal side, tooth apex acute, attenuate as long as 2.0 mm, secondary and tertiary vein enters tooth medially; sinuses angular, acute; venation pinnate, craspedodromous; primary vein moderate, straight to curved; secondary veins thick, at least ten pairs, diverging from the primary at an angle of ca. 40 to 50 degrees on the middle portion, angle smoothly increasing toward the base, decurrent near the divergence, straight or sinuous, slightly curved near the margin, exmedially sending off several thick tertiaries that feed into marginal smaller teeth; tertiary veins very thin, predominantly opposite percurrent, closely spaced (6/cm), usually convex, generally obtuse to the midvein, angle decreasing apically; quaternary and quinternary veins moderate, orthogonal, forming well-developed areolations; areoles typically four- or more-sided, medium in size; veinlets branched more than twice.

Discussion.—*Betula oobae* was originally described by Suzuki (1961) from the late Early Miocene Ryozen Formation of the Soma Area in Fukushima Prefecture. This species is characterized by a widely ovate shape and an obtusely cuneate base, as well as by a conspicuous marginal configuration. Figured specimens of this species yield prolonged marginal serrations. According to the author's investigation of topotypes, however, there are more specimens that yield less conspicuous marginal serrations, which is more similar to the current materials from the Ito-o Formation. Consequently, the author compared the materials with this species. *B. oobae* is related to *B. protoglobispica* Tanai et Onoe from the Late Miocene Onbara Formation (Tanai and Onoe, 1961), but can be distinguished from the latter in number and divergent angle of the secondary veins, as well as in conspicuous marginal serration.

Materials.—FPDM-P-468-2 (Loc. 2), 550 (Loc. 1); FCMNH-GF0524 (Loc. 1).

Betula uzenensis Tanai, 1961

(Figs. 4-4, 5, 6; 8-7)

Betula uzenensis Tanai, 1961 (non 1955), p. 291, pl. 8, figs. 7, 9.

Description.—Lamina symmetrical, microphyll, widely elliptic in shape; apex missing; base middle to wide acute, straight to convex; length estimated 4.9 to 5.9 cm, width 2.3 to 3.5 cm; length to width ratio 1.7 to 2.1; petiole marginal, 9-12 mm long; margin serrate; teeth compound, two to four teeth between two secondaries on middle portion, usually flexuous sometimes straight on the apical side, flexuous to convex on the basal side, tooth apex acute, shortly attenuate with blunt tip, secondary and tertiary vein enters tooth medially; sinuses angular, acute; venation pinnate, craspedodromous; primary vein moderate, straight; secondary veins thick, at least 9 pairs, diverging from the primary at an angle of 32 to 38 degrees on the middle portion, the angle slightly decreasing toward the base, decurrent near the divergence, typically spreading exmedially, sending sub-secondary veins into marginal smaller teeth, basal three pairs of secondaries forming compound agrophic venation; tertiary veins thin, closely spaced (5 to 7/cm), predominantly opposite percurrent, usually convex, generally obtuse to the midvein, angle decreasing toward the apex; quaternary and quinternary veins moderate, orthogonal, forming well-developed areolations; areoles typically four-sided, sometimes more, medium in size; veinlets branched more than twice.

Discussion.—The current materials are assigned to *Betula uzenensis* in acute base, number and course of secondary veins, and acute marginal teeth with blunt tip. This species is somewhat similar to some species belonging to the genus

Carpinus and *Ostrya* of the same family. But this species is distinguished from them in prolonged marginal teeth and areole features bearing veinlets branched more than twice (Wolfe, 1966; Uemura, 1988). *B. uzenensis* was first introduced by Tanai (1955), based on two leaves from the Lower Miocene Aburato Coal-bearing Member yielding the Aniai-type flora. However, Tanai (1955) did not give a description or diagnosis at that time, and the species was not validly published until Tanai (1961). Among the living birch in Japan, *B. uzenensis* can be compared with the modern *B. schmidti* Regel, which grows in Honshu, Shikoku and Kyushu of Japan.

Materials.—FPDM-P-471-2 (Loc. 2), 528-1, 542-2 (Loc. 1).

Genus *CARPINUS* Linnaeus, 1753

Carpinus heigunensis Huzioka, 1938

(Fig. 4-11)

Carpinus heigunensis Huzioka, 1938, p. 149, text-fig. 1

Discussion.—One detached involucre has been collected from the formation. The specimen is marked by inequilateral rhomboid shape, and a few thick secondaries running one side of the lamina, which expand exmedially to the marginal teeth. From these characters, the specimen was assigned to *Carpinus heigunensis*. This species was originally established based on a single involucre from the Middle Miocene flora of Yamaguchi Prefecture (Huzioka, 1938) and subsequently reported from many Tertiary floras of Japan. This species is closely similar to the modern *C. tschonoskii* Blume, which grows in the temperate forests of Japan, Korea, and Central to South China.

Material.—FPDM-P-529-1 (Loc. 1).

Carpinus subcordata Nathorst, 1883

(Fig. 4-12)

Carpinus subcordata Nathorst, 1883, p. 39, pl. 2, figs. 13, 15-18, 20 (excluding fig. 14)

Description.—Laminae symmetrical, microphyll, widely elliptic in shape; apex probably middle acute and acuminate; base obtuse, cordate; petiole missing; length estimated 3.1 cm, width 1.6 cm; length to width ratio 1.93; margin serrate; teeth compound, three teeth between two secondaries on the middle portion, flexuous to concave on the apical side, usually flexuous on the basal side, principal vein enters tooth medially or slightly basally and usually bends up within the teeth, tooth apex middle acute and pointed; sinuses angular, acute; venation pinnate, craspedodromous; primary vein moderate, straight; secondary veins moderate, at least nine pairs, irregularly spaced, relation to the midvein ca. 35 degrees on the middle portion, mostly parallel to one other, course curved; intercostal tertiaries moderate to thin, predominantly opposite percurrent, closely spaced, generally obtuse to the midvein; quaternary and higher order venation not observable.

Discussion.—The current material was assigned to *Carpinus subcordata* due to its wide elliptic shape, cordate base, compound serration with small acutely pointed teeth, and craspedodromous secondary veins that are arranged parallel to one another. This species is common in the Neogene floras of East Asia, and has been regarded as a direct progenitor of the modern *C. cordata* Blume, which is luxuriantly flourishing in humid valley forests in Japan, Korea, and China.

Material.—FPDM-P-527 (Loc. 1).

Carpinus sp. sect. *Distegocarpus* (Siebold et Zuccarini) Sargent, 1896

(Fig. 4-13, 14)

Discussion.—Although present materials are fragmentary and their marginal characters are not sufficiently clear, they are marked by mostly equilateral shape, rounded base, and at least four primary veins diverged radially from the base to the marginal teeth. These characters match with involucres of hornbeams belonging to the section *Distegocarpus* (Berger, 1953). Occurrence of *C. subcordata* of the same section also conforms to the identification of the present materials.

Materials.—FPDM-P-484-1 (Loc. 2), FCMNH-G174-244 (Loc. 1).

Betulaceae gen. et sp. indet.

(Fig. 4-3)

Discussion.—One detached fruit was obtained. A slightly protruding apex perhaps represents a remnant of styles. Although the wing was not preserved, it is identical to a fruit of genus *Alnus* or *Betula* with its flattened, narrow obovate shape, as well as its size.

Material.—FPDM-P-561 (Loc. 1).

Family FAGACEAE Dumortier, 1829

Genus *FAGUS* Linnaeus, 1753

Fagus antipofi Heer in Abich, 1858

(Figs. 5-2, 3; 8-8; 9-1)

Fagus antipofi Heer in Abich, 1858, p. 572, pl. 8, fig. 2.

Description.—Laminae incomplete, both ends missing, slightly asymmetrical, microphyll, narrowly elliptic in shape; apex apparently acute, probably straight on both sides; base middle acute, convex; length estimated 8.4 cm, width estimated 2.9 cm; petiole not preserved; margin serrate; teeth small and simple, regularly arranged, straight on the apical side, convex or weakly flexuous on the basal side, tooth apex acute with blunt tip, apically oriented, secondary vein enters tooth basally; sinuses rounded; venation pinnate, craspedodromous; primary vein moderate, gently curved on apical part; secondary veins moderate, at least 9 to 13 pairs, regularly spaced, arising at angles of 40 to 50 degrees on middle portion, angle smoothly increasing toward the base, straight or curved, decurrent at divergence on the basal part, abruptly bends up within the marginal teeth; tertiary veins thin, closely spaced, predominantly opposite percurrent, nearly perpendicular to oblique to the secondaries, course sinuous, obtuse to the midvein in general trends, angle against the midvein increasing toward the base, one prominent tertiary vein arising admedially from the secondary below the marginal teeth, extending along the margin joining supra-adjacent secondary vein, mostly parallel to contiguous tertiaries; quaternaries moderate, orthogonal, forming well-developed areolations; areoles typically four- or five-sided, medium in size; veinlets absent.

Discussion.—These simple serrate leaves with minute teeth are referable to the genus *Fagus* in the following features: both the primary and secondary veins are thick and distinct; the secondary veins are evenly-arranged and nearly parallel to one another; the secondaries are nearly straight and abruptly curved-up below the teeth; the admedial tertiary vein that departs from the secondary vein below the marginal teeth is nearly parallel to the intercostal tertiary veins; intercostal tertiaries

FIGURE 5. Plant megafossils from the Ito-o Formation. All figures in natural size, unless otherwise stated. **1**, **11**. *Pterocarya protostenoptera* Tanai (11: winged-nut); 1, FPDM-P-568, Loc. 1; 11, FPDM-P-594-2, x1.5, Loc. 2. **2**, **3**. *Fagus antipofi* Heer 1; 2, FCMNH-GF0529, Loc. 1; 3, FPDM-P-73, Loc. 2. **4**. *Fagus* sp. (cupule), FPDM-P-74-1, Loc. 2. **5**, **6**. *Quercus miovariabilis* Hu et Chaney, Loc. 2; 5, FPDM-P-472-1; 6, FPDM-P-468-3, x0.85. **7**. *Rhus* sp., FPDM-P-533, Loc. 1. **8**. *Juglans miochinensis* (Tanai et Onoe) Suzuki, FPDM-P-468-1, Loc. 2. **9**, **10**. *Pterocarya japonica* (Tanai) Uemura: 9, FPDM-P-582-1, Loc. 2; 10, FCMNH-GF0532b, Loc. 1. **12**. *Populus* sp., FCMNH-GF0485, x0.8, Loc. 1.

are relatively weak as compared with the secondary and quaternary veins. The current specimens are also characterized by elongated shapes that fall within the variation of *F. antipofi* (Tanai, 1974: text-fig. 4). They are also similar to *F. uemurae* Tanai described from the Oligocene of Hokkaido (Tanai, 1955) and *F. evenensis* Chelebaeva from the Middle Miocene of

Kamchatka (Chelebaeva, 1980). But, the current specimens can be distinguished from these two species by the fewer number of secondary and intercostal tertiary veins.

Materials.—FPDM-P-73 (Loc. 2); FCMNH-GF0529 (Loc. 1).

Fagus sp.

(Fig. 5-4)

Description.—Cupule compressed, suborbiculate to widely ovate in shape, 20.0 mm long (estimated) and 12.9 mm wide; probably cleft into four lobes (two lobes are visible on one side); each lobe covered with linear appendages (ca. 0.7 mm long) on outer surface; pedicel thick, short, ca. 6.0 mm long.

Discussion.—The specimen is identical to the genus *Fagus* in its shape, number of lobes and the presence of linear appendages on the surface. Although the co-occurrence with beech leaves from the same locality suggest their belonging to the same species, the author hesitated to assign it because knowledge of the cupule of *F. antipofi* is still limited. The specimen resembles those reported from the Abura and Hiyoshi floras (Tanai, 1961: pl. 16, figs. 1, 2, 10) and from the Oguni Flora (Onoe, 1974: pl. 5, figs. 6, 7) under the name of *F. antipofi*.

Material.—FPDM-P-74-1 (Loc. 2).

Genus *QUERCUS* Linnaeus, 1753

Quercus miovariabilis Hu et Chaney, 1938

(Fig. 5-5, 6)

Quercus miovariabilis Hu et Chaney, 1938, p. 36, pl. 15, fig. 5 (excluding fig. 6).

Discussion.—A few fragmentary leaves with simple, spinose teeth were obtained from the Locality 2 of the Ito-o Formation. They are identical to the genus *Quercus* from their very narrow elliptic shape, craspedodromous secondary veins arranged parallel to one another, and closely spaced percurrent intercostal tertiary veins. Among the fossil leaves belonging to the genus *Quercus*, they are referable to *Q. miovariabilis*, originally described from the Middle Miocene Shanwang Flora of China. *Q. miovariabilis* is one of the common elements of the Daijima-type flora and has been described under different species names, such as *Q. ryozenensis* Suzuki (Suzuki, 1961) and *Q. subvariabilis* Tanai (Tanai, 1961).

Materials.—FPDM-P-468-3, 472-1 (Loc. 2).

Family JUGLANDACEAE Perleb, 1818

Genus *JUGLANS* Linnaeus, 1753

Juglans miochinensis (Tanai et Onoe) Suzuki, 1961

(Fig. 5-8)

Corylus miochinensis Tanai et Onoe, 1959, p. 20, pl. 4, fig. 1; text-fig. 2.

Juglans miochinensis (Tanai et Onoe) Suzuki, 1961, p. 32, pl. 4, figs. 1, 4-8; pl. 5, fig. 1.

Discussion.—Although they are not well-preserved, a few fragmentary leaves from the Ito-o Formation were referred to the genus *Juglans* in the following features: inequilateral shape; simple serrate margin with bluntly pointed teeth, which are generally distantly arranged; semi-craspedodromous secondary veins; closely-arranged percurrent tertiary veins; well-developed small areolations. One secondary vein on the upper left of the specimen shown in Fig. 5-8 represents a bifurcating feature and both veins perhaps terminate directly into marginal teeth. This is also a character of the genus *Juglans*.

Among the fossil leaves or leaflets assigned to the genus *Juglans*, the present materials are most similar to *J. miochinensis* as described from the Shichiku Flora of the Joban area (Tanai and Onoe, 1959), in their size, shape, as well as number of secondary veins. Suzuki (1961) compared this species with the modern *J. sieboldiana* Maximowicz (= *J. mandshurica* Maximowicz subsp. *sieboldiana* (Maximowicz) Kitamura), which inhabits the riparian forests in Japan.

Material.—FPDM-P-468-1 (Loc. 2).

Genus *PTEROCARYA* Kunth, 1824

Pterocarya japonica (Tanai) Uemura, 1988

(Fig. 5-9, 10)

Juglans japonica Tanai, 1961, p. 275, pl. 6, fig. 10 (non fig. 9).

Pterocarya japonica (Tanai) Uemura, 1988, p. 132, pl.8, fig. 1.

Description.—Leaflets microphyll, narrowly oblong to oblong in shape; apex missing; base asymmetrical, middle acute, convex, rounded or cordate; length estimated 7.5 to 12.0 cm, width 2.6 to 4.2 cm; length to width ratio 2.8 to 3.7; petiolule short, thick, ca. 4.0 mm long; margin serrate; teeth more or less equal in size, closely spaced (5 to 6/cm) on middle portion, usually straight on the apical side, straight or convex on the basal side, angle between the apical and basal side of teeth acute, tertiary vein from the marginal loop enters tooth medially, length of the basal flank of teeth usually three times longer than the apical one; sinuses angular, acute; venation pinnate, weak brochidodromous; primary vein stout, curved basally; secondary veins moderate, at least 11 pairs, irregularly spaced, middle to wide acute, course curved; intersecondaries common, arising at nearly the same or higher angles than contiguous secondaries; tertiaries moderate, predominantly opposite percurrent, closely spaced (6/cm), straight or sinuous, obtuse to the midvein, angle decreasing exmedially; quaternary and quinternary veins thick, orthogonal, forming small to medium meshes; ultimate veinlets not observable.

Discussion.—The materials are assigned to the genus *Pterocarya* in basally inequilateral oblong shape, evenly-spaced triangular teeth, weak brochidodromous secondary veins, as well as well-developed areolations. They are also characterized by having numerous secondaries curved smoothly toward the margin. These characters correspond with those of *P. japonica* (Tanai) Uemura, which was originally described as a genus *Juglans* by Tanai (1961) from the Late Miocene Shanabuchi Formation. This species also resembles the extant *P. rhoifolia* Siebold et Zuccarini growing in riverside forests in Japan.

Materials.—FPDM-P-582-1 (Loc. 2); FCMNH-GF0532b (Loc. 1).

Pterocarya protostenoptera Tanai, 1961

(Figs. 5-1, 11; 9-2)

Pterocarya protostenoptera Tanai, 1961, p. 278, pl. 4, fig. 10.

Description.—Fruit with two wings, V-shaped in general outline; nut ellipsoid, pointed at base; apex probably with two styles curved outwardly; length 8 mm, width 3.3 mm, shallow irregular ridges on the apical two-thirds of shell wall; wing oblong, abruptly rounded at apex, ca. 13.0 mm long, 5.3 mm wide; venation of wing not observable. Leaflet fragmentary, size microphyll, probably oblong or narrowly oblong in shape; both the apex and base missing; margin serrate; teeth variable in size, relatively distant (≧ 4/cm on middle portion), length of the basal flank of teeth usually four times longer than the apical one, apical side of teeth straight, basal side straight or gently convex, angle between the trend of apical and basal sides wide acute with blunt tip, tertiary vein from the marginal loop enters tooth medially; sinuses angular, acute; venation pinnate, weak brochidodromous; primary vein stout; secondary veins moderate, at least eight pairs, irregularly spaced, wide acute to the midvein, course curved; intersecondaries sometimes present, short, arising at higher angles than the contiguous secondaries; intercostal tertiary veins moderate, mixture of alternate and opposite percurrent, usually sinuous, generally obtuse to the midvein; quaternary veins thick, orthogonal; quinternary veins thick, relatively randomly oriented, forming well-developed areolations; areoles polygonal, small to medium in size; ultimate veinlets present, but cannot be observed in detail.

Discussion.—Both the winged-nut and leaflet bear resemblance to extant *Pterocarya stenoptera*, and *P. protostenoptera* originally described based on fossil fruits from the Upper Miocene Takamine Formation (Tanai, 1961: pl. 4, fig. 10). Leaflets of this species, initially described from the Middle Miocene Shanabuchi Flora (Tanai and Suzuki, 1965), can be distinguished from that of *P. japonica* by relatively remote secondary veins and marginal teeth, and less conspicuous intercostal tertiary veins.

Materials.—FPDM-P-568 (Loc. 1), 594-2 (Loc. 2).

Order MALPIGHIALES Martius, 1835
Family SALICACEAE Mirbel, 1815
Genus *POPULUS* Linnaeus, 1753
Populus sp.
(Fig. 5-12)

Discussion.—One large fragmentary leaf was referable to the genus *Populus* in combination of the following characters: wide-ovate foliar shape; simple serrate margin probably with rounded tip; distinct primary and secondary veins, the latter forming loops just below the margin; closely-spaced percurrent tertiary veins.

Material.—FCMNH-GF0485 (Loc. 1).

Order ROSALES Perleb, 1826
Family ULMACEAE Mirbel, 1815
Genus *ULMUS* Linnaeus, 1753
Ulmus carpinoides Goeppert, 1855
(Fig. 6-2, 3, 4, 5)

Ulmus carpinoides Goeppert, 1855, p. 28, pl. 13, figs. 4-8; pl. 14, fig. 1.

Description.—Laminae asymmetrical, microphyll to mesophyll in size, ovate to elliptic in shape; length estimated 3.0 to 14.0 cm, width estimated 1.6 to 6.0 cm; length to width ratio 1.88 to 2.48; apex middle acute, acuminate; base wide acute to obtuse, usually cordate, sometimes convex; petiole thick below, at least 8 mm long; margin serrate, slightly revolute; teeth compound; primary teeth flexuous on the apical side, convex on the basal side, angle between the trend of apical and basal sides acute to right angles, secondary vein enters tooth slightly basally and usually bends up; subsidiary teeth sometimes present, small, situated along the basal flanks of large primary teeth; sinuses angular, acute; venation pinnate, craspedodromous; primary vein moderate, straight or sinuous; secondary veins thick, at least 15 pairs, irregularly spaced, arising at approximately 40 degrees from the midvein, angle smoothly increasing toward the base, decurrent near the divergence on the basal few pairs, straight or slightly sinuous in course, forked several times; tertiary veins thin, percurrent or relatively randomly oriented, closely spaced (ca. 6/cm); higher order venations and veinlets not observable.

Discussion.—*Ulmus carpinoides* is one of the most common elm species found among the Tertiary floras of the Northern Hemisphere. Because this species shows a wide range of variation in leaf form (Reimann, 1917), it still needs further study to determine its taxonomic placement. The author follows here the treatment mentioned by Huzioka (1963a) that this species was applicable to the ulmaceous leaves showing ovate to elliptic leaf form, cordate base, acuminate apex, and compound marginal serration with acutely pointed teeth. Among the living Asiatic species of elms, Huzioka (1963a) compared it with *U. pumila* Linnaeus of China.

Materials.—FPDM-P-501, 505, 512, 581 (Loc. 1).

Ulmus longifolia Unger, 1847
(Fig. 6-1)

Ulmus longifolia Unger, 1847, p. 101, pl. 26, figs. 5, 6.

Description.—Lamina asymmetrical, size microphyll, narrowly elliptic in shape; length estimated 7.1 cm, width 1.5 cm; length to width ratio 4.7; apex missing but apparently narrowly acute; base middle acute, convex or straight; petiole very thick, 6.0 mm long; margin serrate, slightly revolute, fringed with a fimbrial vein; teeth compound; primary teeth typically flexuous on the apical side, convex on the basal side, angle between the trend of the apical and basal sides mostly right angles at middle portion, secondary vein enters tooth basally and bends up; secondary teeth sometimes situated along the basal flanks of large primary teeth; sinuses angular, wide acute to obtuse; venation pinnate, craspedodromous; primary vein moderate, curved basally; secondary veins thick, at least 20 pairs, diverging at an angle of approximately 40 degrees on middle portion, angle smoothly increasing toward the base, course straight or gently curved, abruptly curving up near the margin and thence curved abmedially to enter teeth; intersecondaries occasional, short, parallel to contiguous secondaries; intermediate veins between the secondary and tertiary orders arising abmedially from secondary veins, entering either small teeth or sinuses; intercostal tertiary veins indistinct, sometimes percurrent; higher order venation and veinlets not observable.

Discussion.—The fossil is marked by a narrow elliptic shape, a cuneate or slightly convex base and indistinct marginal teeth, both flanks of which typically make right angles. Based on those features as well as the shape of the teeth, the specimen was assigned to *Ulmus longifolia*. According to Mädler (1939), and Oishi and Huzioka (1954), this species is related to some modern Chinese species, such as *U. lanceifolia* Roxburgh ex Wallich of Yunnan Province and *U. castaneifolia* Hemsley of southern China. This species is one of the most common elements of the Daijima-type flora.

Material.—FCMNH-GF4900 (Loc. 1).

Genus *ZELKOVA* Spach, 1841
Zelkova ungeri (Ettingshausen) Kovats, 1851
(Figs. 3-1a, b; 6-6, 7)

Planera Ungeri Ettingshausen, 1851, p. 14, pl. 2, figs. 5-18.
Zelkova ungeri (Ettingshausen) Kovats, 1851, p. 178.

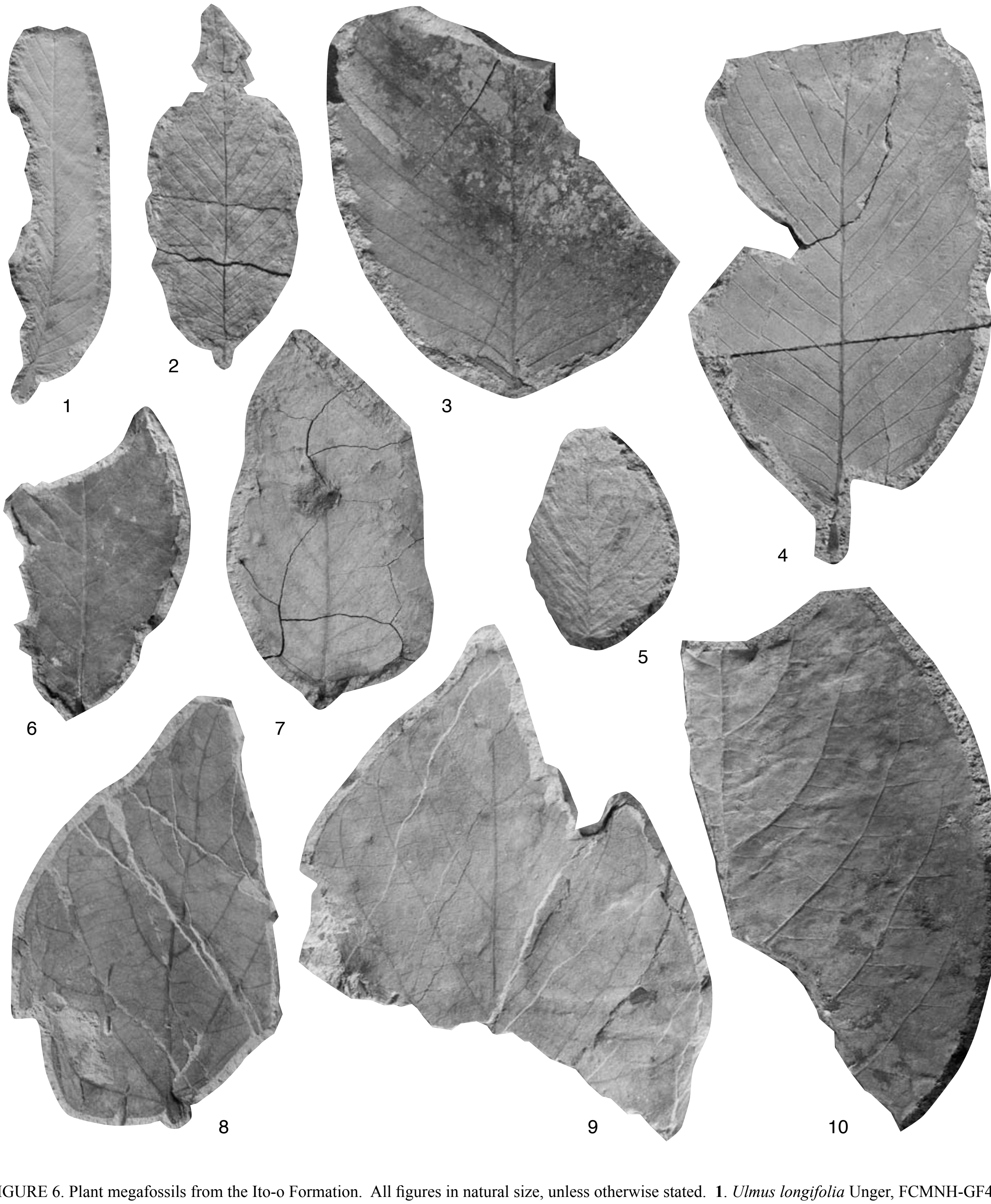

FIGURE 6. Plant megafossils from the Ito-o Formation. All figures in natural size, unless otherwise stated. **1**. *Ulmus longifolia* Unger, FCMNH-GF4900, Loc. 1. **2**, **3**, **4**, **5**. *Ulmus carpinoides* Goeppert, Loc. 1; 2, FPDM-P-501; 3, FPDM-P-505; 4, FPDM-P-581; 5, FPDM-P-512, x1.5. **6**, **7**. *Zelkova ungeri* (Ettingshausen) Kovats, Loc. 1; 6, FPDM-P-513; 7, FPDM-P-519. **8**, **9**. Fabaceae gen. et sp. indet., Loc. 2; 8, FPDM-P-67; 9, FPDM-P-69-3. **10**. *Stewartia* sp. cf. *S. submonadelpha* Tanai et Onoe, FCMNH-GF0467, x0.9, Loc. 1.

Description.—Laminae slightly asymmetrical, microphyll, narrowly ovate to elliptic in shape; apex narrowly acute, probably acuminate; base wide acute, convex to rounded; length estimated 3.1 to 6.8 cm, width estimated 1.4 to 3.1 cm; petiole thick, at least 3 mm long; margin serrate; teeth simple, large, regularly arranged, typically flexuous on the apical side, convex on the basal side, angle between the trend of apical and basal side of teeth widely acute to right angles, apex pointed with mucronate tip, apically oriented, secondary vein enters tooth slightly basally; sinuses angular, acute; venation pinnate, craspedodromous; primary vein moderate, straight, sometimes sinuous; secondary veins moderate, at least eight pairs, irregularly spaced, divergent angle against the midvein middle acute on the middle portion, course usually curved, sometimes recurved near the base, rarely forked near the divergence; tertiary vein moderate to thin, random reticulate, rarely percurrent, obtuse to the midvein; quaternary veins thick, relatively randomly oriented, forming meshes of irregular size and shape; ultimate veinlets not observable.

Discussion.—These fossil leaves characterized by pinnate venation, simple serrate margin, with ulmaceous teeth are readily identical to the genus *Zelkova*. *Z. ungeri* is one of the most common elements in the temperate forests in the Northern Hemisphere during the Tertiary. It has a wide range of variation in leaf form, and it is suspected to be an aggregate. Detailed examination of reproductive organs, which are less common in occurrence, is needed to solve the problem. This species superficially resembles the extant *Z. serrata* (Thunberg) Makino, which grows in temperate to warm-temperate forests of Honshu, Shikoku, and Kyushu in Japan, extending into Korea, Taiwan and China.

Materials.—FPDM-P-513, 519, 539-1, 2 (Loc. 1).

Order SAPINDALES Dumortier, 1829
Family ANACARDIACEAE R. Brown, 1818b
Genus *RHUS* Linnaeus, 1753
Rhus sp.
(Fig. 5-7)

Description.—Lamina asymmetrical, size microphyll, oblong; apex missing; base nearly right angle, convex; length estimated 7.2 cm, width 2.8 cm; length to width ratio 1.7 to 2.6; petiolule missing; margin crenate; teeth simple, irregularly spaced, both the apical and basal side of teeth convex with rounded tip, the angle between the trend of both sides of the teeth obtuse, principle vein enters tooth basally and typically bends up along the basal margin; sinuses angular, obtuse to nearly right angle; venation pinnate, craspedodromous; primary vein stout, gradually tapering till the apex, weakly sinuous; secondary veins moderate, more than ten pairs, irregularly spaced, acute (50- to 60-degree angles) to the midvein, course straight as much as three-fourths the distance toward the margin, rarely sinuous, abruptly curved, sometimes forked near the margin; intersecondaries often present, as thick as contiguous secondaries, usually long, extending near the margin, parallel to the secondaries; intercostal tertiary veins moderate to thick, derived from both the abmedial and admedial side of secondaries, directed exmedially, dichotomizing, rarely percurrent; higher order venation and veinlets not observable.

Discussion.—The materials are characterized by inequilateral foliar shape, irregular secondary veins that bend abruptly near the margin, and dichotomizing intercostal tertiaries. From these characters, they are referable to the genus *Rhus*. Among fossil species belonging to the genus *Rhus*, *R. hinokinaiensis* Huzioka bear crenate margins. However, the present material is too fragmentary and does not show fine venation characters to classify it at the species level. *R. ezoense*, described by Tanai (1961) from the Yoshioka Formation, also yields distinct marginal serration; however, it is distinguished from the present one in its equilateral shape, rounded base and percurrent intercostal tertiaries.

Material.—FPDM-P-533 (Loc. 1).

Family SAPINDACEAE Jussieu, 1789
Genus *ACER* Linnaeus, 1753
Section *MACRANTHA* Pax, 1885
Acer palaeorufinerve Tanai et Onoe, 1961
(Fig. 7-4)

Acer palaeorufinerve Tanai et Onoe, 1961, p. 49, pl. 16, figs. 2, 3.

Description.—Leaf notophyll, palmately three- or five-lobed, pentagonal in outline, base cordate; length estimated 7.2 cm, width estimated 6.0 cm; length to width ratio 1.2; petiole missing; margin serrate; teeth compound, usually one or two smaller teeth situated on the basal flank of large primary teeth, distant, primary teeth flexuous/convex, secondary teeth convex/convex, tooth apex acutely pointed, angles between the apical and basal flanks of teeth acute to obtuse, secondary or tertiary vein enters tooth medially; sinuses angular, acute to obtuse; medial lobe largest, triangular in shape, length of each lobe abruptly decreasing basally; apex of each lobe probably long acuminate; lobes shallowly dissected by obtuse sinuses; venation basal actinodromous with three or five primary veins; primary veins weak to moderate; medial primary sinuous, medial lateral primaries gently curved, 50 to 65 degrees from the midvein, basal primaries (or thick secondaries) curved, obtuse to the midvein; secondary veins thick, semi-craspedodromous, irregularly spaced, usually wide acute against the primaries, curved, abruptly curving up around two-thirds the distance toward the margin, exmedially sends off secondary branch or tertiaries that feed into marginal teeth; intersecondaries not observable; intercostal tertiary veins moderate, random reticulate or percurrent, sinuous in course; higher order veins and ultimate veinlets not observable.

Discussion.—Although the present material is not clear in its fine venation characters, it is readily assigned to the section *Macrantha* of the genus *Acer* in its pentagonal foliar shape, long acuminate lobe apex, and marginal characters. Among two leaf species belonging to the section *Macrantha* from Tertiary of East Asia (Tanai, 1983), *A. palaeorufinerve* Tanai et Onoe and *A. uemurae* Tanai et Ozaki (Tanai and Ozaki, 1977), the present material coincides with the former in all characters described above. The latter species is distinguished in much deeply incised sinuses as well as a marginal large tooth that bears minute subsidiary teeth on both the apical and basal flank. *A. palaeorufinerve* has been reported from the late Early to Late Miocene floras of East Asia. This species resembles the extant *A. rufinerve* Siebold et Zuccarini growing in temperate forests in Japan. Tanai (1983) also compared it with the modern *A. pennsylvanicum* Linnaeus of eastern North America.

Material.—FPDM-P-552-1 (Loc. 1).

Section *PALMATA* Pax, 1885
Acer protojaponicum Tanai et Onoe, 1959
(Fig. 7-8)

Acer protojaponicum Tanai et Onoe, 1959, p. 281, pl. 6, figs. 5, 7, 8.

Discussion.—Although the present material is fragmentary, it is assignable to *Acer protojaponicum* in the following characters: at least a palmately seven-, or probably nine-lobed leaf, shallowly dissected by narrow acute sinuses; cordate base;

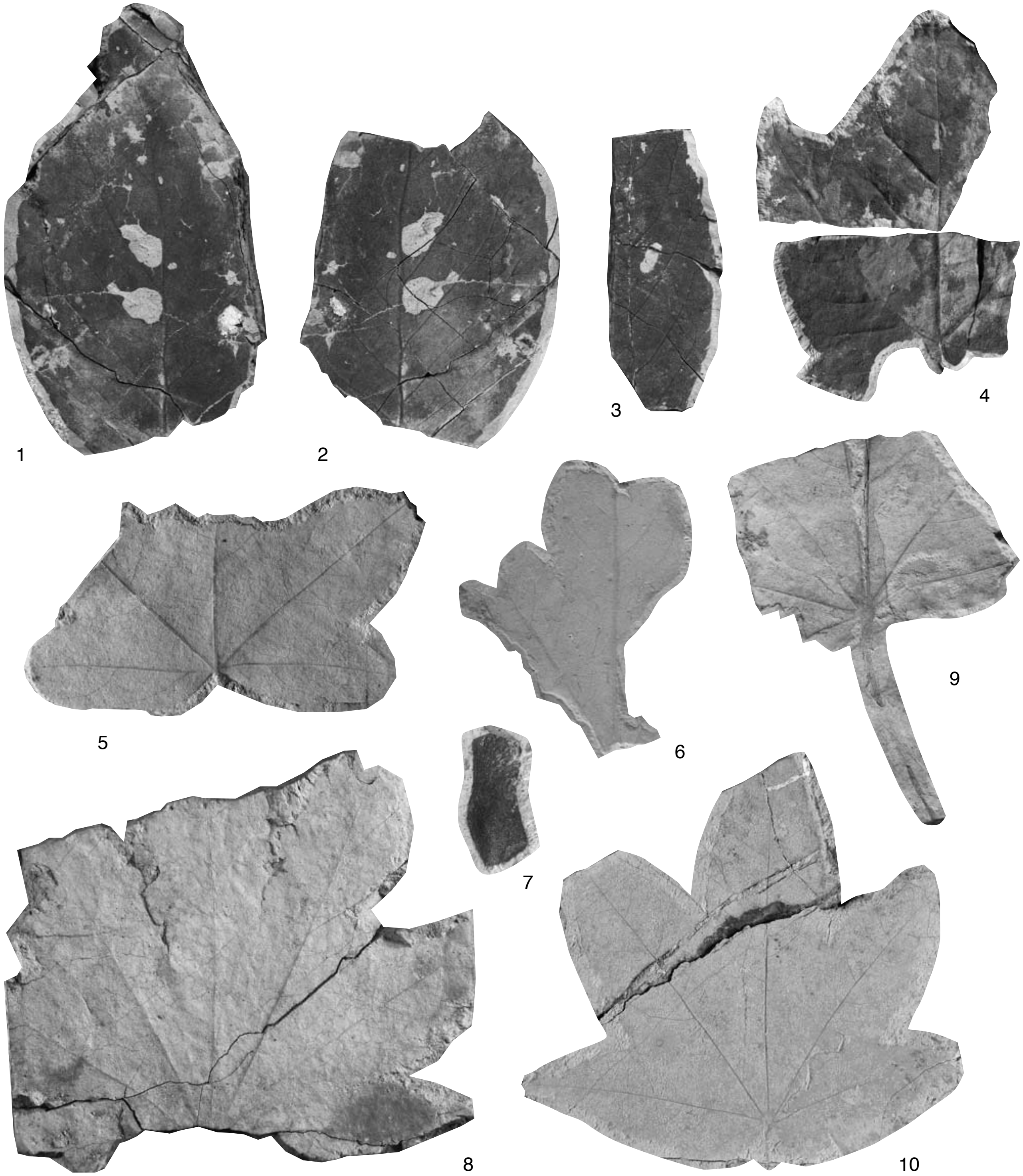

FIGURE 7. Plant megafossils from the Ito-o Formation. All figures in natural size, unless otherwise stated. **1**, **2**. *Styrax protojaponica* Tanai, FPDM-P-554&555, Loc. 1. **3**. *Stewartia* sp. cf. *S. submonadelpha* Tanai et Onoe, FPDM-P-573, Loc. 1. **4**. *Acer palaeorufinerve* Tanai et Onoe, FPDM-P-552-1, Loc. 1. **5–7**. *Acer nordenskioeldi* Nathorst; 5, FCMNH-GF4902a, Loc. 1; 6, FPDM-P-477-2, x1.2, Loc. 2; 7, FPDM-P-575, x2.5, Loc. 1. **8**. *Acer protojaponicum* Tanai et Onoe, FCMNH-GF0541, Loc. 1. **9**, **10**. *Acer rotundatum* Huzioka, Loc. 1; 9, FCMNH-G174-255; 10, FPDM-P-580, x0.9.

relatively large, compound marginal teeth with acutely pointed tip; craspedodromous secondary veins. *A. protojaponicum* was established based on samara and one fragmentary leaf from the Shichiku Formation in Fukushima Prefecture (Tanai and Onoe, 1959). It was subsequently supplemented by a well-preserved leaf found from the Late Miocene Shanabuchi Formation in Hokkaido (Tanai, 1961). This species has a general resemblance with the extant *A. japonicum* Thunberg that grows widely in Japan.

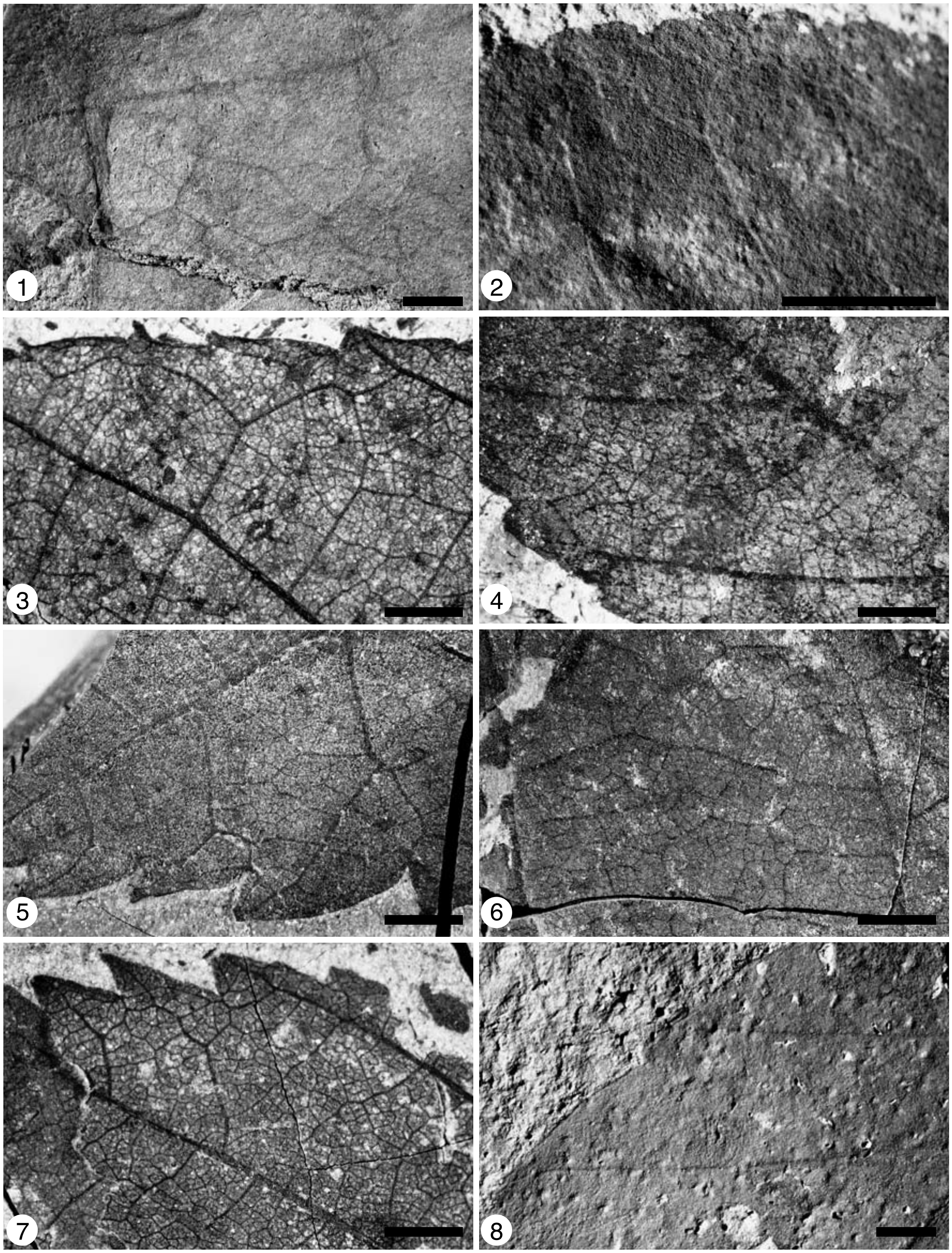

FIGURE 8. Photomicrographs of selected species of the Ito-o Flora. Scale bar equals 2 mm long. **1**. *Parrotia pristina* (Ettingshausen) Stur, FPDM-P-495-3. **2**. *Gleditsia miosinensis* Hu et Chaney, FPDM-P-536-1. **3**. *Alnus miojaponica* Tanai, FPDM-P-572-1. **4**. *Betula oobae* Suzuki, FPDM-P-550. **5**, **6**. *Betula mioluminifera* Hu et Chaney, FPDM-P-551-1. **7**. *Betula uzenensis* Tanai, FPDM-P-542-2. **8**. *Fagus antipofi* Heer, FPDM-P-73.

Material.—FCMNH-GF0541 (Loc. 1).

Acer nordenskioeldi Nathorst, 1883
(Figs. 7-5, 6, 7; 9-4)

Acer nordenskioeldi Nathorst, 1883, p. 60, pl. 11, figs. 11-17.

Discussion.—Two fragmentary leaves and a winged-seed obtained from the formation were independently compared with *Acer nordenskioeldi* Nathorst. Leaf remains are characterized

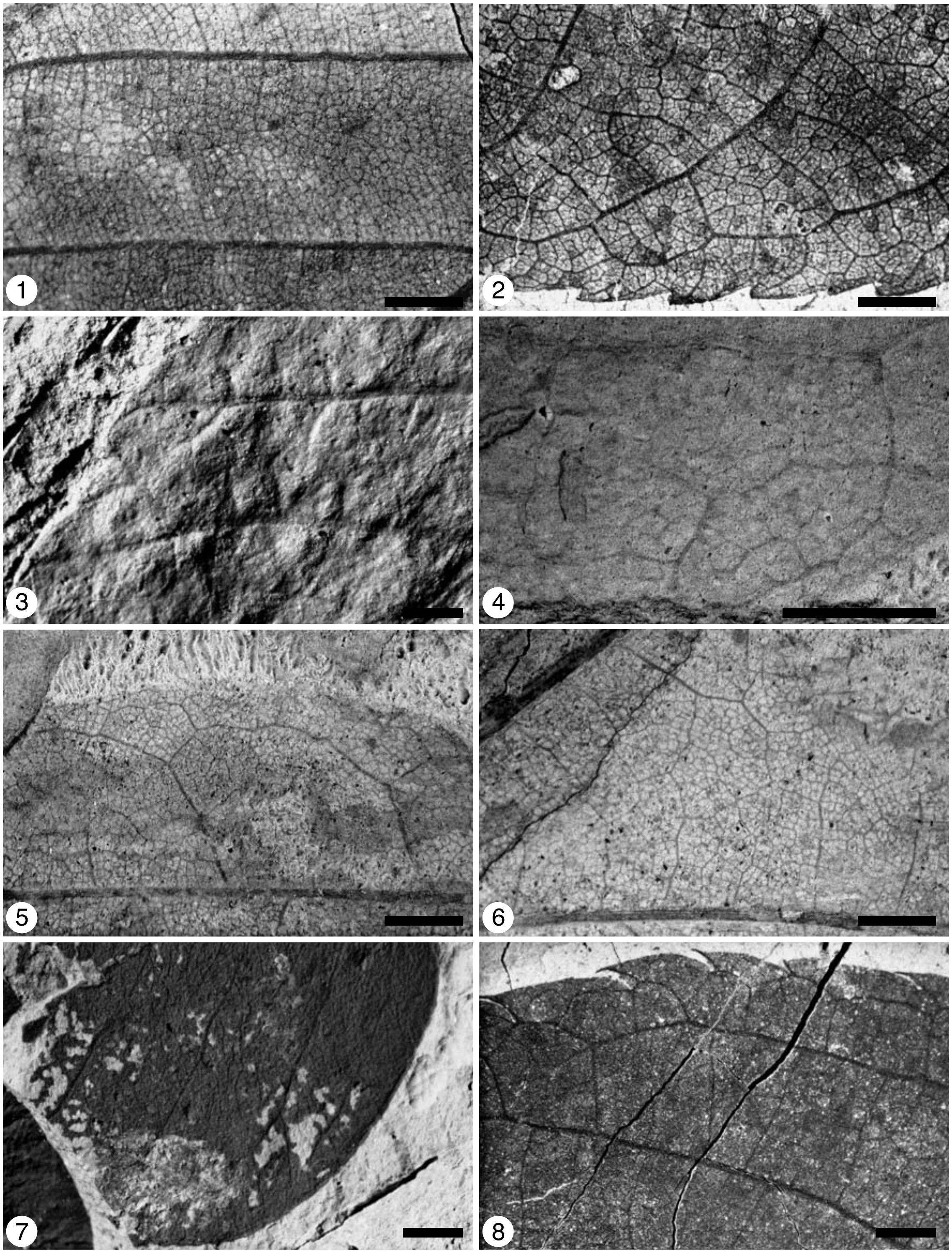

FIGURE 9. Photomicrographs of selected species of the Ito-o Flora. Scale bar equals 2 mm long. **1**. *Fagus antipofi* Heer, FCMNH-GF0529. **2**. *Pterocarya protostenoptera* Tanai, FPDM-P-568. **3**. *Rhus* sp., FPDM-P-533. **4**. *Acer nordenskioeldi* Nathorst, FPDM-P-477-2. **5**, **6**. *Acer rotundatum* Huzioka, FCMNH-G174-255. **7**. *Gleditsia miosinensis* Hu et Chaney, FPDM-P-477-3. **8**. *Stewartia* sp. cf. *S. submonadelpha* Tanai et Onoe, FPDM-P-573.

by palmately five-lobed leaves dissected by medium to shallow sinuses. The leaf margin appears entire but with tiny acute teeth which are generally distantly arranged (Fig. 7-5, 6). The areoles are well-developed with large polygonal meshes that give rise to veinlets branched several times (Fig. 9-4). The winged-seed is characterized by its small size, thick seed part bulged outwardly from the margin of the wing, inner margin of the wing extending to the contact scar, and a divergent angle of ca. 120 degrees.

This species is closely related to the extant *A. palmatum* Thunberg of Japan.

Materials.—FPDM-P-477-2 (Loc. 2), 575 (Loc. 1); FCMNH-GF4902a (Loc. 1).

Section *PLATANOIDEA* Pax, 1885
Acer rotundatum Huzioka, 1943
(Figs. 7-9, 10; 9-5, 6)

Acer rotundatum Huzioka, 1943, p. 129, pl. 24, figs. 1-3; pl. 25, fig. 2.

Description.—Leaves palmately seven-lobed, slightly inequilateral; lobes narrowly oblong to narrowly elliptic, medial lobe nearly as same width as adjacent ones, length of each lobe gradually decreasing basally; apex of each lobe missing, but apparently narrowly acute, probably acuminate; lobe sinuses angular, medium to widely acute, dissected for no more than half the lamina length; lamina mesophyll, very widely ovate; base deeply cordate; length estimated 8.4 cm, width 8.5 cm; length to width ratio ca. 1.0; petiole thick, at least 3.4 cm long; margin entire; venation basal actinodromous with seven primary veins; primary veins moderate, sinuous, curved exmedially; secondary veins moderate to thick, brochidodromous, at least five pairs on each lobe, arising at 45 to 70 degrees from the primaries, angle decreasing basally, curved or nearly straight up to three-fifths the way, abruptly curving up to form large loop with adjacent secondary veins; intersecondaries occasional, weak, arising at slightly higher angles than secondaries; tertiary veins moderate, random reticulate; quaternary veins moderate, regular polygonal reticulate; areoles well-developed, polygonal, small to medium in size; ultimate veinlets absent, simple or rarely branched once; marginal ultimate venation looped.

Discussion.—The present materials are readily identical to the section *Platanoidea* of the genus *Acer* in their shape, entire margin, and thick quaternary and quinternary veins comprising small to medium areoles with no or single ultimate veinlets, and are assigned to *A. rotundatum* Huzioka. Characters distinguishing them from the other species in the section *Platanoidea* include such characters as: palmately seven-lobed leaf; shallowly dissected sinuses; entire margin. This species is assumed to relate to the modern *A. mono* Maximowicz of East Asia.

Materials.—FPDM-P-580 (Loc. 1); FCMNH-G174-255 (Loc. 1).

Order ERICALES Dumortier, 1829
Family STYRACACEAE De Candolle & Sprengel, 1821
Genus *STYRAX* Linnaeus, 1753
Styrax protojaponica Tanai, 1976
(Fig. 7-1, 2)

Styrax japonicum Siebold et Zuccarini fossilis Nathorst, 1883, p. 50, pl. 14, figs. 6-8.

Styrax protojaponica Tanai, 1976, p. 340, pl. 2, fig. 4; text-figs. 6-m&n.

Discussion.—The specimen was assigned to *Styrax protojaponica*, originally described from the Pliocene Mogi Flora of Nagasaki Prefecture in the following characters: wide elliptic foliar shape; remote, tiny teeth with bar-like projections situated on the upper half of the blade; festooned brochidodromous secondaries often bifurcated at middle acute angle; basally close-spaced secondary veins. *S. protojaponica* is similar to the modern *S. japonica* Siebold et Zuccarini, which grows in the temperate to subtropical forests of Japan, Korea and China. However, the present specimen yields a larger number of secondaries than the modern relative.

Materials.—FPDM-P-554, 555 (Loc. 1).

Family THEACEAE Mirbel ex Ker-Gawler, 1816
Genus *STEWARTIA* Linnaeus, 1753
Stewartia sp. cf. *S. submonadelpha* Tanai et Onoe, 1961
(Figs. 6-10; 7-3; 9-8)

Compare: *Stewartia submonadelpha* Tanai et Onoe, 1961, p. 53, pl. 18, fig. 6.

Discussion.—Two fragmentary leaves were obtained from Locality 1 of the Ito-o Formation. Although they are different from one another in size and shape, both of them bear characters common to the genus *Stewartia* as follows: regularly serrate margin; spinose tooth, primary vein of which runs closely to the apical side; festooned brochidodromous secondary veins; percurrent tertiary veins oriented nearly perpendicular to the midvein. Among fossil *Stewartia* described so far from the Tertiary floras of Japan, they are most similar to *S. submonadelpha*, which was originally described from the Late Miocene Tatsumitoge Flora, in number of secondaries and marginal characters. However, the author hesitates to decide on a specific name, owing to their fragmentary nature, as well as their lack of fine venation characters.

Materials.—FPDM-P-573 (Loc. 1); FCMNH-GF0467 (Loc. 1)

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