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Cenozoic History of Evergreen Broad-leaved Forest in Japan

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Abstract The floral and vegetation history of Japan from the Eocene to the Pleistocene is reviewed based mainly on plant macrofossils and pollen. Changes in the distribution of evergreen broad-leaved forests are discussed with reference to paleotopographical changes. Eocene floras in Hokkaido and southwestern Japan include many evergreen broad-leaved trees. However, the fossil evidence showing the existence of evergreen broad-leaved forest since the Oligocene is limited spatially and temporally to Honshu in the late Early and earliest Middle Miocene, the Pacific Coast of central Honshu in the Late Miocene, Kyushu in the middle Pliocene and the Pacific Coast of central Honshu and Kyushu in the late Middle Pleistocene. The distribution of evergreen broad-leaved forest was limited to more southern and littoral areas than these fossil localities. The distribution can be explained in general by the configuration of land and sea, as the distribution is assumed to have been influenced by warm sea currents at each stage. The lack of evergreen broad-leaved forest in most areas throughout the late Cenozoic indicates that these areas have always been subject to a continental climate even in maritime regions during warmer ages.

Key words: Cenozoic, evergreen broad-leaved forest, paleoclimate, paleovegetation, plant macrofossils.

Japan is situated along the northern border of the evergreen broad-leaved forest zone in eastern Asia. Most of the southern half of the country is thought to have been potentially covered by evergreen broad-leaved forest in the late Holocene (Suzuki, 1982). Although most areas of the forest zone have been changed to plantations and secondary coniferous or deciduous broad-leaved forests, the fragmented semi-natural forests are dominated by evergreen Fagaceae such as *Cyclobalanopsis* and *Castanopsis*. This type of evergreen broad-leaved forest is characteristic of the humid warm-temperate zone in eastern Asia and termed "lucidophyll forest" (Kira, 1991).

Extensive pollen and plant macrofossil data from the Holocene sediments have reconstructed the paleovegetation before devastation in historical ages (Tsuji, 1989) and clarified the process of development of evergreen broad-leaved forests in Japan since the Last Glacial (Matsushita, 1992). However, Tertiary vegetation history in eastern Asia has been reviewed in more detail for deciduous broad-leaved trees (e.g. Tanai, 1972, 1992) and the paleobotany of the Quaternary has mentioned mainly conifers and deciduous broad-leaved trees (e.g. Minaki, 1989). The vegetational history of evergreen broad-leaved trees to the Quaternary has been clarified less. This is because fossil assemblages showing the existence of evergreen broad-leaved forests before the Holocene are few except for the Eocene and the late Early and earliest Middle Miocene. In addition, it is harder to identify fossil evergreen tree taxa than deciduous trees because the thick leaves lack conspicuous characteristics in their architecture. The present paper reviews records of fossil evergreen broad-leaved trees with the quantitative data for fossil assemblages to summarize the temporal and spatial distribution of evergreen broad-leaved forest in relation to topographical changes in Japan.

Material and Method

Fig. 1 shows the horizontal distribution of evergreen broad-leaved forest zone in Japan

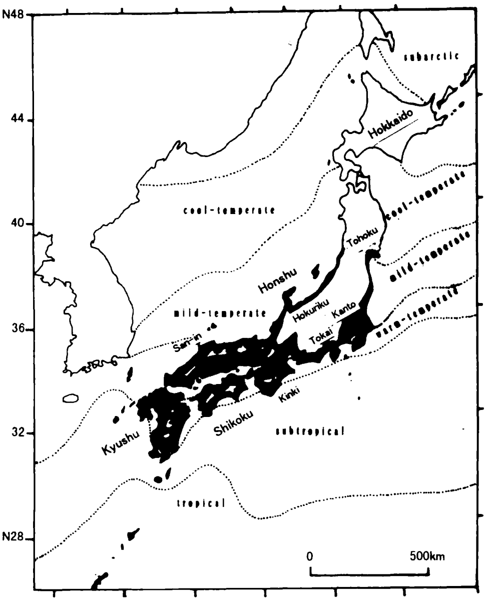

Fig. 1. Recent horizontal distribution of the evergreen broad-leaved forest zone and modern marine zoogeographic divisions according to Nishimura (1981) and Ogasawara (1994). Black area indicates the evergreen broad-leaved forest zone according to Suzuki (1982).

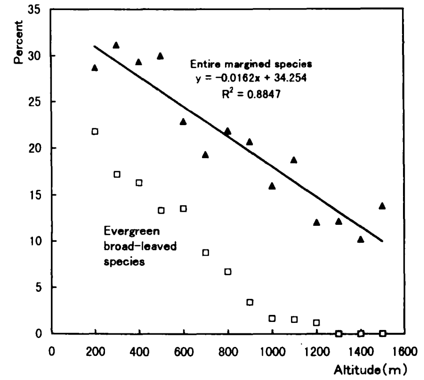

Fig. 2. Vertical distribution of percent entire-margined species and evergreen broad-leaved species in the flora in transects along the Ohi-gawa Valley along the Pacific coast of central Japan based on data by Takahashi (1962). The lower limit of beech (*Fagus crenata*) forest and upper limit of the distribution of *Cyclobalanopsis* is 800 m.

based on the composition of the recent fragmented semi-natural vegetation (Suzuki, 1982). The forest zone is dominated by evergreen oaks of *Cyclobalanopsis*, *Castanopsis*, and *Pasania* associated with rich evergreen tree taxa such as *Machilus*, *Cinnamomum*, *Ilex*, *Symplocos* and *Camellia* (Kira, 1991). This type of forest is peculiar to the warm-temperate zone of the eastern Asia and is known as "lucidophyll forest". The characteristics of the evergreen broad-leaved forest in eastern Asia are less xeromorphic than the Sclerophyll or Mediterranean Forest Formation on the western side of Eurasia and other continents (Kira, 1991). For instance, there are larger shiny leaves, a richer flora including many epiphytes and woody lianas, and a larger tree size (Kira, 1991). The climate of the forest zone is characterized by high annual rainfall amounting to 1300–2500 mm, and especially its high summer and autumn rainfall, which contrasts with the Sclerophyll Forest Formation which has little summer rainfall (Kira, 1991).

Evergreen broad-leaved forest borders on cool temperate deciduous broad-leaved forest dominated by beech (*Fagus crenata*) under a maritime climate in Japan (Kira, 1991). For example, in the mountains along the Pacific Coast in central Honshu the number of evergreen broad-leaved tree taxa decreases towards higher elevations and becomes fewer around the lower limit of beech forest (Fig. 2). Fig. 2 shows the percent of entire-margined species among broad-leaved tree species as a climatic indicator correlated with the mean annual temperature (Wolfe, 1979). However, the horizontal and vertical distribution of evergreen broad-leaved taxa actually tends to be limited by the duration of low temperatures in winter rather than the mean annual temperature and warmth during the growing season (Kira, 1949). Evergreen broad-leaved taxa become fewer and evergreen broad-leaved forest is lacking in the inland districts of central Japan where growing season temperatures are within the range of the warm-temperate zone, but where there is increased winter coldness (Fig. 1).

The present paper compares the distribution of evergreen broad-leaved forest with the past marine climates. This is because the marine climate in the late Cenozoic was reconstructed in detail based on well-studied fossil molluscan fauna (e.g. Ogasawara, 1994)

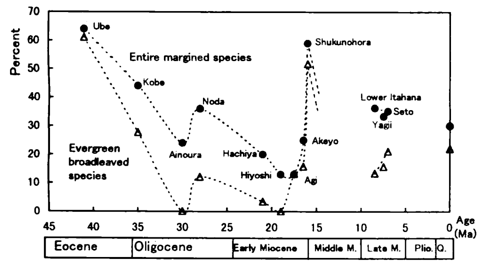

Fig. 3. Temporal changes in percent of entire-margined species and evergreen broad-leaved species in the fossil flora in southwestern Japan. Letters in the figure indicate the fossil localities. References for the fossil floras are Huzioka and Takahashi (1970) for Ube, Hori (1976) for Kobe, Ina (1992) for Hachiya, Hiyoshi, Agi, Akeyo and Shukunohora, Ozaki (1991) for Lower Itahana, Yagii and Seto, and Tanai (1961) for Ainoura, Tanai and Uemura (1991a, b) for Noda Floras. The ages of the Paleogene floras are based on Ozaki (1992). The values at 0 on the time scale are based on the floristic data in a transect at 200 m above sea level along the Ohi-gawa Valley on the Pacific coast of central Japan (Takahashi, 1962).

and the terrestrial climate has been influenced by the marine climate. Fig. 1 indicates the division of recent marine climate zones along Japan (Ogasawara, 1994). The distribution of the marine climate relates to the distribution of terrestrial climatic zones based on forest physiognomy. However, the tropical zone with a marine climate corresponds to a subtropical zone with a terrestrial climate along the shoreline; subtropical, warm-temperate and most parts of mild-temperate zones with a marine climate correspond to a warm-temperate zone with a terrestrial climate.

The author classifies fossil taxa into evergreen or deciduous based on the characteristics of recent descendants of fossil taxa. This is because the texture (coriaceous or membranous, lustrous or not) of fossil leaves does not always indicate leaves which persisted during winter and the conditions for preservation may have changed the texture. However, intensive studies based on leaf venation patterns (e.g. Tanai, 1983; Ozaki, 1991; Uemura, 1988) have clarified detailed phylogenetic relationships between fossil and recent species, and among fossil species. As a result of these studies, many fossil ancestors of recent evergreen broad-leaved species have been described.

Cenozoic History of Evergreen Broad-leaved Forest in Japan

Japan was situated in and around the boundary between evergreen broad-leaved forest and deciduous broad-leaved forest zones for most of the Cenozoic (Tanai, 1972, 1992). In response to climatic fluctuations through the Cenozoic, the northern limit of the distribution of evergreen broad-leaved tree taxa migrated horizontally. Fig. 3 shows the change in evergreen broad-leaved species with the percent of entire-margined species for selected fossil flora at each stage in southwestern Honshu. The percent of the evergreen broad-leaved taxa is related to percent entire-margined species as a whole. That is, the floras in warmer stages such as the Middle Eocene and late Early to earliest Middle Miocene are characterized by the richness in evergreen broad-leaved taxa compared with the flora in cooler stages like the Oligocene and early Early and Late Miocene.

1. Paleogene

Paleocene sediments including plant macrofossils have not been described in Japan; however, many Eocene-Oligocene floras have been reported. Among them, the Middle Eocene to Lower Oligocene flora in Hokkaido has been studied well and correlated stratigraphically in detail by Tanai (1989, 1990, and 1992). The Middle Eocene floras in Hokkaido include abundant evergreen broad-leaved trees with many subtropical plants, representing the "Notophyllous Broad-leaved Evergreen Forest" (Wolfe, 1979; Tanai, 1992). Many evergreen elements such as *Cyclobalanopsis*, *Myrica*, *Cinnamomophyllum*, *Litseaphyllum* and *Myrtophyllum* are included with typical subtropical elements like *Sabalites* (Palmae). Compared with the flora in the Middle Eocene, the fossil floras in the early Late Eocene and late Early Oligocene are composed mainly of deciduous broad-leaved trees and conifers. In these floras evergreen broad-leaved trees are very rare and extant

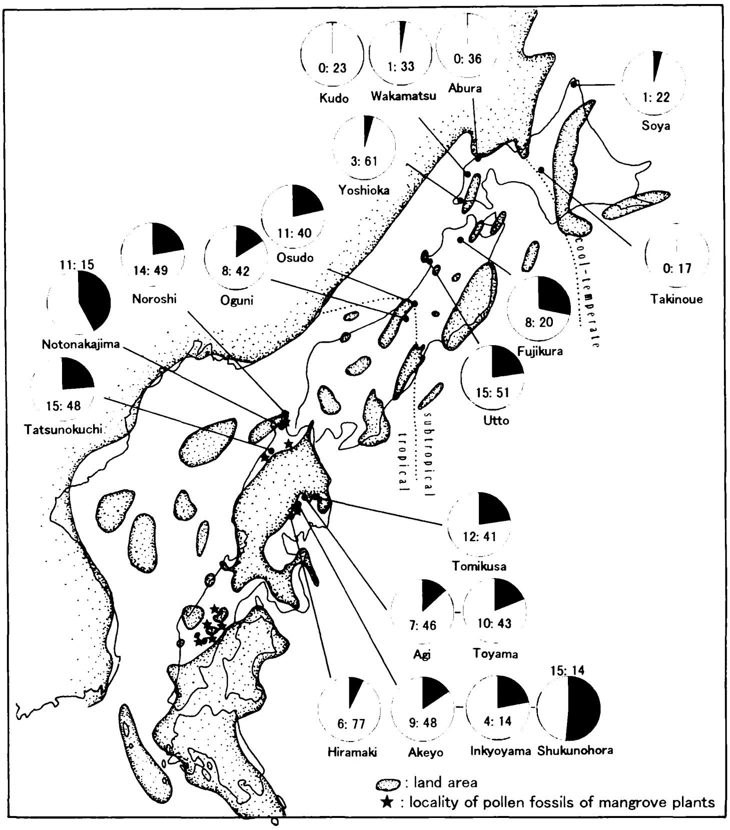

Fig. 4. Paleogeography and marine climate at 16 Ma, Earliest Middle Miocene (Ogasawara, 1994) and the percent evergreen taxa in broad-leaved tree flora in selected late Early Miocene to earliest Middle Miocene fossil floras (Ma 18–15). Letters in each circle indicate the number of evergreen (left) and deciduous (right) broad-leaved tree taxa. References for fossil floras are Ina (1988) for Akeyo and Ozaki (1974) for Inkyoyama in addition to the fossil floras in Table 1.

temperate genera such as *Alnus*, *Carpinus*, *Corylus*, *Quercus*, *Ulmus* and *Prunus* appeared and increased, though the early Late Eocene flora still includes many deciduous subtropical elements such as Euphorbiaceae, Sterculiaceae, Icacinaceae and Menyspermaceae (Tanai, 1992). Tanai (1990) related the floral change from the Middle to Late Eocene with the climatic deterioration in "Terminal Eocene Events" (Wolfe, 1978).

Eocene and Early Oligocene floras in southwestern Japan include more evergreen broad-leaved taxa than Hokkaido. The Eocene flora of the Ube Coal-field includes 60% of evergreen broad-leaved taxa among total dicotyledons (Huzioka and Takahashi, 1970). The flora includes evergreen taxa such as *Cyclobalanopsis*, *Castanopsis* and *Pasania* of Fagaceae, *Cinnamomum*, *Litsea* and *Machilus* of Lauraceae, *Ardisia*, *Maesa* and *Myrsine* of Myrsinaceae, and *Pittosporum*, *Distylium*, *Ilex*, *Ternstroemia*, *Syzygium*, *Sideroxylon* and *Cerbera* together with other subtropical elements whose modern relatives are distributed in southeastern Asia. The flora of the Kobe Group (Hori, 1976, 1987) in the late Eocene and earliest Oligocene (Ozaki, 1992) also includes many evergreen broad-leaved taxa. Hori (1987) listed 46 supposed evergreen broad-leaved taxa in this flora, including *Myrica*, *Castanopsis*, *Cyclobalanopsis*, *Pasania*, *Actinodaphne*, *Cinnamomum*, *Machilus*, *Neolitsea*, *Distylium*, *Camellia*, *Eurya*, *Eugenia*, *Aucuba*, *Dendropanax*, *Fatsia*, *Hedera*, *Pieris*, *Maesa*, *Myrsine*, *Nerium*, *Damnacanthus* and *Uncaria*. However, deciduous broad-leaved trees such as *Zelkova ungeri*, *Fagus stuxbergii*, *Castanea miomollissima* and *Liquidambar*

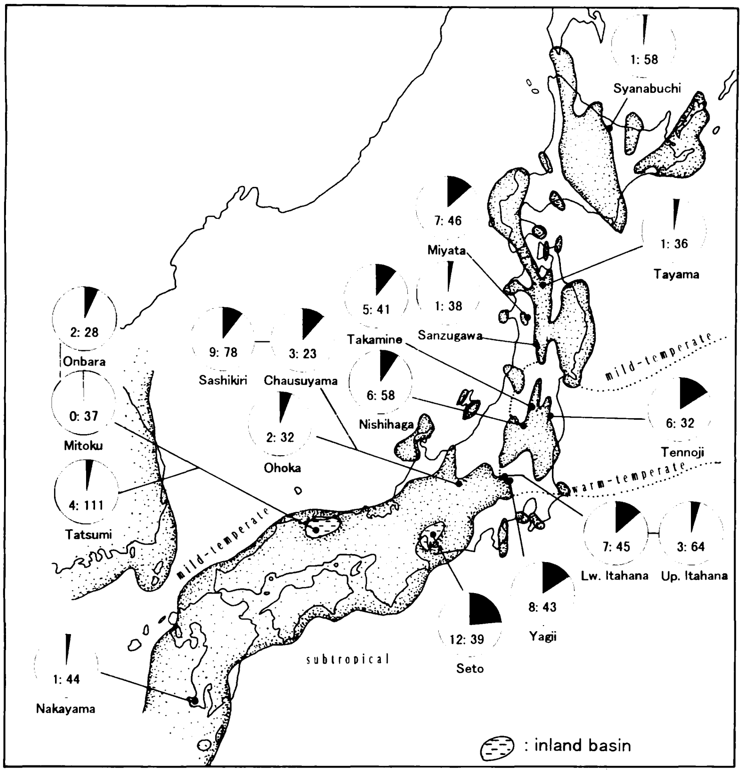

Fig. 5. Paleogeography and marine climate at 10–6 Ma, Late Miocene (Ogasawara, 1994) and the percent evergreen taxa in broad-leaved tree flora in selected Late Miocene fossil floras (Ma 9–6). Letters in each circle indicate the number of evergreen (left) and deciduous (right) broad-leaved tree taxa. References for fossil floras are Ozaki (1991) for Chausuyama and Ohoka, Suzuki (1959a) for Tennoji, and Suzuki (1959b) for Nishihaga in addition to the fossil floras in Table 2.

miosinica, and taxodiaceous conifers as *Sequoia* and *Metasequoia*, dominate the fossil assemblages in this flora and the quantity of evergreen fossil broad-leaves are small (Hori, 1976).

The Late Oligocene flora in southwestern Japan includes fewer evergreen broad-leaved trees than the Early Oligocene flora. The Ainoura flora in the Sasebo Coal-field is composed of deciduous broad-leaved trees and conifers without evergreen broad-leaved trees (Tanai, 1961). The Noda flora in the Hioki Group in western Yamaguchi Prefecture includes *Litseaphyllum* sp., *Lithocarpus* sp., *Cyclobalanopsis nagatoensis* and *Eurya* sp., with 28 deciduous broad-leaved trees and 1 conifer (Tanai and Uemura, 1991a, b).

2. Miocene

The paleogeographic change in the Miocene has been reconstructed by many authors (e.g. Ogasawara, 1994) based on abundant geological data and marine invertebrate fossils. According to the data from paleomagnetism, Japan segregated from the Asian Continent and the Sea of Japan expanded with volcanic activity from 18 to 14 Ma in the late Early Miocene. By the earlier stage of the Middle Miocene (13 Ma), the expansion of the Sea of Japan ceased and Japan was settled near its recent position. The marine climate in the Miocene has been reconstructed in detail based on molluscan fauna (e.g. Ogasawara, 1994), indicating it was warmer in the late Early and earliest Middle Miocene and cooler in the early Early Miocene and later Middle and Late Miocene (Fig. 4, 5). Based on the occurrence of tropical mollusca such as *Geloina* and *Vicarya*, a "mangrove front", that is, a tropical zone border with a marine climate occurred across Northeast Honshu during a short stage in 16 Ma (Oga-

Table 1. Occurrence of selected fossil plants in the late Early to earliest Middle Miocene (18–15 Ma) floras. Abundance of fossil taxa in each flora are based on numerical data, except for the data concerning Soya, Kamigo, Osudo and Hiramaki that are represented only as letters indicating abundant, common and rare. References for fossil floras are Huzioka (1963) for Utto, Huzioka and Koga (1981) for Kamigo and Ikazuchi, Ina (1993) for Agi and Toyama, Ina (1988) for Tomikusa, Ina (1974,1981) for Hiramaki, Ishida (1970) for Noroshi, Kamoi (1976) for Osudo, Kitanaka and Fuji (1988) for Tatsunokuchi, Matsuo (1963) for Notonakajima, Onoe (1974) for Oguni, Tanai (1961) for Soya, Tanai and Suzuki (1963) for Abura and Yoshioka, Tanai and Suzuki (1972) for Wakamatsu and Kudo, and Tanai and Uemura (1988) for Takinoue and Fujikura Floras.

			Hokkaido						Tohoku						Hokuriku			Tokai			
	Fossil taxa	Modern relatives	Soya	Takinoue	Abura	Wakamatsu	Kudo	Yoshioka	Fujikura	Utto	Kamigo	Ikazuchi	Osudo	Oguni	Noroshi	Notonakajima	Tatsunokuchi	Tomikusa	Agi	Toyama	Hiramaki
	Cercidiphyllum crenatum	*C.japonicum*	+		+		+	+													
	Acer protonegundo	*(A. negundo)*			+	○	○	○													+
	Fagus antipofi	*(F.grandifolia)*			●	◎	●			+	+			+					+		
	Picea ugoana	*P.bicolor*			○	+	◎	+				*		+							
	Alnus protomaximowiczii	*A.maximowiczii*			+	○	◎	○		○		*									
	Acer rotundatum	*A.mono*			○	○	◎	○		○	+			+	+						
	Glyptostrobus europaeus	*(G.pensilis)*	◎	*	○		+	+	*	◎		*	○		+	+					
	Acer ezoanum	*A.miyabei*	+		○	○	●	◎			+				+			○	◎	+	
	Castanea miomollissima	*(C.mollissima)*			○	●		●		◎	◎	*	○	◎	○	○	○	◎	○	○	○
	Zelkova ungeri	*Z.serrata*		*	+	●	◎	●	*	◎	◎		●	●	●	○	◎	◎	◎	◎	◎
	Metasequoia occidentalis	*(M.glyptostroboides)*	◎	*	◎	○		○		◎	+		+	+	○	+	+	◎	○	○	○
	Pterocarya spp.		+	*		+	+	+	*	◎	○	*	○	○	○			●	○	○	◎
	"Ficus" tilliaefolia	(extinct genus)	+			+				○	+	*		◎	+	+	+		◎		+
	Comptonia naumanni	*(C.peregrina)*		*	+	+	●	+	*	◎	◎	*	+	●	◎	○	◎	◎		●	
	Liquidambar miocinica	*(L.formosana)*		*	+			○	*	◎	+	*	○	○	○	+	◎		○	○	◎
	Quercus miovariabilis	*Q.variabilis*		*		◎					+	*	●	◎	○		◎	●	●	●	◎
	Pinus miocenica	*P.densiflora*			+	○		◎	*	○	+		◎		+	●		○		◎	+
	Carpinus heigunensis	*C.tshonoskii*			+	○	○	+		+	+	*	◎	+	○	○		○	○	○	+
	Cyclocarya ezoana	*(C.paliurus)*			○	+		○			+	*		○	+		●				◎
	Keteleeria ezoana	*(K.davidiana)*				+	+	◎			+	*	◎	○	◎	+	+	◎	○	◎	+
e	*Camellia protojaponica*	*C.japonica*				+		+		+	+	*		+	○	◎					
	Carpolithes japonica	(unknown)					+			+	+		○	◎	○	+					+
	Ulmus carpinoides	*(U.davidiana)*					+			○		*						◎	●		○
	Diospyros miokaki	*D.kaki*						+		○			+	○		●				+	+
	Parrotia fagifolia	*(P.persica)*						○		◎	+	*	+	○	+			+	○	○	○
e	*Cyclobalanopsis mandraliscae*	*C.myrsinaefolia*							*	+	○	*	○	+	+	○		○			
e	*Cyclobalanopsis nathorstii*	*C.glauca*							*	○		*	○		○	●				○	+
e	*Actinodaphne* spp.								*	+		*		○					○		+
e	*Cinnamomum miocenum*	*C.camphora*							*	○		*	+	○	○		◎	○		+	
e	*Machilus ugoana*	*M.japonica*							*	○	+	*	○	○	○				+	○	
e	*Machilus nathorstii*	*M.thunbergii*								+	+	*	○		+	◎					
	Libocedrus notoensis	*(L.formosana)*								○		*	◎	+	◎	◎		◎		+	
	Cunninghamia protokonishii	*(C.konishii)*								+	+	*			+	+		○	+	○	
e	*Cyclobalanopsis praegilva*	*C.gilva*								+	+	*	○		○	○			+	●	
e	*Castanopsis miocuspidata*	*C.cuspidata*								+	+	*			+	○		○		○	
e	*Cinnamomum oguniense*	*C.reticulata*									+		○	○	+	+		○	+	+	
	Podogonium knorrii	(extinct genus)									+	*		+	◎			+			
e	*Ternstroemia maekawai*	*T.gymnanthera*										*			+	+		+			
	percent of evergreen broad-leaves in plant fossils in each flora(%)				0	0.3	0	0.5		7				6	15	27		6	1	19	

e: evergreen broad-leaved taxa, ●: very abundant (more than 11%), ◎: abundant (4 – 10%), ○: common (1 – 3%), +: rare (less than 1%), ＊ : uncounted data

sawara, 1994), when Japan was composed of many isolated small islands (Fig. 4). Miocene plant macrofossil localities are widely distributed in Japan (Tanai, 1961). Fossil-bearing horizons are distributed all through the Miocene except for the later Middle Miocene.

Early Early Miocene floras, ranging be-

Table 2. Occurrence of selected fossil plants in the Late Miocene (9–6 Ma) floras. References for fossil floras are Hase (1988) for Nakayama, Huzioka and Uemura (1974) for Sanzugawa, Murai (1962) for Gosyo, Ozaki (1981) for Tatsumitoge, Ozaki (1991) for Sashikiri, Lower Itahana, Upper Itahana, Yagii and Seto, Tanai and Onoe (1961) for Mitoku and Onbara, Tanai and Suzuki (1965) for Syanabuchi, and Uemura (1988) for Tayama, Miyata and Takamine Floras.

		Hokkaido	Tohoku					Hokuriku	Kanto			Tokai	San-in			Kyushu
Fossil taxa	Modern relatives	Syanabuchi	Tayama	Miyata	Gosyo	Sanzugawa	Takamine	Sashikiri	L Itahana	U.Itahana	Yagii	Seto	Mitoku	Onbara	Tatsumitoge	Nakayama
Alnus protomaximowiczii	*A.maximowiczii*	+				+										
Betula miomaximowicziana	*B.maximowicziana*		○		+	●										
Cryptomeria miyataensis	*C.japonica*		+	○		◎										
Thuja nipponica	*T.standishii*	○		○	○	○								○		
Picea spp.		○	+	○	+	◎									+	+
Acer palaeodiabolicum	*A.diabolicum*		◎	+		+							●	○		
Betula protoglobispica	*B.ermanii*	◎		+	+			○					+	○	+	+
Abies spp.		○	+	○	+	○			+					○	+	○
Fagus protojaponica	*(F.multinervis)*	●	●	◎	◎	+		○		+		○		+	+	
Cercidiphyllum crenatum	*C.japonicum*	◎				+	+	+			+				+	
Castanea miocrenata	*C.crenata*		+		○	+					+	○	+	◎	○	◎
Ulmus protojaponica	*U.japonica*	◎	+	○		+	+	○	○	○	+	○	○		○	+
Salix spp.		◎	+	+	+	●	◎	○	○	●	◎				+	
Populus spp.		○	◎	+	○	●	◎	+		+	○	◎	+	○	○	
Carpinus heigunensis	*C.tschonoskii*	○	○	○	+		+	○		○	+	○	+	○	○	◎
Fagus stuxbergii	*(F.hayatae)*	+	●	●	●	+	●	●	○	○		○	●	●	●	○
Zelkova ungeri	*Z. serrata*	○	○		○	+	○	○	○	○	○	○	●	○	○	○
Sorbus spp.		○		○	○	○		○	+	+	+		○		○	
Wisteria fallax	*W.floribunda*	+	○	○	○		◎	+	○	+	◎	○	◎	○	+	
Liquidambar spp.		+			○		◎	○		○	○	○	○			
Alnus miojaponica	*A.japonica*	+					●	+	○	◎	◎			○	+	
e *Cinnamomum* cf. *camphora*	*C.camphora*	+		+	+		+	+	○	+	+	◎				
Acer rotundatum	*A.mono*		○	○	○	○		○		+	○		○	○	○	
Banbusites & Sasa			◎		○		◎	○	●	○	◎	○			○	
Quercus protoaliena & Q.miocrispula	*Q.aliena & crispula*		○	○				○		+	+	○	+	●	+	●
Acer nordenskioeldi	*A.palmatum*		+	+			○	○	○	○	+	◎	○		○	○
e *Buxus protojaponica*	*B.japonica*		○	○				+			◎			○	+	
Tilia spp.				+	+	○	○	○	+	+	○	◎	○		○	◎
Lindera spp.				+	+		+		●	+	+	○			+	
e *Cyclobalanopsis protoacuta*	*C.acuta*			○	+						+	○				
Metasequoia occidentalis	*(M.glyptostroboides)*				○		○	+	◎	○	●				○	
e *Cyclobalanopsis protosalicina*	*C.salicina*				○			+	○		+	○			+	
Quercus miovariabilis	*Q.variabilis*				○			◎	+	◎	+					
e *Persea* cf. *thunbergii*	*P.thunbergii*							+	○		+	○				
"Ficus" tiliaefolia	(extinct genus)							+	◎	●	○	○				
e *Actinodaphne* cf. *lancifolia*	*A.lancifolia*								○	+	○	○				
e *Cinnamomum* cf. *japonica*	*C.japonica*								+	+	○	○				
e *Cyclobalanopsis nathorstii*	*C.glauca*											◎				
percent of evergreen broad-leaves in plant fossils in each flora (%)		0.1	3	2	7		2	2	5	0.2	8	15	0	1	0.4	0.2

e: evergreen broad-leaved taxa, ●: very abundant (more than 11%), ◎: abundant (4 – 10%), ○: common (1 – 3%),
+: rare (less than 1%)

tween ca 24 and 18 Ma, are characterized by the dominance of deciduous broad-leaved trees as Betulaceae, Ulmaceae, Juglandaceae and Aceraceae together with conifers like *Picea*, *Metasequoia* and *Glyptostrobus* (Huzioka, 1964; Tanai, 1961). The diversity of the early Early Miocene floras, representing the number of taxa in each flora, is very low compared with the late Early and earliest Middle Miocene flora (Tanai, 1992). In the early Early Miocene, Japan was covered widely by deciduous broad-leaved forest, although fossil floras in the southern area include some evergreen broad-leaved taxa: e.g. *Machilus ugoana* and *Elaeocarpus notoensis* in the Hiyoshi flora (Ina, 1992).

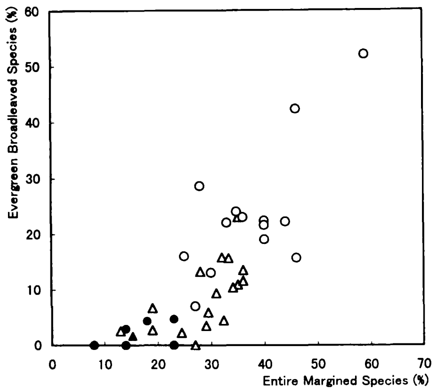

Fig. 6. Relationships between the percent entire-margined and evergreen broad-leaved species in the late Early to earliest Middle Miocene floras (Fig. 4) and Late Miocene floras (Fig. 5). Open circles indicate the late Early to earliest Middle Miocene floras in Honshu and open triangles indicate Late Miocene floras in Honshu and Kyushu. Closed circles and triangle indicate floras in Hokkaido.

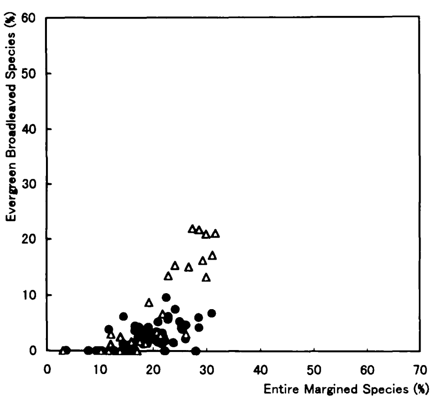

Fig. 7. Relationships between the percent entire-margined and evergreen broad-leaved species in the recent floras of the temperate forest zone in central Japan based on the floristic data by Takahashi (1962). Open triangles: floras along the Pacific Coast, closed circles: floras in inland Honshu.

The late Early Miocene to earliest Middle Miocene floras, approximately from 18 to 15 Ma, are characterized by their high species diversity with abundance of evergreen broad-leaved trees and subtropical elements. The percentages of evergreen broad-leaved tree taxa in each flora are high (7–52%) in all Honshu, but very low in Hokkaido (Fig. 4). The percent of evergreen broad-leaves in total plant fossils in each flora increases from 7 to 27% in the more southern floras (Table 1) with the increase in number of evergreen taxa (Fig. 4). The floras in Honshu include many evergreen Fagaceae such as *Cyclobalanopsis*, *Castanopsis* and *Pasania* and Lauraceae like *Cinnamomum*, *Actinodaphne*, *Machilus* and *Neolitsea*. However, the dominant species in those floras are deciduous trees such as *Comptonia naumanni*, *Zelkova ungeri* and *Quercus miovariabilis* except for some floras dominated by evergreen taxa like *Cyclobalanopsis nathorstii* and *C. praegilva*.

Late Early and earliest Middle Miocene pollen flora have been studied well and some are from the plant macrofossil-bearing strata (Yamanoi, 1992). Pollen floras in Hokuriku and Tokai Districts in central Japan are dominated by *Carya*, *Juglans-Pterocarya*, *Fagus*, *Quercus*, *Ulmus-Zelkova* and *Liquidambar* with *Cyclobalanopsis* (Yamanoi, 1992; Saito and Morohoshi, 1992). The percent of *Cyclobalanopsis* pollen reaches 50% among total tree pollen in and around 16 Ma. Pollen floras in 16 Ma also include characteristic mangrove plants such as *Excoecaria*, *Rhizophora* and *Sonneratia*, suggesting the existence of mangrove forest in western and central Honshu (Fig. 4, Yamanoi and Tsuda, 1986). The pollen data with plant macrofossils indicates the existence of mixed evergreen broad-leaved forests with deciduous broad-leaved trees and conifers in central Honshu in late Early and earliest Middle Miocene. The northernmost distribution of many evergreen species is recognized in the Fujikura flora or Utto flora in northern Tohoku District (Table 1). That is, the mixed evergreen and deciduous forest changed to deciduous broad-leaved forest in a narrow zone between northern Tohoku and southern Hokkaido in northeastern Japan (Tanai and Uemura, 1988).

Fossil floras from the middle and later stage (15 to 10 Ma) of the Middle Miocene are very rare in Japan and only a few in Hokkaido have been studied. The Middle Miocene floras in Hokkaido such as Onnebetsu and Niupu (Uemura, 1991) are characterized by the dominance of deciduous broad-leaved trees including *Fagus palaeojaponica* and *Cer-*

cidiphyllum crenatum and include no evergreen broad-leaved taxa.

The Late Miocene floras covering from 10 to 5 Ma are characterized by the dominance of deciduous broad-leaved trees with conifers (Table 2, Fig. 5). Compared with late Early and earliest Middle Miocene floras, the percent of evergreen broad-leaved trees for the percent entire-margined species are lower in Late Miocene floras (Fig. 6) and similar to the values of the recent forests in central Japan (Fig. 7). The most dominant species in Late Miocene floras are *Fagus paleojaponica* in Hokkaido and northernmost Honshu and *F. stuxbergii* in Tohoku and San-in Districts and the percentage of *Fagus* in fossil assemblages is sometimes more than 50% (Table 2). *Salix*, *Populus* and *Alnus* became frequent in floodplain vegetation at the stage with divergence of deciduous broad-leaved trees like *Ulmus*, *Betula*, *Carpinus*, *Quercus*, *Sorbus* and *Acer*. The composition overwhelmed with beeches indicates the appearance of cool temperate deciduous broad-leaved forest similar to recent beech forest. In addition to the deciduous trees, temperate evergreen conifers including *Cryptomeria*, *Thuja*, *Thujopsis*, *Abies* and *Picea* appeared or expanded their distribution into western Japan.

The percent of evergreen broad-leaves in fossil assemblages in northern and western Honshu decreases to less than 15 % (Table 2), although the percent of evergreen broad-leaved taxa in the fossil flora is not so low (15–24%) in fossil floras along the Pacific coast of Central Japan (Fig. 5). The fossil floras in Seto, Lower Itahana and Yagii along the Pacific Ocean in central Japan include many evergreen broad-leaved trees such as *Cyclobalanopsis*, *Cinnamomum* and *Machilus* with exotic elements like *"Ficus" tiliaefolia*, *Pinus trifolia*, and *Calpolites japonica*, which are remnants of late Early and earliest Middle Miocene flora or Paleogene flora (Miki, 1941; Ozaki, 1991). The pollen assemblages in Seto Porcelain Clay Formation include over 75% *Cyclobalanopsis* pollen (Nasu, 1972). On the other hand the fossil floras along the Sea of Japan include fewer evergreen broad-leaved trees. The Mitoku flora around the western border of the Sea of Japan has no evergreen broad-leaved trees.

3. Early and Middle Pliocene

Plio-Pleistocene sediments are widely distributed around the recent sedimentary basins all over Japan and are well studied stratigraphically with abundant tephrochronological data. The topography of Japan became more similar to the recent; that is, land areas expanded in the Tohoku District and wider inland basins became formed east and westward in the center of central and western Japan. Most of the fossil localities at this stage are distributed in these inland basins. Studies on Plio-Pleistocene floras are based mainly on fruits and seeds in contrast with the Miocene floras based mainly on leaves, because fossil leaf specimens are difficult to get from the softer sediments in the Plio-Pleistocene except for harder volcanic ashes and diatomite.

Early and middle Pliocene (5–3 Ma) fossil leaf assemblages have often been found in Hokkaido, Tohoku, western Kanto, and Kyushu Districts. Among them, the Rubeshibe flora in northeastern Hokkaido (Tanai and Suzuki, 1965), the Kabutoiwa flora in western Kanto (Ozaki, 1991), and the Shigehira flora in southern Kyushu (Hase, 1988) have been well investigated numerically and taxonomically, based on abundant fossil leaf materials.

Evergreen broad-leaved trees were not dominant in the paleovegetation of Hokkaido and Honshu in the early and middle Pliocene. The Rubeshibe flora in the early Pliocene in northeastern Hokkaido includes no evergreen taxa. The early and middle Pliocene floras in Sendai (Okutsu, 1955), Shinjo (Tanai, 1961) and Koyanaizu (Suzuki, 1968) in southern Tohoku District include a few evergreen species such as *Cinnamomum miocenum*, *Buxus mirophylla* var. *japonica* and *Ilex cornuta*. The Kabutoiwa flora in the middle Pliocene (3.7 Ma, by K-Ar age) volcanic lake sediment in western Kanto was studied intensively by Ozaki (1991). The 111 taxa include many exotic ones like *Taiwania*, *Liriodendron*, *Tetracentron*, *Fortunearia*, *Liquidambar*, *Davidia*, *Koelreuteria*, *Catalpa* and *Heptacodium*, but only 3 evergreen taxa, *Neolitsea* sp., *Machilus*? and *Cyclobalanopsis protosalicina*. The percent of evergreen taxa among broad-leaved trees in the Kabutoiwa flora is 3%; a relatively low value compared with percent entire-margined species (26%). The early and middle Pliocene floras from southern Kanto (Uemura and Momohara, 1991), Tokai (Tsukagoshi and Tado Coll. Res. Gr., 1995) and middle Kinki Districts (Miki, 1941; Momohara, 1992) are well studied based on fruit and seed materials and some leaf fossils. These fossil floras are dominated by conifers, including *Metasequoia*, *Sequoia*, *Chamaecyparis*, *Glyptostrobus*, *Pseudolarix* and *Picea koribai* together with deciduous trees such as *Fagus microcarpa* and *Liquidambar*. The percent of evergreen broad-leaved tree fossils is less than 1%, including *Cyclobalanopsis gilva*, *Cinnamomum macropodum*, *Umbellularia japonica*, *Ficus* cf. *pumila*, *Buxus microphylla* var. *japonica*, *Eurya* sp., *Ilex cornuta* and *Symplocos myrtacea*.

In contrast to the Pliocene floras in Honshu, the middle Pliocene floras in Kyushu are characterized by the richness of evergreen taxa. The Shigehira flora in southern Kyushu includes 29 evergreen broad-leaved taxa, with 54 deciduous broad-leaved and 7 coniferous taxa (Hase, 1988). The percent of evergreen broad-leaves in the fossil assemblages is 56%, including 41% *Cyclobalanopsis* and 10% evergreen Lauraceae. The evergreen species in the fossil flora include Fagaceae such as 5 *Cyclobalanopsis* species including *C. praegilva* and *Castanopsis cuspidata*, Lauraceae such as *Cinnamomum* cf. *camphora*, *C.* cf. *japonicum*, *C. lanceolatum*, *Litsea* cf. *acuminata*, *L.* cf. *akoensis*, *Neolitsea* cf. *aciculata*, *Machilus thunbergii*, *M. japonica* and *Phoebe* sp., Theaceae such as *Camellia palaeosasanqua*, *C. nangoi* and *Schima tanaii*, Hamamelidaceae such as *Distylium* sp. and *Sycopsis chaney*, and Aquifoliaceae such as *Ilex integra*, *I.* cf. *sugerokii* and *I.* cf. *rotunda*. The flora includes many exotic genera now growing in Taiwan and southern China such as *Keteleeria*, *Taiwania*, *Cunninghamia*, *Calocedrus*, *Phoebe*, *Sycopsis* and *Liquidambar*. The high dominance of evergreen taxa among the late Cenozoic floras with such exotic taxa shows the existence of evergreen broad-leaved forest similar to extant subtropical forest in southern China. Other well-studied Pliocene floras in Kyushu are Daiwa and Nagano (Hase, 1988), Mogi (Tanai, 1976) and Tsubusagawa (Iwauchi, 1994). These floras include 4 to 6 evergreen genera (*Cyclobalanopsis*, *Cinnamomum*, *Machilus*, *Elaeocarpus*, *Ilex* and *Symplocos*); however, deciduous genera such as *Zelkova* and *Acer* are dominant in the fossil floras.

4. Late Pliocene and Pleistocene

Fossil floras from the late Pliocene to Middle Pleistocene have been studied well based on pollen and plant macrofossils and the floral changes have been discussed with reference to the paleoenvironmental changes in central Kyushu (Iwauchi, 1994), middle Kinki (Tai, 1973; Momohara, 1994), northern Hokuriku (Niigata Fossil Plant Research Group and Niigata Pollen Research Group, 1983), and southern Tohoku (Manabe and Suzuki, 1988). The fossil pollen and macrofossil assemblages showing the richness of evergreen broad-leaved taxa during the stages are limited geographically to Tokai, Kinki and Kyushu and considerably limited temporally.

The strata from the late Early Pleistocene to Middle Pleistocene in the Osaka Group in central Kinki are composed of alternate marine and nonmarine sediments, which are correlated with interglacial and glacial stages (Itihara, 1961). The plant macrofossil assemblages in marine sediments are composed mainly of species growing in warm and maritime areas such as *Paliurus nipponicus*, *Sapium sebiferum* var. *pleistoceaca*, *Melia azedarach* and *Vitex rotundifolia*, but few evergreen taxa are included in marine sediments without "Ma 8 Marine Clay Bed". The pollen assemblages showing the dominance of *Cyclobalanopsis* are limited to "Ma 3", "Ma 6", and "Ma 8 (or "Ma 9" in Furutani, 1984) Marine Clay Beds" among thirteen marine clay beds between the late Early Pleistocene and the Late Pleistocene (Nasu, 1970; Tai, 1973; Furutani, 1984).

The plant macrofossil assemblages in "Ma 8 marine clay" around ca 0.4 Ma are characterized by the dominance of evergreen broad-leaved trees such as *Myrica rubra*, *Cyclobalanopsis gilva*, *C. glauca*, *Cinnamomum doederleinii*, *Machilus thunbergii*, *Illicium religiosum*, *Distylium racemosum*, *Cleyera japonica*, *Ca-*

mellia sasanqua, *Syzygium buxifolium* and *Symplocos prunifolia*, together with conifers such as *Abies firma*, *Tsuga sieboldii* and *Cryptomeria japonica* (Miki *et al*., 1957). Similar fossil assemblages were also found in the Tahara Formation in Tokai (Kuroda, 1966) and the Byobugaura Formation in southern Kanto (Ozaki, 1971) at the same age. These fossil floras include many evergreen Fagaceae and Lauraceae such as *Cyclobalanopsis*, *Castanopsis*, *Cinnamomum*, *Neolitsea* and *Machilus*, accompanied by *Abies* cf. *firma*, *Fagus crenata* and *Fagus microcarpa*.

Fossil pollen and plant macrofossil floras from central Kyushu also indicate that dominance of evergreen taxa in paleovegetation was scares in the Pleistocene. The dominance of more than 50% *Cyclobalanopsis* pollen occurs only at ca 0.5 Ma in the pollen spectrum from 1.4 to 0.1 Ma in 5 sedimentary basins in central Kyushu. The stages characterized by dominance of *Cyclobalanopsis* pollen with *Fagus* pollen were found in the lower part of the Nogami Formation and the lower part of the Yoshino Formation (Iwauchi, 1994). The plant macrofossil assemblages ("Nogami A" flora) from the same horizon as the *Cyclobalanopsis* dominance (up to 50%) in pollen assemblages include 17 evergreen broad-leaved taxa (49%) among 35 broad-leaved taxa: these include *Castanopsis cuspidata*, *Cyclobalanopsis* spp., *Cinnamomum japonica*, *Neolitzea aciculata*, *Machilus japonica* and *Camellia japonica*. The pollen assemblages from the lower part of the Yoshino Formation include abundant *Cyclobalanopsis* pollen (up to 63%) and plant macrofossil assemblages (Ph-2) from the same horizon include 12 evergreen broad-leaved taxa with 1 deciduous broad-leaved tree and 3 gymnosperms (Iwauchi, 1994). The percentages of fossil broad-leaved taxa among 186 samples include 41% *Cyclobalanopsis acutissima*, 16% *Castanopsis cuspidata* and 15% *Machilus thunbergii* (Iwauchi and Hase, 1992)

The fossil assemblages in the "Ma 8 Marine Clay Bed" in the Osaka Group in central Kinki, the Tahara Formation in Tokai, the Byobugaura Formation in southern Kanto, and the Nogami and Yoshino Formations in central Kyushu indicate the existence of evergreen broad-leaved forests dominated by evergreen Fagaceae and Lauraceae. The composition of the forests is very similar to that of the recent lucidophyll forest in southwestern Japan. The correlation of the ages based on tephrostratigraphy using widely distributed volcanic ashes has not been attempted among those formations. However, the fission track ages of volcanic ashes lying in and around formations range between 0.4 and 0.6 Ma. These data show that the evergreen broad-leaved forests expanded from Kyushu to southern Kanto once or twice in and around 0.5 Ma.

The pollen spectra during later Middle and Late Pleistocene in central Kyushu (Iwauchi, 1994), central Kinki (Furutani, 1984) and southern Kanto (Nishimura, 1980) do not record the dominance of *Cyclobalanopsis*, which was always less than 20%. The pollen and plant macrofossils in the Late Pleistocene last interglacial sediments have been studied in detail at many sites throughout Japan (Sohma and Tsuji, 1988). The plant macrofossil floras in the Late Pleistocene in Kinki, Tokai and southern Kanto include many tree species distributed in warm-temperate regions, including *Sapium sebiferum*, *Vitex cannabifolium*, and *Paliurus nipponicus* and pollen assemblages at this stage are dominated by *Cryptomeria* and *Lagerstroemia* (Sohma and Tsuji, 1988). However, there are few fossil broad-leaved evergreen trees in the plant macrofossil and pollen floras of Honshu. Fossil pollen floras in central Kyushu are dominated by *Cryptomeria* and *Alnus* as in Honshu (Iwauchi, 1994). The only plant macrofossil flora including many evergreen broad-leaved trees in the earlier late Pleistocene is the Ebino flora in southern Kyushu (Onoe, 1971). The Ebino flora is composed of 13 evergreen and 28 deciduous broad-leaved tree species with 6 conifers and includes 24% of evergreen broad-leaves among the total fossils. The most abundant fossils are *Osmanthus ilicifolius* (14% total fossils) with *Tsuga sieboldii* and *Abies firma* (13 and 12%, respectively). Fossil pollen assemblages in the Ikemure Formation including the Ebino flora record the dominance of *Picea* and *Abies* with only one horizon including *Cyclobalanopsis* (25%) and *Podocarpus* (10%) (Hase and

Hatanaka, 1984). These fossil data indicates that the paleovegetation in southern Kyushu was composed of mixed coniferous and deciduous broad-leaved forests and that evergreen broad-leaved trees were less dominant.

Discussion

Eocene floras in Hokkaido and southwestern Japan indicate that Japan was covered widely by evergreen broad-leaved forest. However, since the Oligocene the fossil evidence showing the existence of evergreen broad-leaved forest is limited spatially and temporally to Honshu in the late Early and earliest Middle Miocene, the Pacific Coast of central Honshu in the Late Miocene, Kyushu in the Middle Pliocene and the Pacific Coast of central Honshu and Kyushu in the late Middle Pleistocene. The distribution of evergreen broad-leaved forest was limited to more southern and littoral areas than these fossil localities. This distributional pattern seems to be related to the configuration of land and sea as a general rule, since the distribution is assumed to have been influenced by the mildness of the winter climate at each stage as in the present. However, the lack of evergreen broad-leaved forest in most parts of Japan from the Oligocene to the Pleistocene indicates that most parts of Japan have always been subject to a continental climate, even in maritime regions during warmer ages. Evergreen broad-leaved forest could expand its distribution only in some limited ages when the winter climate was ameliorated.

The floral change from the Eocene to the Oligocene in both Hokkaido and southwestern Japan reflects the worldwide climatic deterioration representing the "Terminal Eocene Event" (Wolfe, 1978; Tanai, 1992). Wolfe (1978) discussed the increase of annual range of temperature with the decrease of mean annual temperature between the Late Eocene and Early Oligocene based on the change of fossil leaf physiognomy in North America. The Oligocene floras like Kobe, Ainoura, and Noda in western Japan include a lower percent evergreen broad-leaved species for the percent entire-margined species than the Eocene floras like Ube (Fig. 3). The paucity of evergreen broad-leaved trees in the Oligocene floras is assumed to reflect the enlargement of the annual range in temperature as shown in North America. The severe winter representing a continental or inland climate restricted the distribution of evergreen broad-leaved forest and increased the deciduous broad-leaved forests to allow the appearance and diversification of modern deciduous elements like *Betula*, *Corylus*, *Carpinus*, *Fagus*, *Quercus*, *Ulmus* and *Acer*.

The increase and spread of evergreen broad-leaved trees in the late Early Miocene and earliest Middle Miocene were caused by the amelioration in winter climate, influenced in part by the isolation of Japan from the Asian Continent. Japan in the late Early and earliest Middle Miocene was segregated into many small islands and these were influenced similarly by the oceanic climate (Fig. 4) except for Hokkaido where was influenced directly by a cold sea current. On the other hand, the decrease of evergreen broad-leaved trees in Late Miocene floras indicates the deterioration in winter climate characteristic of inland or continental climates compared with the oceanic climate in the late Early and earliest Middle Miocene. Japan in the Late Miocene merged into larger islands than in the earliest Middle Miocene (Fig. 5). The narrow contiguity with the Asian Continent along the Korean Peninsula prevented warm current from flowing into the Sea of Japan, although the Sea of Japan was as large as now. The marine climate along the Sea of Japan became cooler and this accelerated the deterioration in winter climate, especially in western Honshu surrounded by the large land areas of the Asian Continent. The oceanic environment should have remained in the part of Tohoku composed of islands and in Tokai influenced directly by warm sea current.

In the Plio-Pleistocene, the distribution of the evergreen broad-leaved forest became more limited to the southern areas as in southern Kyushu and the Pacific Coast in Honshu and also limited temporally to one or two short stages like the middle Pliocene and late Middle Pleistocene. The paucity of evergreen taxa in central Japan may be explained by the continental climate, just as in the late Miocene. This is because the area of land increased to more than that of the Late Miocene and most fossil assemblages have been obtained from non-marine sediment in inland basins. However, the expansion of evergreen broad-leaved forest did not occur except for a few stages in the late Middle Pleistocene, although the topography of Japan changed to its modern form by the Middle Pleistocene. That is, the deciduous broad-leaved trees still dominated the paleovegetation in coastal areas, although the distribution of marine sediments was expanded considerably into inland basins in the Middle and Late Pleistocene warm stages. This fact indicate that most parts of Japan have always been subject to a continental climate with a winter climate too severe for the growth of evergreen broad-leaved trees even along the coast during warmer stages in the Plio-Pleistocene.

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日本の新生代における常緑広葉樹林の植生史

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大型植物化石資料と花粉化石資料に基づいて，始新世から更新世までの日本のフロラと植生の歴史を総説し，日本列島の地形発達史と関連させて常緑広葉樹林の分布変遷を議論した．北海道と西南日本の始新世フロラには多くの常緑広葉樹が含まれており，常緑広葉樹林が広く分布していたと考えられる．一方，漸新世以降では，常緑広葉樹林の存在を示す化石群は前期中新世末から中期中新世初頭の本州，後期中新世の本州中部の太平洋岸，中期鮮新世の九州，中期更新世後半の本州中部と九州の太平洋岸からしか報告されておらず，常緑広葉樹林の分布はそれらより南の地域に限られていたと考えられる．常緑広葉樹林の分布は，大局的には各時代の陸と海の配置に規定され，暖流による影響を受けていたと考えられる．しかしながら，後期新生代を通して日本の大部分で常緑広葉樹林が分布していなかったことからは，大陸気候のような寒冷な冬季の気候によって温暖期の沿海地域でも常緑広葉樹林の分布が制限されていたことが考えられる．