Miocene Floral Changes in the Circum-Japan Sea Areas—Their Implications in the Climatic Changes and the Time of Japan Sea Opening

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Abstract. The Miocene plant megafossil assemblages from the circum-Japan Sea areas, including southern Primorye, Korea, and Japan, were reviewed in terms of floristic composition and physiognomic characters. These attributes were used to understand the vegetation history during the formation of the Sea of Japan with its effects on floristic changes in each area. There was a temperature increase from the early early Miocene to the middle Miocene with a peak at the earlymiddle Miocene boundary, and subsequent temperature drop in the late Miocene in all floral successions. The early Miocene assemblages from each area are similar to one another, but the number of common species between those from the southern Primorye and Japanese Islands decreased since the middle Miocene, suggesting an influence of geographic separation of these areas possibly due to the rifting of the Sea of Japan. The degree of temperature increase was larger in the southern part (the Japanese Islands and southern Korean Peninsula), whereas it was much smaller in the northern part (southern Primorye and northern Korean Peninsula). Effects of cold and warm water currents both toward the north and south of the Sea of Japan were suggested for floristic differentiation of these areas.

Key words: Plant megafossil assemblages, Forest vegetation, Paleoclimate, Circum-Japan Sea areas, Miocene

Introduction

Extant forest vegetation in southern Primorye and the Japanese Islands show quite different pictures, even though they are situated at similar latitudes (Fig. 1). Southern Primorye is covered by a mixture of conifers and deciduous angiosperms (Mixed Coniferous and Broad-leaved forest), which developed under cooler-temperate conditions with low mean annual temperatures (Krestov, 2003). Although this forest type is sporadically distributed in the mountains in the Japanese Islands, most parts of the Japanese Islands are covered by those dominated by a mixture of deciduous and evergreen angiosperms that change their composition latitudinally and altitudinally. Forest vegetation of these areas and their differences are severely controlled by the monsoonal climate (Asian summer and winter monsoons) and the prevalence of warm and cold oceanic currents (Fig. 1). The summer monsoon brings high precipitation in these areas, while the winter monsoon brings strong cold and dryness to the continental side. Because of the effect of the Tsushima warm current that transports humid air to the Sea of Japan, a strong northwesterly from the continent brings heavy snow to the Japan Sea-side of the Japanese Islands (Vitvitsky, 1980), which is considered to be critical for developing the beech forest in Japan (Hara, 2010).

Modern geographic configurations of these areas are thought to have primarily formed dur-



Fig. 1. Geographic configurations of the study area with plant megafossil localities treated in the study. Warm and cold oceanic currents around the Japanese Islands were shown.

ing the Miocene due to the rifting of the Sea of Japan. A number of geologic evidences support connections between Japan and the Eurasian continent before the rifting (Golozoubov, 2006). In fact, floristic compositions of Paleogene floras in these areas are quite similar to one another and plenty of common species exist (Pavlyutkin & Petrenko, 2010). Therefore, the onset of floristic differentiation in these areas should be highly dependent on the formation of the Sea of Japan.

The rifting and opening of the Japan Sea basin have been considered to occur at a short time interval during the mid-Miocene (Otofuji, 1996). However, recent revision of the tectonic development of the marginal Eurasian continent indicates a much longer phenomenon initiated in the Paleogene (Golozoubov *et al.*, 2007, 2009, 2012; Kano et al., 2007).

To better understand the history of floristic change in the circum-Japan Sea areas, a number of studies have been carried out (Baikovskaya, 1974; Klimova, 1983; Ablaev & Vassiliev, 1988). However, the ages of the plant-bearing deposits in southern Primorye were controversial (Pavlyutkin *et al.*, 1985) and this hampered the detailed discussion about the time and diversification of each flora in light of the Japan Sea formation. Some of the present authors have worked on the geology and plant fossil assemblages in southern Primorye and revised the previously established geologic framework based on detailed stratigraphic correlation and newly obtained radiometric ages (Pavlyutkin & Petrenko, 2010).

In this study, we compare floristic data

obtained from the circum-Japan Sea areas including southern Primorye, the Korean Peninsula, and the Japanese Islands, based on the latest floristic and geologic studies in order to show the vegetation history and climate during the Miocene. We discuss time and possible effects of the Sea of Japan formation on the vegetation differentiation between the continent and the Japanese Islands.

Materials and methods

Regional floral data from southern Primorye, the Korean Peninsula, and Japan (mainly from the Sea of Japan side) were compared floristically and vegetationally. For climate analysis, we used a simple linear regression analysis termed the Leaf Margin Analysis (LMA: Wolfe, 1979; Wing & Greenwood, 1993) to obtain quantitative data on mean annual temperature (MAT). This method is based on the relationship between the MAT of a given area and the percentage of woody dicotyledons with a smooth leaf margin in a given flora under humid to mesic conditions (Wolfe, 1979; Wing & Greenwood, 1993). Among published regression equations, we used the one provided by Wolfe (1979), which has been developed based on East Asian vegetation. Errors for the analysis were calculated based on Wilf (1997). Classification of forest vegetation was followed after Wolfe (1979).

Floral data

Southern Primorye

The Miocene floral succession of southern Primorye has been a matter for continuous debates (Baikovskaya, 1974). Klimova (1983) revised the former stratigraphic scheme and recognized two horizons, namely the Sineutesovsky (the lower–middle Miocene) and the Ust-Suifunsky (the upper Miocene). At that moment, the 'Miocene' Ust Davydovsky Formation was rejected from the Miocene records and was newly compared with the Eocene–Oligocene Harutori Formation in Hokkaido (Klimova, 1983). Cenozoic floras from Primorye were principally compared with those of Japan and Sakhalin, however the current status for the age of Japanese floras has not been critically cited in the scheme. One of the present authors (BP) has worked on the Cenozoic stratigraphy and floral succession of southern Primorye and concluded that some of the 'Miocene' floras accepted by Klimova (1983) and other authors (e.g., Ablaev & Vassiliev, 1998) should be assigned to the early Oligocene based on floristic comparison with Paleogene floras in Japan (Pavlyutkin & Petrenko, 2010). Consequently, they recognized four Miocene floral horizons: Sine-Utesovsky (lower lower Miocene), Nezhinsky (upper lower Miocene), Novokachalinsky (middle Miocene), and Ust-Suifunsky (upper Miocene).

The Sine-Utesovsky horizon is represented by a plant assemblage from the Sine-Utesovsky Formation in the Ivanovsky depression, southwest of Vladivostok. The Sine-Utesovsky horizon is characterized by deciduous angiosperms with a small amount of conifers: Metasequoia occidentalis, Sequoia langsdorfii, Kadzura sp., Ulmus pseudolongifolia, Zelkova elongata, Fagus evenensis, F. palaeocrenata, Quercus yoshiokaensis, Betula mitai, Alnus usyuensis, A. prenepalensis, A. duensis, A. schmalhausenii, Carpinus subyedoensis. Tilia hommashinichii. Cladrastis chaney, Hemitrapa borealis, Acer protomiyabei, Alangium kryshtofovichii (Pavlyutkin, and unpublished data). No evergreen angiosperm has been recorded so far. The Sine-Utesovsky horizon is comparable to the earliest Miocene Aniaitype floras of Japan (Huzioka, 1964; Tanai, 1961) because they share many common species as well as physiognomic characters (Pavlyutkin & Petrenko, 2010). The age of the Sine-Utesovsky Formation is assumed to be the earliest Miocene based on a K-Ar age of 22.0 ± 1.0 Ma from the overlying basalt rock (Popov et al., in Pavlyutkin & Petrenko, 2010).

The Nezhino Flora that typifies the late early Miocene Nezhinskii horizon was recently described by Pavlyutkin *et al.* (2012) from the Nezhinsky Formation in the Pavlovsky depression. Its age was estimated between 20.9– 17.1 Ma based on radiometric dating. There were 127 species described from the formation that are characterized by temperate angiosperms belonging to the family Ulmaceae, Betulaceae, Fagaceae, Salicaceae, Fabaceae, and Sapindaceae, with minor amounts of warm-temperate elements, such as *Davidia*, *Nyssa*, *Idesia*, and *Eurya*. Some species that are the same or close to the elements of the Daijima-type floras of Japan (Tanai, 1961), which range from the late early to early middle Miocene, were also recognized: *Pinus miocenica*, *Liquidambar europaea*, *Ulmus carpinoides*, *Castanea miomollissima*.

The Novokachalinsky horizon is represented by the Khanka Flora from the western coast of Lake Khanka near the border between Russia and China (Pavlyutkin, 2005). The flora is characterized by the predominance of Fagus chankaica with subordinate elements like Metasequoia disticha, Taxodium dubium, Sorbus iljinskajae, Zelkova elongata, Acer rotundatum, and Aesculus iljinskajae. This flora is comprised of 165 species belonging to 82 genera and 39 families, and it is dominated by deciduous angiosperms. No evergreen species has been recognized from the flora. Many common genera exist between the Miocene floras of Primorye and Japan; however, the percentage of endemic species is high in the Khanka Flora.

The type section of the Ust-Suifunsky horizon is located in the Pushkinsky depression near Vladivostok. The Ust-Suifunsky Formation and its correlatives contain several fossil plants common to the lower Novokachalinsky horizon (Pavlyutkin, 2002). But it is characterized by the dominance of *Ulmus*, *Cercidiphyllum*, *Populus*, and *Salix*, as well as by the rarity of *Fagus* and conifers in its lower part, although *Fagus* dominate in the upper part. Fission-track ages obtained at the type section indicate a late Miocene age of the flora $(10.8 \pm 1.1 \text{ and } 11.8 \pm 0.9 \text{ Ma: Pavlyutkin et al.}, 1985).$

No age data is available for the Novokachalinsk horizon but we assumed it to be middle Miocene based on stratigraphic and floristic correlations (Fig. 2).

Korean Peninsula

Miocene strata bearing plant fossils are well exposed in the Pohang Bay area, North Gyeongsang Province, South Korea. Classical localities are also known in the Myongchong–Kilchu district in North Hamgyong Province and Tongchon in Gangwon (Kangwon) Province, North Korea (Huzioka, 1972).

Three levels of plant-bearing strata have been recognized in the Pohang Bay area. The lower most stratum is the lacustrine Geumgwangdong Formation of the Jianggi Group, which yields the early early Miocene Jianggi Flora (Huzioka, 1972; Paik *et al.*, 2012). The Yeonil Flora was reported from the marine Duho Formation of the upper most part of the Pohang Group, that unconformably overlies the Jianggi Group (Huzioka, 1972). Palynofloral assemblage of the formation was reported by Yamanoi (1992b).

The Jianggi and Yeonil floras consist of 36 and 35 species, respectively. More than 70% of Jianggi species are common to the Aniai-type floras, while ca. 65% of the Yeonil species are known in the Daijima-type Noroshi (Ishida, 1970) and Notonakajima (Matsuo, 1963) floras in Noto Peninsula, Japan. Thus, they were compared to the Aniai-type and Daijima-type floras, respectively (Huzioka, 1972).

Jeong et al. (2004, 2009) reported two fossil wood assemblages from the Sinjeongri Formation that overly the Geumgwangdong Formation in the Jianggi Group. They are characterized by an appearance of some wood species known in the Daijima-type wood assemblage (Terada, 1998), such as Taxodioxylon cunninghamioides, Camellia japonoxylum, Distrylium chiharuhirayae, and Wataria miocenica, in association with the ones known in the Aniai-type wood assemblage (Terada, 1998), Fagus hondoensis. Leaf fossils are dominated by Fagus antipofii (K. Uemura, personal communication with AY). Therefore, Lim et al. (2010) concluded that these assemblages should be transitional ones between two floral types.

The Jianggi Group is dated by Ar/Ar ages of extrusive $(19.4 \pm 2.1 \text{ Ma})$ and intrusive $(16.8 \pm 2.2 \text{ Ma})$ rocks; both indicate an early Miocene age for this group (Paik *et al.*, 2012). The marine Duho Formation is assumed to be late middle Miocene based on dinoflagellate cysts (14-12 Ma: Yun et al., 1997) and a paleomagnetic study (14.5-11.5 Ma: Kim et al., 1993).

Two plant bearing strata have been recognized in the Miocene deposits in the Myongchong-Kilchu district (Huzioka, 1972). The Yongdong Flora from the Yongdong Formation is composed of 21 species of deciduous angiosperms and conifers; all of its components are common to the Jianggi Flora. The Hamjindong Flora was reported from the marine Hamjindong Formation in the Myeoncheon Group, which unconformably overlies the Yongdong Group. It consists of 45 species belonging to 31 genera and 23 families, and it is dominated by deciduous angiosperms and deciduous and evergreen conifers. Although it also resembles the Jianggi Flora or the Aniaitype floras of Japan, it is comparable to the Daijima-type floras due to the occurrence of some index species as Quercus miovariabilis, Liquidambar miosinica, and Parrotia fagifolia (Huzioka, 1972). The diatom assemblage from the Hamjindong Formation was correlated to the upper part of the Denticulopsis hyalina zone to the D. dimopha zone (14-9.5 Ma) (Koizumi, 1988), suggesting a late middle to early late Miocene age.

A Miocene plant assemblage from the freshwater deposits in Tongchon, Kangwon Province, referred to as the Tongchon Flora, consists of 20 species of deciduous angiosperms and conifers. No evergreen plants were recognized. Most of its components are common to the Aniai-type floras (Huzioka, 1972), but it was also compared with the Daijima-type floras with the occurrence of the key species, *Comptonia naumanni*. Although we have no data for the age of this plant-bearing stratum at the moment, we herewith follow Huzioka's (1972) opinion that it was situated between the Jianggi and Yeonil floras based on its composition.

Japan

Miocene floras in the Japanese Islands are classified into three types: the Aniai-type, Daijima-type, and Mitoku-type floras in ascending stratigraphic order (Tanai, 1961, 1992).

The Aniai-type flora of the early early Miocene age (Tanai, 1961; Huzioka, 1964) in central and northern Japan is characterized by the predominance of deciduous angiosperms and deciduous and evergreen conifers with representative elements of Fagaceae, Betulaceae, Ulmaceae, Juglandaceae, Salicaceae, and Sapindaceae. In terms of physiognomic characters, it corresponds with the Mixed Northern Hardwood forest that develops under cold-temperate climate conditions (Tanai, 1992).

The Daijima-type flora of late early to earliest middle Miocene (Tanai, 1961, 1992; Huzioka, 1963) has been recognized throughout the Japanese Islands. The strata bearing the Daijima-type flora unconformably covers those bearing the Aniai-type and it often contains marine organisms in its upper part or conformably overlying beds. These fossils, represented by the Arcid-Potamid molluscan fauna, clearly indicate an influence from the warm oceanic climate. Most of the Japanese Islands were inundated by marine conditions during the latter part of the middle Miocene, and thus, few fossil assemblages have been recognized.

The floras in Honshu are characterized by a mixture of deciduous and evergreen angiosperms that correspond to the Notophyllous Broadleaved Evergreen forest indicating warm-temperate climate conditions. Latitudinal and altitudinal differences of floristic composition have been recognized in the Daijima-type floras (Tanai & Uemura, 1988). Those from southern Hokkaido and northern most Honshu were compared to the Mixed Broad-leaved Deciduous forest (Wolfe & Tanai, 1980). Moreover, earlier part of the Daijima-type flora in Honshu is also enriched in temperate elements. They were compared to the Mixed Broad-leaved Deciduous or Mixed Broadleaved Evergreen and Deciduous forest (Yabe, 2008a, b). They can be recognized due to the occurrence of key species of deciduous angiosperms: *Comptonia naumanni*, *Quercus miovariabilis, Liquidambar miosinica*, and *Parrotia pristina*.

The Mitoku-type flora of the late Miocene– Pliocene age (Tanai, 1961) is characterized by the predominance of beech species (*Fagus stuxbergii* and *F. paleojaponica*) in association with various deciduous dicotyledons, conifers, and a few evergreen dicotyledons. Constituents of this type of floras are more modernized than previous ones and their composition also resembles those in modern vegetation.

Temporal floristic changes that occurred during the Miocene in Japan were revealed to have occurred at the same time as changes in climate conditions during that time interval (Kano & Yanagisawa, 1989; Tanai, 1992; Yabe, 2008b). Based on accumulated radiometric ages and stratigraphic revisions, the boundary age of the Aniai-type and Daijima-type floras is considered to be approximately 20Ma (Yabe, 2008b). The transition between the Daijima-type and Mitokutype floras are not well understood because plant-bearing terrestrial strata are scarce in Japan during the middle Miocene. Some plant fossil assemblages from marine strata have been recorded previously (Kawase & Koike, 2001; Uemura et al., 2006); however, their compositions were skewed due to taphonomic effects in many respects. Based on a palynological study of offshore deposits in the Sea of Japan, Yamanoi (1992a) proposed that the Daijima-type pollen assemblage (NP-2) was traceable until 13 Ma and the Mitoku-type assemblage (NP-4) appeared since 7 Ma. Yamanoi (1989) defined the zone NP-3 as transitional vegetation between the Daijima-type and Mitoku-type floras. However, recently obtained radiometric ages suggested that some assemblages that are comparable with the Mitoku-type flora had appeared much earlier (i.e., Yagii Floras: 10 Ma, Kobayashi et al., 2011; Pinus-trifolia bed: 12 Ma, Tsukagoshi, 2011). Although the appearance of the Mitoku-type flora might differ site-wise, we tentatively assigned the boundary age between the Daijimatype and Mitoku-type floras to the middle-late Miocene boundary. The correlation of each flora from the three different areas is shown in Fig. 2.

Geol. Age Horizon			Primorye	N.Korea		S.Korea	Japan	NP	
Miocene	ate	IV	Ust Suifun				Mitoku-tvpe	4	
	<u></u>		oot ounum				Willond Typo	2	
	middle	III	Novokachalinsk	Hamjin- dong		Yeonil	1	3	
								2	
	early	II	Nezhino		Tong- chon	Sinjeongri	Daijima-type		
		I	Sinij Utes	Yong- dong		Jianggi	Aniai-type	1	

Fig. 2. Correlation of Miocene floras in the southern Primorye, North and South Korea and the Japanese Islands. NP: palynofloral zonation proposed by Yamanoi (1992a). MNCO: mid-Neogene climatic optimum. The upper limit of the Daijima-type floras in Japan was followed after Yamanoi (1992a). It can be extended toward the end of the middle Miocene (allow) based on the correlation with the Yeonil and Hamjindong floras in Korea. For further details see main text.

Correlation and climate analysis

Floristic correlation

On the basis of the stratigraphic correlation of each area in association with additional radiometric and biostratigraphic ages, we recognized four Miocene phytolevels in the circum-Japan Sea areas. They were defined here as Stages I to IV.

Stage I is represented by the Aniai-type floras of Japan and its equivalents (Jianggi and Yongdong floras) from the earliest Miocene age. The Sinij Utes Flora was also compared to this stage (Pavlyutkin & Petrenko, 2010). The floristic composition of fossil assemblages of this stage are similar to one another, and they have been compared to the Mixed Northern Hardwood forest, which indicate cool-temperate climatic conditions (Wolfe, 1979).

Stage II is represented by the Nezhino Flora and the lower part of the Daijima-type floras, which were dated between 20-16 Ma. The Sinjeongri and Tongchong floras from the Korean Peninsula can be correlated to this stage. Floras of this stage, especially in the Japanese Islands, are characterized by an appearance of many thermophilic species in its latter part and are comparable to the Notophyllous Broad-leaved Evergreen forest. Whilst the earlier part of this stage can be correlated to the Mixed Broad-leaved Deciduous or Mixed Broad-leaved Evergreen and Deciduous forest. The occurrence of pollen grains from mangrove plants, which are though to be the elements of tropical-subtropical conditions, has been recorded in central and northeast Japan during the transition between Stage II and III (Yamanoi et al., 1980, 2008, 2010, 2011; Saito et al., 1995). Some common species exist among these assemblages, though the total number of it is smaller in the Tongchong and Nezhino floras in continental Asia (Huzioka, 1972; Pavlyutkin et al., 2012).

Stage III is represented by the Khanka Flora. The Hamjindong and Yeonil floras in the Korean Peninsula, and the upper part of the Daijima-type floras were compared stratigraphically. The age range of this stage is assumed to be 16-12 Ma. Most assemblages other than the Khanka Flora were found in marine deposits. Although only a few fossil assemblages are available in this stage in Japan, the floristic similarities between the Daijima-type Stage II assemblage and the Yeonil Flora conform to a prevalence of the Daijimatype floras until the latter part of the middle Miocene (Stage III). Fossil assemblages from this stage are characterized by a mixture of thermophilic and temperate elements. The Yeonil flora is assignable to the Notophyllous Broad-leaved Evergreen forest like that in the previous stage, while the Hamjindong and Khanka floras, enriched more in temperate elements, are comparable to the Mixed Broad-leaved Deciduous forest.

Stage IV is represented by the Ust-Suifunsky horizon and is comparable with the Mitoku-type floras. They are dominated more by temperate elements than those of the preceding stage, although the Ust-Suifun Flora show unique features distinct from the Mitoku-type floras in Japan. Latitudinal floristic changes are much clearer in this time period and the assemblages from central Japan can be compared to the Mixed Mesophytic forest, while those in the lowland vegetation in northeast Honshu and southern Primorye are comparable to the Mixed Northern Hardwood forest.

Climate analysis

Miocene plant fossil assemblages mentioned in the previous section always contain notophyllclass leaves, indicating a mesic to humid condition. Therefore, changes in floristic composition are considered to be principally controlled by changes in temperature values. Thus, we analyzed each stage assemblage in terms of the temperature change during the Miocene. For Stage I, II, and III assemblages from the Japanese Islands, those from Akita (Aniai and Daijima floras), southwest Hokkaido (Kaminokuni and Yoshioka floras), and Noto (Noroshi and Notonakajima floras) were selected for study. In order to examine the Stage IV assemblage, we added

Area	Flora	Stage	# of species	# of entires	Е	MAT	Error	Reference
Southern Primorye	Nezhino*1	II	94	11	11.70	4.72	1.01	Pavlyutkin et al. (2012)
	Khanka	Ш	99	17	17.17	6.40	1.16	Pavlyutkin (2005)
	Ust-Suifun L ^{*2}	IV	24	3	12.50	4.97	2.07	Pavlyutkin (2002)
	Ust-Sullun U	1 V	82	11	13.41	5.25	1.15	Paviyulkin (2002)
Korean Peninsula	Jianggi*3	Ι	31	8	25.81	9.04	2.40	Huzioka (1972)
	Yeonil*4	III	27	9	33.33	11.34	2.78	Huzioka (1972)
	Hamjindong*5	III	38	6	15.79	5.97	1.81	Huzioka (1972)
Japanese Islands	Kaminokuni*6	Ι	32	2	6.25	3.05	1.31	Tanai and Suzuki (1963)
	Aniai*7	Ι	37	6	16.22	6.10	1.85	Huzioka (1964)
	Yoshioka*8	II	57	11	19.30	7.05	1.60	Tanai and Suzuki (1963)
	Utto ^{*9}	II	69	25	36.23	12.23	1.77	Huzioka (1963)
	Noroshi ^{*10}	II	61	25	40.98	13.68	1.93	Ishida (1970)
	Notonakajima ^{*11}	II–III	28	11	39.29	13.16	2.82	Matsuo (1963)
	Shanabuchi*12	IV	59	8	13.56	5.29	1.36	Tanai and Suzuki (1965)
	Yagii ^{*14}	IV	47	15	31.91	10.91	2.08	Horiuchi (1996)
	Onbara ^{*15}	IV	39	7	17.95	6.63	1.88	Uemura (1986)

Table 1. Quantitative estimates for Mean Annual Temperature based on Leaf Margin Analysis (Wolfe, 1979).

MAT: Mean Annual Temperature; E: Percentage of woody species with smooth leaf margin. MATs and their errors were calculated after equations shown in Wolfe (1979) and Wilfe (1997), respectively. Uste-Suifunsk Flora was divided in the lower (L) and upper (U) floras according to Pavlyutkin (2002). The age of each flora was based on the following literatures: *1, 20.9–17.1 Ma, Pavlyutkin *et al.*, 2012; *2, 11.8–10.8 Ma, Pavlyutkin *et al.*, 1985; *3, 20.9–17.1 Ma, Paik *et al.*, 2012; *4, 14.5–11.5 Ma, Jung and Lee, 2009; *5, 14–9.5 Ma, Koizumi, 1988; *6, 24–23 Ma, Ganzawa, 1992; *7, 24.0–19.4 Ma, Kano *et al.*, 2012; *8, 18–17 Ma, Suzuki *et al.*, 1992; *9, 18.2–16.4 Ma, Yoshikawa *et al.*, 2002; *10, 19–18 Ma, Yoshikawa *et al.*, 2002; *11, 16.3–15.7 Ma, Yoshikawa *et al.*, 2002; *12, 8.2–6.3 Ma, Yahata and Nishido, 1995; *13, ca. 4 Ma, Uemura, personal communication in 2015; *14, 10 Ma, Kobayashi *et al.*, 2011; *15, 6 Ma, Kano and Nakano, 1985.

those from central (Yagii Flora) and western Japan (Onbara Flora) in order to understand the temporal changes in each area as well as its latitudinal difference (Table 1). Most of the estimated values are concordant with physiognomic characters of each assemblage, but others show distinctly lower temperatures. This is probably because LMA tends to be influenced by the number of angiosperm species and because deciduous species were highly divided into morphospecies in some fossil assemblages.

The LMA for floras in Japan indicates a clear trend of temperature increase from Stages I to II. There was a four or six degrees increase in temperature observed in southwest Hokkaido (Kaminokuni to Yoshioka floras) and northeast Honshu (Aniai to Utto floras). The Stage I Jianggi Flora in South Korea show a similar temperature value with that in Japan. The Stage II–III transition, represented by the Notonakajima Flora indicates one of the warmest conditions, while the Stage III Yeonil Flora indicates a slightly cooler condition than the preceding one. The Stage IV assemblages indicate cooler conditions and a latitudinal temperature gradient is observable from Hokkaido (Shanabuchi Flora) to Central Japan (Yagii Flora). The Onbara Flora yielded in the intramountain basin of western Japan represents a similar temperature condition as Northeast Honshu.

In southern Primorye, the Stage II Nezhino Flora indicate a mean annual temperature of less than 5 degrees, which is similar to the Aniai-type floras in northeast Honshu or southwest Hokkaido in Japan. The Stage III Khanka Flora together with the Hamjindong Flora in North Korea indicate slightly warmer conditions but are much lower than that indicated by the Yeonil Flora in South Korea. During Stage IV, the Ust-Suifun floras indicate lower temperature than the Khanka Flora and specify similar values estimated in the assemblage from northern Hokkaido.

Discussion

Miocene floral changes in the circum-Japan Sea areas

Floristic comparisons among southern Primorye, Korea, and Japan clearly show similarities and differences in composition of each flora and their floral changes among these areas.

A synchronized pattern of floristic changes can be recognized in Japan and in the southern part of the Korean Peninsula. Namely, climate warming started prior to 20 Ma and became obvious near the transition between Stages II and III, when mangrove swamps developed in many places in the Japanese Islands. A similar pattern of floristic change has been shown to occur during the early Miocene on the Pacific-side of northeast Japan (Yabe, 2008b). Terrestrial vegetation change in that area is synchronized with shallow marine climate and two warming episodes were recorded there at around 20 Ma and 16 Ma (Yabe, 2008b). The transition between Stages II and III has been known as 'the mid-Neogene climatic optimum (MNCO)' (Tsuchi, 1986), and it lasted from ca. 16.5 to 15 Ma, when warm oceanic climate prevailed throughout the coastal areas in East Asia. In Japan, mollusks typical of 'tropical-subtropical' marine conditions expanded their distribution further north (Ogasawara & Nagasawa, 1992). Pollen grains from mangrove plants were also recorded from these strata in the Japanese Islands (Yamanoi et al., 2011). The earlier part of the Stage II assemblage is known to occur in the Ito-o Formation in Fukui Prefecture, central Japan, where floristic composition is more temperate and comparable with the Mixed Broad-leaved Deciduous forest (Yabe, 2008a).

After a short warming period, the climate became slightly colder, which is represented by the presence of Yeonil Flora. Yamanoi (1992a) distinguished palynofloras of this time period as zone NP-3. This assemblage represents a cooler climate than zone NP-2 with the common occurrence of *Fagus* and the paucity of evergreen *Quercus*. Cooling probably started just after the Stage II–III transition as represented by the Tatsugoroshi Flora from the marine deposits dated 15.9–15.7 Ma, which contain elements of both the Daijima-type and Aniai-type floras (Uemura *et al.*, 2006).

In terms of marine conditions, molluscs typical to the temperate oceanic conditions flourished after MNCO (Ogasawara *et al.*, 2008). Molluscan fossils co-occurring with the Yeonil Flora (i.e., Yeonil Fauna) contains both deep sea and shallow marine mollusks and the latter indicate a warm-temperate marine climate (Ogasawara, personal communication with AY). The expansion of temperate molluscs was considered to have started around 14 Ma (Suzuki, 2003).

Stage IV, represented by the Mitoku-type floras, indicates a more temperate climate condition. Equivalent pollen zone NP-4 is characterized by the dominance of *Fagus* and Taxodiaceae and a sharp decline of *Carya* and *Liquidambar* pollen grains, indicating much cooler climate conditions. It probably represents a cooling trend known to occur in the Late Miocene and thereafter (Zachos *et al.*, 2001).

Floral succession recognized in North Korea and southern Primorye, on the other hand, are not concordant with that in Japan and South Korea. Although there is a trend of climate warming from Stages II to III and probably between Stages I and II, Miocene climate changes in those areas appear to be gentle. Stage II Nezhino and Stage III Khanka floras are both enriched in temperate elements, and the reconstructed temperature value also supports a cool-temperate climate similar to the Stage I assemblage in Japan and South Korea or the Stage II Yoshioka Flora in southwest Hokkaido. The Stage IV Ust-Suifun assemblages also show temperate aspects. However, the absence of beech species as well as the paucity of conifers probably indicates slightly colder and dryer conditions than the preceding one. Therefore, a distinct warming period was not recorded on the continental side.

Floristic similarities between the continental

side and the Japan side started to be disrupted prior to Stage III. Floras in Stage III and IV in southern Primorye consist more of endemic elements. Moreover, a strong difference in floristic composition between the Yeonil and Hamjindong floras were observed, even though they are found in coeval strata. The Tongchon Flora, geographically located between the above two assemblages, is also enriched in temperate elements. Thus, this may represent a latitudinal temperature gradient during that time. However, the latitudinal temperature gradient estimated based on the Daijima-type floras of Honshu Island in Japan is much lower (Tanai, 1991). Besides, the floristic gap was detected around northernmost Honshu (Tanai & Uemura, 1988). Considering that there is no tectonic distinction among these areas, the influence of extra-terrestrial effects should be considered.

Based on marine diatom assemblages from the sediments in the Sea of Japan, Tsoy & Shastina (1999) reported the prevalence of warm-water low-latitude species in the southeast part of the Sea of Japan, which is distinct from those in the northwestern part, where cold-water species dominated. Similarly, molluscan assemblage from the Hamjindong Formation is dominated by boreal genera (Yoldia, Portlandia, Mya) with the rare occurrence of subtropical genera (Macoma) (Ablaev et al., 1990). It shows a strong contrast not only with the Ryeongryukdong fauna (Makiyama, 1936) from the underlying Ryeongryukdong Formation but also with those from the Duho Formation. Therefore, the influence of the cold current, which resembles the modern day cold current, i.e., the Liman Cold Current, on northernmost Honshu, Hokkaido, and the coastal area of the continent, and the effect of a warm oceanic current on Honshu and the southern Korean Peninsula were suggested as major contributing factors that helped to develop the terrestrial vegetation of each area.

Cause of the coastal-inland distinctions

The contrast between the floral assemblages northwest (southern Primorye and North Korea)

and southeast (Japanese Islands and South Korea) of the Sea of Japan became evident from Stage III and were more obvious in Stage IV assemblages. This can be explained by the geographic separation of the Japanese Islands due to the opening of the Sea of Japan since the earlymiddle Miocene and subsequent diversification of local flora. Pavlyutkin & Golozoubov (2010) inferred the effect of the winter monsoon on this floral contrast in association with a strong warm oceanic current that came northeastward across the Sea of Japan since MNCO. The onset of monsoonal climate occurred as early as the late Eocene (Wang et al., 2013). Most scientists, however, confirmed that the intensification of a monsoonal climate occurred later than the Late Miocene (Jacques et al., 2012). If the diversity of Khanka Flora (165 species) and the dominance of beech species in the assemblage are taken into considerations, the effect of monsoonal climate, i.e., low mean annual temperature, high summer precipitation and low winter precipitation, seems unlikely. Rather, it supports a more humid and relatively warmer conditions than modern day Primorye, which is in line with the suggestion that is based on physiognomic analysis. Jacques et al. (2012) discussed that the xeric vegetation in northeast China started to develop when the winter monsoon became stronger during the late Miocene to Pliocene. Interestingly, there is no strong sign of a mid-Neogene climatic optimum that can be recognized in the interior of China. Therefore, peculiar features of the Khanka Flora can probably be explained by the distance from the coast. Whether the Stage IV Ust-Suifun floras represent the effect of intensified monsoonal climate needs to be tested based on further study because pollen grains of beech species are abundant in the upper horizon of this stage.

Implications for the period of Japan Sea formation

The rifting and opening of the Sea of Japan basin caused a key geographic barrier between continental East Asia and Japan. It may have further influenced the regional climatic conditions



Fig. 3. Dynamics of the Sea of Japan opening (modified and supplemented after Golozoubov, 2006). A, the early Paleogene (ca. 50Ma). B, the late early Miocene (ca. 20Ma). C, the early middle Miocene (ca. 15Ma). 1: Pre-Cenozoic terranes. 2: areas of the newly formed oceanic crust. 3: the Okhotsk Sea Plate. 4: the Pacific Plate. 5: the axial part of the Izu–Bonin arc. 6: strike-slip fault zones, including HSF (Hokkaido–Sakhalin faults), TnF (Tanakura fault), FMF (Fossa-Magna faults), TsF (Tsushima fault). 7: extension axes. 8: directions of plate displacements. 9: subduction zones. 10: directions of block rotation. Letters in circles show underwater rises: Ya, Yamato; EK, East-Korean; Kr, Krishtofovich; K, Kita-Oki.

and lead to the distinct vegetation of each area. A detailed correlation of Miocene floras in this study revealed that its effect became obvious during Stage III.

The Japan Sea basin was formed by the clockwise rotation of southwest Japan and counter clockwise rotation of northeast Japan during the short time period between the late early to early middle Miocene (i.e., 15-17 Ma: Otofuji, 1996). Jolivet & Tamaki (1992) discussed that the opening of the Sea of Japan could have started ca. 25 million years ago based on the oldest sedimentary rocks studied during deep-water drilling in the newly formed depressions of the Sea of Japan (up to 20 Ma). Earlier rifting has often been proposed (Kano et al., 2002, 2007). In order to accept that the pull-apart sedimentary basins, which are located along the Strait of Tatar (Golozoubov et al., 2012), Sikhote-Alin (Golozoubov et al., 2007, 2009), south of the Korean Peninsula (Martynov et al., 2006), were formed simultaneously with the major depressions of the Sea of Japan, the origin and development of the basin could be as early as the early Eocene, as long as it is not younger than 50 Ma.

However, late Paleogene floras in Primorye are quite similar to those found in the Japanese Islands. The two areas have many common species and climate change trends inferred from the flora in these areas are parallel to one another (Tanai & Uemura, 1991a, b, 1994; Ablaev, 2000; Pavlyutkin, 2007), so that a geographic distinction between these areas during that time is unlikely. Thus, two major stages were distinguished in the course of the development of the Sea of Japan basin. The first stage was settled when the Japanese Islands separated from the mainland. A series of pull-apart intra-continental basins were formed (Fig. 3A & B). The separate blocks between the basins were close to each other, as well as to the continental side and to the Japan side. This may provide the preservation of floristic links. It is worthy to note that fragments, which have broken off the continent during their movement, did not undergo significant rotation of each block at this time period. At the second stage, the further rather fast drift of Japan occurred within the limits of a so-called twodoor model by Otofuji (1996) with considerable anticlockwise rotation of northeast Japan and the clockwise rotation of southwest Japan (Fig. 3B & C). Since this time period, Japan and the continent have been separated by vast water spaces and it does not only provide geographic separation but also climatic differentiation between the island and the continental sides of the Sea of Japan, which leads to the distinction of forest vegetation in these areas.

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中新世における環日本海植物化石群の変化 一古気候変化と日本海拡大の影響に注目して

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ロシア沿海州南部,韓半島および日本列島に分布する中新世植物化石群集を層位的に 対比し,同地域における中新世の森林植生変化と推測される古気候変化を明らかにする とともに,日本海の拡大による植生への影響を議論した.全地域において前期中新世から 前期/中期中新世境界への温暖化とその後の寒冷化の傾向が確認できたが,南部と北部 とで温暖化の規模に違いがあることが明らかとなった.また,中期中新世以降,各地の化 石群集に地域性が現れ,後期中新世にさらに顕著となった.これらの現象は日本海の拡大 にともなう地理的分断の影響に加え,大陸沿岸を洗う寒流と日本列島沿岸を流れる暖流 の影響をうけた可能性が推測された.