

6 Migration and adaptation of late Cenozoic cold-water molluscs in the North Pacific

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6.1 Abstract

Cold-water molluscan fauna originated in the North Pacific in accordance with the worldwide cooling events around the latest Eocene. The westward trans-Pacific migration of the cold-water molluscs occurred during the early to early middle Miocene, owing to shifting climatic belts and “ecological opportunity” rather than current direction. In contrast, the eastward migration of the cold-water molluscs occurred in cool climate ages from the early Oligocene to Holocene. As a result of the Plio-Pleistocene cooling, cold-water species spreaded to the Yellow and the East China Sea through the Japan Sea. Shifting climatic belts thus affected the zoogeographic range of cold-water species.

Keywords: Migration, Late Cenozoic, cold-water, Mollusca, North Pacific.

6.2 Introduction

The cold-water molluscan fauna in the North Pacific has a long and complex history involving species formation, migration and adaptation against a backdrop of changing climate and oceanographic conditions.

Migration and adaptation of molluscan species have been studied in relation to climate change and the opening of Bering Strait in the northern Pacific. Three types of migrations have been recognized among the North Pacific taxa (Amano 2000). The first type appeared in the northwestern Pacific and migrated to the northeastern Pacific. It includes *Mya* (MacNeil 1965), *Neptunea* (Strauch 1972), *Mizuhopecten* (Masuda 1986), Turrilloidea and Buccinoidea (Titova 1994). The species of the second type originated in the northeastern Pacific, then spread westward. The taxa

include *Penitella* and *Platyodon* (Adegoke 1967), *Panomya* (Strauch 1972), *Littorina* (Reid 1996), *Liracassis* (Kanno 1973), *Nucella* (Amano et al. 1993), *Ceratostoma* (Amano and Vermeij 1998b), *Macoma* (*Rexithaerus*) (Amano et al. 1999), *Kaneharaia* (Amano and Hikida 1999) and *Lirabuccinum* (Amano and Vermeij 2003). The species of the third type such as *Cyrtodaria* (Strauch 1972) and Astartidae (Ogasawara 1986) invaded the North Pacific after the opening of the Bering Strait from the Arctic Sea region.

When Vermeij (2001) synthesized the history of North Pacific biota, he noted that the genera in the first two types appeared during the latest Eocene or the early Oligocene as a response to cooling. Based on Amano and Vermeij (1998b), he also emphasized the Oligocene to early Miocene origin of groups that subsequently migrated westward during the early middle Miocene. Vermeij (2001) also suggested that the turrid *Aforia* and *Yoldia* group might have been originated in the Southern Hemisphere. Based on a molecular study, Ozawa et al. (2001) noted that the buccinid *Kelletia* originated in Southern Hemisphere and reached the northwestern Pacific via the northeastern Pacific. However, a detailed scenario of the northward migration of the above mentioned genera remains speculative. Thus, these taxa are not included in this paper.

In consequence of the establishment of a new time table of the Pacific coast Cenozoic in North America based mainly on magnetostratigraphy (Prothero 2001), it is necessary to reexamine the timing of the molluscan migration events. Moreover, the bathymetric difference between the eastward and westward spreading molluscan groups has also not been discussed in detail.

The Pliocene trans-arctic interchange through the Bering Strait has been studied by many authors (e.g. Durham and MacNeil 1967; Vermeij 1991; Marincovich and Gladenkov 1999; Marincovich 2000; Marincovich et al. 2002; Gladenkov and Gladenkov 2004). When the Bering Strait opened, astartids and other bivalves invaded the Pacific from the Arctic region. Based on a drastic frequency change of calcareous nannofossil, *Coccolithus pelagicus* at 2.74Ma, Sato et al. (2004) concluded that this frequency change was correlated with the closure of the Central American Seaway and with onset of heavy glaciation in the Arctic Sea and the North Pacific Ocean. However, no detailed examination has been done on the route of southward expansion of the cold-water molluscs, including the astartids in the northwestern Pacific.

The purposes of this paper are to: (1) extend the list on the trans-Pacific migrants, (2) explore the bathymetric difference between different groups of migrants, and (3) specify routes of migration of cold-water species in the northwestern Pacific during the Plio-Pleistocene.

6.3 Material and Methods

Stratigraphic and geographic distributions of the North Pacific cold-water taxa listed by Amano (2000) and Vermeij (2001) are reexamined. Among them, the turbinid *Phanerolepida*, the muricid *Boreotrophon*, the buccinids *Japelion*, and *Sulcosipho* were not previously discussed in this context. In this paper, I reexamine their migration routes and ages in detail. Material stored at Joetsu University of Education (JUE) and Tohoku University (IGPS) was used in addition to a critical review of the literature.

I divided the North Pacific into western and eastern regions from the paleobiogeographic viewpoint. The northwestern Pacific includes Japan, Sakhalin, Kamchatka and Koryak Upland while the northeastern Pacific includes Alaska, Vancouver Island, Washington, Oregon and California. After checking the age of the oldest fossil record for each genus on both sides of the Pacific, I treat the older age as an appearance and the younger age as a migration age for each genus. It is possible for these ages to be younger than the real origin and migration timings mainly because of taphonomic reasons.

These Cenozoic ages are based mainly on the synthesized micropaleontological or magnetostratigraphic scheme by Kano et al. (1991) for Japan, Kurita et al. (2000) and Gladenkov et al. (2000) for Sakhalin, Gladenkov (1998) for Kamchatka, Marincovich (1990) for Alaska, and Prothero (2001) for Vancouver to California. Ecological data of Recent molluscs are mainly based on Higo et al. (1999), Coan et al. (2001) and McLean (1996).

For the Plio-Pleistocene, I examined the distribution of some cold-water molluscan species. In addition, the southern limits of some boreal species were investigated. As the Japan Sea was semi-enclosed and separated from the Pacific Ocean during the Plio-Pleistocene (e.g. Ogasawara 1994), the hydrographic condition of the Japan Sea differed from that of the Pacific. So, it is necessary to separately examine the southernmost limits of boreal species in the Pacific and Japan Sea. For this purpose, material housed at Joetsu University of Education (JUE), Tohoku University (IGPS) and University Museum of University of Tokyo (UMUT) was used.

6.4 Trans-Pacific migration

6.4.1 Case studies of some gastropods

Migration of *Phanerolepida*

The deep-water turbinid, *Phanerolepida transenna* (Watson 1879) is the only extant species of this genus and lives in warm-water habitats ranging from Sagami Bay, central Honshu to Southern Kyushu (200-1100 m in depth; Higo et al. 1999). However, the migration route is the same as that of some cold-water genera such as *Nucella*, *Ceratostoma* and *Lirabuccinum*.

Noda and Ogasawara (1976) and Majima and Murata (1992) compiled the fossil records of *Phanerolepida* species; *P. oregonensis* Hickman 1972, *P. expansilabrum* (Kuroda 1931), *P. pseudotransenna* Ozaki 1956, *P. rehderi* MacNeil 1960 (= *P. pseudotransenna* by Majima and Murata 1992), *P. transenna* (Watson 1879) and *P. okinawana* Noda 1988. *P. okinawana* resembles *Homalopoma granuliferum* Nomura and Hatai 1940 in having distinct spiral cords despite having coarser shagreen sculpture. In this paper, this species is excluded from the genus *Phanerolepida*.

According to Majima and Murata (1992) and Hickman (2003), the earliest species *P. oregonensis* was collected from the upper Eocene Keasy Formation (middle member) in Oregon and evolved from the middle Eocene *Nehalania hieroglyphica* Hickman 1974 in Oregon (Fig. 1). The Pliocene to Recent *P. transenna* evolved by the way of *P. pseudotransenna* during the late Miocene in southwest Japan.

Two additional Miocene species were found in eastern Kamchatka and Hokkaido. Titova in Gladenkov et al. (2000) only illustrated *P. ozernensis* from the lower Miocene Ozernovsky Formation in eastern Kamchatka as a new species without any description. Judging from her illustration, this species is more similar to the Recent *P. transenna* than any fossil species especially in having fine shagreen sculpture. Fujii Environmental Geology Institute (1998) illustrated an ill-preserved specimen from the uppermost lower to lowermost middle Miocene Ponsubetsu Formation in Hokkaido as *Phanerolepida* sp.

The fossil record indicates the following history for this genus. The earliest deep-water species, *P. oregonensis* appeared in Oregon during the late Eocene. The genus reached eastern Kamchatka by the early Miocene. Then, it moved southward to central Honshu *via* Hokkaido in the latest early to earliest middle Miocene during the climatic warm interval.

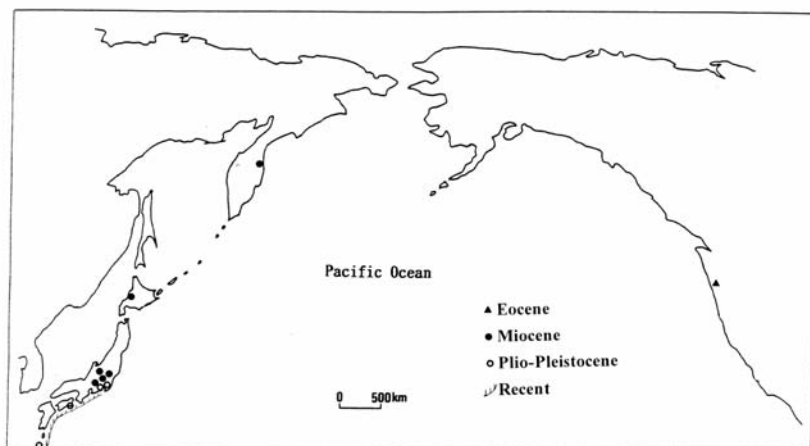


Fig. 1. Distribution of *Phanerolepida*

In the Pliocene, the genus adapted to the deep-water of warm area from central Honshu to Okinawa Islands and now lives there. This migration pattern is partly similar to the other shallow-water westward spreading group in its direction, but differs from the latter in that eastern Pacific members became extinct. No species now live in the North Pacific region and the northwestern part of America.

Migration of *Boreotrophon*

Many species of the muricid gastropod *Boreotrophon* occur in the sublittoral zone of the North Pacific, Arctic and North Atlantic (Tiba and Kosuge 1985; Egorov 1993; Houart 2001). The earliest fossil species are *Boreotrophon osawanoensis* (Tsuda 1959) from the lower Miocene Yamanouchi Formation in Gifu Prefecture, central Japan or *B. sp. indet.* described by Matsubara (1996) from the lower Miocene Yotsuyaku Formation in Iwate Prefecture, northeast Japan. Associated faunas of these species suggest that they might have lived in the upper sublittoral zone under the influence of warm water. I obtained a specimen of *B. cf. beringi* (Dall) from the middle Miocene Shibiutan Formation in the northern Hokkaido in association with *Anadara hokkaidoensis* Noda 1966, *Spisula onnechiuria* (Otuka 1940), *Megangulus protovenulosus* (Nomura 1935), *Kaneharaia ausiensis* (Ilyina 1954) and *Securella chitanana* (Yokoyama 1926). Thus, in the middle Miocene, the genus adapted to temperate-water

in North Korea, Honshu and reached northern Hokkaido (Fig. 2). Sinelnikova in Gladenkov and Sinelnikova (1990) described *B. etolonica* as a new species from the middle Miocene Etolon Formation in western Kamchatka.

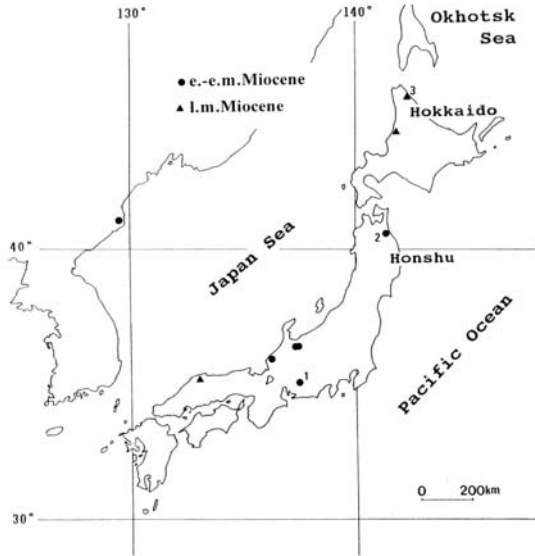


Fig. 2. Distribution of *Boreotrophon* in the early to middle Miocene. 1. Yamanouchi Formation in Gifu Prefecture, 2. Yotsuyaku Formation in Iwate Prefecture, 3. Shibiutan Formation in Hokkaido (see also the text)

However, as the type and only specimen lacks a basal part, it is difficult to determine the validness of this species within the genus *Boreotrophon*. There is no early to middle Miocene record of this genus in northeastern Pacific side. The oldest record is *Boreotrophon* from the upper Miocene to Pliocene Rio Dell Formation in California (Faustman 1964).

The genus originated in the warm water environment around Honshu during the early Miocene. Then, by the late Miocene, *Boreotrophon* spread to the northeastern Pacific. After the opening of the Bering Strait, the genus spread to the Arctic and North Atlantic regions in the Pliocene (Durham and MacNeil 1967). In the Pliocene, this genus diversified both on northwestern and northeastern sides of the Pacific Ocean (Grant and Gale 1931; Hatai and Nisiyama 1952; Masuda and Noda 1976).

Migration of *Japelion*

The Recent buccinid *Japelion* consists of *J. hirasei* (Pilsbry 1901), *J. pericochlion* (Schrenck 1862), *J. adelphicus* (Dall 1907) and *J. latus* (Dall 1918). The first two species live in the lower sublittoral to upper bathyal depths from central Honshu and northward to the Bering Sea. *J. latus* is an endemic species living mainly in the lower sublittoral of the Tsushima Strait, East China Sea and Yellow Sea.

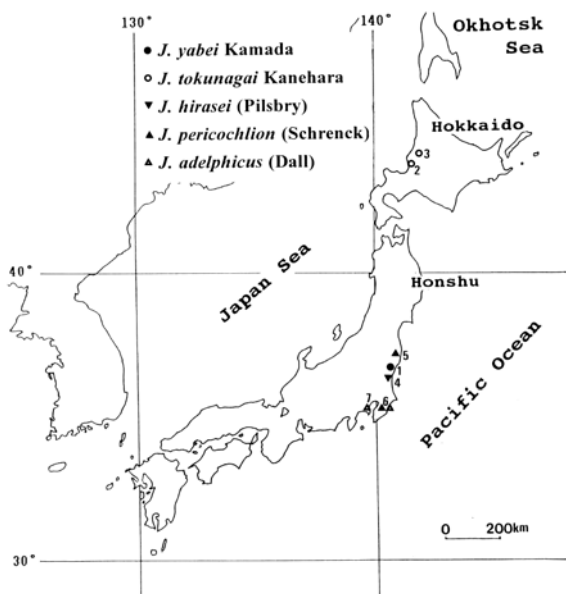


Fig. 3. Distribution of fossil *Japelion*. 1. Mizunoya Formation in Joban coal-field, 2. Morai Formation in Hokkaido, 3. Mashike Formation in Hokkaido, 4. Hitachi Formation in Ibaraki Prefecture, 5. Futaba-Tomioka Formation in Fukushima Prefecture, 6. Kazusa Group and Semata Formation in Chiba Prefecture, 7. Kazusa Group in Kanagawa Prefecture (see also the text)

J. adelphicus dwells in the lower sublittoral of warm-water area from central Honshu to southernmost Kyushu (Higo et al. 1999).

The fossil record of *Japelion* is confined to Japan. The oldest fossil species is *J. yabei* Kamada 1955 from the lower Miocene Mizunoya Formation in the Joban coal-field (Fig. 3). Concerning the upper Miocene fossil record, *J. tokunagai* Kanehara 1937 was collected from the Morai (Kanehara 1937) and Mashike (this study) Formations both in western Hokkaido.

In the Plio-Pleistocene, three Recent species appeared mainly in and around the Kanto Region, central Honshu. *J. hirasei* was described by Noda et al. (1995) from the Pliocene Hitachi Formation, Ibaraki Prefecture. *J. pericochlion* has been recorded from the Pliocene Futaba-Tomioka Formation in Fukushima Prefecture by Nemoto and O'Hara (1979) and from the Pleistocene Kazusa Group in Chiba Prefecture by Baba (1990). *J. adelphicus* has been known from the Pleistocene Kazusa Group and Semata Formation in Chiba and Kanagawa Prefectures (Okutani 1968; Baba 1990).

Based on the above fossil records, the genus originated in central Honshu during the early Miocene and may have spread recently to the Bering Sea, south Kyushu and East China Sea. However, it has never reached the northeastern part of the Pacific.

Migration of *Sulcosipho*

Sulcosipho was proposed by Dall (1916) as a new section of *Chrysodomus* Swainson 1840 (= *Neptunea* Roeding 1798), based on *Chrysodomus tabulatus* Baird 1863. *Sulcosipho tabulatus* now lives in 50-200 m depth of Petersburg, Alaska to Newport Bay, California (McLean 1996).

When he summarized the Neogene biogeography of *Neptunea*, Nelson (1978) included *N. "sachalinensis"* Khomenko 1938, *N. lamellosa* Golikov 1962 and *N. uwasoensis* Otuka 1935 (= *N. eos* (Kuroda 1931)) in *Sulcosipho*. However, as pointed by Goryachev (1987) and Amano (1997a), they should be classified as *Neptunea* (*Neptunea*) because the shell is not slender form and the shoulder is not tabulated. On the other hand, Goryachev (1987) treated *S. tabulatus*, *S. lawsoni* (Martin 1914) and *S. andersoni* (Martin 1914) as belonging to the Melongenidae (= Melongenidae) without any reasons. However, these species lack spines or nodes which are characteristic of the Melongenidae and the narrow siphonal canal resembles that of *Neptunea*. Dall (1919) stated that *S. tabulatus* was included in the same section of *Japelion adelphicus* by having the slender form and the tabulated shoulder. From these reasons, *Sulcosipho* should be treated as a genus of the Buccinidae rather than the Melongenidae.

The earliest fossil record of *Sulcosipho* is *Neptunea (Sulcosipho) cf. tabulatus* described by Kanno (1971) from the middle Miocene Yakataga Formation in Alaska. Then, this species migrated southward during the late Miocene. In contrast with *Japelion*, this genus did not reach the northwestern Pacific.

6.5 Pattern of origin, migration and adaptation

North Pacific cold-water genera or subgenera are classified into three groups as mentioned by Amano (2000). Among them, the group originating in the northwestern Pacific can be subdivided into two subgroups. The first subgroup (W1) migrated to the northeastern Pacific while the second one (W2) did not. The W1 subgroup consists of 21 genera or subgenera including *Boreotrophon* as mentioned above (Table 1).

On the origination age, the late Eocene (8 taxa) dominates the subgroup W1. Four taxa each originated in the early Oligocene and early Miocene. In contrast, there is no conspicuous age of migration ranging from the early Oligocene onwards.

On the other hand, only four genera are included in the W2 subgroup; *Ocenebrellus*, *Clinopegma*, *Japelion* and *Volutomitra*. Their appearances in the early to early middle Miocene are younger than those of the W1 subgroup. As pointed out by Vermeij (2001), most taxa of this group live on sandy mud or mud bottom at sublittoral to bathyal depths. It is noteworthy that 14 among 23 extant taxa are able to live in the bathyal zone.

Table 1. Origin and migration ages of W Group. *M, mud; sM, sandy mud; fS, fine-grained sand; cS, coarse-grained sand; S, sand; R, rock

Genera or subgenera	NW Pacific	NE Pacific	Depth (m)	Bottom*	References
W1 Group					
<i>Turritella (Neohaustor)</i>	e.Miocene	e.m.Miocene	30–1500	sM	Titova, 1994
<i>T. (Hataiella)</i>	e.Eocene	e.m.Miocene	–	–	Titova, 1994; Oleinik and Marincovich, 2003
<i>Tachyrhynchus</i>	l.Eocene	l.Pliocene	12–1500	cS, sM	Titova, 1994
<i>Boreotrophon</i>	e.Miocene	l.Miocene	0–964	cS, sM	This study
<i>Neptunea</i>	l.Eocene	l.Oligocene	0–1380	sM	Strauch, 1972; Oleinik and Marincovich, 2003
<i>Ancistrolepis</i>	l.Eocene	e.Oligocene	100–690	M	Titova, 1993
<i>Tromina</i>	l.Eocene	e.Oligocene	–	–	Titova, 1994
<i>Buccinum</i>	e.Oligocene	l.Oligocene	0–1500	M	Titova, 1994
<i>Arctamelon</i>	m.Eocene	Holocene	100–200	M	Oleinik, 1996
<i>Acila</i>	Cretaceous	e.Oligocene	0–990	fS, M	Vermeij, 2001
<i>Yoldia (Cnesterium)</i>	m.Eocene	m.Miocene	9–400	sM	Vermeij, 2001
<i>Portlandia (Megayoldia)</i>	l.Eocene	Holocene	25–760	M	Vermeij, 2001
<i>Mizuhopecten</i>	e.Miocene	l.Miocene	2–80	cS, sM	Masuda, 1986
<i>Cyclocardia</i>	l.Eocene	e.Oligocene	10–400	sM	Popov, 1983
<i>Clinocardium (Keenocardium)</i>	e.Oligocene	l.Oligocene	10–200	sM	Kafanov, 1999, 2000
<i>C. (Ciliatocardium)</i>	l.Eocene	l.Oligocene	10–200	M	Kafanov, 2001
<i>Serripes</i>	e.Oligocene	l.Miocene	0–260	sM	Kafanov, 2003
<i>Siliqua</i>	l.Eocene	e.m.Miocene	0–100	S	Vermeij, 2001
<i>Solen (Ensisolen)</i>	e.m. Miocene	l.Miocene	0–50	S	Vermeij, 2001
<i>Liocyma</i>	e.Oligocene	l.Oligocene	0–1500	sM	Amano, 2000
<i>Mya</i>	m.Eocene	l.Oligocene	0–100	M	MacNeil, 1965
W2 Group					
<i>Ocenebrellus</i>	e.m. Miocene	–	0–200	R	Amano and Vermeij, 1998a; Matsubara and Amano, 2000
<i>Clinopegma</i>	e.m. Miocene	–	50–650	sM	Amano, 2000
<i>Japelion</i>	e.Miocene	–	50–500	M	This study
<i>Volutomitra</i>	e.Miocene	–	100–200	M	Amano, 1997b

The group evolving in the northeastern Pacific also consists of two subgroups. One of them (E1) spread northwestward while the other (E2)

remained restricted to the Northeast Pacific. The E1 subgroup is composed of 22 genera or subgenera including *Phanerolepida* (Table 2).

Table 2. Origin and migration ages of E Group. *M, mud; sM, sandy mud; fS, fine-grained sand; cS, coarse-grained sand; S, sand; R, rock

Genera or subgenera	NE Pacific	NW Pacific	Depth (m)	Bottom*	References
E1 Group					
<i>Puncturella</i>	l.Eocene	e.m.Miocene	0-1200	R	Vermeij, 2001; Squires, 2003
<i>Phanerolepida</i>	l.Eocene	e.Miocene	200-1100	cS, M	This study
<i>Littorina</i>	m.Eocene	e. Miocene	0	R	Reid, 1996; Squires, 2003
<i>Trichotropis</i>	l. Eocene	e. Miocene	20-100	M	Amano, 2000; Squires, 2003
<i>Euspira</i>	Paleocene	m.Eocene	0-620	sM	Marincovich, 1977; Majima, 1989
<i>Glossaulax</i>	m. Eocene	e.m.Miocene	0-100	fS	Marincovich, 1977; Majima, 1989
<i>Cryptanatica</i>	e.Miocene	e.m.Miocene	20-300	sM	Marincovich, 1977; Majima, 1989
<i>Liracassis</i>	l.Eocene	e.Miocene	-	-	Kanno, 1973; Squires, 2003
<i>Fusitriton</i>	l.Eocene	e.m.Miocene	0-620	sM, fS	Smith, 1970; Squires, 2003
<i>Nucella</i>	e.Oligocene	e.m.Miocene	0-20	R	Amano et al., 1993
<i>Ceratostoma</i>	e.Miocene	e.m.Miocene	0-135	R	Amano and Vermeij, 1998b
<i>Lirabuocinum</i>	e.Oligocene	e.m.Miocene	0-270	R	Amano and Vermeij, 2003
<i>Nuttalia</i>	m. Eocene	e.Oligocene	0-20	sM, fS	Vermeij, 2001
<i>Spisula (Mactromeris)</i>	Paleocene	m.Eocene	0-200	fS, M	Vermeij, 2001
<i>S. (Pseudocardium)</i>	Paleocene	m.Eocene	0-30	fS	Vermeij, 2001
<i>Macoma (Rexithaerus)</i>	l.Oligocene	e.m.Miocene	0-100	S	Amano et al., 1999
<i>Securella</i>	e.Oligocene	e.m.Miocene	0-150	fS	Vermeij, 2001
<i>Kanaharaia</i>	e.Oligocene	e.m.Miocene	-	-	Amano and Hikida, 1999
<i>Compsomyax</i>	e.Oligocene	e.Miocene	2-500	M	Amano, 2000
<i>Panomya</i>	l.Oligocene	e.Miocene	0-300	sM, M	Strauch, 1972
<i>Penitella</i>	e.Oligocene	e.Miocene	0	R	Adegoke, 1967
<i>Platyodon</i>	e.Oligocene	e.Miocene	0-20	R	Adegoke, 1967
E2 Group					
<i>Ocinebrina</i>	e.Miocene	-	0-60	R	Marko and Vermeij, 1999
<i>Sulcosipho</i>	m.Miocene	-	54-392	sM	This study
<i>Crassadoma</i>	e.Miocene	-	0-80	R	Vermeij, 2001
<i>Cumingia</i>	Pliocene	-	0-65	R	Vermeij, 2001

Seven genera or subgenera first appeared in the early Oligocene, and four taxa each appeared in the middle and late Eocene. The migration age is also concentrated in the early to early middle Miocene (18 taxa). Only four genera belong to the E2 subgroup; *Ocinebrina*, *Sulcosipho*, *Crassadoma* and *Cumingia*. They originated after the early Miocene like did subgroup W2. As noted by Amano and Vermeij (1998b) and Vermeij (2001), this group includes many hard bottom- as well as soft bottom-dwellers mainly living in the intertidal to sublittoral zones. Fifteen taxa among 24 extant genera or subgenera are confined to these zones. *Phanerolepida* living in the bathyal zone is the single exception.

6.6 Causes of origin, migration and adaptation

During the Eocene-Oligocene transition, a global cooling affected both deep-water and shallow-sea molluscan faunas (Squires 2003; Oleinik and

Marincovich 2003; Nesbitt 2003; Hickman 2003). As noted by Vermeij (2001), the cold-water taxa appeared during the latest Eocene or the early Oligocene representing the first cooling interval of the Cenozoic. Most cold-water taxa evolved in the late Eocene and early Oligocene. It is noteworthy that no shallow-sea cold-water species evolved from the tropical Pacific biota in the latest Eocene to early Oligocene cooling. However, the reason for this is unknown.

The eastward migration took place at intervals from the early Oligocene to the Holocene, but there were few instances in the early to early middle Miocene. In contrast, the westward spreading occurred during the short interval of the early to early middle Miocene.

The deeper water W1 subgroup had opportunities to move northward and eastward in any cooling climate ages. As also noted by Amano and Vermeij (1998b) and Vermeij (2001), the northwestward migration of subgroup E1 occurred during the Neogene warm maximum. Two plausible causes for the westward migration are available.

For benthic organisms, current is usually considered as an important factor of larval transport (e.g. Cecca 2002). As noted by Kafanov (1982), many high latitude molluscs have a non-planktotrophic larval life; therefore planktonic dispersal would be unimportant. However, as the current sometimes transports the adult on algae, it may be important for the direction of migration. If there was a westward current during the Neogene warm maximum, it is easy to explain why many E1 taxa migrated westward but few W1 taxa spread eastward. However, it is difficult to explain the reason why circulation reversed only during the Neogene warm period.

Another plausible reason is the combination of a shifting climate belt and “ecological opportunity”. In the Neogene warmest age, the northernmost Pacific lay in the temperate zone (Marincovich 1988; Ogasawara 1994; Amano et al. 1996). As the temperate zone extended northward, eastern Pacific taxa could move westward easily along the coast. The reason why the W1 subgroup could not migrate eastward is an “ecological opportunity” postulated as the most important reason for the trans-Arctic interchange by Vermeij (1991).

The E1 subgroup includes many rocky shore dwellers which are never found in the W1 subgroup. Only two muricid species and one boring bivalve species are known from the Paleogene of the northwestern Pacific region: *Ocenebra ashियाensis* Nagao 1928 from the upper Oligocene Ashiya Group, in Fukuoka Prefecture, Kyushu, *Ocenebra tsuzurensis* Yokoyama 1924 from the lower Oligocene Iwaki Formation in the Joban coal-field, central Honshu, and *Parapholas satoi* Nagao 1928 from the upper Oligocene Meinohama Formation in Fukuoka Prefecture, Kyushu.

In other words, by the early Miocene, the hard bottom communities in shallow water were an open niche for species coming from the east.

In contrast, ten deep-water species among the twenty one species of W1 subgroup already migrated and adapted to the northeastern part by the end of Oligocene.

Moreover, similar niches of another species had been already occupied by the well established soft-bottom fauna. For example, the trophonines, volutids, yoldiids and pectinids appeared in the northeastern Pacific during the Paleocene and Eocene (Squires 2003; Moore 1983 1984). Thus, it was difficult for the W1 subgroup to adapt on the soft bottom in the northeastern Pacific.

The taxa restricted to either the northeastern or the northwestern Pacific (W2, E2) originated in the early Miocene or later. Five genera or subgenera first appeared in the early or early middle Miocene belong to the W1 subgroup.

As mentioned above, this interval is a timing of migration for most E1 and a few W1 taxa. The later appeared W2 and E2 taxa such as *Japelion* and *Sulcosipho* could not participate in the migration.

6.7 Plio-Pleistocene expansion of cold-water species

6.7.1 Recent cold-water species in Yellow Sea and East China Sea

A warm-water current flows at the surface of the East China Sea and the Yellow Sea. By contrast, there is a deep cold-water mass in the Yellow Sea (Tsuchida 1975). Seventeen cold-water species other than *Ancistrolepis vietnamensis* and *Arctomelon tamikoe* now live in the modern water of the sublittoral zone of the Yellow Sea (Yamashita 1978; Zhao et al. 1982; Qi et al. 1989; Table 3).

The southern limits of eight of these species in the Japan Sea are located at Tsushima or off Yamaguchi near the Yellow Sea. Populations of nine other species in the Yellow Sea are separated from the northern populations in the Japan Sea. Two Recent species of *Arctomelon* occur in Alaska and northwestern America (Weaver and du Pont 1970).

The distribution of *Arctomelon tamikoe* Kosuge 1970 living in 100-200 m depth of the East China Sea is isolated from the main distributional area of this genus.

Table 3. Cold-water species now living in the Yellow Sea, the East China Sea and the South China Sea

Species	Depth (m)	Bottom*	S.L.**	References
<i>Acmaea pallida</i> (Gould)	0-20	R	Tsushima	Qi et al., 1989
<i>Homalopoma amussitatum</i> (Gould)	0-300	cS, R	Niiigata	Zhao et al., 1982; Qi et al., 1989
<i>Turritella (Neohaustator) fortilirata</i> Sowerby	30-300	sM	Yamaguchi	Yamashita, 1978
<i>Trichotropis bicarinata</i> Sowerby	20-100	M	Hokkaido	Yamashita, 1978; Zhao et al., 1982
<i>Boreotrophon beringi</i> (Dall)	20-389	S	Hokkaido	Yamashita, 1978
<i>Japellion latus</i> (Dall)	50-200	sM	Tsushima	Qi et al., 1989
<i>Ancistrolepis vietnamensis</i> Sirenko and Goryachev	400-700	M	-	Sirenko and Goryachev, 1990
<i>Plicifusus rhyssoides</i> Dall	100-300	M	Tsugaru	Yamashita, 1978
<i>Neptunea cumingi</i> Grosse	0-200	R	Hyogo	Yamashita, 1978; Zhao et al., 1982
<i>Buccinum plectrum</i> Stimpson var.	-	-	Kuril Is.	Zhao et al., 1982; Qi et al., 1989
<i>Volutharpa perryi</i> (Jay)	10-70	sM	Yamaguchi	Qi et al., 1989
<i>Arctomelon tamikoeae</i> Kosuge	100-200	M	-	Kosuge, 1970
<i>Acila (Truncacila) insignis</i> (Gould)	0-200	fS, M	Tsushima	Yamashita, 1978
<i>Ennucula tenuis</i> (Montagu)	0-2200	sM	Yamaguchi	Yamashita, 1978
<i>Yoldia (Cnesterium) johanni</i> Dall	10-100	sM	Hokkaido	Yamashita, 1978
<i>Musculus nexus</i> (Gould)	10-230	M	Primorie	Qi et al., 1989
<i>Clinocardium (Keenocardium) californiense</i> (Deshayes)	10-200	sM	Tsushima	Yamashita, 1978
<i>Potamocorbula amurensis</i> (Schrenck)	2-20	M	-	Qi et al., 1989
<i>Cardiomya behringensis</i> (Leche)	50-2900	sM	Hokkaido	Yamashita, 1978

Ancistrolepis vietnamensis Sirenko and Goryachev 1990, a descendant form of the cold-water genus *Ancistrolepis*, now lives in 400-700 m depth of the South China Sea. As proposed by Oleinik (1996), these species resulted from southward expansion in the Quaternary. However, there has been no discussion on the migration route of these species.

6.7.2 Plio-Pleistocene migration route

There are two ways for cold-water species to expand their distribution. One is the Japan Sea route and the other is the Pacific side route. However, the Pacific side of southwestern Japan lies in the subtropical zone affected by the warm Kuroshio Current during the late Cenozoic (e.g. Ogasawara 1994). Thus, it is difficult to assign the migration route to the Pacific side. *Tridonta borealis* and *T. alaskensis* are known from the Plio-Pleistocene strata in Hokkaido and the Japan Sea borderland (Fig. 4), but there is no Plio-Pleistocene record of this genus from the Pacific side of northeastern Honshu other than the Pliocene Togawa Formation and Pleistocene Hamada Formation. Ten cold-water species now living in Hokkaido and are known from the Japan Sea borderland at the horizon younger than the Datum A (Sato and Kameo 1996) which coincides in timing with the increasing abundance of *Coccolithus pelagicus* (Amano et al. 1987; Amano, 1994, 1996; Yoon 1988; Amano et al. 1996; Kase et al. 1996; Sato et al. 2003; Table 4).

In the late Pliocene, the southernmost occurrences of the following species are located at Akita Prefecture (Sasaoka Formation) and Niigata

Prefecture (Tanihama Formation): *Cyclocardia crassidens*, *C. isaotakii*, *Felaniella ohtai*, *Macoma middendorffi*, *M. lama meridionalis* and *Nuttallia commoda* (Fig. 5).

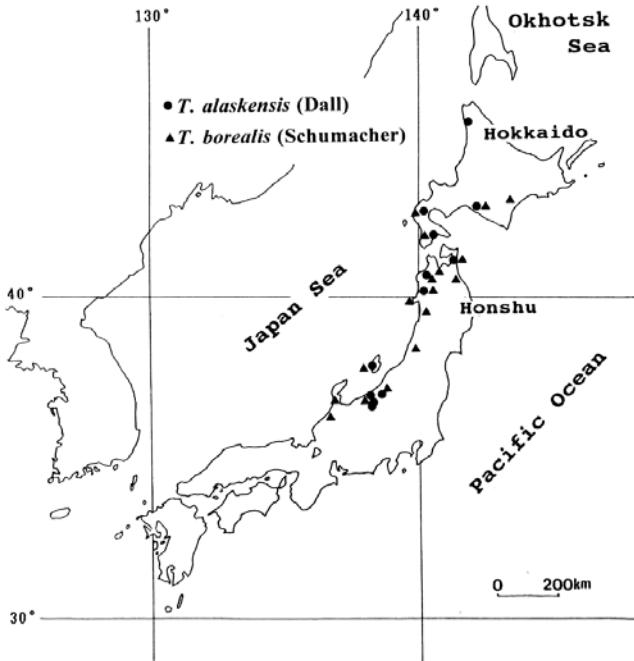


Fig. 4. Distribution of fossil *Tridonta alaskensis* (Dall) and *T. borealis* (Schumacher)

Later, *Siliqua alta* occurred from the lower Pleistocene Seoguiipo Formation in Jeju Island near the Yellow Sea (Yoon 1988; Kang 1995). *Felaniella ohtai* was also found from the lower Pleistocene Sawane Formation in Sado Island, Niigata Prefecture. Four species have been recorded from the lower Pleistocene Omma Formation in Ishikawa Prefecture: *Ancistrolepis grammatus*, *Macoma middendorffi*, *M. lama meridionalis* and *Mya truncata*.

Table 4. Southernmost formation occurring the cold-water species during the late Pliocene to the middle Pleistocene

Species	l.Plio.	e.Pleist.	m.Pleist.	References
<i>Ancistrolepis grammatus</i> (Dall)	–	Omma F.	–	Amano et al., 1996
<i>Chlamys (Chlamys) straegus</i> (Dall)	–	–	Shibikawa F.	Amano, 1996
<i>Cyclocardia crassidens</i> (Broderip and Sowerby)	Sasaoka F.	–	Shibikawa F.	Amano, 1996, 2001
<i>C. isaotaki</i> (Tiba)	Tanihama F.	–	–	Amano et al., 1987
<i>Felaniella ohtai</i> Kase and Miyauchi	Sasaoka F.	Sawane F.	–	Kase et al., 1996
<i>Siliqua alta</i> (Broderip and Sowerby)	–	Seoguiipo F.	–	Yoon, 1988
<i>Macoma (Macoma) middendorffi</i> Dall	Sasaoka F.	Omma F.	–	Amano, 1996
<i>M. (M.) lama meridionalis</i> Scarlato	Sasaoka F.	Omma F.	Shibikawa F.	Amano, 1996; Sato et al., 2003
<i>Nuttallia commoda</i> (Yokoyama)	Sasaoka F.	–	–	Sato et al., 2003
<i>Mya (Mya) truncata</i> Linnaeus	–	Omma F.	–	Amano, 1996

**Fig. 5.** Plio-Pleistocene formations yielding some species living at present in Hokkaido and northwards. 1. Sasaoka Formation in Akita Prefecture, 2. Tanihama Formation in Niigata Prefecture, 3. Sawane Formation in Niigata Prefecture, 4. Omma Formation in Ishikawa Prefecture, 5. Seoguiipo Formation in Korea, 6. Shibikawa Formation in Akita Prefecture (see also the text)

In the late middle Pleistocene, *Chlamys strategus*, *Cyclocardia crassidens* and *Macoma lama meridionalis* again reached Akita Prefecture (Shibikawa Formation).

Sato et al. (2002) showed that the cold-water calcareous nannofossil *Coccolithus pelagicus* assemblage migrated through the Japan Sea via the East China Sea to the South China Sea during 2.75–1.97Ma. Kitamura and

Kimoto (2004) showed that the southern strait to the Japan Sea existed in the glacial period during 1.45-1.32 Ma and during all interglacials as well. The horizon of the above cold-water species in the Sasaoka Formation is assigned in age to the late Pliocene just after 2.75 while that in the Omma Formation to the time interval of 1.45-1.32Ma.

Ancestral populations of some cold-water species migrated westward into the Yellow Sea and East China Sea through the Japan Sea during 2.75-1.97Ma and 1.45-1.32 Ma. Upper middle Pleistocene deposits are scarce in the Japan Sea coast. Although, some cold-water molluscs which live now in Hokkaido and northwards are known from the Shibikawa Formation, it is uncertain if these species could migrate to the Yellow Sea in the late middle Pleistocene. Because *Ancistrolepis vietnamensis* and *Arctomelon tamikoae* are known only from their type locality and have no fossil records, they may have arisen recently.

6.8 Conclusions

Cold-water taxa originated in the temperate zone of the North Pacific as a response to the worldwide cooling events around the latest Eocene. The taxa of northeastern origin migrated via the north to the northwestern Pacific mainly during the early to early middle Miocene, the warmest period of the Neogene. Such westward migration seems to be owing to the combination of shifting the climatic belts and the “ecological opportunity” rather than the current direction. On the other hand, species originating in the northwest migrated during the cooling climate ages from the early Oligocene to Holocene. Cold-water species of the North Pacific spread to the Arctic, North Atlantic regions through the Bering Strait and to the Yellow and East China Seas through the Japan Sea in the Pliocene to Pleistocene as climate cooled.

No shallow-sea cold-water species evolved from the tropical northwestern Pacific biota in the latest Eocene to early Oligocene cooling. In contrast, some species of cold-water taxa originated in the northeastern Pacific became adapted to warm waters in the western Pacific. For example, *Phanerolepida transenna* (Watson 1879), *Ceratosoma fournieri* (Crosse 1861) and *Securella chitanihana* (Yokoyama 1926) live or lived in the warm waters of southwestern Japan. The reason for the different histories of trans-Pacific species originated in the east and in the west remains unclear.

6.9 Acknowledgements

I am very grateful to Prof. Geerat J. Vermeij (University of California at Davis), Prof. Kazushige Tanabe (University of Tokyo) and Dr. Enrico Savazzi (Institute of Earth Sciences, Uppsala, Sweden) for their critical reading of this manuscript and comments. This study was partly supported by Grant-in-aid for Scientific Research of the Japan Society for the Promotion of Science (C, 15540450, 2003-2005).

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