Online ISSN 2435-0931 Print ISSN 0385-0900
DOI: 10.50897/bmfm.51.1_75

Bulletin of the Mizunami Fossil Museum, vol. 51, no. 1, p. 75–109, 2 pls., 3 figs., 12 tables.

Manuscript accepted on November 24, 2024; online published on December 25, 2024
http://zoobank.org/urn:lsid:zoobank.org:pub:776FFCCD-9000-4260-B6DF-2E534A30470F

Speciation, extinction and survival of molluscan species in the marginal sea –Plio-Pleistocene Omma-Manganji fauna in the Japan Sea borderland–

Kazutaka Amano*

*Department of Geology and Paleontology, National Museum of Nature and Science Tokyo, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan < amano@juen.ac.jp >

Abstract

The Plio-Pleistocene Omma-Manganji fauna shed light on the mechanism of speciation, extinction and survival in the Japan Sea. The semi-enclosed Japan Sea accelerated speciation by interrupting gene flow since the Late Miocene. During some cold events such as NHG, MIS 22 and LGM, most shallow-water species became extinct because of cooling and reduced salinity. In addition, many deep-sea species became extinct because of anoxia. Some large-sized bivalves such as pectinids and some predator gastropods such as buccinids were vulnerable because of their high metabolic rates and cold conditions. On the other hand, some species dwelling in the intermediate marine zone (200 to 300 m in depth) could survive the deteriorated environments in the glacial periods.

Key words: Omma-Manganji fauna, speciation, extinction, survival, Japan Sea

1. Introduction

1.1. General outline of the Recent Japan Sea

The Japan Sea is a typical marginal sea having deep basins (max. depth, 3700 m) connected to open ocean by four shallow straits: the Tsushima and Tsugaru Straits (about 130 m in depth), Soya Strait (55 m in depth) and Mamiya Strait (15 m in depth) (e.g., Tada, 1994).

The temperature of the surface water is influenced by the Tsushima Warm Current (TWC) through the Tsushima Strait. On the other hand, below 300m, the cold temperature (0–0.5℃) as well as high dissolved oxygen (5 ml/l) water prevails below 300 m and is called “Japan Sea Proper Water” (JSPW) (e.g., Gamo et al., 1986).

1.2. Environmental change of the Japan Sea

The Japan sea became a semi-enclosed marginal sea since the Pliocene (Ogasawara, 1994). The deep-water connection between the Japan Sea and the Pacific Ocean was interrupted at 4.5 Ma by the uplift of the backbone range of Northeastern Honshu (Kozaka et al., 2018; Nakajima, 2018). In the Pliocene to Early Pleistocene, many cold-water species lived in the semi-enclosed Japan Sea because of relatively wide northern straits in contrast with narrow and shallow southern strait (Ogasawara, 1986; Tada, 1994; Amano, 2007; Itaki, 2016; Nakajima, 2018). Especially, by the cooling of Northern Hemisphere at 2.75 Ma (Datum A by Sato and Kameo, 1996), northern species currently confined from Hokkaido and northward extended south to Akita and Toyama Prefectures on the Japan Sea side of Honshu (Amano et al., 2011, 2012).

Judging from the appearance of warm-water species, the Tsushima warm current flowed into the Japan Sea through the Tsushima Strait since 4 Ma (Amano et al., 2008), not 3.5 Ma (Tada, 1994; Kitamura and Kimoto, 2006). Along the formation of the present-day southern channel at 1.71 Ma, TWC began to flow in the interglacial period to a depth as deep as today (Kitamura and Kimoto, 2006).

These geographic and climate changes in this semi-enclosed marginal sea led to speciation of the endemic species and adaptation of warm-water species to cold water areas (Kamiya, 2003; Amano, 2007). The Plio-Pleistocene molluscan fauna including such endemic extinct species of the Japan Sea was named as the Omma-Manganji fauna by Otuka (1939a).

1.3. Historical review of the studies on the Omma-Manganji fauna

Otuka (1936) proposed Manganzian fauna for the “Pliocene” [Early Pleistocene] molluscan fossils from Manganzi, Kotomo-mura [Yuri-Honjo City] in Akita Prefecture. He also pointed out that it shares some characteristic species with the Onma Series in Ishikawa Prefecture. Otuka (1939a) proposed Omma-Manganzian fauna from the Japan Sea-side area, from Teshio to Saishu-to [Cheju Island in Korea] in his text fig. 2 when he described the Pliocene molluscan fossils from Tanabu [Mutsu City] in Aomori Prefecture. Summarizing the geography, crustal deformation and faunal succession by Otuka (1939b), he stated that the Manganzi (or Onma) fauna is the Oyashio (cold-water current) fauna in the Pliocene. He also used Onma-Manganzi sea in this paper.

Chinzei (1963) called the Pliocene fauna in the Japan Sea borderland as Omma-Manganji type fauna which is characterized by offshore species. When Chinzei (1978, 1991) summarized the Neogene to Quaternary molluscan succession, he defined the Pliocene to Early Pleistocene molluscan fauna of the Japan Sea coast of Honshu as the Omma-Manganji fauna. I follow his usage herein as the Omma-Manganji fauna. He also showed that the general character of the fauna comprises cold-water species and extinct species. Three associations were recognized in the Omma-Manganji fauna by him; coastal water sandy bottom associations, coastal water gravelly bottom associations, and offshore muddy bottom associations.

Noda and Amano (1977) first collected one of the characteristic species of Omma-Manganji fauna, *Anadara amicula elongata* Noda [=*A. amicula* (Yokoyama)] from the Kume Formation in the Kanto area, Pacific side of central Honshu. They proposed the Transitional Zone to the mixed faunal area from where the cold-water Tatsunokuchi and Omma-Manganzian faunas and the warm-water Kakegawa fauna cooccurred.

Masuda and Ogasawara (1981) summarized the species lists of Omma-Manganzian fauna from various localities. Ogasawara (1981) noticed that the fauna from the upper part of the Omma Formation in Ishikawa Prefecture does not include any characteristic species of Omma-Manganji fauna and he proposed the Younger Ommaian fauna for the species from the upper part of the Omma Formation in Ishikawa Prefecture. The age of this change was MIS 22 (0.9 Ma), elucidated by Kitamura (2016).

Among the type localities of the Omma-Manganji fauna, many well-preserved molluscan fossils occur from the Omma Formation in Ishikawa Prefecture. Yokoyama (1927) first described the molluscan fossils from the Omma Formation. Later, Kaseno and Matsuura (1965) listed and illustrated many molluscan fossils from the formation. Ogasawara (1977) analyzed the assemblage of the molluscan fauna from the Omma Formation and described the molluscan species. Kitamura and Kondo (1990) found the cycles of glacial and interglacial sediments in the Omma Formation by analyzing the stratigraphy and the molluscan assemblages in detail.

Ogasawara (1986) stated that the Omma-Manganzian fauna consists of 250 to 300 species including 45 extinct species. Although there are many cold-water species in the fauna, some warm-water species are included. Judging from the species composition, he divided the Omma-Manganzian province into four subprovinces; southern (Cheju Island and Off Mishima), central (Ishikawa Prefecture to Akita Prefecture), northern (northern Akita Prefecture to Hokkaido) and Kuril. Paleoclimate of the southern subprovince corresponded to the warm-temperate zone while the central and northern subprovince to the mild-temperate zone according to Ogasawara (1994).

Amano (1994a) tried to estimate the paleotemperature of the Early Pleistocene Omma-Manganji fauna based on the distribution of each species. As a result, he estimated SST (annual mean) in the Early Pleistocene was 0.5 to 3℃ lower than today. This lower SST in the Early Pleistocene was supported by the distribution of rock-boring bivalve associations (Shinada and Amano, 1995). When Amano (2001) summarized the “Pliocene” [Pliocene and Early Pleistocene (Gelasian)] Omma-Manganji fauna, he found the Miocene relict species became extinct by the cooling event at the Datum A (2.75 Ma). Moreover, he also found that the extinct species of the Omma-Manganji fauna increased during the Pliocene and warm-water species living in the upper sublittoral depth first appeared in the Late Pliocene. Based on the distribution pattern of neogastropods, Amano (2004) estimated that the shallow-water species became extinct during the Middle to Late Pleistocene glacial age due to prevailing low-salinity water in the enclosed Japan Sea while most deep-water species became extinct due to anoxic deep water. He also estimated the existence of intermediate marine water even in the glacial time period including the Last Glacial Maximum (LGM).

Amano (2007) summarized the Pliocene and Pleistocene Omma-Manganji fauna from the viewpoints of stratigraphic ranges of extinct species, occurrences of warm-water and cold-water species and timing of extinction of Miocene relict species. As a result, after the Late Pliocene, some cold-water species now living in Hokkaido and northwards were collected from the Japan Sea side of Honshu. The warm-water species first appeared at 4 Ma and increased their diversity in the Late Pliocene. Moreover, it is confirmed that many characteristic species became extinct at 0.9 Ma.

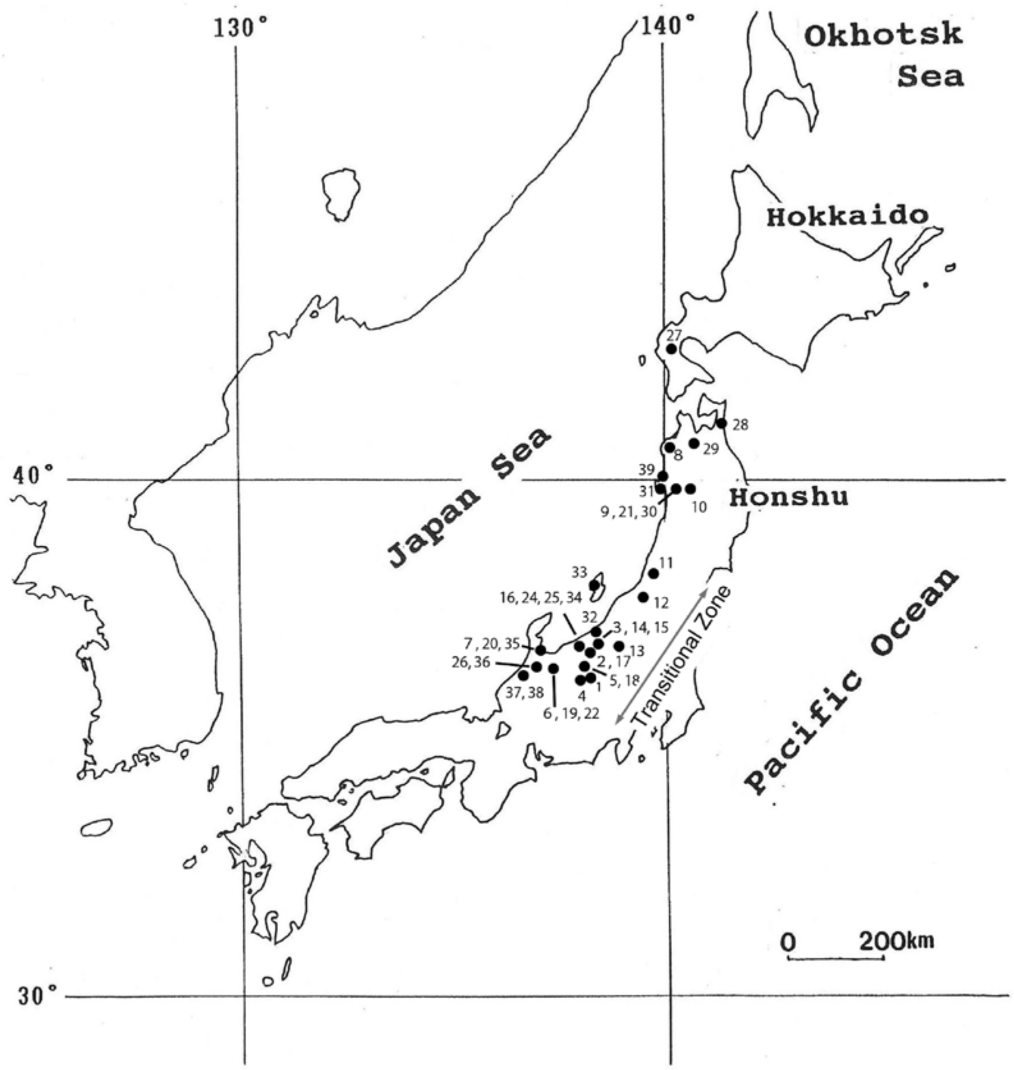

Fig. 1. Locality of the Omma-Manganji fauna. Number of localities are listed in Table 1.

Table 1. Formations and their ages treated in this study. *numbers of localities are the same as in Fig. 1.

Geologic age	No.*	Formation	Prefecture	References
Late Miocene	1	Ogawa F.	Nagano	Amano and Koike (1993)
Early Pliocene	2	Tomikura and Nagasawa Fs.	Nagano and Niigata	Nakata and Amano (1991)
	3	Upper part of Kurokura F.	Niigata	Amano (1994c)
	4	Joshita F.	Nagano	Amano and Sato (1995)
	5	Arakurayama F.	Nagano	Amano and Karasawa (1988)
	6	Lower part of Mita F. (Loc. 1, 2, 5–9, 17, 18, 22, 25, 26)	Toyama	Amano et al. (2008)
	7	Lower part of Zukawa F. (Loc. Z-1, 5–7)	Toyama	Amano et al. (2012)
Late Pliocene	8	Kitakanegasawa F.	Aomori	Amano (2020)
	9	Sasaoka F. (Loc. TH1–5, MH1)	Akita	Amano et al. (2011)
	10	Tentokuji F.	Akita	Ogasawara et al. (1986), Amano et al. (2000a)
	11	Kannonji F.	Yamagata	Ogasawara and Naito (1983)
	12	Kuwae F.	Niigata	Amano et al. (2000b)
	13	Shitoka F.	Niigata	Amano et al. (2009)
	14	Ikenosawagawa F.	Niigata	Amano (1994c)
	15	Higashigawa F.	Niigata	Amano (1994c)
	16	Kawazume F.	Niigata	Amano et al. (1990)
	17	Seguchi F.	Nagano and Niigata	Nakata and Amano (1991), Amano (2019c)
	18	Ogikubo F.	Nagano	Amano and Karasawa (1988, 1993), Nagamori (1998, 2014)
	19	Upper part of Mita F. (Loc. 3–4, 9–13, 19, 23, 24)	Toyama	Amano et al. (2008)
	20	Upper part of Zukawa F. (Z-9)	Toyama	Amano et al. (2012)
Younger than 2.75 Ma	21	Sasaoka F. (Loc. TH 8–10, MH2)	Akita	Amano et al. (2011)
	22	Uppermost part of Mita F. (Loc.14–16, 27–29)	Toyama	Amano et al. (2008)
	23	Uppermost part of Zukawa F. (Loc. Z-2–4, Z-11)	Toyama	Amano et al. (2012)
e. Early Pleistocene	24	Tanihama F.	Niigata	Amano et al. (1987)
(Gelasian)	25	Upper part of Nadachi F.	Niigata	Amano et al. (1988), Amano and Kanno (1991)
	26	Lowermost part of Omma F. (Loc. 5, 11)	Toyama	Kaneko et al. (2016)
l. Early Pleistocene	27	Setana F.	Hokkaido	Sawada (1962), Suzuki (1989, 1991)
(Calabrian)	28	Hamada F.	Aomori	Hatai et al. (1961), Shimaguchi and Nara (2015)
	29	Daishaka F.	Aomori	Nomura and Hatai (1935), Iwai (1965)
	30	Upper part of Sasaoka F. (Loc. TH 6, 10, MH3–7)	Akita	Amano et al. (2011)
	31	Kitaura F.	Akita	Takayasu (1962)
	32	Haizume F.	Niigata	Kobayashi et al. (1986)
	33	Sawane F.	Niigata	Omori (1977), Endo (1986)
	34	Kota F.	Niigata	Mizuno and Amano (1988)
	35	Itaya F.	Toyama	Amano et al. (2014)
	36	Omma F.	Toyama	Amano and Ogihara (2012), Kaneko et al. (2016)
	37	Lower and Middle parts of Omma F.	Ishikawa	Ogasawara (1977), Matsuura (1985, 1992, 2009)
Younger than 0.9 Ma	38	Upper part of Omma F.	Ishikawa	Ogasawara (1981), Amano (2023)
Middle Pleistocene	39	Shibikawa F.	Akita	Takayasu (1962), Ogasawara et al. (1986)

1.4. Purpose of this study

The semi-enclosed Japan Sea can provide a good model to examine genetic separation and speciation of deep-sea animals (Kojima et al., 2001). Some Recent deep-water molluscs are endemic to the Japan Sea (Scarlato, 1981; Amano, 2004; Hasegawa, 2014).

In this paper, based on occurrences of all cold-water and warm-water species in the Omma-Manganji fauna, the paleoclimatic changes and the responses of the Omma-Manganji fauna are summarized. Moreover, adding to the results of studies after 2007, the geologic ranges of the extinct species of the Omma-Manganji fauna are also reexamined. Based on the environmental change and ecological viewpoints, the speciation and extinction in the marginal sea such as the Japan Sea are discussed.

2. Materials and methods

The Pliocene to Early Pleistocene molluscan faunas in the Japan Sea borderland have been examined (Fig. 1). All species in the lists by the authors in Table 1 were checked. Mainly calcareous nannoplankton fossils, diatom fossils and tephrochronology were used for age control in this study. Considering the faunal change recognized in my previous studies (e.g., Amano, 2007), the interval from the Early Pliocene to the Early Pleistocene is subdivided into the six time bins in the following lines; A) Early Pliocene, B) Late Pliocene (older than 2.75 Ma), C) Latest Pliocene (younger than 2.75 Ma), D) early Early Pleistocene (Gelacian), E) late Early Pleistocene (Calabrian, older than 0.9 Ma) and F) latest Early Pleistocene (Calabrian, younger than 0.9 Ma). Moreover, for examining the geological range of the characteristic species, the faunal lists from the Upper Miocene Ogawa Formation in Nagano Prefecture (Kanno and Tomizawa, 1959; Amano and Koike, 1993), the Upper Miocene Togeshita Formation (upper part) in Hokkaido (Amano, 1983) and the Middle Pleistocene Shibikawa Formation (Takayasu, 1962; Ogasawara et al., 1986) were examined. Consequently, the following number of localities were examined for each time bin; A) 120, B)168, C) 14, D) 55, E)143, F) 1 (Table 1). Moreover, data on 14 taxa of gastropods and 22 taxa of bivalves (Table 2) were used herein.

Based on the geographic distribution data of Higo et al. (1999), I defined the species residing in the Boso Peninsula and northwards (Oyashio area) as cold-water species while those in the Boso Peninsula and southwards (Kuroshio area) as warm-water species.

3. Results

3.1. Cold-water extant species

As mentioned in the previous studies, many cold-water species have been recorded in the Plio-Pleistocene Omma-Manganji fauna. A total of 124 species is counted, consisting of 70 bivalves (Table 3) and 54 gastropod species (Table 4). Among six age time bins, the largest number of cold-water bivalve species (58 species) are recorded in the late Early Pleistocene, Calabrian before 0.9 Ma (Table 5). However, the ratio of the number of species for each locality (number of cold-water bivalves/number of localities) is highest (1.2) in the Late Pliocene after 2.75 Ma, except for only one locality of the Early Pleistocene after 0.9 Ma. Moreover, among 70 cold-water bivalves, 25 species are now living in Iwate Prefecture and northwards, according to Higo et al. (1999). The highest ratio of these species (0.4) is also found in the Late Pliocene after 2.75 Ma.

On the other hand, 54 cold-water gastropods have been recorded. Among them, the highest ratio (0.6) is recognized also in the Late Pliocene after 2.75 Ma (Table 9). Moreover, fifteen gastropod species are now residing in Iwate Prefecture and northwards. The highest ratio (0.1) of the gastropods residing in Iwate Prefecture and northward is found in the Late Pliocene after 2.75 Ma and the Early Calabrian before 0.9 Ma.

Table 2. Taxonomic work on the Omma-Manganji fauna herein cited.

Taxa	References
Monodonta	Amano (2019b)
Pomaulax	Amano (2019b)
Vermeijia	Amano (2019a)
Cymatiidae	Amano (1997a)
Cyllene	Amano (2019a)
Ancistrolepidinae	Amano et al. (1996)
Neptunea	Amano (1997c)
Neptunea sakurai	Amano et al. (2021)
Lirabuccinum	Amano and Vermeij (2003)
Buccinum	Amano and Watanabe (2001)
Ceratostoma	Amano and Vermeij (1998b)
Ocinebrellus	Amano and Vermeij (1998a)
Trophonopsis	Amano (2006)
Volutomitra	Amano (1997b)
Robaia	Amano and Narita (1992)
Megayoidia toyamaensis	Amano (1996a)
Scapharca broughtonii	Amano and Komori (2021)
Scapharca	Amano (2023)
Limopsis	Amano and Lutaenko (2004)
Chlamys	Amano and Karasawa (1986), Amano (1994d), Amano et al. (1991)
Chlamys islandica group	Kubota (1950), Masuda and Sawada (1961), Masuda (1962), Shikama and Ikeya (1964), Uozumi and Akamatsu (1975)
Fortipecten kenyoshiensis	Chinzei and Hiramatsu (1988)
Astartidae	Amano (1994b)
Cyclocardia	Amano (2024)
Megacardita	Amano (in press)
Miodontiscus	Amano et al. (2024)
Thracia	Amano (1995)
Divalucina	Amano (2019c)
Felaniella	Kase et al. (1996)
Calyptogena	Kanno et al. (1989), Amano and Kiel (2007), Amano and Jenkins (2011), Amano et al. (2019b)
Profulvia	Amano and Tanaka (1992)
Humilaria	Amano (1998)
Kaneharaia	Amano and Hikida (1999)
Macoma	Amano (1996b), Amano et al. (2024)
Nuttallia	Amano and Ogihara (2012)
Cardillia	Amano (2019c)

Table 3. Occurrences of the cold-water extant bivalves included in the Omma-Manganji fauna. *Species living in Iwate Prefecture, Northeast Honshu and northwards.

Species \ Age	Early Pliocene	Late Pliocene	2.75 Ma	Early Pleistocene: Gelasian	Calabrian	0.9 Ma
Agriodesma naviculoides (Yokoyama)	+					
Calyptogena pacifica Dall	+					
Nuttallia ezonis Kuroda and Habe	+					
Gobraeus kazusensis (Yokoyama)	+					
Panomya priapus (Tilesius)*	+	+				
Acila (*Truncacila*) *insignis*	+	+		+	+	
Nuculana (*Nuculana*) *pernula* (Müller)	+	+		+	+	
Yoldia (*Cnesterium*) *notabilis* Yokoyama	+	+		+	+	
Portlandia (*Megayoldia*) *thraciaeformis* (Storer)	+	+			+	
Glycymeris (*Glycymeris*) *yessoensis* (Sowerby)	+	+		+	+	+
Crenella yokoyamai Nomura	+				+	
Modiolus difficilis Kuroda and Habe	+	+	+	+	+	
Solamen columbiana (Dall)*	+	+		+		
Swiftopecten swiftii (Bernardi)	+	+		+	+	
Mizuhopecten yessoensis (Jay)	+	+	+		+	
Monia macroschisma (Dehshayes)	+	+	+	+	+	
Astarte hakodatensis Yokoyama	+	+		+	+	
Tridonta borealis Schumacher*	+	+	+	+	+	
T. alaskensis (Dall)*	+	+	+	+	+	
Thracia kakumana Yokoyama	+	+	+		+	
Pandorella wardiana A. Adams	+	+		+	+	
Adontorhina subquadrata (A. Adams)	+			+	+	
Felaniella usta (Gould)	+	+	+	+	+	+
F. ohtai Kase and Miyauchi*	+		+		+	
Clinocardium (*Keenocardium*) *californiense* (Deshayes)	+				+	
Serripes groenlandicus (Bruguière)*	+	+		+	+	
Securella stimpsoni (Gould)	+	+	+	+	+	
Ezocallista brevisiphonata (Carpenter)	+	+	+	+	+	
Megangulus zyonoensis Hatai and Nisiyama	+	+		+	+	
Cadella lubrica (Gould)	+	+	+	+	+	
Macoma (*Macoma*) *calcarea* (Gmelin)	+	+		+	+	
Solen krusensterni Schrenck	+	+			+	
Siliqua alta (Broderip and Sowerbty)	+			+	+	
Spisula (*Pseudocardium*) *sachalinensis* (Schrenck)	+	+			+	
S. (*Mactromeris*) *grayana* (Schrenck)	+	+		+	+	
Musculus laevigatus (Gray)		+				
Clinocardium (*Clinocardium*) *nuttallii* (Conrad)*		+				
Panomya arctica (Lamarck)*		+				
Mytilus (*Crenomytilus*) *grayanus* Dunker		+		+	+	
Parvamussium alaskense (Dall)		+			+	
Miodontiscus prolongatus (Carpenter)*		+		+	+	
M. annakensis (Oinomikado)		+			+	
Heteroclidus pulchellus (Yokoyama)*		+			+	
Clinocardium (*Ciliatocardium*) *ciliatum* (Fabricius)		+		+	+	
Liocyma fluctuosa (Gould)*		+			+	
Megangulus venuosus (Schrenck)		+			+	
Mya (*Mya*) *truncata* Linnaeus*		+		+	+	
M. (*Arenomya*) *japonica* Jay		+			+	
Adula falcatoides Habe*			+			
Thracia itoi Habe			+			
Panomya nipponica Nomura and Hatai*			+	+		
Macoma (*Macoma*) *middendorffi* Dall*			+		+	
Callithaca adamsi (Reeve)			+	+	+	
Mya (*Mya*) *pseudoarenaria* Schlesch			+	+	+	
Tridonta filatovae Habe*				+	+	
Cyclocardia (*Cyclocardia*) *isaotakii* (Tiba)*				+	+	
C. (*Crassicardia*) *crassidens* (Broderip and Sowerby)*				+	+	
Hiatela arctica (Linnaeus)*				+	+	
Leucoma euglypta (Sowerby III)				+	+	
Macoma (*Macoma*) *lama meridionalis* Scarlato				+	+	
Leionucula tenuis (Montagu)					+	
Yoldia (*Cnesterium*) *johanni* Dall					+	
Musculus niger (Gray)					+	
Chlamys (*Chlamys*) *albida* (Dall)*					+	
C. (*C.*) *behringiana* (Middendorff)*					+	
C. (*C.*) *strategus* (Dall)*					+	
Tridonta vernicosa (Dall)					+	
Cyclocardia crebricostata (A. Krause)*					+	
Macoma (*Macoma*) *lipara* Dall*					+	
Gari californica (Conrad)*					+	

Table 4. Occurrences of the cold-water extant gastropods included in the Omma-Manganji fauna. *Species living in Iwate Prefecture, Northeast Honshu and northwards.

Species \ Age	Early Pliocene	Late Pliocene		Early Pleistocene	
			2.75 Ma	Gelasian	Calabrian (0.9 Ma)
Turritella (*Neohaustator*) *nipponica* Yokoyama	+				
Lirabuccinum fuscolabiata (Smith)	+				
Neptunea (*Neptunea*) *pribioloffensis* (Dall)*	+				
N. (*N.*) *rugosa* Golikov*	+				
Volutharpa ampullacea perryi (Jay)	+				
Rectiplanes isaotakii (Habe)	+				
Buccinum unuscarinatum Tiba*	+	+			
Turritella (*Neohaustator*) *fortilirata* Sowerby III	+	+			+
Littorina (*Neritrema*) *sitkana* Philippi	+	+			+
Crepidula grandis Middendorff	+				+
Euspira pila (Pilsbry)	+	+			+
Cryptonatica janthostoma (Deshayes)	+	+	+		+
C. affinis (Gmelin)	+	+			+
Boreoscala greenlandica (Perry)	+	+	+		+
Neptunea (*Barbitonia*) *arthritica* (Valenciennes)	+	+			+
Antiplanes vinosa (Dall)	+	+			+
Rectiplanes sanctiioannis (Smith)	+	+			+
Cocculina japonica Dall		+			
Euspira pallida (Broderip and Sowerby)		+			
Buccinum rhodium Dall*		+			
Admete viridula (Fabricius)		+			
Lepeta concentrica (Middendorff)*		+	+	+	
Tugalina gigas (v. Martens)		+		+	
Clinopegma borealis Tiba		+		+	
Niveotectura pallida (Gould)		+	+	+	+
Homalopoma amussitatum (Gould)		+	+	+	+
Puncturella nobilis (A. Adams)		+	+	+	+
Pseudoliomesus ooides (Middendorff)		+			+
Boreotrphon candelaburum (Reeve)		+			+
Propebela assimilis (Sars)*		+			+
Lepeta caeca Müller*			+		+
Cryptobranchia kuragiensis (Yokoyama)			+		+
Tachyrhynchus septencostatus Golikov*					+
Trichamathina nobilis (A. Adams)*					+
Frigidoalvania asura (Yokoyama)					+
Fusitriton oregonensis (Redfield)					+
Acirsa ochotenseis (Middendorff)*					+
Mitrella burcardi (Dunker)					+
Ancistrolepis grammatus (Dall) *					+
Beringius indentatus Dall*					+
Plicifusus plicatus (A. Adams)					+
Neptunea (*Neptunea*) *constricta* (Dall)					+
N. (*N.*) *polycostata* (Scarlato)*					+
N. (*N.*) *vinosa* (Dall)*					+
N. (*N.*) *lamellosa* Golikov*					+
N. (*N.*) *eulimata* (Dall)*					+
Buccinum ochotense Middndorff*					+
B. sakhalinense Dall					+
B. inclytum Pilsbry					+
Nucella freycineti (Deshayes)					+
N. lamellosa (Gmelin)					+
Boreotrophon beringi Dall					+
B. pacificus Dall					+
Volutomitra gloenlandica alaskana Dall					+

Table 5. Summarized table of the cold-water, warm-water and extinct molluscan species included in the Omma-Manganji fauna. *Cold-water species living in Iwate Prefecture, Northeast Honshu and northwards. **Warm-water species not living in the Japan Sea.

Item \ Age	Total number of sp.	E. Pliocene	L. Pliocene (before 2.75Ma)	L. Pliocene (after 2.75Ma)	E. Pleistocene (Gelasian)	E. Pleistocene (Calabrian)	E. Pleistocene (after 0.9Ma)
Number of localities	-	120	168	14	55	143	1
Cold-water bivalves	70	35	39	17	35	58	2
Cold-water bivalves/loc.	-	0.3	0.2	1.2	0.6	0.4	2.0
Cold-water bivalves*	25	6	11	6	11	19	0
Cold-water bivalves*/loc.	-	0.1	0.1	0.4	0.2	0.1	0.0
Cold-water gastropods	54	17	23	8	6	40	0
Cold-water gastropods/loc.	-	0.1	0.1	0.6	0.1	0.3	0.0
Cold-water gastropods*	15	3	4	2	1	11	0
Cold-water gastropods*/loc.	-	0.0	0.0	0.1	0.0	0.1	0.0
Cold-water molluscs	124	52	62	25	41	98	2
Cold-water molluscs/loc.	-	0.4	0.4	1.8	0.7	0.7	2.0
Cold-water molluscs*	40	9	15	8	12	30	0
Cold-water molluscs*/loc.	-	0.1	0.1	0.6	0.2	0.2	0.0
Warm-water bivalves	61	7	28	4	11	42	6
Warm-water bivalves/loc.	-	0.1	0.2	0.3	0.2	0.3	6.0
Warm-water bivalves**	6	0	4	0	1	3	0
Warm-water bivalves**/loc.	-	0	0.0	0.0	0.0	0.0	0.0
Warm-water gastropods	71	3	34	1	8	41	15
Warm-water gastropods/loc.	-	0.0	0.2	0.1	0.1	0.3	15.0
Warm-water gastropods**	10	1	3	0	1	2	3
Warm-water gastropods**/loc.	-	0.0	0.0	0.0	0.0	0.0	3.0
Warm-water molluscs	132	10	62	5	19	83	21
Warm-water molluscs/loc.	-	0.1	0.4	0.4	0.3	0.6	21.0
Warm-water molluscs**	16	1	7	0	2	5	3
Warm-water molluscs**/loc.	-	0.0	0.0	0.0	0.0	0.0	3.0
Extinct bivalves	55	31	42	9	23	25	2
First appearance of extinct bivalves	-	17	15	1	1	3	0
Last occurrence of extinct bivalves	-	7	15	1	6	22	2
Extinct gastropods	58	9	32	1	9	37	0
First appearance of extinct gastropods	-	4	24	0	1	22	0
Last occurrence of extinct gastopods	-	2	16	0	3	34	0
Extinct molluscs	113	40	74	10	32	62	2
First appearance of extinct molluscss	-	21	39	1	2	25	0
Last occurrence of extinct molluscs	-	9	31	1	9	56	2

The highest ratio per localities of cold-water molluscs (1.8) is recorded in the Late Pliocene after 2.75 Ma, except for only one locality of the Early Pleistocene after 0.9 Ma. Confined to the cold-water molluscs residing in Iwate Prefecture and northwards, the highest ratio is in the Late Pliocene after 2.75 Ma.

3.2. Occurrence of warm-water extant species

Although the number of specimens of each warm-water species is less than the cold-water ones, many warm-water species are unexpectedly included in the Omma-Manganji fauna. A total of 132 species is recognized, consisting of 61 bivalves (Table 6) and 71 gastropod species (Table 7). Among six age time bins, only 10 species (7 bivalves and 3 gastropods) are recognized in the Early Pliocene. In contrast, the largest number of warm-water bivalve species (42 species) are recorded in the late Early Pleistocene, Calabrian before 0.9 Ma (Table 5). However, the ratio of the number of species for each locality (number of warm-water bivalves/number of localities) is highest (6.0) in the Early Pleistocene (Calabrian) after 0.9 Ma. However, this time bin has only one locality. The second highest value is 0.3 in the Late Pliocene after 2.75 Ma and the Calabrian before 0.9 Ma.

Table 6. Occurrences of the warm-water extant bivalves included in the Omma-Manganji fauna. *Species is not living in the Japan Sea.

Species \ Age	Early Pliocene	Late Pliocene		Early Pleistocene		
			2.75 Ma	Gelasian	Calabrian	0.9 Ma
Leionucula niponica (Smith)	+	+		+	+	
Striarca symmetrica (Reeve)	+	+		+	+	
Limatula kurodai Oyama	+	+			+	
Megacardita ferruginosa (Adams and Reeve)	+	+	+	+	+	
Keenaea samarangae (Makiyama)	+	+		+	+	
Clementia vatheleti Mabille	+	+			+	
Cardiomya gouldiana (Hinds)	+				+	
Lamellinucula tokyoensis (Yokoyama)		+				
Saccella confusa (Hanley)		+				
Glycymeris (*Veletuceta*) *fulgurata* Dunker*		+				
Divalucina soyoae Habe*		+				
Mactrotoma depressa (Spengler)		+				
Cardilia semisulcata (Lamarck)		+				
Merisca margaritina (Lamarck)		+				
Semele zebuensis (Hanley)		+				
Coralliophaga collaiophaga (Gmelin)		+				
Placamen foliaceum (Phillipi)		+				
Glycydonta marica (Linnaeus)		+				
Circe scripta (Linnaeus)		+				
Clementia papyracea (Gmelin)*		+				
Irus mitis (Deshayes)		+				
Timoclea micra (Pilsbry)		+		+		
Acila (*Acila*) *divaricata* (Hinds)		+		+	+	
Glycymeris (*Tucetonella*) *munda* (Sowerby III)*		+		+	+	
Limopsis cumingii (A. Adams)		+		+	+	
Glycymeris (*Tucetilla*) *pilsbryi* (Yokoyama)		+			+	
Saccella sematensis (Suzuki and Ishizuka)		+			+	+
Cycladichama cumingii (Hanley)		+	+		+	+
Solen grandis Dunker		+				+
Petricola divergens (Gmelin)			+			
Indocrassaetlla oblongata (Yokoyama)			+	+	+	
Myrtea soyoae (Habe)				+		
Leptomya cuspidariaeformis Habe				+		
Saccella gordonis (Yokoyama)					+	
Barbatia amygdalumtostum (Röding)					+	
Barbatia decussata (Sowerby)					+	
Didimarca tenebrica (Reeve)					+	
Acar plicata (Dillwyn)					+	
Cryptopecten vesiculosus (Dunker)					+	
Chlamys (*Chlamys*) *jousseaumei* Bavay					+	
Neopycnodonte cochlear (Poli)					+	
Monia umbonata (Gould)					+	
Gonimyrtea soyoae Habe					+	
Bellucina civica (Yokoyama)					+	
Cycladichama nomurai (Habe)					+	
Lutraria sieboldii Reeve					+	
Oxyperas bernardi (Pilsbry)					+	
Macoma (*Macoma*) *praetexta* (v. Martens)					+	
Timoclea mindanensis (E. A. Smith)					+	
Paphia schnelliana (Dunker)					+	
Paphia vernicosa (Gould)					+	
Eufistulana grandis (Deshayes)					+	
Barnea japonica (Yokoyama)					+	
Offadesma nakamigawai Kuroda and Horikoshi*					+	
Cyathodonta conccina (Gould)					+	
Cyathodonta granulosa Hutton					+	
Cardiomya reticulata (Kuroda)*					+	
Plectodon ligula (Yokoyama)					+	
Lima zushiensis Yokoyama					+	+
Pillucina yamakawai (Yokoyama)					+	+
Wallucina striata (Tokunaga)					+	+

Table 7. Occurrences of the extant warm-water gastropods included in the Omma-Manganji fauna. *Species is not living in the Japan Sea.

Species \ Age	Early Pliocene	Late Pliocene		Early Pleistocene		
			2.75 Ma	Gelasian	Calabrian	0.9 Ma
Leucotina dianae (A. Adams)	+	+			+	+
Emarginula sp.	+			+		
Mammilla sp.	+	+			+	+
Neritina aff. *paralella* Röding*		+				
Emarginula imaizumi Dall*		+				
Cerithium dialeucum Philippi		+				
Mammilla mammata (Röding)		+				
Eunaticina papilla (Gmelin)		+				
Cypraea sp.		+				
Cantharus cecillei (Philippi)		+				
Mitra sp.		+				
Pusia sp.*		+				
Pteropurpura stimpsoni (A. Adams)		+				
Reticunassa fuscolineata (E. A. Smith)		+				
Ithycythara sp.		+				
Conus sp.		+				
Punctoterebra sp.		+				
Duplicaria dussumieri (Kiener)*		+				
Leucotina sp.		+				
Splendrillia braunsi (Yokoyama)		+				
Retusa minima Yamakawa		+				
Punctacteon kajiyamai Habe		+				
Pupa strigosa (Gould)*		+				+
Siphonaria acmaeoides Pilsbry		+				
Astralium haemaetragum (Menke)		+			+	
Onustus exutum (Reeve)		+			+	
Calyptraea yokoyamai Kuroda		+	+		+	
Glossaulax reiniana (Dunker)		+			+	
Siphonalia modificata (Reeve)		+			+	
Mitrella (*Indomitrela*) *lischkei* (E. A. Smith)		+			+	
Fulgoraria prevostiana (Crosse)		+			+	
Granulina tantilla (Gould)		+			+	
Paradrillia patruelis (Smith)		+			+	
Phalium flammiferum (Röding)		+				+
Oliva mustellina Lamarck		+			+	+
Turcica monilifera A. Adams				+		
Siphonalia aspersa Kuroda and Habe*				+		
Glossaulax vesicalis (Philippi)				+	+	
Habesolatia nodulifera (Sowerby)				+	+	
Mitrella (*Mitrella*) *anachisoides* Nomura and Niino				+	+	
Paradrillia inconstans (E. A. Smith)				+	+	
Guraleus tabatensis (Tokunaga)				+	+	
Minolia pseudobscura (Yokoyama)					+	
Petaroconchus tokyoensis (Pilsbry)					+	
Syphopatella walshi (Reeve)					+	
Proterato callosa (Adams and Reeve)					+	
Diala semistriata (Philippi)					+	
Semicassis bisulcata (Schubert and Wagner)*					+	
Bittium urashimanum Nomura and Niino					+	
Triphora sp.					+	
Engina sp.					+	
Hima japonica (A. Adams)*					+	
Telasco sufflatus (Gould)					+	
Neadmete okutanii Petit					+	
Ithycythara oyuana (Yokoyama)					+	
Brevimyurella awajiensis (Pilsbry)					+	
Duplicaria evoluta (Deshayes)					+	
Ringicula yokoyamai Takeyama					+	
Decorifer insignis (Pilsbry)					+	
Adamnestia japonica (A. Adams)					+	
Entalinopsis intercostata (Boissevain)					+	
Doxander japonicus (Reeve)					+	+
Mitrella (*Indomitrella*) *yabei* Nomura					+	+
Zeuxis caelatus (A. Adams)					+	+
Spiniscala japonica (Dunker)					+	+
Syrnola cinnamomea (A. Adams)					+	+
Brunneifusus ternatanus (Gmelin)*						+
Brevimyurella japonica (E. A. Smith)						+
Duplicaria reticostata (Yokoyama)						+
Endemoconus sieboldi (Reeve)*						+
Lophiotoma leucotropis (Adams and Reeve)						+

Table 8. Families including more than two extinct bivalve species and their maximum length of the Omma-Manganji fauna. *P, Pectinidae; V, Veneridae; C, Cardiidae; A, Arcidae; L, Limopsidae; G, Glycymerididae; Th, Thraciidae; Pe, Periplomatidae; Ca, Carditidae.

Species \ Family and maximum length	Family*	L (mm)
Chlamys (*Chlamys*) *cosibensis* (Yokoyama)	P	70
C. (*C.*) *ingeniosa tanakai* Akiyama	P	67
C. (*C.*) *insolita* (Yokoyama)	P	30
C. (*C.*) *tamurae* Masuda and Sawada	P	38
C. (*C.*) *foeda* (Yokoyama)	P	87
C. (*C.*?) *lioica shigaramiensis* Amano and Karasawa	P	40
C. (*Leochlamys*) *tanassevitschi* (Khomenko)	P	112
Swiftopecten djoserus Yoshimura	P	75
Mizuhopecten naganoensis (Masuda)	P	121
M. tryblium (Yokoyama)	P	155
M. yamasakii (Yokoyama)	P	90
M. tokyoensis (Tokunaga)°	P	150
M. yokoyamae (Masuda)	P	132
M. poculum (Yokoyama)	P	130
Yabepecten tokunagai (Yokoyama)	P	157
Fortipecten kenyoshiensis Chinzei	P	120
Pecten (*Pecten*) *byoritsuensis* Nomura°	P	60
Neogenella hokkaidoensis (Nomura)	V	73
Kaneharaia ausiensis (Ilyina)	V	58
Leucoma tateiwai (Makiyama)	V	31
Securella chitaniana (Yokoyama)	V	64
Pseudamiantis tauyensis (Yokoyama)	V	87
Phacosoma tomikawensis (Takagi)	V	63
Humilaria perlaminosa (Conrad)	V	75
Clinocardium decoratum (Grewingk)	C	23
C. fastosum (Yokoyama)	C	90
Serripes makiyamai (Yokoyama)	C	77
"*Dinocardium*" *angustum* (Yokoyama)	C	43
Profulvia kurodai (Hatai and Nisiyama)	C	120
Anadara amicula (Yokoyama)	A	80
Scapharca ommaensis (Otuka)°	A	54
S. pseudosubcrenata (Ogasawara)°	A	39
Limopsis satoi Amano and Lutaenko	L	16
L. tokaienis (Yokoyama)	L	30
L. hokkaidoensis Amano and Lutaenko	L	27
Glycymeris (*Glycymeris*) *nipponica* (Yokoyama)	G	30
G. (*G.*) *minochiensis* (Yokoyama)	G	60
Thracia kamayasikiensis Hatai	Th	44
T. higasinodonoensis Oinomikado	Th	27
Periploma pulchella Hatai and Nisiyama	Pe	27
P. plane Ozaki	Pe	40
Cyclocardia myogadaniensis (Itoigawa)	Ca	21
Megacardita ommaensis Ogasawara°	Ca	28

On the other hand, the largest number of numerous warm-water gastropod species (41 species) are recorded in the late Early Pleistocene (Calabrian) before 0.9 Ma (Table 5). However, the ratio of the number of species for each locality (number of warm-water bivalves/number of localities) is highest (15.0) in the Early Pleistocene (Calabrian) after 0.9 Ma and the second highest value 0.3 is recognized in the Calabrian before 0.9 Ma.

Table 9. Families including more than two extinct gastropod species and their maximum length of the Omma-Manganji fauna. *B, Buccinidae; T, Turritellidae; M, Muricidae; Can, Cancellariidae; M, Mangeliidae; Ce, Cerithiidae; Tr, Trochidae; N, Naticidae; Cap, Capulidae; R, Ranellidae; E, Epitoniidae; P, Pyramidellidae.

Species \ Family and maximum size	Family*	H or D (mm)
Neptunea (*Neptunea*) *modesta* (Kuroda)	B	43
N. (*N.*) *eos* (Kuroda)	B	43
N. (*N.*) *hataii* Noda	B	107
N. (*N.*) *sakurai* (Ozaki)	B	117
N. (*Golikovia*) *nikkoensis* Nomura	B	35
Buccinum sinanoense Makiyama	B	48
B. shibatense Amano and Watanabe	B	40
B. saitoi Amano and Watanabe	B	59
Ancistrolepis koyamai (Kuroda)	B	19
A. masudaensis Nomura	B	21
Lirabuccinum japonicum (Yokoyama)	B	21
Retifusus yanamii (Yokoyama)	B	21
Plicifusus ozawai (Yokoyama)	B	24
Turritella (*Neohaustator*) *saishuensis motidukii* Otuka	T	60
T. (*N.*) *saishuensis saishuensis* Yokoyama	T	56
T. (*N.*) *saishuensis etigoensis* Ikebe	T	40
T. (*N.*) *nipponica nomurai* Kotaka	T	40
T. (*N.*) *fortilirata habei* Kotaka	T	88
Tachyrhynchus venustellus (Yokoyama)	T	11
T. tubeculosus (Yokoyama)	T	20
Trophonopsis uyemurai (Yokoyama)	M	33
T. sasae Sawada	M	24
T. vermeiji Amano	M	20
Boreotrophon solitarius (Yokoyama)	M	13
Chicoreus totomiensis Makiyama°	M	44
Ocinebrellus ogasawarai Amano and Vermeij	M	39
Scalptia kurodai (Makiyama)°	Can	16
Mesalia ommaensis Ogasawara	Can	51
Merica kobayashii (Yokoyama)°	Can	26
Admete murayamai (Yokoyama)	Can	6
Neadmete lishchkei (Yokoyama)	Can	10
Oenopota kagana (Yokoyama)	Ma	18
Ophiodermella kuromatsunaiensis (Sawada)	Ma	17
O. maekawaensis Hatai, Masuda and Suzuki	Ma	34
Granotoma kotakae Sawada	Ma	17
Bittium asatoi (Oinomikado and Ikebe)	Ce	23
B. etigoense (Oinomikado and Ikebe)	Ce	23
B. horinjiense (Oinomikado and Ikebe)	Ce	8
Umbonium (*Suchium*) *akitanum* Suzuki	Tr	19
Monodonta joetsuensis Amano°	Tr	10
Glossaulax coticazae (Makiyama)°	N	42
G. hagenoshitensis (Shuto)°	N	14
Vermeijia japonica Amano	Cap	27
Trichotropis chikagawaensis Hatai, Masuda and Suzuki	Cap	13
Ranella yasumurai Amano	R	60
Fusitriton izumozakiensis Amano	R	53
Boreoscala angulatosimile (Otuka)	E	43
B. yabei echigonum (Kanehara)	E	28
Menestho incisa (Yokoyama)	P	5
Turbonilla inscitula Yokoyama	P	10

Table 10. Characteristic species of the Omma-Manganji fauna recorded from the Transitional Zone.

Species	Age	Formation	Reference
Umbonium akitanum Suzuki	L. Plio.	Tomioka	Nemoto and O'Hara (2005)
Ranella yasumurai Amano	L. Plio.	Tomioka	Nemoto and O'Hara (2005)
Trophonopsis uyemurai (Yokoyama)	L. Plio.	Tomioka	Nemoto and O'Hara (2005)
Retifusus yanamii (Yokoyama)	L. Plio.	Tomioka	Nemoto and O'Hara (1979)
Propebela kagana (Yokoyama)	L. Plio.	Tomioka	Nemoto and O'Hara (2005)
Oenopota candida (Yokoyama)	E.~M. Pleist	Kazusa G., Iioka	Baba (1990)
Anadara amicula (Yokoyama)	L. Plio.	Dainenji	Ogasawara et al. (1988)
	L. Plio.	Tomioka	Nemoto and O'Hara (1979)
	E. Plio.	Kume	Noda and Amano (1977), Takahashi (1986)
	Plio.?	Kazusa G.?	Aoki and Baba (1982)
	L. Plio.	Nakatsu	Okumura and Ueda (1998)
	E. Plio.	Akebono G.	Yamanashi Prefecture (1970)
Glycymeris (*Glycymeris*) *nipponica* (Yokoyama)	E.~M. Pleist.	Umegase, Mandano, Nojima, Koshiba, Kakio	Baba (1990)
Limopsis tokaiensis Yokoyama	L. Plio.	Tomioka	Nemoto and O'Hara (1979)
	L. Plio.	Nakatsu	Okumura and Ueda (1998)
	E.~M. Pleist.	Tomiya, Umegase, Kakinokidai, Nojima, Ofuna, Koshiba	Yokoyama (1910), Baba (1990)
Chlamys (*Leochlamys*) *tanassevitchi* (Khomenko)	Plio.	Hitachi	Masuda (1962)
	L. Plio.	Tomioka	Nemoto and O'Hara (1979)
C. (*Chlamys*) *cosibensis* (Yokoyama)	L. Plio.	Tomioka	Nemoto and O'Hara (1979)
	Plio.	Hitachi	Noda et al. (1995)
	E.~M. Pleist.	Ichijuku, Koshiba	Baba (1990)
Mizuhopecten poculum (Yokoyama)	L. Plio.	Tomioka	O'Hara and Nemoto (1988)
M. tokyoensis (Tokunaga)	E.~L. Pleist	Kazusa G., Shimosa G.	Baba (1990)
Yabepecten tokunagai (Yokoyama)	L. Plio.~ E. Pleist.	Tomioka, Koshiba	Yokoyama (1911), Nemoto and O'Hara (1979)
Megacardita ommaensis (Ogasawara)	E. Pleist.	Umegase	Amano (in press)
Pseudamiantis tauyensis (Yokoyama)	L. Plio.	Tomioka	Nemoto and O'Hara (2005)
	Plio.?	Kazusa G.?	Aoki and Baba (1982)

Consequently, the highest ratio per localities of warm-water molluscs (21.0) is recorded in the Early Pleistocene (Calabrian) after 0.9 Ma and the second highest value 0.6 is also in the Calabrian before 0.9 Ma. Confined to the warm-water molluscs, not living in the Japan Sea, the highest ratio (3.0) is found in the Calabrian after 0.9 Ma.

3.3. Extinct species and their geologic ranges

A total of 113 species of molluscs is recognized as the extinct species and known as the characteristic species of the Omma-Manganji fauna. They are composed of 55 species of bivalves and 58 gastropod species.

The extinct bivalve species consists of 21 families. It is noteworthy that 17 species (30.9%) belong to Pectinidae and 18 species (32.7%) are included in Pectinoidea (Table 8). Adding to Pectinoidea, seven species belong to Veneridae and five species to Cardiidae. Moreover, a total of 32 species (58.2%) are estimated as non-siphonate bivalves because of no pallial sinus and the ecology of Recent counterparts.

Most extinct species of bivalves are derived from the cold-water or temperate species. Among them, only one specimen of *Fortipecten kenyoshiensis* Chinzei has been collected from the Upper Pliocene Usuizawa Formation in Futatsui, Akita Prefecture (Chinzei and Hiramatsu, 1988). This species is a characteristic Pliocene species in the Pacific-side northern Pacific area (Nakashima, 2002). However, the following three species of bivalves were derived from the warm-water ancestral species in the Japan Sea: *Scapharca ommaensis* Otuka, *S. pseudosubcrenata* Ogasawara and *Megacardita ommaensis* Ogasawara (Amano, 2023, in press). *Pecten byoritsuensis*

Nomura and *Amussiopecten praesignis* (Yokoyama) are extinct bivalve species which are characteristic of the Kakegawa fauna (Otuka, 1939b) distributed on the Pacific side of southwestern Japan. Among them, *Pecten byoritsuensis* was described from the Plio-Pleistocene Toukoushan Formation? in Taiwan and migrated to the Japan Sea in the late Early Pleistocene (Amano and Ohno, 1988; Amano et al., 2014). *Ammusiopecten praesignis* were recorded from the Plio-Pleistocene sea bed (precise age unknown) of western Japan Sea (Okamoto and Honza, 1978).

On the geological range, 18 bivalve species appeared earlier than the Late Miocene. Of these, four species such as *Periploma pulchella* Hatai and Nisiyama, *Neogenella hokkaidoensis* (Nomura), *Kaneharaia ausiensis* (Ilyina), and *Megangulus protovenulosus* (Nomura) became extinct by the end of the Early Pliocene (Fig. 2). And three local species such as *Mizuhopecten naganoensis* (Masuda), *Lucinoma motidukii* (Kuroda) and *Archivesica kannoi* Amano and Kiel have fossil records only from the Lower Pliocene formations. Including the above three species, a total of 17 species first appeared in the Early Pliocene. In the late Pliocene before 2.75 Ma, 15 species are added to the Omma-Manganji fauna. On the other hand, 15 species became extinct by the cooling at 2.75 Ma. The largest number of species (22 species) became extinct by the mid-Pleistocene Climate Transition at 0.9 Ma.

The extinct gastropod species consists of 20 families. Most numerous species (13 species, 22.4%) are included in Buccinidae (Table 9). Seven species and subspecies (12.1%) are recognized in Turritellidae. Moreover, Muricidae occupies third place and includes six species (10.3%). Five species (8.6%) belong to Cancellariidae while four species (6.9%) belong to Mangeliidae.

Most species of gastropods are also derived from the cold-water or temperate species. However, the following five species are shared with the warm-water Kakegawa fauna: *Chicoreus totomiensis* Makiyama, *Scalptia kurodai* (Makiyama), *Glossaulax hagenoshitensis* (Shuto), *Babylonia elata* (Yokoyama) and *Pomaulax omorii* (Shibata). Of these, *Babylonia elata* first appeared in the Early Pliocene while *Chicoreus totomiensis*, *Scalptia kurodai* and *Pomaulax omorii* did in the Late Pliocene before 2.75 Ma. *Glossaulax hagenoshitensis* first appeared in the Calabrian before 0.9 Ma.

On the geological range of gastropods in the Omma-Manganji fauna, seven species appeared earlier than the Late Miocene (Fig. 3). Of these, only *Glossaulax coticazae* (Makiyama) became extinction by the end of Early Pliocene. The following three species and one subspecies first appeared in the Early Pliocene: *Ancistrolepis koyamai* (Kuroda), *Neptunea* (*Golikovia*) *nikkoensis* Nomura, *Babylonia elata* (Yokoyama) and *Turritella* (*Neohaustator*) *saishuensis saishuensis* Yokoyama. Expansion of diversity of endemic species is observed in the Late Pliocene before 2.75 Ma. Twenty-four species first appeared at that age. The second expansion is observable in the Calabrian before 0.9 Ma. A total of 22 species first appeared in this time bin. Sixteen species became extinct by the cooling event at 2.75 Ma while 30 species and four subspecies became extinct by the mid-Pleistocene Climate Transition at 0.9 Ma.

Moreover, deep-sea families and subfamilies suffered from extinction in the Japan Sea. Vesicomyidae is a representative bivalve of the deep-sea hydrocarbon seep. The last occurrences of this family were from the Lower Pliocene in the Japan Sea (Amano et al., 2019b). Ancistrolepidinae is a deep-sea buccinid gastropod and became extinct by MIS 22 (Amano et al., 1996). Some species of Vesicomyidae and Ancistrolepidinae having fossil records are living in the Pacific side whereas no species has been found from the Japan Sea.

3.4. Transitional Zone

Noda and Amano (1977) proposed the Transitional Zone on the Pacific side area where the formations yield some characteristic species of the Omma-Manganji fauna between Yamanashi Prefecture (Akebono Formation) and Fukushima Prefecture (Kumagai Formation) as a mixed faunal area. Moreover, in this zone, some Miocene relict species have also been reported.

Ogasawara et al. (1988) found a characteristic species of the Omma-Manganji fauna such as *Anadara amicula elongata* Noda [= *A. amicula* (Yokoyama)] from the Upper Pliocene Dainenji Formation in Sendai, Miyagi Prefecture. Based on this record, the Transitional Zone extends northward to Miyagi Prefecture.

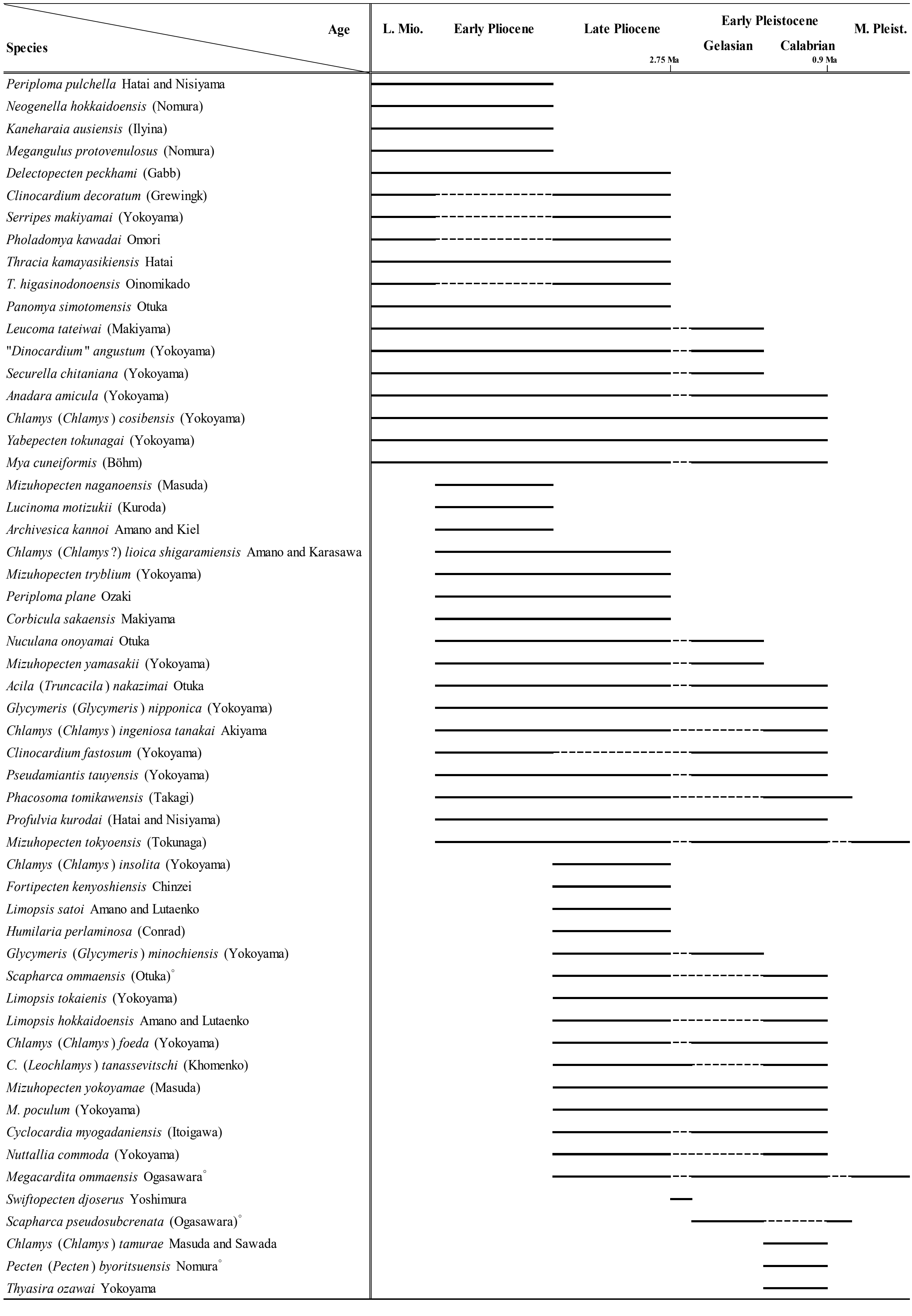

Fig. 2. Geologic ranges of the extinct bivalve species of the Omma-Manganji fauna. Species with small open circle were derived from warm-water species.

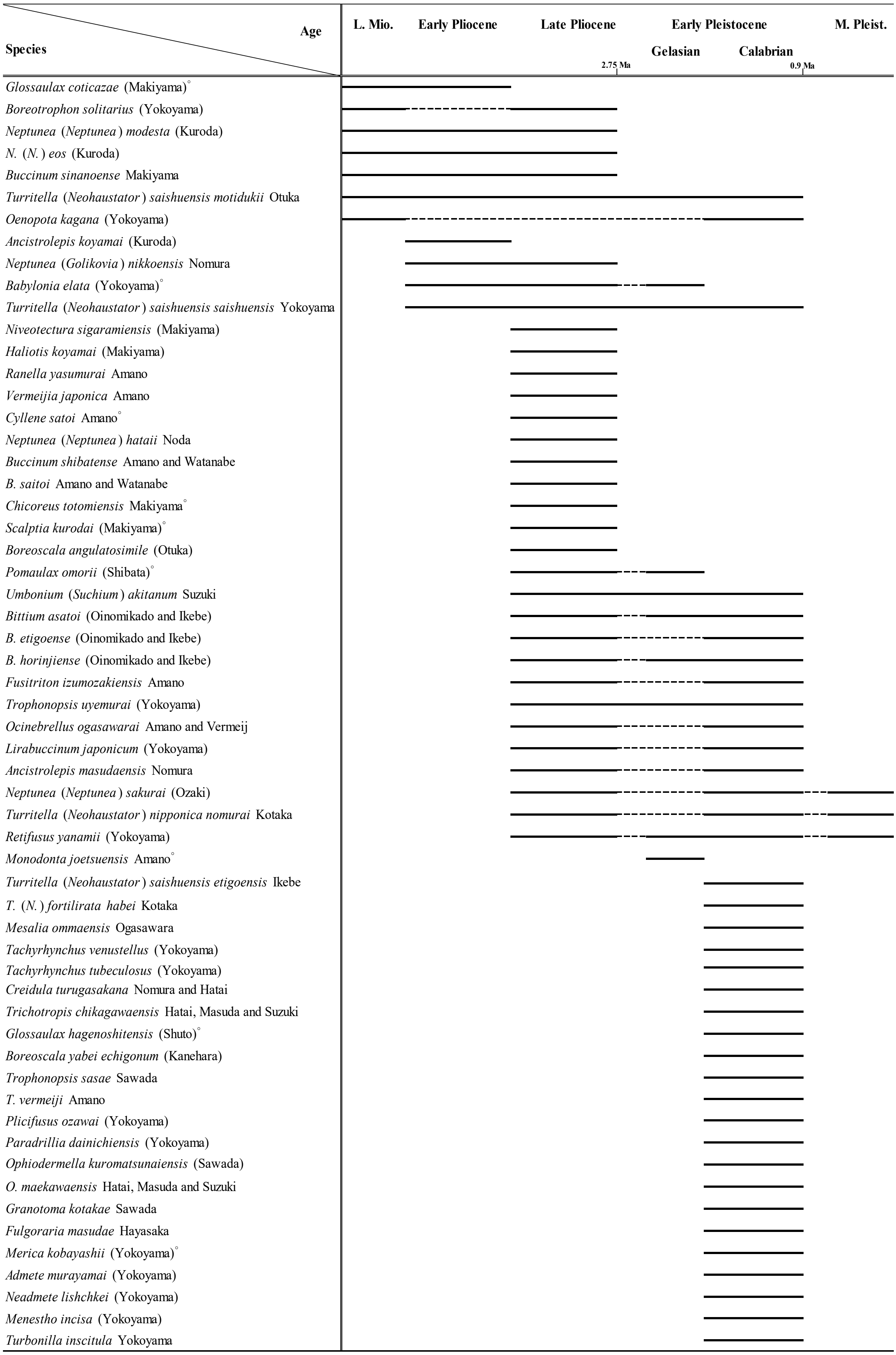

Fig. 3. Geologic ranges of the extinct gastropod species of the Omma-Manganji fauna. Species with small open circle were derived from warm-water species.

Twelve species of the Omma-Manganji fauna were found from the Upper Pliocene Tomioka Formation in Fukushima Prefecture (Nemoto and O'Hara, 1979, 2005; O'Hara and Nemoto, 1979). Recently, Amano (in press) noticed that *Venericardia* sp. described by Baba (1990) from the Lower Pleistocene Umegase Formation in Chiba Prefecture was synonymous with *Megacardita ommaensis* (Ogasawara). Consequently, six gastropod and 10 bivalve species of the characteristic species have been recorded (Table 10). Most of these occurred from the Upper Pliocene or the Lower to Middle Pleistocene mainly in the Kanto area, Pacific-side central Honshu.

3.5. Recent endemic species of the Japan Sea

As the Japan Sea is now a semi-enclosed sea, some endemic species are found. Sixteen species of bivalves (Table 11) and 31 species and two subspecies of gastropods (Table 12) have been recorded only from the Japan Sea. On the depth range, 12 species of bivalves are mainly living in water deeper than 100 m. On the other hand, 24 species and one subspecies of gastropods mainly reside around 100 m and deeper water.

Four species of bivalves have fossil records from the Japan Sea borderland. Namely, *Robaia robai* (Kuroda) has been recorded from the Upper Pliocene to the Middle Pleistocene formations in the Japan Sea borderland and the Lower Pleistocene Iioka Formation in Chiba Prefecture, Pacific side of central Honshu (Amano and Narita, 1992). *Megayoldia toyamaensis* (Kuroda) occurred also from the Upper Pliocene to the Lower Pleistocene in the Japan Sea borderland (Amano, 1996a). It is interesting to note that both species appeared in the Early to Middle Miocene in Sakhalin and then migrated southward since the Late Pliocene in the Japan Sea side of Honshu. On the other hand, seven species of gastropod have fossil records mainly from the Lower Pleistocene. Exceptionally, *Alvania awa* Chinzei was described from the Upper Miocene Shitazaki Formation on the Pacific-side Northeast Honshu (Chinzei, 1959). Moreover, *Buccinum striatissimum* Sowerby was described from the Lower Pliocene Kurokura Formation in Niigata Prefecture (Amano, 1994).

4. Discussion

4.1. Responses of molluscs to the environmental change

Basically, the Japan Sea was opened to the Okhotsk Sea and northern Pacific Ocean. In the Late Miocene to the Early Pleistocene, the cold current flowed into the Japan Sea through the northern straits (e.g., Itaki, 2016; Matsuzaki et al., 2018). A total of 124 cold-water species migrated into the Japan Sea by this current. Based on the calcareous nannoplankton, the Miocene relict species became extinct by the cooling event at the Datum A (2.75 Ma) related to the beginning of Northern Hemisphere Glaciation (NHG). Amano et al. (2011, 2012) stressed that some species living in Hokkaido and northwards first appeared in Honshu just above the Datum A. Results of this study support this conclusion. The ratio of the number of cold-water species to the total number of localities is highest (1.8) in the Late Pliocene after 2.75 Ma (Table 5). Moreover, the ratio of species living in Iwate Prefecture and northwards to the total number of localities suddenly increased from 0.1 to 0.6 above the Datum A (2.75 Ma). This trend is more distinct in the bivalve species than the gastropods.

The mid- to Late Pliocene warm climate was recognized in the ~4.2–2.8 Ma (e.g., Caballero-Gill et al., 2019). During the mid-Pliocene warmest period (3.264–3.025 Ma) , the global mean annual temperature was 2.7–4.0℃ higher and sea level was 10–30 m higher than today (Dwyer and Chandler, 2009; Haywood et al., 2013, 2016).

The Tsushima Strait was formed by a tectonic event and was widely opened as it is today in 1.7 Ma (Kitamura and Kimoto, 2006; Zhao et al., 2022).

The first invasion of the Tsushima Warm Current (TWC) began to inflow after 4 Ma as mentioned above probably because of the high sea level and tectonically formed shallow strait. However, in the Early Pliocene (4–3.6 Ma), only 11 species (seven bivalves, three gastropods and one scaphopod) are recognized (Tables 6, 7). The shallowest living depths of 10 species are shallower than 50 m in depth (Higo et al., 1999). From these, the thickness of TWC at the interglacial age of the Early Pliocene can be estimated around 50 m which is nearly the same as the estimate for the interglacial stages in the Late Pliocene to early Early Pleistocene (Gelacian) by Kitamura and Kimoto (2006). It is interesting to note that most warm-water species that appeared in the Early Pliocene continued into the late Early Pleistocene (Calabrian).

The largest number of warm-water species (83 species) have been recorded from the late Early Pleistocene (Calabrian) (Table 5). The highest ratio of warm-water species per locality (21.0) is observed in the Calabrian after 0.9 Ma, and the second higher ratio (0.6) is found in the Calabrian before 0.9 Ma. In spite of being younger than the mid-Pliocene Warm Period, the reason why so many warm-water species are found might be related to the depth and width of the Tsushima Strait. Among the Calabrian species, three species are now living in water deeper than 100 m (Higo et al., 1999): *Neadmete okutanii* Petit, *Gonimyrtea soyoae* Habe and *Cardiomya reticulata* Kuroda. These results are concordant with the estimate by Kitamura and Kimoto (2006) who estimated thickness of TWC at MIS 47 as 100 m.

4.2. Origin of the extinct species of the Omma–Manganji fauna

On the geological range, 18 species of bivalves and seven species of gastropods were also recognized in the Late Miocene Younger Shiobara-Yama fauna (Ogasawara, 2002; Ogasawara et al., 2008) in Honshu and the Lower and Upper Togeshita fauna (Amano, 1983, 1986) in Hokkaido. These species survived the Late Miocene Cooling (LMC) between 7 and 5.5 Ma (see Steinthorsdottir et al., 2020). Houlbourn et al. (2018) estimated the ephemeral Northern Hemisphere glaciation between 6.0 and 5.5 Ma. However, on the Pacific side, very few species of the Younger Shiobara fauna survived. Noda and Amano (1977) pointed out that some Miocene relict species had been recorded in the Transitional Zone. Okumura and Ueda (1998) described two Miocene relict species such as *Laevicardium shiobarense* (Yokoyama) and *Cultellus izumoensis* in association with *Anadara* (*Anadara*) cf. *amicula amicula* Yokoyama and many characteristic species of the Kakegawa fauna from the Lower Pleistocene Kanzawa Member of the Nakatsu Formation in Kanagawa Prefecture. One reason for these contrasts between the Japan Sea side and the Pacific side is the difference in climate. According to Ogasawara (1994), the Younger Shiobara-Yama fauna lived in warm-temperate to mild-temperate water zones. In the Early Pliocene, the mild-temperate zone widely prevailed in the Japan Sea while the northern cool-temperate zone was in contact with the southern subtropical zone on the Pacific side. A very narrow mild-temperate zone was recognized in the northern Kanto area (a northern part of the Transitional Zone). Among 25 Miocene relict species, sixteen became extinct at the cooling event at 2.75 Ma.

Among 55 extinct bivalves, 17 species first appeared in the Early Pliocene and 15 species in the Late Pliocene before 2.75 Ma. In contrast, among 61 extinct gastropods, 24 species first appeared in the Late Pliocene before 2.75 Ma and 25 species appeared in the Calabrian. Most of them were derived from cold- to temperate-water species while six species, such as *Scapharca ommaensis* (Otuka), *S. pseudosubcrenata* (Ogasawara), *Megacardita ommaensis* (Ogasawara), *Cyllene satoi* Amano, *Monodonta joetsuensis* Amano and *Merica kobayashii* (Yokoyama) were derived from warm-water species (Figs. 2, 3). It is possible that they might have been derived from some warm-water species of the Kakegawa fauna which invaded into the Japan Sea.

One plausible reason why many species first appeared in the Late Pliocene is the closure of the Japan Sea by the uplift of Northeastern Honshu in the Late Miocene to Late Pliocene (Matsuzaki et al., 2018; Kozaka et al., 2018; Nakajima, 2018). This interrupted gene flow between the Japan Sea and Pacific Ocean. Another reason is the first main influx of the TWC into the cold-water Japan Sea in the Late Pliocene (Kitamura and Kimoto, 2006; Gallapher et al, 2015; Itaki, 2016). Warm water influx might have accelerated the temperate-water adaptation of both cold-water and warm-water taxa. Temperate-water adaptation for the warm-water species are shown in the diversification of the arcid bivalve, *Scapharca* in the Late Pliocene (Amano, 2023). In contrast with bivalves, many gastropod species also first appeared in the Calabrian when the TWC significantly intruded into the Japan Sea via the widely opened Tsushima Strait as today (Kitamura and Kimoto, 2006; Itaki, 2016).

Some species of *Cythere* (Ostracoda) now living in the boreal seas originated from ancestral warm-water species in the Japan Sea during the Plio-Pleistocene. In other words, the Japan Sea acted as a place for adaptation of warm-water species to the boreal environments (Kamiya, 2003, 2006). However, there is no cold-water molluscan species derived from the warm-water species during the Plio-Pleistocene age. Although the exact reason for this difference between ostracods and molluscs is unknown, the ecology and distribution of *Cythere* accelerated its speciation. *Cythere* species live in the intertidal zone, attaching to calcareous algae (Kamiya, 2006) which is affected by the surface water climate and has limited geographic area.

4.3. Extinction of the characteristic species of Omma-Manganji fauna

There were two extinction events of the Omma-Manganji fauna; the 2.75 Ma (Datum A) and 0.9 Ma (MIS 22) cooling events. Thirty-one molluscan species became extinct at 2.75Ma while 56 species did at 0.9 Ma. As mentioned by Amano (2007), most temperate Miocene relict species became extinct at 2.75 Ma when many cold-water species now living in Hokkaido and northward migrated to central Honshu (Amano et al., 2011, 2012; Amano, 2024). Almost all species of the Omma-Manganji fauna became extinct at MIS 22 (0.9 Ma). According to Kitamura (2016), the sea-level during MIS 22 (Mid-Pleistocene Climate Transition) was its lowest ever and at most 20 m lower than during MIS 34 and 26. These low sea stands caused the closure of the straits of the Japan Sea and accelerated decreasing salinity of the sea surface water and anoxic condition of deep water. The semi-enclosed Japan Sea together with cold climate caussed the extinction of shallow- as well as deep-water molluscs (Amano, 2004). On the other hand, two bivalve species and three gastropod species survived the extinction event but might have become extinct in the Late Pleistocene glacial age. These are *Mizuhopecten tokyoensis* (Tokunaga), *Megacardita ommaensis* (Ogasawara), *Neptunea* (*Neptunea*) *sakurai* (Ozaki), *Turritella* (*Neohaustator*) *nipponica nomurai* Kotaka and *Retifusus yanamii* (Yokoyama) (Figs. 2, 3). Of these, the two bivalves and *N.* (*N.*) *sakurai* were known also from the Transitional Zone on the Pacific side (Amano et al., 2021; Amano, 2024). Some Recent arcid *Scapharca* first appeared in the Japan Sea during the Late Pliocene and then migrated to the Pacific side in the Early Pleistocene (Amano, 2023).

From the viewpoints of ecology of bivalves, the large-size and epifaunal Pectinoidea (32.7% of all extinct bivalves), the infaunal venerids (12.7%) and the infaunal cardiids (9.1%) are shallow-water dwellers. The highest extinction ratio of Pectinoidea is also observed for the Plio-Pleistocene fauna in the northeastern Pacific (Stanley, 1986) and the Pliocene Mediterranean bivalves (Danise and Domnici, 2022). The reasons for the high extinction rate observed in the Pectinoidea was the high predation pressure (Stanley, 1986) and the high metabolic rates related to large body size of Pectinoidea (Danise and Dominici, 2022). Based on the Pliocene to Recent molluscs in the West Atlantic, Stroz et al. (2018) stressed the importance of metabolic rates related to body size as an important influence on extinction. As discussed by Danise and Dominici (2022), there is no evidence of high predation pressure at the extinction event. The high extinction rate of Pectinoidea, venerids and cardiids in the Omma-Manganji fauna is partly attributed to high metabolic rates and large body size.

On the other hand, many extinct gastropods might have non-planktotrophic early development stages (Amano, 2007). Among them, the buccinids occupy 22.4% of all extinct gastropods. They were deep-water dwellers and became extinct because of deep-sea anoxia during the lower sea level stand in the glacial age (Amano et al., 1996; Amano, 1997c, 2004; Amano and Watanabe, 2001). Except for the plankton feeding turritellids, most of the extinct gastropods are predators (Taylor et al., 1980; Allmon, 2011). Their high metabolic rates might have also accelerated the extinction of gastropods during cooling.

In the Transitional Zone (Pacific-side), the following five shallow-water species survived the MIS 22 cooling; *Oenopota candida* (Yokoyama), *Glycymeris* (*Glycymeris*) *nipponica* (Yokoyama), *Limopsis tokaiensis* Yokoyama, *Chlamys* (*Chlamys*) *cosibensis* (Yokoyama) and *Mizuhopecten tokyoensis* (Tokunaga) (Table 10). The reasons for their survival are unknown but less severe deterioration of shallow water than the semi-enclosed Japan Sea and the possibility to migrate southward on the Pacific side might have enabled them to survive. However, except for *M. tokyoensis*, they became extinct in the Late Pleistocene glacial age.

4.4. Survival of the Plio-Pleistocene species in the Japan Sea

Three modern endemic bivalves of the Japan Sea have fossil records in the Omma-Manganji fauna; *Robaia robai* (Kuroda), *Megayoldia toyamaensis* (Kuroda), and *Felanuiella ohtai* Kase and Miyauchi (Table 11). Five modern endemic gastropods of the Japan Sea were found from the Lower Pliocene and Lower Pleistocene Japan Sea borderland; *Alvania akibai* (Yokoyama), *Acirsa morsei* (Yokoyama), *Buccinum striatisimum* Sowerby, *B. tsubai* Kuroda in Teramachi and *Oenopota candida* (Yokoyama) (Table 12). The fossil and Recent distributions of these species are confined to the Japan Sea. Except for *Felaniella ohtai*, the other eight species commonly live in 200 to 300 m depth.

Amano (1996a, 2004) estimated that these species could survive the deteriorated environment in the Plio-Pleistocene glacial age including LGM in the intermediate marine water (100–400 m in depth). This estimation is supported by the radiolarian fossils. Itaki (2001, 2007) estimated the existence of the marine layer as 200–300 m depth during the last glacial period. His depth range is concordant with my estimated depth herein.

5. Concluding remarks

Studies on speciation and extinction of the Omma-Manganji fauna reveals the following conclusions for the marginal sea fauna.

(1) Speciation in a marginal sea like the Japan Sea occurred by the separation of the sea from the open ocean and the influx of the warm-water current (TWC) into the cold-water sea during the interglacials.

Table 11. Endemic bivalve species of the Japan Sea and their living depth.

Species	Living depth (m)	Fossils	Reference on the living depth
Robaia robai (Kuroda)	200–1200	L. Pliocene to M. Pleistocene	Kurozumi et al. (2017a)
Yoldia kikuchii Kuroda	100–400	-	Kurozumi and Tsuchida (2017)
Megayoldia toyamaensis (Kuroda)	200–500	L. Pliocene to E. Pleistocene	Kurozumi and Tsuchida (2017)
Neilonella profunda Okutani and Fujiwara	5225–7320	-	Kurozumi et al. (2017b)
Limopsis crassula Habe	100–170	-	Matsukuma (2017a)
Musculus koreanus Ockelmann	60–950	-	Kurozumi (2017)
Nipponocrassatella adamsi (Kobelt)	100–150	-	Matsukuma (2017b)
Megacardita coreensis (Deshayes)	20–50	-	Matsukuma (2017c)
M. koreana Habe and Ito	20–50	-	Matsukuma (2017c)
Miodontiscus popovi Amano, Lutaenko and Haga	6–75	-	Amano et al. (2024)
Lyonsia nuculaniformis Scarlato	0–20	-	Scarlato (1981)
Cuspidaria ascolida Scarlato	200–275	-	Okutani (2017c)
Cardiomya (*Kurodamya*) *fujitai* (Kuroda)	100–300	-	Higo et al. (1999)
Lucinoma japonica (Habe)	100–150	-	Matsukuma (2017d)
Thyasira inadai Amano and Haga	169–1021	Holocene	Amano and Haga (2023)
Axinulus yamatotaiensis Okutani and Izumidate	375	-	Okutani (2017d)
Felaniella ohtai Kase and Miyauchi	23–28	E. Pleistocene	Kase et al. (1996), Lutaenko (2005)

Table 12. Endemic gastropod species of the Japan Sea and their living depth. *Pacific-side of Honshu.

Species	Living depth (m)	Fossils	Reference on the living depth
Cantharidus bisbalteatus (Pilsbry)	0	-	Sasaki (2017a)
Emarginula hataii Habe	80–250	-	Sasaki (2017b)
Alvania akibai (Yokoyama)	220–635	E. Pleistocene	Hasegawa (2014, 2017)
A. awa Chinzei	200–300	L. Miocene (P*)	Hasegawa (2014, 2017)
A. yamatoensis Hasegawa	316–328	-	Hasegawa (2014, 2017)
Punctulum soyomaruae Hasegawa	679–839	-	Hasegawa (2014, 2017)
Frigidoalvania tanseimaruae Hasegawa	369–1360	-	Hasegawa (2014, 2017)
Stilapex suzuki Habe	46–54	-	Hori and Matsuda (2017)
Onchidiopsis nihonkaiensis Okutani and Numanami	400–500	-	Okutani (2017a)
Acirsa morsei (Yokoyama)	120–320	E. Pleistocene	Hasegawa and Nakayama (2009), Tsuchida and Hasegawa (2017)
Mokumea albomarginata (Okamoto and Habe)	0	-	Tsuchiya (2017a)
Hima hizenensis (Pilsbry)	-	-	Tsuchiya (2017b)
Lussivolutopsius. furukawai (Oyama)	200–350	-	Okutani (2017b)
Retimohnia micra (Dall)	300–400	-	Higo et al. (1999)
R. japonica (Dall)	300–400	-	Higo et al. (1999)
Neptunea (*Neptunea*) *elegantula* Ito and Habe	225–230	-	Okutani (2017b)
N. (*N.*) *cybaea* Fraussen and Terryn	200	-	Fraussen and Terryn (2007)
Microfusus adamsi (Kuroda)	100–200	-	Okutani (2017b)
Buccinum kawamurai Habe and Ito	200–	-	Okutani (2017b)
B. bayani Jousseaume	100–200	-	Okutani (2017b)
B. senshumaruae Kosuge and Ishiyama	180–400	-	Okutani (2017b)
B. tenuissimum Kuroda in Teramachi	400–1000	-	Okutani (2017b)
B. striatissimum Sowerby	200–500	E. Pliocene	Okutani (2017b)
B. terebriforme Habe and Ito	300–450	-	Okutani (2017b)
B. tsubai Kuroda in Teramachi	100–300	E. Pleistocene	Okutani (2017b)
B. suzumai Habe and Ito	-	-	Okutani (2017b)
Volutharpa ampullacea nipponkaiensis Habe and Ito	120	-	Okutani (2017b)
V. a. limnaeformis Habe and Ito	35–60	-	Okutani (2017b)
Oenopota candida (Yokoyama)	200–300	E. Pleistocene, M. Pleistocene (P*)	Hasegawa et al. (2017)
Obesotoma okutanii Bogdanov and Ito	200–300	-	Hasegawa et al. (2017)
Cylichna inedita A. Adams	66–115	-	Hori (2017a)
Enotepteron hayashii Hamatani	-	-	Hamatani (2017)
Parthenina shibana (Yokoyama)	93–95	L. Pleistocene (P*)	Hori (2017b)

(2) The extinction of species occurred during cold periods and accompanied low sea level. On the other hand, there was no extinction during the warm interglacials.

In three cold events (NHG, MIS 22 and LGM), shallow-water species became extinct because of lower temperature, lower salinity of surface water and anoxia for deep-sea species. Moreover, species with high metabolic rates (large-sized pectinids and predatory buccinids) were more susceptible to extinction.

(3) Species' survival depends on the depth distribution of the species. A few species survived the shallow and deep water deteriorated environments by dwelling in the intermediate marine layer (200 to 300 m in depth) in the Japan Sea. As result, these species form the modern endemic species of the Japan Sea.

6. Acknowledgements

I am so grateful to Geerat J. Vermeij (UC Davis) for his critical reading of the manuscript and useful suggestions. I thank Kenshiro Ogasawara (Emeritus Professor of University of Tsukuba) for his review. I also thank Takenori Sasaki (The University Museum, The University of Tokyo) and Takuma Haga (National Museum of Nature and Science) for their help in examining the fossil specimens.

7. References

Allmon, W. D. 2011. Natural history of Turritelline Gastropods (Cerithiodea: Turritellidae): A status report. Malacologia 54: 159–202.
DOI: 10.4002/040.054.0107

Amano, K. 1983. Paleontological study of the Miocene Togeshita molluscan fauna in the Rumoi district, Hokkaido. Science Reports of the Institute of Geoscience, the University of Tsukuba, Sec. B. 4: 1–72.

Amano, K. 1986. Age and characteristics of the so-called "Atsunai-Togeshita fauna in Hokkaido. Paleontological Society of Japan, Special Papers (29): 187–198.

Amano, K. 1994a. An attempt to estimate the surface temperature of the Japan Sea in the Early Pleistocene by using a molluscan assemblage. Palaeogeography, Palaeoclimatology, Palaeoecology 108(3/4): 369–378.

Amano, K. 1994b. Astartidae (Bivalvia) from the Pliocene and Lower Pleistocene strata in the Shin'etsu district, Central Japan. Bulletin of the Joetsu University of Education 14(1): 241–249. (in Japanese with English abstract)

Amano, K. 1994c. Diversity of *Chlamys* (Bivalvia) from the Pliocene Ogikubo Formation, Central Japan. Transactions and Proceedings of the Palaeontological Society of Japan, New Series (176): 661–676.

Amano, K. 1994d. Pliocene molluscan fauna and its paleoenvironment in Matsunoyama-machi, Niigata Prefecture. Journal of Geography 103(6): 653–673. (in Japanese with English abstract)
DOI: 10.5026/jgeography.103.6_653

Amano, K. 1995. Two relict species of *Thracia* (Bivalvia) from the Pliocene Ogikubo Formation in Nagano Prefecture, Central Japan. Venus 54(2): 143–151.
DOI: 10.18941/venusjjm.54.2_143

Amano, K. 1996a. *Portlandia toyamaensis* (Kuroda) as an endemic bivalve of Japan Sea. In H. Noda, and K. Sashida, eds., Prof. H. Igo Commemorial Volume on Geology and Paleontology of Japan and Southeast Asia. Gakujutsu Tosho Insatsu Co. Tokyo. p. 141–146.

Amano, K. 1996b. Taxonomy and distribution of boreal species of *Macoma* (Bivalvia) from the Plio-Pleistocene strata in the Japan Sea borderland. Bulletin of the Joetsu University of Education 16(1): 289–297. (in Japanese with English abstract)

Amano, K. 1997a. Taxonomy and distribution of Cymatiidae (Gastropoda) from the Pliocene and Lower Pleistocene in the Japan Sea Borderland. Venus 56(2): 121–129.
DOI: 10.18941/venusjjm.56.2_121

Amano, K. 1997b. Taxonomy and distribution of the fossil *Volutomitra* (Gastropoda) from Japan. Bulletin of the Joetsu University of Education 17(1): 377–383. (in Japanese with English abstract)

Amano, K. 1997c. Biogeography of the genus *Neptunea* (Gastropoda: Buccinidae) from the Pliocene and the lower Pleistocene of the Japan Sea borderland. Paleontological Research 1(4): 274–284.
DOI: 10.2517/prpsj.1.274

Amano, K. 1998. First discovery of fossil *Humilaria* (Bivalvia:Veneridae). Venus 57(4): 271–280.
DOI: 10.18941/venusjjm.57.4_271

Amano, K. 2001. Pliocene molluscan fauna of Japan Sea borderland and the paleoceanographic conditions. Biological Science 53(3): 178–184. (in Japanese, title translated)

Amano, K. 2004. Biogeography and the Pleistocene extinction of neogastropods in the Japan Sea. Palaeogeography, Palaeoclimatology, Palaeoecology 202(3/4): 245–252.
DOI: 10.1016/S0031-0182(03)00637-0

Amano, K. 2005. Migration and adaptation of late Cenozoic cold-water molluscs in the North Pacific. In A. M. T. Elewa, ed., Migration of Organisms. Springer-Verlag. Berlin Heidelberg. p. 127–150.

Amano. K. 2006. *Trophonopsis* Bucquoy, Dautzenberg and Dollfus, 1882 (Gastropoda, Muricidae) from the Plio–Pleistocene deposits in Japan. Paleontological Research 10(2): 163–176.
DOI: 10.2517/prpsj.10.163

Amano, K. 2007. The Omma-Manganji fauna and its temporal change. Fossils (Palaeontological Society of Japan) (82): 6–12. (in Japanese with English abstract)

Amano, K. 2019a. Two new gastropods from the late Pliocene Omma-Manganji fauna in the Japan Sea borderland of Honshu, Japan. Paleontological Research 23(2): 85–94.
DOI: 10.2517/2018PR011

Amano, K. 2019b. Two warm-water species of Trochoidea (Gastropoda) from Pliocene deposits on the Japan Sea side of Honshu, Japan, with remarks on the influence of the onset of Northern Hemisphere glaciation. The Nautilus 133(2): 57–66.

Amano, K. 2019c. Two rare warm-water bivalves from the Pliocene Seguchi Formation in Nagano Prefecture, Central Japan. Venus 78(1–2): 45–56.
DOI: 10.18941/venus.78.1-2_45

Amano, K. 2020. Molluscan fossils from the Kitakanegasawa Formation in Aomori Prefecture, Japan, with remarks on the northern limit of the Tsushima Warm Current during the late Pliocene. Bulletin of the National Museum of Nature and Science, Series C 46: 87–98.

Amano, K. 2023. Invasion, diversification and extinction of *Scapharca* (Bivalvia: Arcidae) in the Japan Sea borderland during the Plio-Pleistocene. Venus 81(1–4): 61–74.
DOI: 10.18941/venus.81.1-4_61

Amano, K. 2024. Taxonomy and distribution of *Cyclocardia* (Bivalvia: Carditidae) of the Plio-Pleistocene Omma Manganji fauna in the Japan Sea borderland. Venus 82(1–4): 67–100.
DOI: 10.18941/venus.82.1-4_67

Amano, K. in press. Taxonomy and distribution of *Megacardita* (Carditidae, Bivalvia) from the Plio-Pleistocene Omma-Manganji fauna. Venus.

Amano, K., and T. Haga. 2023. A new species of *Thyasira* Lamarck, 1818 (Bivalvia: Thyasiridae) from the Japan Sea. Venus 81(1–4): 47–60.
DOI: 10.18941/venus.81.1-4_47

Amano, K., M. Hamuro, and T. Hamuro. 2014. New fossil record of two warm-water bivalves from the Pleistocene Itaya Formation, Toyama Prefecture, Central Japan. Venus 72(1–4): 65–76.
DOI: 10.18941/venus.72.1-4_65

Amano, K., M. Hamuro, and T. Sato. 2008. Influx of warm-water current to Japan Sea during the Pliocene-based on analyses of molluscan fauna from the Mita Formation in Yatsuo-machi of Toyama City. Journal of the Geological Society of Japan 114(10): 516–531. (in Japanese with English abstract)
DOI: 10.5575/geosoc.114.516

Amano, K., M. Hamuro, T. Hamuro, T. Sato, and R. Ogihara. 2012. Influence of the latest Pliocene cooling to the benthic fauna from the central part of the Japan Sea borderland: Molluscan fauna from the Zukawa Formation in Toyama Prefecture. Journal of Geological Society of Japan 118(12): 810–822. (in Japanese with English abstract)
DOI: 10.5575/geosoc.2012.0058

Amano, K., K. Hasegawa, A. Inada, and T. Sato. 2021. *Neptunea sakurai* (Ozaki, 1958) (Gastropoda: Buccinidae) from middle to upper Pleistocene deposits in the southern part of the Japan Sea. The Nautilus 135(2): 53–58.

Amano, K., and Y. Hikida. 1999. Evolutionary history of the Cenozoic bivalve genus *Kaneharaia* (Veneridae). Paleontological Research 3(4): 249–258.
DOI: 10.2517/prpsj.3.249

Amano, K., A. Ichikawa, and S. Koganezawa. 1988. Molluscan fauna from the Nadachi Formation around Osuga Bridge in Nadachi Town, Nishikubiki-gun. – Studies on the molluscan fossils from the western part of Joetsu district, Niigata Prefecture (Part 3) –. Bulletin of the Joetsu University of Education 7(3): 63–71. (in Japanese with English abstract)

Amano, K., A. Inada, and T. Sato. 2024. Boreal species of *Macoma* (Bivalvia: Tellinidae) from the Middle to Upper Pleistocene deposits in the southwestern part of the Japan Sea. Bulletin of the Mizunami Fossil Museum 51(1): 15–37.
DOI: 10.50897/bmfm.51.1_15

Amano, K., and R. G. Jenkins. 2011. Fossil records of extant vesicomyid species from Japan. Venus 69(3–4): 163–176.
DOI: 10.18941/venus.69.3-4_163

Amano, K., and S. Kanno. 1991. Composition and structure of Pliocene molluscan associations in the western part of Joetsu City, Niigata Prefecture.

Fossils (Palaeontological Society of Japan) (51): 1–14. (in Japanese with English abstract)

Amano, K., S. Kanno, A. Ichikawa, and Y. Yanagisawa. 1987. Molluscan fauna from the Tanihama Formation in the western part of Joetsu City. –Studies on the molluscan fossils from the western part of Joetsu district, Niigata Prefecture (Part 2)–. Bulletin of the Joetsu University of Education 6(3): 157–170. (in Japanese with English abstract)

Amano, K., S. Kanno, H. Nagai, N. Sasabe, and H. Ban. 1990. Molluscan fauna from the Kawazume Formation in the western part of Joetsu City. –Studies on the molluscan fossils from the western part of Joetsu district, NiigataPrefecture (Part 5)–. Bulletin of the Joetsu University of Education 9(3): 67–75. (in Japanese with English abstract)

Amano, K., and S. Karasawa. 1988. *Yabepecten* and *Pseudamiantis* from the Shigarami Formation in Nagano Prefecture, Central Japan. Saito Ho-on Kai, Special Publication (2): 507–517.

Amano, K., and S. Karasawa. 1993. Molluscan fauna and paleoenvironment of the Pliocene Ogikubo Formation in the northern part of Nagano Prefecture, central Japan. Journal of Geography 102(5): 572–582. (in Japanese with English abstract)
DOI: 10.5026/jgeography.102.572

Amano, K., and S. Karasawa. 1986. A new subspecies of *Chlamys lioica* (Dall) from the Pliocene Shigarami Formation in the environs of Nagano City, central Japan. Monograph of the Mizunami Fossil Museum (6): 41–47.

Amano, K., and S. Kiel. 2007. Fossil vesicomyid bivalves from the North Pacific Region. The Veliger 49(4): 270–293.

Amano, K., and K. Koike. 1993. Molluscan fauna from the Miocene Ogawa Formation in the western part of Nagano City, Nagano Prefecture. Bulletin of the Joetsu University of Education 13(1): 287–300. (in Japanese with English abstract)

Amano, K., and K. Komori. 2021. Origin and biogeographic history of *Scapharca broughtonii* (Schrenck, 1867) (Bivalvia: Arcidae) and its related species. Venus 79(1–4): 15–28.
DOI: 10.18941/venus.79.1-4_15

Amano, K., and K. A. Lutaenko. 2004. New fossil and Recent *Limopsis* (Bivalvia) from the northwestern Pacific. The Veliger 47(1): 13–20.

Amano, K., K. A. Lutaenko, and T. Haga. 2024. Taxonomy, reproduction and evolution of the small carditid *Miodontiscus* (Bivalvia) in the northern Pacific. The Nautilus 138(3–4): 59–74.

Amano, K., Y. Miyajima, R. G. Jenkins, and S. Kiel. 2019. The Miocene to Recent biogeographic history of vesicomyid bivalves in Japan, with two new records of the family. The Nautilus 133(2): 48–56.

Amano, K., K. Nagata, T. Sato, Y. Yanagisawa, and Y. Kurita. 2009. Influence of a warm water current on the northern Fossa Magna Region during the Pliocene, based on analyses of molluscan fauna from the Shitoka Formationand the lowest part of the Uonuma Group along the Kamakurazawa River in Minato-Uonuma City, Nagano Prefecture. Journal of the Geological Society of Japan 115(11): 597–609. (in Japanese with English abstract)
DOI: 10.5575/geosoc.115.597

Amano, K., and K. Narita. 1992. Origin and migration of *Robaia robai* (Kuroda) (Bivalvia: Nuculoida). Venus 50(4): 287–295.
DOI: 10.18941/venusjjm.50.4_287

Amano, K., and R. Ogihara. 2012. Taxonomy of large *Nuttallia* (Bivalvia: Psammobiidae) in the northwestern Pacific, with remarks on the evolution of the genus. Paleonotological Research 16(2): 146–158.
DOI: 10.2517/1342-8144-16.2.146

Amano, K., and Y. Ohno. 1988. *Pecten* (*Pecten*) *byoritsuensis* Nomura from the Pleistocene Omma Formation in Ishikawa Prefecture, central Japan. Venus 47(1): 37–49.
DOI: 10.18941/venusjjm.47.1_37

Amano, K., and H. Sato. 1995. Relationship between embaymental associations and relict species. –Molluscan fauna from the Pliocene Joshita Formation in the northern part of Nagano Prefecture. Fossils (Palaeontological Society of Japan) (59): 1–13. (in Japanese with English abstract)

Amano, K., T. Sato, and T. Koike. 2000b. Paleoceanographic conditions during the middle Pliocene in the central part of Japan Sea borderland –Molluscan fauna from the Kuwae Formation in Shibata City,

Niigata Prefecture, central Japan–. Journal of the Geological Society of Japan 106(12): 883–894. (in Japanese with English abstract)
DOI: 10.5575/geosoc.106.883

Amano, K., M. Suzuki, and T. Sato. 2000a. Warm-water influx into Japan Sea in the middle Pliocene. –Molluscan fauna from the Tentokuji Formation around Mt. Taihei in Akita Prefecture–. Journal of the Geological Society of Japan 106(4): 299–306. (in Japanese with English abstract)
DOI: 10.5575/geosoc.106.299

Amano, K., K. Tanaka, and S. Karasawa. 1991. *Chlamys* (*Chlamys*) *foeda* (Yokoyama) from the Shigarami Formation in Nagano Prefecture, Central Japan. Bulletin of Joetsu University of Education 10(2): 305–313.

Amano, K., and K. Tanaka. 1992. An Omma-Manganjian Bivalvia, *Profulvia kurodai* (Sawada), from the Plio-Pleistocene strata of Japan. Bulletin of Joetsu University of Education 12(1): 115–124.

Amano, K., M. Ukita, and S. Sato. 1996. Taxonomy and distribution of the subfamily Ancistrolepidinae (Gastropoda: Buccinidae) from the Plio-Pleistocene of Japan. Transactions and Proceedings of the Palaeontological Society of Japan, New Series (176): 467–477.

Amano, K., and G. J. Vermeij. 1998a. Origin and biogeographic history of *Ceratostoma* (Gastropoda: Muricidae). Venus 57(3): 209–223.
DOI: 10.18941/venusjjm.57.3_209

Amano, K., and G. J. Vermeij. 1998b. Taxonomy and evolution of the genus *Ocinebrellus* (Gastropoda: Muricidae) in Japan. Paleontological Research 2(3): 199–212.
DOI: 10.2517/prpsj.2.199

Amano, K., and G. J. Vermeij. 2003. Evolutionary adaptation and geographic spread of the Cenozoic buccinid genus *Lirabuccinum* in the north Pacific, Journal of Paleontology 77(5): 863–872.
DOI: 10.1666/0022-3360(2003)077<0863:EAAGSO>2.0.CO;2

Amano, K., and M. Watanabe. 2001. Taxonomy and distribution of Plio-Pleistocene *Buccinum* (Gasrtopoda: Buccinidae) in northeast Japan. Paleontological Research 5(3): 215–226.
DOI: 10.2517/prpsj.5.215

Amano, K., A. Yoshida, and T. Sato. 2011. Influence of cooling event at 2.75 Ma on the molluscan fauna of the Japan Sea borderland: Molluscan fauna from central and northern parts of Akita Prefecture. Journal of the Geological Society of Japan 117(9): 508–522. (in Japanese with English abstract)
DOI: 10.5575/geosoc.117.508

Aoki, N., and K. Baba. 1982. Molluscan fossils from the boring core at the University of Tsukuba. Study on the environment of Tsukuba (6): 167–171. (in Japanese, title translated)

Baba, K. 1990. Molluscan Fossil Assemblages of the Kazusa Group, South Kwanto, Central Japan. Keio-Yochisha. Tokyo. 445 pp., 40 pls. (in Japanese with English description of new taxa)

Caballero-Gill, R. P., T. D. Herbert, and H. J. Dowsett. 2019. 100-kyr paced climate change in the Pliocene warm period, Southwest Pacific. Paleoceanography and Paleoclimatology 34: 524–525.
DOI: 10.1029/2018PA00346

Chinzei, K. 1959. Molluscan fauna of the Pliocene Sannohe Group of Northeast Honshu, Japan. 1. The faunule of the Kubo Formation. Journal of the Faculty of Science, University of Tokyo, Section 2 12(1): 119–132.

Chinzei, K. 1963. Notes on historical change of Neogene molluscan assemblages in Northeast Honsu. Fossils (Paleontological Society of Japan) (5): 20–26. (in Japanese)

Chinzei, K. 1978. Neogene molluscan faunas in the Japanese Islands: An ecologic and zoogeographic synthesis. Veliger 21(2): 155–170.

Chinzei, K. 1991. Late Cenozoic zoogeography of the Sea of Japan area. Episodes 14(3): 231–235.
DOI: 10.18814/epiiugs/1991/v14i3/006

Chinzei, K., and C. Hiramatsu. 1988. First occurrence of Pliocene *Fortipecten* from the Japan Sea area of northern Honshu. Special Publication of Saito Ho-On Kai (2): 469–476.

Danise, S., and S. Dominici. 2022. Biodiversity change and extinction risk in Plio-Pleistocene Mediterranean bivalves: the families Veneridae, Pectinidae and Lucinidae. Special Publications of the Geological Society, London: 529.
DOI: 10.1144/SP529-2022-44

Dwyer, G. S., and M. A. Chandler. 2009. Mid-Pliocene sea level and continental ice volume based on coupled benthic Mg/Ca palaeotemperatures and

oxygen isotopes Philosophical Transactions of the Royal Society A 367: 157–168.
DOI: 10.1098/rsta.2008.0222

Endo, K. 1986. Mode of occurrence and significance of warm-water fauna in the Sawane Formation, Sado Island. Journal of the Gological Society of Japan 92(1): 77–80. (in Japanese)
DOI: 10.5575/geosoc.92.77

Fraussen, K., and Y. Terryn. 2007. The family Buccinidae: genus *Neptunea*. In G. T. Poppe, and K. Groh, eds., A Conchological Iconography. ConchBooks. Hackenheim. 166 pp.

Gallapher, S. J., A. Kitamura, Y. Iryu, T. Itaki, I. Koizumi, and P. W. Hoiles. 2015. The Pliocene to recent history of the Kuroshio and Tsushima Currents: a muli-proxy approach. Progress in Earth and Planetary Science 2: 17.
DOI: 10.1186/s40645-015-0045-6

Gamo, T., Y. Nozaki, H. Sakai, T. Nakai, and H. Tsubota. 1986. Spatial and temporal variations of water characteristics in the Japan Sea bottom layer. Journal of Marine Research 44: 781–793.

Hamatani, I. 2017. Family Gastropteridae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1093. (in Japanese and English)

Hasegawa, K. 2014. A review of bathyal Rissoidae in the Sea of Japan and adjacent waters. In T. Fujita, ed., Deep-sea fauna of the Sea of Japan. National Museum of Nature and Science Monographs (44): 75–148.

Hasegawa, K. 2017. Family Rissoidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 806–811. (in Japanese and English)

Hasegawa, K., and T. Nakayama. 2009. Rediscovery of "T*urbonilla* (*Cingulina*)" *morsei* Yokoyama, 1926 from the Recent fauna in the Sea of Japan, and its relocation in the genus *Acirsa* (Gastropoda: Epitoniidae). Venus 67(3–4): 135–143.
DOI: 10.18941/venus.81.1-4_27

Hasegawa, K., T. Okutani, and E. Tsuchida. 2017. Family Mangeliidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1018–1023. (in Japanese and English)

Hatai, K., K. Masuda, and Y. Suzuki. 1961. A note on the Pliocene megafossil fauna from the Shimokita Peninsula, Aomori Prefecture, Northeast Honshu, Japan. Saito Ho-on Kai Museum Research Bulletin (30): 18–38.

Haywood, A. M., H. J. Dowsett, and A. M. Dolan. 2016. Integrating geological archives and climate models for the mid-Pliocene warm period. Nature Communications 7: 10646 (2016).
DOI: 10.1038/ncomms10646

Haywood, A. M., D. J. Hill, A. M. Dolan, B. L. Otto-Bliesner, F. Bragg, W.-L. Chan, M. A. Chandler, C. Contoux, H. J. Dowsett, A. Jost, Y. Kamae, G. Lohmann, D. J. Lunt, A. Abe-Ouchi, S. J. Pickering, G. Ramstein, N. A. Rosenbloom, U. Salzmann, L. Sohl, C. Stepanek, H. Ueda, Q. Yan, and Z. Zhang. 2013. Large-scale features of Pliocene climate: results from the Pliocene Model Intercomparison Project. Climate of the Past 9: 191–209.
DOI: 10.5194/cp-9-191-2013, 2013.

Higo, S., P. Callomon, and Y. Goto. 1999. Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan. Elle Scientific Publication. Yao. 749 pp.

Hori, S. 2017a. Family Cylichnidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1085–1087. (in Japanese and English)

Hori, S. 2017b. Family Pyramidellidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1105–1123. (in Japanese and English)

Hori, S., and H. Matsuda. 2017. Family Eulimidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 823–832. (in Japanese and English)

Holbourn, A. E., W. Kuhnt, S. C. Clemens, K. G. Kochhann, J. Jöhnck, J. Lübbers, and N. Andersen. 2018. Late Miocene climate cooling and intensification of southeast Asian winter monsoon. Nature Communications 9: 1–13.
DOI: 10.1038/s41467-018-03950-1

Itaki, T. 2001. Radiolarian fauna change in the eastern Japan Sea during the last 30kyr. News of Osaka Micropaleontologists (NOM) Special Volume (12): 359–374. (in Japanese with English abstract)

Itaki, T. 2007. Historical changes of deep-sea radiolarians in the Japan Sea during the last 640 kyrs. Fossils

(Palaeontological Society of Japan) (82): 43–51. (in Japanese with English abstract)

Itaki, T. 2016. Transitional changes in microfossil assemblages in the Japan Sea from the Late Pliocene to Early Pleistocene related to global climate and local tectonic events. Earth and Planetary Science (2016) 3: 11.
DOI: 10.1186/s40645-016-0087-4

Iwai, T. 1965. The geological and paleontological studies in the marginal area of the Tsugaru Basin, Aomori prefecture, Japan. Bulletin of the Faculty of Education, Hirosaki University (15): 1–68.

Kamiya, T. 2003. Environmental significance of the Japan Sea, a marginal sea, for the shallow marine organisms. –A perspective from Ostracoda (Crustacea). Proceedings of the International Symposium of the Kanazawa University 21st-Century COE Program 1: 102–105.

Kamiya, T. 2006. 5. Environmental change and marine organism of the Japan Sea. Japan Sea Rim Studies: Images of forest, sea and sky (Research Report of the Kanazawa University 21st-Century COE Program): 33–40. (in Japanese, title translated)

Kaneko, A., K. Amano, T. Sato, M. Hamuro, and T. Hamuro. 2016. Influence of environment change on benthic fauna during the early Pleistocene in the central part of Japan Sea borderland: Based on analyses of molluscan fauna from the Omma Formation around Tagawa in Oyabe City, Toyama Prefecture. Journal of the Geological Society of Japan 122(5): 193–206. (in Japanese with English abstract)
DOI: 10.5575/geosoc.2016.0009

Kanno, S., and T. Tomizawa. 1959. Fossil molluscan fauna from the environs of the Zenkoji hot-springs, Nagano Prefecture. Transactions and Proceedings of the Palaeontological Society of Japan, New Series (33): 9–14.

Kanno, S., K. Amano, and H. Ban. 1989. *Calyptogena* (*Calyptogena*) *pacifica* Dall (Bivalvia) from the Neogene System in the Joetsu District, Niigata Prefecture. Transactions and Proceedings of the Palaeontological Society of Japan, New Series (153): 25–35.

Kase, T., T. Miyauchi, and K. Amano. 1996. A new species of the Family Ungulinidae from Wakkanai, Hokkaido, Japan. Venus 55(2): 97–103.
DOI: 10.18941/venusjjm.55.2_97

Kaseno, Y., and N. Matsuura. 1965. Pliocene shells from the Omma Formation around Kanazawa City, Japan. Science Report of Kanazawa University 10: 27–62.

Kitamura, A. 2016. Constraints on eustatic sea-level changes during the Mid-Pleistocene Climate Transition: Evidence from the Japanese shallow-marine sediment record. Quaternary International 397: 417–421.
DOI: 10.1016/jquaint.2015.03.004

Kitamura, A., and K. Kimoto. 2006. History of the inflow of the warm Tsushima Current into the Sea of Japan between 3.5 and 0.8 Ma. Palaeogeography, Palaeoclimatology, Palaeoecology 236: 355–366.
DOI: 10.1016/j.palaeo.2005.11.015

Kitamura, A., and Y. Kondo. 1990. Cyclic changes of sediment and molluscan fossil associations caused by glacio-eustatic sea-level changes during the early Pleistocene. –A case study of the middle part of the Omma Formation at the type locality–. Journal of the Geological Society of Japan 96(1): 19–36. (in Japanese with English abstract)
DOI: 10.5575/geosoc.96.19

Kobayashi, I., T. Yahata, S. Sugimoto, and S. Iyoda. 1986. Molluscan fauna from the Haizume Formation in the Nishiyama oil-field, Niigata Prefecture. Monograph of the Mizunami Fossil Museum (6): 105–118. (in Japanese with English abstract)

Kojima, S, R. Segawa, I. Hayashi, and M. Okiyama. 2001. Phylogeography of a deep-sea demersal fish, *Bothrocara hollandi*, in the Japan Sea. Marine Ecology Progress Series 217: 135–143.
DOI: 10.3800/pbr.4.115

Kozaka, Y., K. Horikawa, Y. Asahara, H. Amakawa, and Y. Okazaki. 2018. Late Miocene–mid-Pliocene tectonically induced formation of the semi-closed Japan Sea, inferred from seawater Nd isotopes. Geology 46(10): 903–906.
DOI: 10.1130/G45033.1

Kubota, K. 1950. Illustrated Cenozoic fossils of northern Japan, 9. Fossil Pectinidae of Setana Series. Study on the molluscan fauna from Setana Series, no. 3. Shinseidai-no-kenkyu (6): 94–100. (in Japanese)

Kurozumi, T. 2017. Family Mytilidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1172–1179. (in Japanese and English)

Kurozumi, T., and E. Tsuchida. 2017. Family Yoldiidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1162–1163. (in Japanese and English)

Kurozumi, T., E. Tsuchida, and T. Okutani. 2017. Family Nuculanidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1160–1162. (in Japanese and English)

Lutaenko, K. A. 2005. Bivalve mollusks of Ussuriysky Bay (Sea of Japan). Part 1. The Bulletin of the Russian Far East Malacological Society 9: 59–81. (in English with Russian abstract)

Masuda, K. 1962. Tertiary Pectinidae of Japan. Science Reports of the Tohoku University, Second Series 33(2): 113–238.

Masuda, K., and K. Ogasawara. 1981. On the Omma-Manganzi fauna and Tatsunokuchi fauna. In T. Habe, and M. Omori, eds., Study of Molluscan Paleobiology: Professor Masae Omori Memorial Volume. Editorial Committee of the Professor Masae Omori Memorial Volume. Niigata. p. 223–249. (in Japanese with English abstract)

Masuda, K., and Y. Sawada. 1961. Some new Tertiary pectinids from southwestern Hokkaido, Japan. Japanese Journal of Geology and Geography 32(1): 19–29.

Matsukuma, A. 2017a. Family Limopsidae. In T. Okutani. ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press, Hiratsuka. p. 1171–1172. (in Japanese and English)

Matsukuma, A. 2017b. Family Crassatellidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1203. (in Japanese and English)

Matsukuma, A. 2017c. Family Carditidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1204–1206. (in Japanese and English)

Matsukuma, A. 2017d. Family Lucinidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1217–1219. (in Japanese and English)

Matsuura, N. 1985. Successive change of the marine molluscan faunas from Pliocene to Holocene in Hokuriku Region, central Japan. Bulletin of the Mizunami Fossil Museum (12): 71–158. (in Japanese with English abstract)

Matsuura, N. 1992. Fossils of Ishikawa Prefecture. Hokkoku Shimbun. Kanazawa. 156 pp. (in Japanese, title translated)

Matsuura, N. 2009. Fossils of Ishikawa Prefecture (New Edition). Hokkoku Shimbun. Kanazawa. 273 pp. (in Japanese, title translated)

Matsuzaki, K. M., T. Itaki, R. Tada, and S. Kamikuri. 2018. Paleoceanographic history of the Japan Sea over the last 9.5 million years inferred from radiolarian assemblages (IODP Expedition 346 Sites U1425 and U1430). Progress in Earth and Planetary Science (2018) 5: 54.
DOI: 10.1186/s40645-018-0204-7

Mizuno, T., and K. Amano. 1988. Molluscan fauna from the Kota Formation in the Joetsu City. –Studies on the molluscan fossils from the western part of Joetsu District, Niigata Prefecture (Part 4). Bulletin of the Mizunami Fossil Museum (14): 73–88. (in Japanese with English abstract)

Nagamori, H. 1998. Molluscan fossil assemblages and paleo-environment of the Pliocene strata in the Hokushin District, Nagano Prefecture, Central Japan. Earth Science (Chikyu-Kagaku) 52: 5–25. (in Japanese with English abstract)

Nagamori, H. 2014. Molluscan fossils from the Togakushi District, Nagano City. Togakushi Museum of Natural History. Nagano. 47 pp. (in Japanese)

Nakata, Y., and K. Amano. 1991. Pliocene molluscan associations in the Tomikura District, extended over Niigata and Nagano Prefecrures, Japan. Bulletin of the Mizunami Fossil Museum (18): 77–92. (in Japanese with English abstract)

Nakajima, T. 2018. Tectonics of sedimentary basins in and around Japan since the opening of the Sea of Japan. Journal of the Geological Society of Japan 124(9): 693–722. (in Japanese with English abstract)
DOI: 10.5575/geosoc.2018.0049

Nakashima, R. 2002. Geographic distribution of the late Cenozoic bivalve *Fortipecten* in the northwestern Pacific. Palaeogeography, Palaeoclimatology, Palaeoecology 186: 261–274.
DOI: 10.1016/S0031-0182(02)00509-6

Nemoto, N., and S. O'Hara. 1979. Molluscan fossils from the Taga Group around Futatsunuma in Hirono-machi. Research Report of Taira Geological Society, Special Volume: 1–16. (in Japanese, title translated)

Nemoto, N., and S. O'Hara. 2005. Molluscan fossils from the Tomioka Formation in the northern part of Joban district. Research Report of Taira Geological Society (25): 3–43. (in Japanese with English abstract)

Noda, H., and K. Amano. 1977. Geological significance of *Anadara amicula elongata* from the Pliocene Kume Formation, Ibaraki Prefecture, Japan. Annual Report of the Institute of Geoscience, the University of Tsukuba (3): 37–41.

Noda, H., R. Watanabe, and Y. Kikuchi. 1995. Pliocene marine molluscan fauna from the Hitachi Formation in the northeastern part of Ibaraki Prefecture, Japan. Science Reports of the Institute of Geoscience, University of Tsukuba, Sec. B 16: 39–93.

Nomura, S., and K. Hatai. 1935. Pliocene Mollusca from the Daisyaka shell-beds in the vicinity of Daisyaka, Aomori-ken, Northeast Honshu, Japan. Saito Ho-on Kai Museum, Research Bulletin (6): 83–142.

Ogasawara, K. 1977. Paleontological analysis of Omma fauna from Toyama-Ishikawa area, Hokuriku Province, Japan. Science Reports of the Tohoku University, Second Series 47(2): 43–156.

Ogasawara, K. 1981. Paleogeographic significance of the Omma-Manganzian fauna of the Japan Sea Borderland. Saito Ho-on Kai Museum Research Bulletin (49): 1–17.

Ogasawara, K. 1986. Notes on origin and migration of the Omma-Manganzian fauna, Japan. Palaeontological Society of Japan, Special Papers (29): 227–244.

Ogasawara, K. 1994. Neogene paleogeography and marine climate of the Japanese Islands based on shallow-marine molluscs. Palaeogeography, Palaeoclimatology, Palaeoecology 108: 335–351. DOI: 10.1016/0031-0182(94)90241-0

Ogasawara, K. 2002. Responses of Japanese Cenozoic molluscs to Pacific gateway events. Revista Mexicana de Ciences Geológicas 19(3): 206–214.

Ogasawara, K., K. Masuda, and Y. Matoba. 1986. Neogene and Quaternary Molluscs from the Akita Oilfield, Japan. Commemorative Association of Professor Taisuke Takayasu's Retirement and Supporters' Foundation of Mineral Industry Museum, Mining College, Akita University. Akita. 310 pp. (in Japanese)

Ogasawara, K., and K. Naito. 1983. The Omma-Manganzian molluscan fauna from Akumi-gun, Yamagata Prefecture, Japan. Saito Ho-on Kai Museum, Research Bulletin (51): 41–61.

Ogasawara, K., O. Sasaki, and N. Chiba. 1988. The Dainenji molluscan association from the environs of Sendai, Northeast Honshu and its zoogeographic significance. Saito Ho-on Kai Museum, Research Bulletin (56): 1–15.

Ogasawara, K., M. Takano, H. Nagato, and T. Nakano. 2008. Cenozoic molluscan faunas and climatic changes in the northern Pacific related to Pacific gateways: review and perspective. Bulletin of the Geological Survey of Japan 59(7/8): 355–364.

O'Hara, S., and N. Nemoto. 1988. Pectinids from the Taga Group of the Joban Coalfield. Saito Ho-on Kai, Special Publication (2): 481–496.

Okamoto, K., and E. Honza. 1978. The "Pliocene" fossil molluscan assemblage including *Amussiopecten* collected by GH 77–2 cruise in the southwestern Japan Sea. Journal of the Geological Society of Japan 84(10): 625–628. (in Japanese) DOI: 10.5575/geosoc.84.625

Okumura, K., and T. Ueda. 1998. Molluscan fossils from the Upper Pliocene Nakatsu Formation in the middle part of Sagami River, Kanagawa Prefecture, Japan. Bulletin of the Mizunami Fossil Museum (25): 53–87.

Okutani, T. 2017a. Family Velutinidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 858. (in Japanese and English)

Okutani, T. 2017b. Family Buccinidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 917–939. (in Japanese and English)

Okutani, T. 2017c. Family Cuspidariidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1213–1217. (in Japanese and English)

Okutani, T. 2017d. Family Thyasiridae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 1219–1221. (in Japanese and English)

Omori, M. 1977. Molluscan fossils from the so-called Sawane Formation. Reseach Report of the Sado Museum (7): 63–76. (in Japanese, title translated)

Otuka, Y. 1936. Pliocene Mollusca from Manganzi in Kotomo-mura, Akita Prefecture, Japan. Journal of the Geological Society of Japan 43: 726–736.

Otuka, Y. 1939a. Mollusca from the Cainozoic System of eastern Aomori Prefecture, Japan. Journal of the Geological Society of Japan 46: 23–31.
DOI: 10.5575/geosoc.46.23

Otuka, Y. 1939b. Tertiary crustal deformation in Japan (with short remarks on Tertiary Palaeogeography). Jubilee Publication in the Commemoration of Prof. H. Yabe's 60th Birthday 2: 481–519.

Sasaki, T. 2017a. Family Trochidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 747–754. (in Japanese and English)

Sasaki, T. 2017b. Family Fissurellidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 775–779. (in Japanese and English)

Sato, T., and K. Kameo. 1996. Pliocene to Quaternary calcareous nannofossil biostratigraphy of the Arctic Ocean, with reference to Late Pliocene glaciation. In J. Thiede, A. M. Myhre, J. V. Firth, and W. F. Ruddiman, eds., Proceedings of the Ocean Drilling Program, Science Results 151. Texas A and M University. College Station. p. 39–59.

Sawada, Y. 1962. The geology and paleontology of the Setana and Kuromatsunai areas in Southwest Hokkaido. Memoirs of the Muroran Institute of Technology 4: 1–110.

Scarlato, O. A. 1981. Dvustvorchatye mollyuski umerennykh shirot zapadnoy chasti Tikhogo Okeana [Bivalve molluscs from the middle latitude of the western part of the Pacific Ocean]. Opredeliteli po faune SSSR, Izdavaemye Zoologicheskim Institutom AN SSSR [Keys to the fauna of the USSR, Zoological Institute of the USSR Academy of Sciences] (126): 1–479. (in Russian)

Shikama, T., and A. Ikeya. 1964. On the variation of *Chlamys islandicus* from a part of Setana Formation. Science Reports of the Yokohama National University, Sec. II (11): 29–54.

Shimaguchi, T., and M. Nara. 2015. Molluscan fossils from the Lower Pleistocene Hamada Formation in the Aomori Prefectural Museum. Annual Report of the Aomori Prefectural Museum 39: 1–12. (in Japanese)

Shinada, Y., and K. Amano. 1995. Rock-boring bivalve associations in the early Pleistocene Omma-Manganji fauna. Fossils (Palaeontological Society of Japan) (58): 10–19. (in Japanese with English abstract)

Stanley, S. M. 1986. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. Paleobiology 12: 89–110.
DOI: 10.1017/S0094837300003006

Stedinthorsdottir, M., H. K. Coxall, A. M. de Boer, M. Huber, N. Barbolini, C. D. Bradshaw, N. J. Burls, S. J. Feakins, E. Gasson, J. Henderiks, A. E. Houlbourn, S. Kiel, M. J. Kohn, G. Knor, W. M. Kürschner, C. H. Lear, D. Liebrand, D. J. Lunt, T. Mörs, P. N. Pearson, M. J. Pound, H. Stoll, and C. A. E. Strömberg. 2021. The Miocene: The future of the past. Paleoceanography and Paleoclimatology 36: e2020PA004037.
DOI: 10.1029/2020PA004037

Strotz, L. C., E. E. Saupe, J. Kimmig, and B. C. Lieberman. 2018. Metabolic rates, climate and macroevolution: a case study using Neogene molluscs. Proceedings of the Royal Society B 285: 20181292.
DOI: 10.1098/rspb.2018.1292

Suzuki, A. 1989. Molluscan fauna from the Setana Formation in the Kuromatsunai District, southwestern Hokkaido, Japan. Earth Science (Chikyu-Kagaku) 43(5): 277–289. (in Japanese with English abstract)
DOI: 10.15080/agcjchikyukagaku.43.5_277

Suzuki, A. 1991. Sedimentary environment oif the Setana Formation in the Pirila- Kuromatsunai area, southwestern Hokkaido. Journal of the Geological Society of Japan 97(5): 329–344. (in Japanese with English abstract)
DOI: 10.5575/geosoc.97.329

Tada, R. 1994. Paleoceanographic evolution of the Japan Sea. Palaeogeography, Palaeoclimatology, Palaeoecology 108: 487–508.
DOI: 10.1016/0031-0182(94)90248-8

Takahashi, H. 1986. Characteristics of the molluscan assemblages in the Pliocene Kume Formation in the Hitachi-Ota area, Ibaraki Prefecture, central Japan. Monograph of the Mizunami Fossil Museum (6): 91–104, pls. 12–13. (in Japanese with English abstract)

Takayasu, T. 1962. Molluscan fossils from the Shibikawa Formation in the Oga Peninsula, Akita Prefecture, Japan. Studies of the Cenozoic fauna in the Akita oil field (Part 2). Journal of the Mining College, Akita University, Ser. A. 2(2): 1–19.

Tayor, J. D., N. L. Morris, and C. N. Taylor. 1980. Food specialization and the evolution of predatory prosobranch gastropods. Palaeontology 23(2): 375–409.

Tsuchiya, K. 2017a. Family Collumbellidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 903–910. (in Japanese and English)

Tsuchiya, K. 2017b. Family Nassariidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 910–917. (in Japanese and English)

Tsuchida, E., and K. Hasegawa. 2017. Family Epitoniidae. In T. Okutani, ed., Marine Mollusks in Japan, 2nd edition. Tokai University Press. Hiratsuka. p. 889–901. (in Japanese and English)

Uozumi, S., and M. Akamatsu. 1975. Pliocene pectinids from southwest Hokkaido, Japan. –*Chlamys islandicus* group–. Journal of the Faculty of Science, Hokkaido University, Ser. IV 17(1): 27–71.

Yamanashi Prefecture. 1970. Geology of Yamanashi Prefecture. 240 pp. (in Japanese, title translated)

Yokoyama, M. 1910. On species of *Limopsis* found in the Neogene of Koshiba. Journal of the Geological Society of Tokyo 17: 1–5.

Yokoyama, M. 1911. Pectens from Koshiba Neogene. Journal of the Geological Society of Tokyo 18: 1–5.

Yokoyama, M. 1927. Fossil Mollusca from Kaga. Journal of the Faculty of Science, Imperial University of Tokyo, sec. 2 2(4): 165–182.

Zhao, D., S. Wan, L. Zhai, X. Shi, and A. Li. 2022. Tectonic and orbital imprints in the redox history of Japan Sea since the Pliocene. Paleoceanography and Paleoclimatology 37: e2021PA004333. DOI: 10.1029/2021PA004333

Speciation, extinction and survival of molluscan species in the marginal sea –Plio‑Pleistocene Omma‑Manganji fauna in the Japan Sea borderland–

Kazutaka Amano

Explanation of Plates 1–2

Plate 1. Characteristic species of the Omma-Manganji fauna (1). All scale bars = 10 mm.

Fig. 1. ***Acila* (*Truncacila*) *nakazimai* Otuka.** Paralectotype, UMUT CM 12830, Hamada Formation in Aomori Prefecture.

Figs. 2a, b. ***Glycymeris* (*Glycymeris*) *nipponica* (Yokoyama).** Lectotype, UMUT CM 20625, Koshiba Formation in Kanagawa Prefecture.

Fig. 3. ***Chlamys* (*Chlamys*) *cosibensis* (Yokoyama).** UMUT CM 23275, Sawane Formation in Niigata Prefecture.

Fig. 4. ***Anadara amicula* (Yokoyama).** Lectotype, UMUT CM 22639, Joshita Formation in Nagano Prefecture.

Fig. 5. ***Chlamys* (*Chlamys*) *insolita* (Yokoyama).** Holotype, UMUT CM 22634, Ogikubo Formation in Nagano Prefecture.

Figs. 6, 11. ***Yabepecten tokunagai* (Yokoyama).** UMUT CM 23281 (fig. 6), 23282 (fig. 11), Sawane Formation in Niigata Prefecture.

Fig. 7. **"*Dinocardium*" *angustum* (Yokoyama).** Holotype, UMUT CM 22599, Ogikubo Formation in Nagano Prefecture.

Fig. 8. ***Chlamys* (*Chlamys*) *foeda* (Yokoyama).** Holotype, UMUT CM 23286, Sawane Formation in Niigata Prefecture.

Fig. 9. ***Profulvia kurodai* (Hatai and Nisiyama).** Holotype, UMUT CM 23214, Sawane Formation in Niigata Prefecture.

Figs.10a, b. ***Limopsis tokaiensis* Yokoyama.** Lectotype, UMUT CM 20652, Koshiba Formation in Kanagawa Prefecture.

Plate 1

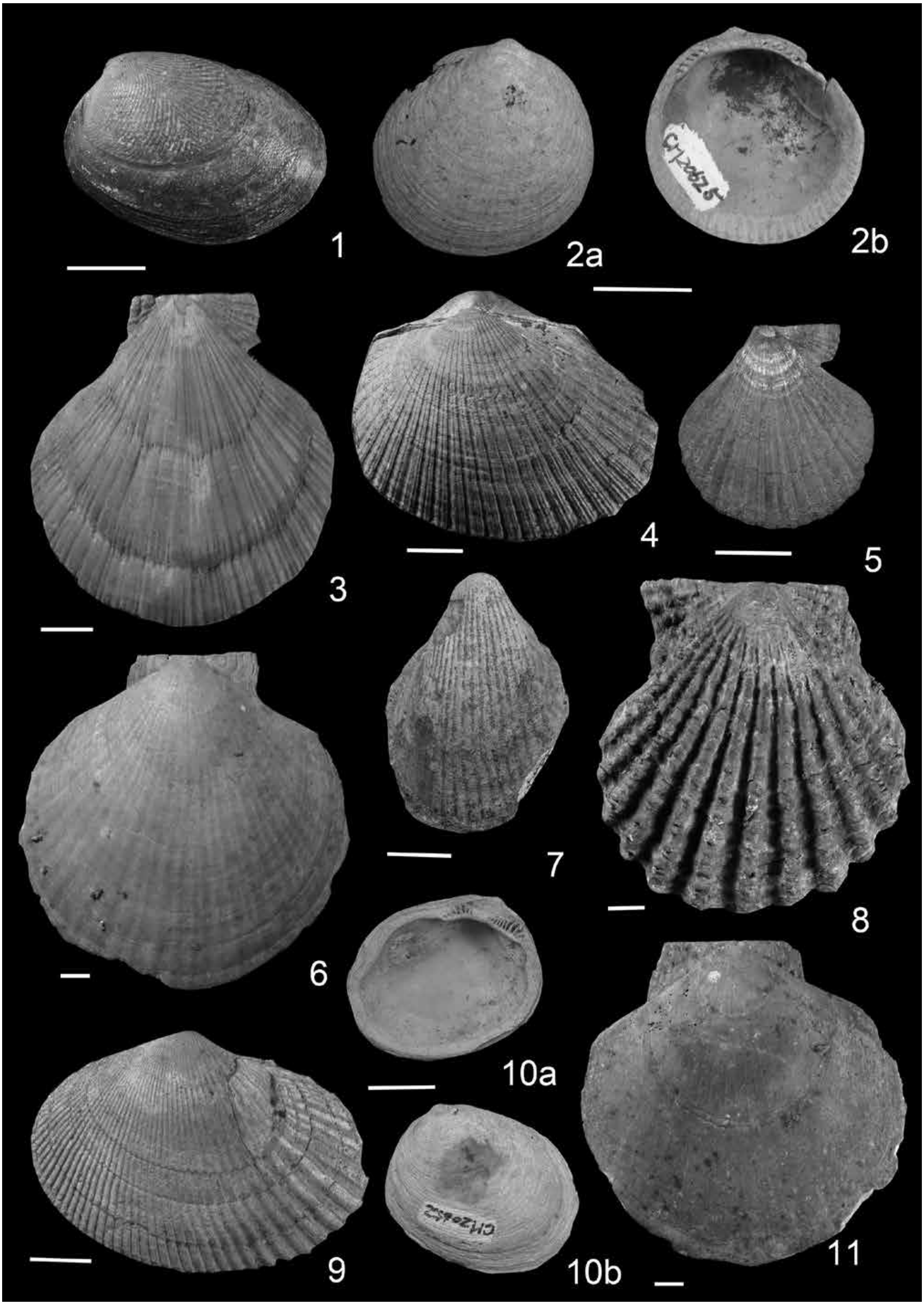

Plate 2. Characteristic species of the Omma-Manganji fauna (2). Scale bars in figs. 1–5, 7, 10 = 5 mm; in figs.6, 8, 9, 11, 12 = 10 mm.

Fig. 1. ***Oenopota kagana*** **(Yokoyama).** Lectotype, UMUT CM 24793, Omma Formation in Ishikawa Prefecture.

Fig. 2. ***Plicifusus ozawai*** **(Yokoyama).** Lectotype, UMUT CM 24801, Omma Formation in Ishikawa Prefecture.

Fig. 3. ***Lirabuccinum japonicum*** **(Yokoyama).** Holotype, UMUT CM 23117, Sawane Formation in Niigata Prefecture.

Fig. 4. ***Merica kobayashii*** **(Yokoyama).** Holotype, UMUT CM 24808, Omma Formation in Ishikawa Prefecture.

Fig. 5. ***Turritella*** **(*Neohaustator*)** ***saishuensis saishuensis*** **(Yokoyama).** UMUT CM 24841, Omma Formation in Ishikawa Prefecture.

Fig. 6. ***Pseudamiantis tauyensis*** **(Yokoyama).** Lectotype, UMUT CM 24903, Omma Formation in Ishikawa Prefecture.

Fig. 7. ***Retifusus yanamii*** **(Yokoyama).** Holotype, UMUT CM 23085, Sawane Formation in Niigata Prefecture.

Fig. 8. ***Nuttallia commoda*** **(Yokoyama).** Holotype, UMUT CM 22588, Ogikubo Formation in Nagano Prefecture.

Fig. 9. ***Mizuhopecten yokoyamae*** **(Masuda).** UMUT CM 24946, Omma Formation in Ishikawa Prefecture.

Fig.10. ***Umbonium akitanum*** **Suzuki.** UMUT CM 12793, Sasaoka Formation in Akita Prefecture.

Fig.11. ***Mizuhopecten tryblium*** **(Yokoyama).** Paralectotype, UMUT CM 22629, Ogikubo Formation in Nagano Prefecture.

Fig.12. ***Mizuhopecten yamasakii*** **(Yokoyama).** Lectotype, UMUT CM 22621, Ogikubo Formation in Nagano Prefecture.

Plate 2