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JAPANESE CENOZOIC MOLLUSCS

—THEIR ORIGIN AND MIGRATION—

Edited by

Tamio KOTAKA

Assisted by

Louie MARINCOVICH, Jr.

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CONTENTS

PREFACE

The waters around the Japanese Islands are zoogeogaphically recognized as the Japonic marine molluscan province and contain a very rich molluscan fauna of more than 6,500 species. Several Japonic genera and species are endemic ones and help to characterize the province. The molluscan fauna along the Pacific coast of Japan has long been influenced by both the warm Kuroshio current and the cold Oyashio current. Similarly, molluscs along the Sea of Japan coast have been influenced by the warm Tsushima current, a nearshore branch of the Kuroshio current, and by the cold offshore Liman current.

Along the Pacific coast we can subdivide the fauna into two parts: one composed of warm water elements inhabiting the region where the Kuroshio current extends in summer as far northward as 39°N. Lat. off Kinkazan Island, Miyagi Prefecture; and another consisting of cold water elements that are found in the realm of the Oyashio current, which extends southward to 36°N. Lat. in winter, near the base of the Boso Peninsula, Chiba Prefecture. The area between 36° and 39°N. Lat. is influenced seasonally by both warm and cold currents.

Along the Sea of Japan coast the warm Tsushima current exerts a fairly strong influence on the shallow bottom molluscan assemblages all the year round as far north as northern Hokkaido (45°N. Lat.). However, boreal molluscs occur in deeper and offshore bottoms where the Tsushima current has been chilled by mixing with the cold Liman current.

According to Hatai and Nisiyama (1952), 1,482 species and subspecies of fossil molluscs were recorded from the Tertiary deposits of Japan up to 1950. Masuda and Noda (1976) catalogued 4,722 species and subspecies described and illustrated from Tertiary and Quaternary strata of Japan between 1950 and 1974. These two works contain a total of 6,204 species and subspecies, but include extinct and living taxa, plus the synonyms and homonyms of different authors. So the total number of valid Cenozoic species of Japanese molluscs is not accurately known.

During the Cenozoic, several taxa immigrated into the Japonic province, some emigrated out to other provinces, and some become extinct within the Japonic province.

The Cenozoic molluscan fauna of Japan, as well as that of the shallow Tethys Sea that extended across Europe, India and Southeast Asia, has long been thought to have originated in the Indo-Pacific region. However, faunal comparisons of large regions usually are compiled from the data of numerous individual studies done in different areas and for different stratigraphic intervals. Consequently, there is a lack of uniformity in the basic data used in making comparisons. However, an accumulation of paleontological studies over the past two decades, plus recent developments in modern continental drift theory and biostratigraphic correlations based on planktonic microfossils have contributed to our understanding of relationships between geographically distant marine faunas.

The Japanese Islands were not situated within the Tethys Sea that formed between the paleocontinents of Laurasia and Gondowana during the Late Paleozoic, though marine invertebrate faunas in the European and Asian regions were long connected through this seaway.

Hatai, K., Nisiyama, S. (1952): Check list of Japanese Tertiary marine Mollusca. *Sci. Rept., Tohoku Univ., 2nd Ser., Spec. Vol.*, no. 3, p. 1–464.

Masuda, K & Noda, H. (1976): *Check list and bibliography of the Tertiary and Quaternary Mollusca of Japan, 1950–1974.* 494 p., The Saito Gratitude Foundation, Sendai, Japan.

During the Miocene the Tethys Sea was subdivided into the Indo-European and Indo-Pacific regions by northward drifting of the Indian subcontinent and its collision against the Eurasian continent. Since that time, the shallow marine benthic faunas of these two regions have become increasingly distinct from each other.

From this background, a project on "Origin and Migration of Japanese Cenozoic Molluscs," supported by the Ministry of Education, Science and Culture of the Japanese Government, was carried out by twenty-two Japanese mollusan paleontologists/geologists from 1982 to 1984. During the course of this project, short field excursions were made by individual collaborators throughout Japan. In addition, small colloquia were arranged by the project leader on 13th–15th December, 1982, on 23rd–25th September, 1983 and on 21st–23rd March, 1984, for the purpose of promoting an exchange of views among collaborators.

The following papers are the result of the colloquia just mentioned, and the editors and contributors of this volume would like to express their appreciation to Dr. Louie Marincovich, Jr.,* a molluscan paleontologist with the United State Geological Survey, Menlo Park, California for his assistance in editing of this volume. Deep gratitude is also given to the Ministry of Education, Science and Culture of the Japanese Government for their financial support.

Tamio Kotaka
Chairman of the Colloquia

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PART I

AN OUTLINE OF CENOZOIC MOLLUSCAN FAUNAS IN JAPAN

A vast amount of information on Cenozoic molluscs in Japan has accumulated since the late Professor Matajiro Yokoyama first described some Paleogene molluscs from central Hokkaido in 1890. This information covers the many aspects of molluscan paleontology, including taxonomic and evolutionary studies, biostratigraphy, paleoecology, plaeogeography, and concerning paleoenvironmental reconstructions.

The first part of the volume is intended as an overview of Cenozoic molluscan faunas in the Japanese Islands. It includes summaries of faunal compositions, biogeographic characteristics, and stratigraphic and geographic occurrences. The origin and evolution of these faunas are also discussed.

In the first paper, Honda shows the presence of the two distinct faunas in the Paleogene System in Hokkaido. The Eocene Ishikari fauna is characterized by many warm water taxa which shows affinity to the Eocene faunas in Kyushu. The Oligocene Poronai fauna, on the other hand, is composed of northern elements and exhibits close relationship to Paleogene faunas of the Northern Pacific regions. The change from the warm to cold water faunas during the Late Eocene-Early Oligocene may reflect a global climatic deterioration during the terminal phase of the Eocene Epoch.

Stratigraphic and geographic distributions of Neogene faunas in Japan are discussed in three papers by Chinzei, Tsuchi and Itoigawa. Chinzei presents a revision of his 1978 paleontologic and biogeographic synthesis, based on new planktonic microfossil age assignments of the mollusc-bearing sediments. Chinzei's synthesis is based on the idae of temporal parallelisms, the time-transgressive occurrence of ecologically analogous molluscan associations. He also stresses a sharp swichover from the warm water Kadonosawa fauna of the early Middle Miocene to the cold water Shiobara-Yama fauna of the Middle Miocene in Japan Sea coast areas. The swichover is dated at about 15 Ma. and is thought to be related to rapid rotation of Southwest Japan and opening of Japan Sea.

Based on an up-dated microbiostratigraphic framework, Tsuchi reviews historical changes of Neogene molluscsn faunas of Japan. He discusses the importance of the Late Miocene through Early Pleistocene Sagara and Kakegawa faunas of Japan to the development of the present-day subtropical Kuroshio fauna. He also discusses the possible origin of the two Neogene faunas and concludes that they were largely established by the independent immigration of tropical elements from the south.

Itoigawa discusses his concept on environmental control of temporal and areal distributions of molluscan assemblages. He emphasizes the different grades of importance of current, water mass, and local factors (such as depth, bottom sediments, etc.) for geographic distribution of molluscan species. Taking the molluscan fauna in the Setouchi Province as an example, he discusses the relationship between similar faunal composition and similar environmental conditions. The distribution of molluscan assemblages in the Japanese Neogene is reevaluated based on the grade of the controlling environmental factors.

These four papers present an up-to-date idea of the historical development of Japanese molluscan faunas.

(Kiyotaka CHINZEI and Ryuichi TSUCHI)

A PALEOGENE MOLLUSCAN FAUNA FROM HOKKAIDO, NORTHERN JAPAN

By

Yutaka HONDA

Introduction

Mizuno (1964b) summarized the Paleogene molluscan faunas of North Japan, and divided them into the lower, middle and upper Ishikarian and the Poronaian faunas, in ascending order. The lower Ishikarian fauna (Eocene) is found in the Noborikawa, the Horokabetsu, the Yubari, the Wakkanabe, and the Bibai Formations, in the lower part of the Ishikari Group; and the Shiroki and the Uryu Formations of the Uryu Group, Rumoi coal field, central Hokkaido (Mizuno, 1964b).

A representative lower Ishikarian fauna is seen in the Wakkanabe Formation, where it is largely composed of shallow marine or brackish warm water dwellers. It is characterized by *Pyrazus* n. sp., *Crassatellites* (*Eucrassatella*) *yessoensis* Minato and Kumano, *Venericardia* (*Venericardia*) *otatsumei* Uozumi, *Geloina hokkaidoensis* (Nagao and Otatume), *Corbicula* (*Corbicula*) *tokudai* (Yokoyama), *Claibornites quinquangulus* Uozumi, *"Paphia" munroei* Yokoyama, and *Mya* (?*Arenomya*) *ezoensis* Nagao and Inoue (Mizuno, 1965).

The middle Ishikarian fauna (Oligocene) is found in the Akabira Formation, forming the middle part of the Ishikari Group (Mizuno, 1964b). It is characterized by *Siphonalia sakakurai* Mizuno, *Portlandia* (*Portlandella*) *watasei ogasawarai* Uozumi, *Acila* (*Acila*) *shimoyamai* Oyama and Mizuno, *Corbicula tokudai, Conchocele bisecta omarui* (Oyama and Mizuno), *"Paphia" munroei,* and *Mya ezoensis,* n. subsp. (Mizuno, 1965).

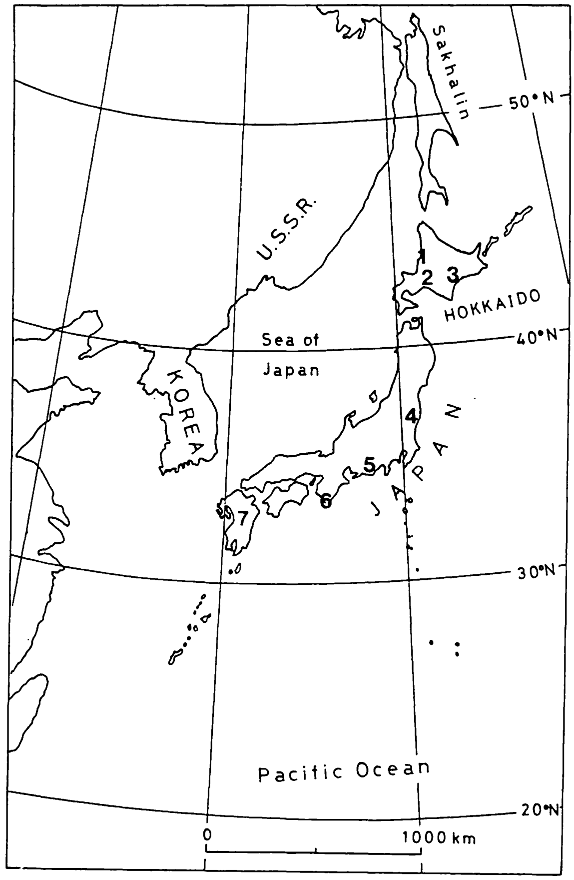
The upper Ishikarian fauna (Oligocene) is found in the Hiragishi and the Ashibetsu Formations, in the upper part of the Ishikari Group; and in the Urahoro Group of the Kushiro coal field, eastern Hokkaido (Mizuno, 1964b). It is characterized by *Corbicula* (*Batissa*) *sitakaraensis* Suzuki, *Portlandia watasei watasei* (Kanehara), *Nemocardium* (*Arctopratulum*) *ezoense* Takeda, *Yoldia* (*Yoldia*) *laudabilis* Yokoyama, and *Mya* (?*Arenomya*) *grewingki* Makiyama (Mizuno, 1965).

The Poronaian fauna (or the Asagai-Poronai fauna, Otuka, 1939; Oligocene) is found in the Poronai Formation of the Ishikari coal field; the Tappu Group of the Rumoi coal field; the Ombetsu Group of the Kushiro coal field; and the Asagai Formation of the Joban coal field, Northeast Japan (Mizuno, 1964b). It is characterized by *Orectospira wadana* (Yokoyama), *Portlandia watasei watasei, Acila* (*Truncacila*) *picturata* (Yokoyama), *Crassatellites teshimai* Inoue and Mizuno, *Cyclocardia akagii* (Kanehara), *Conchocele bisecta* (Conrad), *Periploma* (*Aelga*) *besshoense* (Yokoyama), *Laevicardium* (*Profulvia*) *harrimani* (Dall), and *Yoldia laudabilis* (Mizuno, 1965).

It has been noted by many paleontologists that the Poronaian fauna is closely related to those in Sakhalin, Kamchatka, Alaska, and Northwest America, from the molluscan and the foraminiferal viewpoints (Asano, 1949, 1961; Hatai and Kamada, 1950; Takeda, 1953; Durham and Sasa, 1961; Serova, 1976; and others). The fauna has been regarded as a boreal or cold-water one (Otuka, 1939; Makiyama, 1934, 1939; Hatai and Kamada, 1950), and is a cold-water equivalent of the Ashiya fauna (late Oligocene to early Miocene) of Kyushu, southern Japan (Tsuchi and Shuto, 1984).

Matsumoto (1964) described the Asagai-Poronai fauna from the Ōga Formation (late Oligocene or earliest Miocene), which is unconformably underlain by the so-called Mikura and Setogawa Groups, Shizuoka Prefecture, Central Japan. Iwasaki and Ono (1977) described a molluscan fauna allied to the Asagai-Poronai fauna from the Setogawa Group. Mizuno (1973) summarized the molluscan fauna of the Muro Group of Kii Peninsula, Southwest Japan; the fauna is mostly composed of Poronaian species, and Mizuno tentatively assigned the group to the late Oligocene to early Miocene.

Mizuno (1965, 1977) established two paleozoogeographic provinces in Japan and adjacent regions during Paleogene time: the Northeast (North) Japan-Okhotsk and the Formosa-Southwest (West) Japan Provinces. The Northeast Japan-Okhotsk Province includes the areas of Sakhalin and Kamchatka, and is largely composed of tropical, subtropical, and temperate forms in the Eocene and is dominated by temperate ones in the Oligocene (Mizuno, 1977). On the



Text-fig. 1. Map of Japan showing the areas referred to in the text. 1, Rumoi coal field, central Hokkaido; 2, Ishikari coal field, central Hokkaido; 3, Kushiro coal field, eastern Hokkaido; 4, Joban coal field, Northeast Japan; 5, Shizuoka Prefecture, Central Japan; 6, Kii Peninsula, Southwest Japan; 7, Kyushu.

other hand, the Formosa-Southwest Japan Province is largely composed of tropical and subtropical forms in both Eocene and Oligocene times (Mizuno, 1977).

Tanai (1970) studied the Oligocene floras of the Urahoro Group, including the Harutori, the Tenneru, the Yubetsu, and the Shakubetsu floras in upward sequence; they change gradually upward from warm-temperate to temperate ones. Sato (1970) recorded a temperate pollen flora from the Poronai Formation and a cool-temperate one from the Momijiyama Formation, Ishikari coal field. Sato (1984) also recorded a cool-temperate pollen flora becoming cooler in upward sequence from the Ombetsu Group, and correlated the Charo and Nuibetsu Formations of the Ombetsu Group with the Poronai and Momijiyama Formations.

On the other hand, Kaiho (1984) studied Paleogene foraminifera from Hokkaido, and correlated the Urahoro and the Ombetsu Groups with the Poronai and the Momijiyama Formations. He assigned these strata a late Eocene to early Oligocene age. Tanai (1983) mentioned that the Eocene/Oligocene boundary is placed between the Bibai and the Akabira Formations of the Ishikari Group, in view of their fossil floras and the so-called terminal Eocene event (Wolfe, 1978). A map of Japan indicating the areas referred to here is shown in Fig. 1.

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Geological Setting

The Paleogene strata that crop out in the Kushiro coal field, eastern Hokkaido, are divided into the Urahoro and the Ombetsu Groups in ascending order. The Urahoro Group is unconformably underlain by the Nemuro Group (late Cretaceous to Paleocene), and is largely composed of gray, poorly sorted, fine-grained sandstone and pebbly to granular conglomerate composed of chert pebbles, with intercalated coal seams.

The group is divided into the Rushin, Yubetsu, Shitakara, and Shakubetsu Formations, in ascending order, and attains a thickness of about 1000 m. It yields nonmarine and shallow marine mollusks, including *Ostrea eorivularis* Oyama and Mizuno, *Chlamys shitakaraensis* Honda, *Corbicula* (*Batissa*) *sitakaraensis, C. tokudai, Nemocardium* (*Arctopratulum*) *ezoense, N.* (*A.*) *yokoyamai* Takeda, *Mya grewingki*, etc.

The Ombetsu Group unconformably overlies the Urahoro Group, and is largely composed of gray siltstone, with greenish gray basal sandstone. It is divided into the Omagari, Charo and Nuibetsu Formations, in ascending order. It is more than 1000 m in maximum thickness, and is unconformably overlain by the Atsunai Group (Miocene). The stratigraphic classification of the Kushiro coal field is shown in Table 1.

The Ombetsu Group yields such shallow marine mollusks as *Yoldia laudabilis, Portlandia*

Table 1. Stratigraphic classification in the Kushiro coal field (Yui, 1975MS).

AGE	GROUP	FORMATION
Holocene		Alluvium
Pleistocene		Terrace deposits
Pliocene		Hombetsu Formation
Miocene	Atsunai Group	Atsunai Formation
		Tokomuro Formation
Oligocene	Ombetsu Group	Nuibetsu Formation
		Charo Formation
		Omagari Formation
	Urahoro Group	Shakubetsu Formation
		Shitakara Formation
		Yubetsu Formation
		Rushin Formation
Late Cret.-Paleocene	Nemuro Group	Kawaruppu Formation
		Katsuhira Formation

watasei watasei, *Acila* (*Acila*) *elongata* Nagao and Huzioka, *A.* (*Acila*) *brevis* Nagao and Huzioka, *Cyclocardia ezoensis* (Takeda), *C. expansa* (Takeda), *C. tokudai* (Takeda), *C. laxata* (Yokoyama), *Turritella* (*Hataiella*) *poronaiensis* Takeda, *T. tokunagai* Yokoyama, *T. importuna* Yokoyama, *Dentalium* (*Fissidentalium*) *nunomae* Takeda, *Eocylichna multistriata* (Takeda), *Orectospira wadana* (Yokoyama), *Clinocardium omagariense* Honda, *Neverita* (*Neverita*) *asagaiensis* (Makiyama), *Conchocele bisecta*, *Macoma* (*Macoma*) *sejugata* (Yokoyama), *Periploma besshoense*, *Laevicardium harrimani*, etc. The occurrences of fossil mollusks in the Urahoro and the Ombetsu Groups are shown in Table 2.

The Paleogene strata that crop out in the Ishikari coal field, central Hokkaido, are divided into the Ishikari Group and the Poronai and Momijiyama Formations, in ascending order. The Ishikari Group is unconformably underlain by the Hakobuchi Group (late Cretaceous), and is largely composed of sandstone, shale and mudstone, with intercalated coal seams (Shimokawara, 1963). It attains several hundreds of m in thickness, and is divided into the Noborikawa, Horokabetsu, Yubari, Wakkanabe, Bibai, Akabira, Ikushumbetsu, Hiragishi, and Ashibetsu Formations, in ascending order (Shimokawara, 1963).

The Poronai Formation, which rests unconformably upon the Ishikari Group, is largely composed of dark gray shale, with glauconitic sandstone-bearing gravel at the base, and ranges in thickness from 1350 to 1850 m (Shimokawara, 1963). The Momijiyama Formation, which is unconformably underlain by the Poronai Formation and conformably overlain by the Takinoue Formation (Miocene), is largely composed of dark gray mudstone, bluish gray mudstone and bluish or greenish gray fine- to coarse-grained sandstone, and ranges in thickness from 360 to 480 m (Shimokawara, 1963). The occurrences of fossil mollusks in the Ishikari Group and the Poronai and Momijiyama Formations are shown in Table 3.

Paleogene molluscan faunas in Hokkaido

Several thousand specimens of Paleogene Mollusca were collected at about 600 localities of the Urahoro and the Ombetsu Groups. They are distributed in 44 genera and 58 species of bivalves, 24 genera and 27 species of gastropods, and one genus and one species of scaphopod.

Most specimens are complete, with their original shell material, whereas others are only partly preserved, and some of them have been somewhat deformed after burial. As a rule, molluscan fossils occur closely packed in groups in granule to pebble conglomerate or poorly sorted fine-grained sandstone of the Urahoro Group. *Ostrea eorivularis*, *Corbicula tokudai* and *C. sitakaraensis* frequently form beds attaining several tens of cm in thickness.

Table 2. Occurrences of fossil mollusks in the Kushiro coal field, eastern Hokkaido (Honda, 1984, *partly revised*). Urahoro Group: RN, Rushin Formation; YB, Yubetsu F.; SK, Shitakara F.; SB, Shakubetsu F. Ombetsu Group: OM, Omagari F.; CH, Charo F.; NB, Nuibetsu F.

SPECIES	RN	YB	SK	SB	OM	CH	NB
Solemya (Acharax) cf. dalli Clark							+
Malletia poronaica (Yokoyama)						+	+
Malletia sp.							+
Saccella pseudoscissurara (Takeda)						+	
Saccella sp.						+	+
Yoldia (Yoldia) laudabilis Yokoyama			+		+	+	+
Yoldia (Yoldia) akanensis Uozumi					+		
Yoldia (Tepidoleda) sobrina Takeda					+	+	+
Yoldia sp.						+	+
Portlandia (Portlandella) watasei watasei (Kanehara)			+		+	+	+
Portlandia (Portlandella) watasei semiovata Uozumi						+	
Portlandia (Portlandella) ovata (Takeda)					+		+
Portlandia (Portlandella) sp.						+	+
Portlandia (Megayoldia) yotsukurensis Uozumi						+	+
Portlandia (Megayoldia) thraciaeformis (Storer)						+	+
Portlandia sp.						+	+
Nucula (Ennucula) n. sp.					+	+	+
Nucula (Ennucula) sp.						+	+
Acila (Acila) cf. praedivaricata Nagao and Huzioka					+		
Acila (Acila) elongata Nagao and Huzioka							+
Acila (Acila) brevis Nagao and Huzioka					+		+
Acila (Acila) kusiroensis Nagao and Huzioka					+	+	+
Acila (Acila) sp.					+	+	+
Acila (Truncacila) picturata (Yokoyama)							+
Acila (Truncacila) sp.					+		+
Acila sp.						+	+
Crenella (Megacrenella) n. sp. A			+				
Crenella (Megacrenella) n. sp. B						+	+
Mytilus mabuchii Oyama and Mizuno			+	+			
Mytilus cf. luciferus Yokoyama				+			
Mytilus sp.			+	+			
Modiolus sp.				+	+		
Brachiodontes sp.						+	
Delectopecten ikushyunbetsuense (Utashiro)						+	+
Delectopecten sp.						+	+
Propeamussium kusiroense (Takeda)						+	+
Chlamys shitakaraensis Honda			+				
Lima (Acesta) sp., indet.						+	
Ostrea eorivularis Oyama and Mizuno	+	+	+	+	+	+	
Margaritifera sp.				+			
Anodonta subjapanensis yokoyamai Suzuki				+			
Cyclocardia takedai (Honda)							+
Cyclocardia yokoyamai (Oyama and Mizuno)					+	+	
Cyclocardia laxata (Yokoyama)					+	+	
Cyclocardia akagii (Kanehara)					+	+	+
Cyclocardia expansa (Takeda)					+	+	+
Cyclocardia tokudai (Takeda)					+	+	+
Cyclocardia orbica (Yokoyama)					+		
Cyclocardia tokunagai (Yokoyama)							+
Cyclocardia ezoensis (Takeda)						+	+
Cyclocardia sp.			+			+	+
Geloina cf. takaoi (Nagao and Otatume)			+				
Corbicula (Batissa) sitakaraensis Suzuki	+	+	+	+	+		
Corbicula (Corbicula) tokudai (Yokoyama)		+		+			
Corbicula (Corbicula) kotakai Honda		+					
Corbicula sp.		+	+		+		
Lucinoma hannibali (Clark)					+	+	
Lucinoma sp., indet.							+
Conchocele bisecta (Conrad)			+		+	+	
Conchocele nipponica (Yabe and Nomura)					+		
Nemocardium (Arctopratulum) ezoense Takeda			+		+		
Nemocardium (Arctopratulum) yokoyamai Takeda			+		+		
Nemocardium (Keenaea) iwakiense (Makiyama)					+		
Nemocardium sp.			+	+			
Clinocardium omagariense Honda					+		
Clinocardium sp.					+	+	+
Trachycardium kinsimarae (Makiyama)					+		
Laevicardium (Profulvia) harrimani (Dall)						+	
Laevicardium sp.							+
Hubertschenckia ezoensis (Yokoyama)			+				
Callista sp.			+				
Liocyma terrena (Yokoyama)						+	+
Liocyma furtiva (Yokoyama)							+
Clementia sp.							+
Mactra sp.			+				
Spisula (Mactromeris) sorachiensis Uozumi		+	+				
Spisula sp.			+				

SPECIES	RN	YB	SK	SB	OM	CH	NB
Macoma (Macoma) sejugata (Yokoyama)			+		+	+	+
Macoma (Macoma) optiva (Yokoyama)					+		
Macoma sp.			+		+	+	+
Peronidea sp.			+				
Siliqua sp., indet.						+	
Phaxas sp.						+	
Solen n. sp.			+				
Caryocorbula sp.							+
Mya (?Arenomya) grewingki grewingki Makiyama			+		+		
Mya (?Arenomya) grewingki kusiroensis Nagao and Inoue			+		+		
Mya sp.					+		
Myadora sp., indet.						+	
Periploma (Aelga) besshoense (Yokoyama)			+		+	+	+
Periploma (Aelga) ezoense Mizuno and Inoue			+				
Periploma sp.						+	
Periploma? sp.						+	
Thracia (Thracia) n. sp.			+				
Cardiomya (Cardiomya) n. sp.							+
Cardiomya (Cardiomya) makiyamai (Kanehara)					+		+
Cardiomya (Cardiomya) sp.						+	
"Minolia" funiculata (Yokoyama)						+	+
Machaeroplax eos (Hirayama)						+	
Turcicula (Ginebis) sakhalinensis (Takeda)							+
Turcicula sp.						+	+
Margarites makiyamai Hirayama							+
Margarites sp.							+
Bellamya (Sinotaia) mabutii (Suzuki)				+			
Cipangopaludina isikariensis (Suzuki)				+			
Orectospira wadana (Yokoyama)						+	+
Turritella (Hataiella) n. sp.						+	+
Turritella (Hataiella) poronaiensis Takeda					+	+	+
Turritella tokunagai Yokoyama					+	+	+
Turritella importuna Yokoyama						+	+
Turritella sp.			+		+	+	+
Semisulcospira fiscina yokoyamai Suzuki				+			
Melanoides? sp.				+			
Cerithidea ishikariensis Yokoyama?				+			
Neverita (Neverita) asagaiensis (Makiyama)			+		+		+
Neverita (Neverita) sp.			+	+		+	
Naticidae gen. et sp., indet.			+				+
Crepidula matajiroi Makiyama					+		
Crepidula sp.			+			+	
Colus sp.			+				
Trominina japonica (Takeda)						+	+
Trominina hokkaidoensis (Hayasaka and Uozumi)							+
Trominina ishikariensis (Hayasaka and Matsui)						+	+
Trominina umbelliformis (Hayasaka and Uozumi)						+	+
Trominina cf. umbelliformis (Hayasaka and Uozumi)						+	
Trominina sp.						+	+
Neptunea dispar Takeda						+	+
Neptunea ezoana Takeda					+		
Neptunea modestoidea Takeda			+		+	+	+
Neptunea n. sp.						+	
Siphonalia sp.					+		
Buccinum sp.						+	+
Molopophorus sp.							+
Priscofusus ishijimai Hirayama					+		
Fulgoraria (Musashia) antiquior (Takeda)						+	+
Fulgoraria sp.						+	
Riuguhdrillia rugosa (Takeda)					+	+	+
Eocylichna multistriata (Takeda)					+	+	+
Cylichna sp.						+	
Scaphanderidae gen. et sp., indet.							+
Dentalium (Fissidentalium) nunomae Takeda			+		+	+	+
Dentalium sp.			+		+	+	+
Makiyama chitanii (Makiyama)							+
Annelid tube					+		
Kewia sp.					+		
Balanus sp.			+		+		
Callianassa elongatodigitata Nagao						+	
Callianassa muratei Nagao						+	
Callianassa kusiroensis Nagao						+	
Callianassa sp.						+	+
Myophiuridae gen. et sp., indet.					+	+	
Fish scale						+	
Bryozoa			+				

Table 3. Occurrences of fossil mollusks in the Ishikari Group and the Poronai and Momijiyama Formations, Ishikari coal field, central Hokkaido (Shimokawara, 1963, *partly revised*). Ishikari Group: NK, Noborikawa Formation; HK, Horokabetsu F.; YR, Yubari F.; WK, Wakkanabe F.; BI, Bibai F.; AK, Akabira F.; IK, Ikushumbetsu F.; HR, Hiragishi F.; AS, Ashibetsu F.; PN, Poronai F.; MJ, Momijiyama F.

SPECIES	NK	HK	YR	WK	BI	AK	IK	HR	AS	PN	MJ
Solemya (Acharax) tokunagai Yokoyama										+	
Solemya (Acharax) cf. tokunagai Yokoyama				+							
Malletia poronaica (Yokoyama)										+	
Saccella hokkaidoensis Oyama and Mizuno				+				+		+	
Saccella cf. hokkaidoensis Oyama and Mizuno						+					
Saccella nagaoi (Takeda)				+		+				+	
Nuculana sp.										+	
Yoldia (Yoldia) laudabilis Yokoyama								+		+	
Yoldia (Yoldia) saitoi Uozumi				+						+	
Yoldia (Tepidoleda) sobrina Takeda										+	
Portlandia (Portlandella) watasei watasei*				+		+				+	
P. watasei ogasawarai Uozumi *(Kanehara)						+					
P. watasei semiovata Uozumi										+	
P. (Portlandella) ovata (Takeda)										+	
P. (Megayoldia) breviscapha (Yokoyama)				+							
P. (Megayoldia) cf. thraciaeformis (Storer)				+							
Nucula hokkaidoensis Mizuno and Inoue										+	
Acila (Truncacila) picturara (Yokoyama)										+	
Acila (Acila) shimoyamai Oyama and Mizuno						+					
Acila (Acila) elongata Nagao and Huzioka										+	+
Acila (Acila) brevis Nagao and Huzioka											+
Acila (Acila) sp.										+	
Glycymeris altoumbonata Nagao				+							
Glycymeris cf. cisshuensis Makiyama				+							
Modiolus sp.						+					
Brachiodontes sp.				+		+					
Mytilus mabuchii Oyama and Mizuno				+							
Mytilus sp.				+	+	+					
Delectopecten ikushyunbetsuense (Utashiro)										+	
Delectopecten poronaiense (Utashiro)										+	
Propeamussium kusiroense (Takeda)										+	
Chlamys ashiyaensis (Nagao)				+							
Lima (Acesta) jsuzukii Takeda										+	
Ostrea eorivularis Oyama and Mizuno						+					
Crassostrea sp.				+		+					
Margaritifera perdahurica (Yokoyama)	+	+	+		+	+		+	+		
Margaritifera otatumei Suzuki				+							
Unio uryuensis Suzuki	+	+	+			+		+	+		
Inversidens isikariensis Suzuki						+					
Lanceolaria pisciformis (Yokoyama)	+	+	+			+	+	+	+		
Hyriopsis mabutii Oyama								+			
Lepidodesma septemtrionale Suzuki			+								
Cristaria sasai Suzuki *Minato and Kumano						+					
Anodonta subjapanensis (Yokoyama)	+	+	+			+		+			
A. subjapanensis yokoyamai Suzuki	+	+	+			+		+			
Crassatellites (Eucrassatella) yessoensis*				+		+		+			
Crassatellites teshimai Inoue and Mizuno										+	
Venericardia (Venericardia) otatsumei Uozumi				+		+					
Venericardia (Venericor) subnipponica Nagao				+		+					
Cyclocardia yokoyamai (Oyama and Mizuno)										+	?
Cyclocardia akagii (Kanehara)										+	+
Cyclocardia tokudai (Takeda)										+	
Cyclocardia momijiyamaensis (Masuda and Noda)											+
Cyclocardia tokunagai (Yokoyama)										?	+
Cyclocardia hobetsuensis (Hayasaka and Uozumi)											+
Cyclocardia ezoensis (Takeda)										+	
Cyclocardia satisparva (Mizuno and Inoue)										+	

SPECIES	NK	HK	YR	WK	BI	AK	IK	HR	AS	PN	MJ
Geloina takaoi (Nagao and Otatume)				+		+					
Geloina bibaiensis (Nagao and Otatume)				+							
Geloina hokkaidoensis (Nagao and Otatume)				+		+		+			
Corbicula (Cyrenobatissa) sunagawaensis*				+		+		+			
C. (Cyrenobatissa) muratai (Nagao and Otatume)				+		+					
C. (Corbicula) tokudai (Yokoyama)			+	+	+	+	+	+	+		
Claibornites quinquangulus Uozumi				+							
Anodontia poronaiensis (Yokoyama)										+	
Anodontia sp. * *Nagao and Otatume*				+		+					
Conchocele bisecta omarui (Oyama and Mizuno)						+				+	
Nemocardium (Arctopratulum) yokoyamai Takeda										+	
Nemocardium sp.						+					
Pitar cf. kyushuensis (Nagao)				+							
Pitar sorachiensis Oyama and Mizuno				+							
Pitar matsumotoi (Nagao)				+							
Callista matsuraensis (Nagao)				+		+		+			
Callista hanzawai (Nagao)				+						+	
Hubertschenckia ezoensis (Yokoyama)											
Dosinia sp.				+							
Cyclina sp.				+							
"Paphia" munroei Yokoyama				+		+		+			
Merisca onishii Inoue and Mizuno				+					+	+	
Macoma sp.				+		+				+	
Angulus (Tellinides) maximus (Nagao)				+		+			+		
Lutraria sp.				+							
Nuttallia sp.				+							
Spisula (Mactromeris) sorachiensis Uozumi				+							
Siliqua sp.				+							
Cultellus izumoensis Yokoyama				+							
Solen sp.				+		+			+		
Mya (?Arenomya) ezoensis Nagao and Inoue				+		+		+			
Pholadomya sp.				+						+	
Thracia sp.				+						+	
Periploma (Aelga) besshoense (Yokoyama)				+		+		+		+	+
Periploma (Aelga) ezoense Mizuno and Inoue										+	
Cuspidaria sp.										+	
"Minolia" funiculata (Yokoyama)										+	
Bellamya (Sinotaia) uryuensis (Yokoyama)					+	+		+	+		
Bellamya (Sinotaia) mabutii (Suzuki)									+		
Cipangopaludina isikariensis (Suzuki)									+		
Cipangopaludina soratiensis Oyama								+			
Cipangopaludina jimboi (Suzuki)	+	+	+		+	+	+	+	+	+	
Orectospira wadana (Yokoyama)								?		+	+
Orectospira shimokawarai Urata										+	
Turritella (Hataiella) poronaiensis Takeda										+	
Semisulcospira fiscina (Yokoyama)						+		+			
Semisulcospira fiscina yokoyamai Suzuki						+					
Melanoides otatumei Suzuki								+			
Clathrus cf. submaculosus (Nagao)										+	
Cirsotrema (Cirsotremopsis?) sp.						+		+			
Neverita asagaiensis (Makiyama)										+	
Neverita sp.				+				+			
Euspira sp.										+	
Lunatia sp.				+		+					
Polinices sp.				+		+					
Calyptraea sorachiensis Oyama and Mizuno				+							
Crepidula sp.										+	
Colus aff. fujimotoi Hirayama										+	
Beringius hobetsuensis (Matsui)											+
Trominina angasiana yubariensis*											+
Trominina japonica (Takeda) *(*Hayasaka and Matsui*)										+	
Trominina hokkaidoensis (Hayasaka and Uozumi)											+
Trominina ishikariensis (Hayasaka and Matsui)											+
Trominina umbelliformis (Hayasaka and Uozumi)											+
Neptunea modestoidea Takeda										+	
Siphonalia sakakurai Mizuno				+		+					
Siphonalia ishikariana Oyama and Mizuno				+		+					
Buccinum sp.						+				+	
Molopophorus cf. kusiroensis Takeda				+						+	
Turicla japonica Takeda										+	
Fulgoraria (Musashia) antiquior (Takeda)										+	
Trigonostoma? (Scalptia?) sp.				+		+					
Nekewis sekii (Mizuno)						+					
Eocylichna multistriata (Takeda)				+						+	
Olivella sp.										+	
Dentaliun (Fissidentalium) nunomae Takeda										+	
Dentalium sp.				+						+	

It is noteworthy that *Nemocardium ezoense* and *O. eorivularis* occur together in gray poorly sorted fine-grained sandstone bearing pebbles and granules of the Shitakara Formation. The former occurs in large numbers in sandstone, and the latter occurs where pebbles are closely packed in sandstone.

Molluscan fossils occur sporadically in gray siltstone of the Charo and Nuibetsu Formations, and closely packed in groups in gray fine-grained sandstone or silty sandstone of the Omagari Formation, often parallel with the stratification. These modes of occurrence suggest that they are autochtonous or only slightly allochtonous assemblages.

It is remarkable that these faunas contain many cold water genera such as *Portlandia, Yoldia, Cyclocardia, Mya, Neptunea, Buccinum, Clinocardium, Conchocele, Liocyma, Margarites,* etc., which are widespread today in the northern Pacific. *Neverita* (*Neverita*) is essentially a northern temperate subgenus and lives in temperate and arctic waters of the eastern Pacific and elsewhere (Marincovich, 1977). On the other hand, there are a few warm water forms, including *Geloina* cf. *takaoi* (Nagao and Ōtatume).

Clinocardium and *Neptunea* are considered to have originated during the Oligocene in North Japan and Sakhalin (Kafanov, 1974; Nelson, 1978), and *Mya* during the late Eocene or early Oligocene in Japan (MacNeil, 1965). Furthermore, *Conchocele bisecta* is one of the earliest representatives of the genus, which appeared during the Oligocene in the northern Pacific.

These faunas contain several species that range into the Miocene of Japan, including *Portlandia watasei, Conchocele bisecta, C. nipponica,* etc., and *C. bisecta* and *Portlandia* (*Megayoldia*) *thraciaeformis* (Storer), species that still live in the northern Pacific. Furthermore, the faunas have several species in common with the faunas of other Paleogene strata of northern Japan, including *Yoldia laudabilis, Portlandia watasei, Cyclocardia tokunagai* (Yokoyama), *Periploma besshoense,* etc., and some related to or in common with species in the faunas of Northwest America, including *Cyclocardia laxata, C. tokunagai, Laevicardium harrimani, Conchocele bisecta, Yoldia laudabilis, Neverita asagaiensis, Turritella importuna, T. tokunagai,* etc. (Hatai and Kamada, 1950).

On the other hand, these faunas have a few species in common with those of Paleogene strata of Kyushu, southern Japan. They are *Y. laudabilis, Y.* (*Tepidoleda*) *sobrina* Takeda, *Periploma besshoense,* and *Orectospira wadana,* which are typical representatives of the Poronaian fauna, and in Kyushu are restricted to the Nishisonogian Stage (Mizuno, 1964a).

Y. laudabilis was essentially a cold-water species, which lived on upper neritic fine sand bottoms, as is shown by its occurrence predominantly in sandy rocks and only rarely in muddy ones in northern Japan, whereas it only occurs in muddy rocks of southern Japan, being associated with cold-water species (Mizuno, 1954). In Kyushu, the molluscan fauna in sandy rocks is represented by *Crassatellites* (*Eucrassatella*) *yabei* Nagao, *Glycymeris "cisshuensis* Makiyama", *Septifer nagaoi* Oyama, etc., replacing *Y. laudabilis* in northern Japan (Mizuno, 1954).

Based on the frequency of the number of individuals, a total of nine molluscan assemblages is discriminated in the Urahoro Group, 16 in the Omagari Formation, and 14 in the Charo and Nuibetsu Formations. These assemblages are:

Urahoro Group

Corbicula tokudai assemblage
Corbicula (*Batissa*) *sitakaraensis* assemblage
Ostrea eorivularis assmblage
Nemocardium ezoense assemblage
Chlamys shitakaraensis assemblage
Yoldia laudabilis assemblage
Portlandia watasei assemblage
Cyclocardia assemblage
Mya grewingki kusiroensis assemblage

Omagari Formation

Clinocardium omagariense assemblage
Clinocardium assemblage
Nemocardium ezoense assemblage
Cyclocardia tokudai assemblage
Portlandia watasei-Clinocardium omagariense assemblage
Portlandia watasei-Yoldia laudabilis assemblage
Cyclocardia expansa assemblage
Cyclocardia laxata-Acila brevis assemblage
Acila brevis-Cyclocardia tokudai assemblage
Acila brevis assemblage
Conchocele bisecta assemblage
Mya grewingki assemblage
Neptunea ezoana assemblage
Corbicula (*Batissa*) *sitakaraensis* assemblage
Ostrea eorivularis assemblage
Yoldia laudabilis assemblage

Charo and Nuibetsu Formations

Cyclocardia ezoensis assemblage
Cyclocardia expansa assemblage
Cyclocardia assemblage
Turritella-Cyclocardia assemblage
Turritella poronaiensis assemblage
Turritella tokunagai assemblage
Turritella assemblage
Dentalium assemblage
Portlandia watasei assemblage
Portlandia watasei-Cyclocardia assemblage
Orectospira wadana assemblage
Eocylichna multistriata assemblage
Clinocardium assemblage
Yoldia laudabilis assemblage

Table 4. Species in common with other regions where the Poronaian fauna (or correlative faunas) have been reported. 1, Matchgar, northern Sakhalin (Makiyama, 1934); 2, Maoka Series (Oligocene), southern Sakhalin (Takeda, 1953); 3, Mallenian Stage (Oligocene) of the Koryak Upland, eastern USSR, northern Pacific (exclusive of gastropods and scaphopods; Volobueva, 1980); 4, Momijiyama Formation (Shimokawara, 1963); 5, Tappu Group (Ohara, 1966); 6, Ombetsu Group (Table 2); 7, Asagai Formation, Joban coal field, Northeast Japan (Kamada, 1962); 8, Muro Group of Kii Peninsula, Southwest Japan (Mizuno, 1973); 9, Nishisonogian Stage of Kyushu (Mizuno, 1964a).

SPECIES	1	2	3	4	5	6	7	8	9
Malletia poronaica					+	+		+	
Yoldia laudabilis	+	+			+	+	+	+	+
Yoldia saitoi								+	
Yoldia sobrina					+	+		+	+
Portlandia watasei watasei			+		+	+		+	
Portlandia ovata					+	+			
Acila picturata					+	+			
Acila elongata				+		+		+	
Acila brevis				+	+	+			
Delectopecten ikushyunbetsuense						+			
Propeamussium kusiroense					+	+			
Cyclocardia yokoyamai					+	+			
Cyclocardia akagii				+	+	+		+	
Cyclocardia tokudai					+	+			
Cyclocardia ezoensis		+				+			
Cyclocardia satisparva					+				
Nemocardium yokoyamai					+	+			
Hubertschenckia ezoensis					+				
Periploma besshoense		+	+	+	+	+	+		+
Orectospira wadana		+		+	+	+		+	+
Orectospira shimokawarai					+				
Turritella poronaiensis						+			
Neverita asagaiensis	+				+	+	+		
Trominina japonica						+			
Neptunea modestoidea		+			+	+			
Fulgoraria antiquior		+				+			
Eocylichna multistriata		+				+			
Dentalium nunomae		+			+	+			

Some of the molluscan assemblages discriminated in the Urahoro and the Ombetsu Groups are similar to those of the Asagai Formation in the Joban coal field, Northeast Japan, including the *Pitar-Dentalium*, the *Acila-Venericardia*, the *Clinocardium-Turritella*, the *Papyridea-Mya*, and the *Mya-Turritella* assemblages (Nemoto and O'Hara, 1979). They are also similar to the "C assemblage", characterized by *Portlandia watasei*, *Yoldia laudabilis*, *Cyclocardia tokunagai*, *Trominina japonica* (Takeda), and *Fulgoraria* (*Musashia*) *prevostiana* (Crosse), found on mud bottoms at a depth of about 200 m in the Setogawa Stage, Shizuoka Prefecture, Central Japan (Iwasaki and Ono, 1977).

There are several species in the Ishikari Group in common with the Paleogene strata of Kyushu, southern Japan, including *Venericardia* (*Venericor*) *subnipponica* Nagao, *Pitar matsumotoi*, *Callista matsuraensis* (Nagao), *C. hanzawai* (Nagao), *Angulus maximus* (Nagao), etc. There are many warm water genera in the Ishikari Group, including *Glycymeris*, *Pitar*, *Dosinia*, *Cyclina*, *Venericor*, *Geloina*, etc., as well in the Eocene strata of the Koryak Upland, eastern USSR, northern Pacific, including *Pacificor*, *Crassatella*, *Eucrassatella*, etc. (Volobueva, 1980). In contrast, cool sea temperatures are suggested by the many species of *Cyclocardia* in the Poronai Formation as well as in the Ombetsu Group and in the Oligocene strata of the Koryak Upland, which yielded *Cyclocardia tokunagai* (Yokoyama), *C. laxata*, *Laevicardium harrimani*, *Periploma besshoense*, etc. (Volobueva, 1980).

Several taxa are common to the Momijiyama Formation and the Poronai Formation, including *Acila elongata*, *Cyclocardia akagii*, *Periploma besshoense*, *Orectospira wadana*, and *Trominina* (Table 3), and the Momijiyama Formation is here assigned an Oligocene age rather than a Miocene one. Species common to other regions where the Poronaian fauna (or correlative faunas) have been recorded are shown in Table 4.

Concluding Remarks

The Ishikarian fauna, especially the lower Ishikarian fauna, is composed of many warm water forms, including *Glycymeris, Pitar, Dosinia, Cyclina, Venericor, Geloina,* etc. In contrast, the Poronaian fauna is similar to those of other areas bordering the northern Pacific, including Sakhalin and Kamchatka, and there are some species related to those of Northwest America (Hatai and Kamada, 1950). But there are only relatively few Poronaian species in common with those of Kyushu, where they are restricted to the Nishisonogian Stage (Table 4).

The Poronaian fauna is characterized by many cold water genera, including *Portlandia, Yoldia, Cyclocardia, Mya, Neptunea, Buccinum, Clinocardium, Conchocele, Liocyma, Margarites,* etc., which are widespread at present in the northern Pacific. This fact is consistent with occurrences of a temperate pollen flora in the Poronai Formation (Sato, 1970) and a cool-temperate one in the Ombetsu Group (Sato, 1984).

There are no Eocene species in the Koryak Upland in common with those of Japan and Sakhalin; however, several are common to the Koryak Upland and Northwest America; and many Oligocene species are common to the Koryak Upland, Japan, and Sakhalin, although only a few Oligocene species are common to these areas and Northwest America (Volobueva, 1980). Eocene molluscan faunas in Hokkaido, as a whole, seem to be more allied to those of Kyushu, southern Japan, than to those of Kamchatka and Northwest America, since there are several species in the Ishikari Group in common with Kyushu.

However, Oligocene faunas of Hokkaido are similar to those of Kamchatka and Northwest America; there are many species in the Poronaian fauna in common with or related to those of Kamchatka and Northwest America.

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Plate 1

Explanation of Plate 1

(All figures at natural size, unless otherwise stated)

Fig. 1. *Delectopecten ikushyunbetsuense* (Utashiro)
Nuibetsu Formation, x 2.

Figs. 2a–c. *Acila* (*Acila*) *kusiroensis* Nagao and Huzioka
IGPS* coll. cat. no. 97124, Nuibetsu Formation.

Fig. 3. *Yoldia* (*Tepidoleda*) *sobrina* Takeda
IGPS coll. cat. no. 97115, Charo Formation.

Fig. 4. *Cyclocardia ezoensis* (Takeda)
Charo Formation.

Figs. 5a–c. *Portlandia* (*Portlandella*) *watasei watasei* (Kanehara)
IGPS coll. cat. no. 97126, Charo Formation.

Figs. 6a–c. *Clinocardium omagariense* Honda
IGPS coll. cat. no. 95729, Omagari Formation.

Fig. 7. *Propeamussium kusiroense* (Takeda)
IGPS coll. cat. no. 97097, Charo Formation, x 2.

Fig. 8. *Portlandia* (*Megayoldia*) *thraciaeformis* (Storer)
IGPS coll. cat. no. 97109, Nuibetsu Formation, x 2.

Fig. 9. *Conchocele bisecta* (Conrad)
IGPS coll. cat. no. 97112, Omagari Formation.

Figs. 10a–b. *Corbicula* (*Batissa*) *sitakaraensis* Suzuki
IGPS coll. cat. no. 96764, Shakubetsu Formation.

Figs. 11a–b. *Orectospira wadana* (Yokoyama)
IGPS coll. cat. no. 97130, Charo Formation, x 2.

Figs. 12a–b. *Turritella* (*Hataiella*) *poronaiensis* Takeda
IGPS coll. cat. no. 96781, Charo Formation.

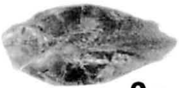
Figs. 13, 14. *Dentalium* (*Fissidentalium*) *nunomae* Takeda
13. IGPS coll. cat. no. 97129, Charo Formation, x 2.
14. IGPS coll. cat. no. 97177, Charo Formation, x 2.

*Abbreviation for the Institute of Geology and Paleontology, Tohoku University, Sendai, Japan.


1


2a


2b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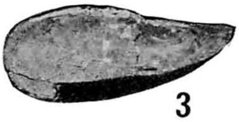
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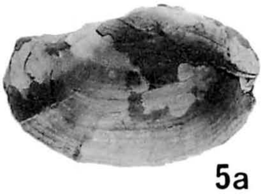
5a


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6a

6b


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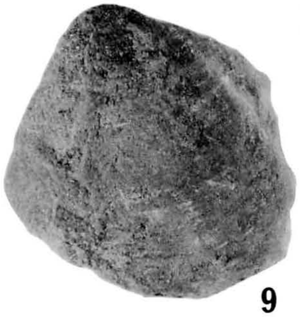
8


6c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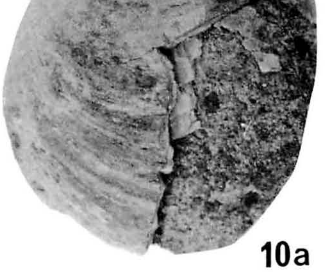
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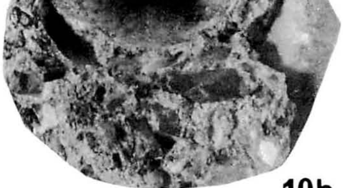
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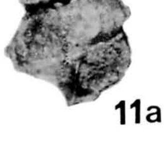
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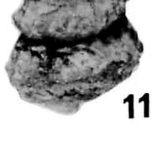

11b


12a


12b


13


14

Plate 2

Explanation of Plate 2

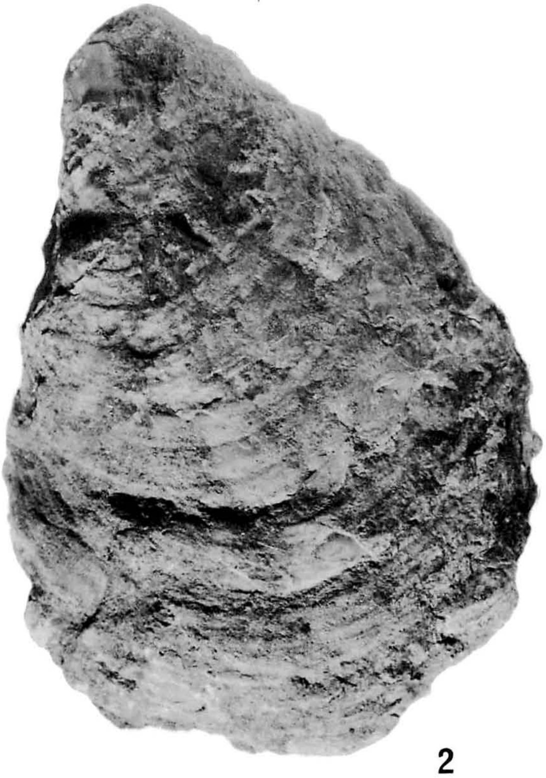
(All figures at natural size, unless otherwise stated)

Fig. 1. *Mytilus mabuchii* Oyama and Mizuno
IGPS coll. cat. no. 96777, Shakubetsu Formation.

Fig. 2. *Ostrea eorivularis* Oyama and Mizuno
Shitakara Formation.

Fig. 3. *Corbicula* (*Corbicula*) *tokudai* (Yokoyama)
IGPS coll. cat. no. 96778, Shakubetsu Formation, x 1/2.

1



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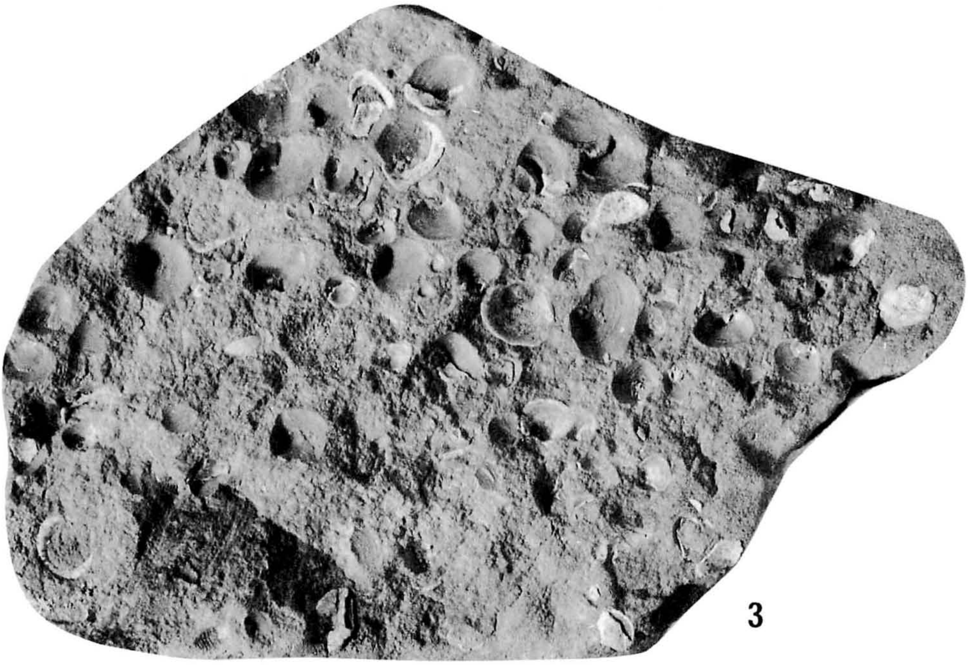


3

FAUNAL SUCCESSION AND GEOGRAPHIC DISTRIBUTION OF NEOGENE MOLLUSCAN FAUNAS IN JAPAN

By

Kiyotaka CHINZEI

Introduction

Microbiostratigraphy of marine deposits containing molluscan fossils has greatly advanced since I outlined the stratigraphic and geographic distributions of the Japanese Neogene molluscan faunas (Chinzei, 1978). This sheds a new light on marine paleobiogeography during the Neogene in and around the Japanese Islands. Based on new biostratigraphic frameworks for Paleogene (Saito et al., eds., 1984) and Neogene (Tsuchi, ed., 1979, 1981; Tanai, ed., 1982) deposits, I will recapitulate the stratigraphic and geographic distributions of Japanese Neogene molluscan faunas.

In his synthesis of Cenozoic marine and terrestrial faunas in Japan, Otuka (1939) recognized two or three marine faunal provinces and described different faunal sequences for each one. Many of the faunal names now used by Japanese paleontologists were proposed by him in this paper. Most later works on Japanese Neogene mollusks are geographically or stratigraphically limited except for biostratigraphic studies on particular taxonomic groups. The Neogene faunal succession in Hokkaido was summarized by Uozumi (1962), and that in northern Honshu was discussed by Kotaka (1958) and Chinzei (1963). Iwasaki (1970) described the distribution of a shallow marine fauna (Shiobara type fauna) in the Middle Miocene in central and northern Honshu. Tropical aspects of early Middle Miocene mollusks in the Japan Sea coast areas were first noticed by Oyama (1950) and have been discussed by Tsuda and his co-workers (e.g., Tsuda et al., 1981). Ogasawara (1981) summarized a Plio-Pleistocene molluscan fauna (Omma-Manganji fauna) in the Japan Sea coast areas and discussed its possible origin. Compositions of late Neogene faunas and their geographic distribution in the Pacific coast of Southwest Japan have become clear through studies by Tsuchi (1960), Shuto (1961) and others. The molluscan fauna and paleogeography of the Setouchi Province, an inland sea area in Southwest Japan during the early Middle Miocene, have been summarized by Itoigawa and Shibata (1973), and Shibata and Itoigawa (1980). I presented a general picture of historic and geographic changes of Neogene molluscan faunas in Japan based on ecologic characters of the faunal constituents, and their local and regional distributions (Chinzei, 1978). Summaries of stratigraphic and geographic distributions of Neogene faunas were also given by Masuda (1973), and by Tsuchi and Shuto (1984) who discussed them in relation to regional molluscan history in the West Pacific. Many other works concerning the ecology and biogeography of Japanese Neogene mollusks are cited herein.

Temporal Parallelism of Molluscan Associations and Paleobiogeographic Province

Neogene deposits in Japan contain abundant and diverse molluscan faunas. The nature and stratigraphic distributions of the faunas are primarily controlled by depositional history, which reflects regional and local tectonic events. The molluscan faunas change remarkably in accordance with a cyclic change of sedimentary facies. The cycle began with rapid transgression in the early Middle Miocene followed by a gradual latest Miocene to Recent regression. Also, the respective waxing and waning of warm and cold water current systems directly influenced faunal composition throughout the Neogene.

Molluscan associations of similar composition repeatedly appeared at different times and in geographic areas where similar environmental conditions prevailed. Similarity of generic composition is remarkable among the shallow water and embayment faunas of different ages. The comparable associations usually consist of the same or allied genera, but are different in species composition. The ecologic similarity seen among these comparable associations was named temporal parallelism by Chinzei (1984), compared with the geographic parallelism seen in coeval associations from different geographic areas.

The similarities of composition indicate that these parallel associations had analogous ecologic structures. The changes in species composition might have resulted from: 1) evolutionalry change induced by discontinuous changes within their environments and resultant isolation, or 2) competitive replacement of the preoccupied species by new immigrants from the north or south (Chinzei, 1984). Both imply biogeographic changes of regional scale in Japanese waters. On a smaller stratigraphic scale, faunas of identical species composition occur at coeval stratigraphic horizons over broad areas. The respective distribution area of these faunas indicates a paleobiogeographic province.

My ecologic and paleobiogeographic division of Japanese Neogene molluscan faunas is based on the phenomena of temporal and geographic parallelisms. Based on the reoccurrence of ecologically analogous associations the historical changes of Neogene molluscan faunas in Japan can be divided into four phases. The four phases are, Early Miocene (before 16.5 Ma ago), early Middle Miocene (c.16.5 – 15 Ma ago), Middle and Late Miocene (c.15 – 5 Ma ago), and Pliocene to early Pleistocene (5 – 1 Ma ago). Late Pleistocene to Recent may be regarded as the fifth phase of molluscan history in Japan. The molluscan faunas in each phase consist of both warm and cold water taxa, and exhibit geographically parallel relationships.

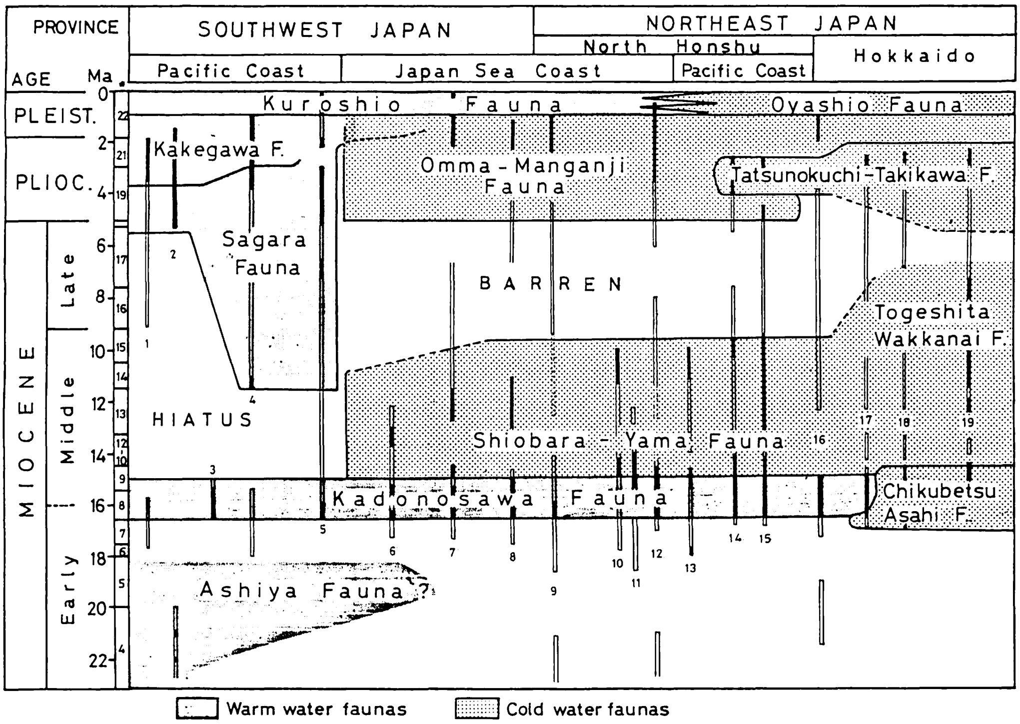
In Japan, a molluscan fauna of distinct species composition and wide geographic distribution has usually been named after a local geographic name of the area where the fauna is typically observed. Such a fauna is usually limited in stratigraphic range and so has presumed biostratigraphic importance. An interval containing the fauna is sometimes used as a biostratigraphic unit. However, it is more productive and useful for these molluscan faunas of benthic nature to primarily have a biogeographic value. The distribution of a fauna represents a zoogeographic province both in time and space. In this paper, a fossil fauna is named and defined so as to include the molluscs that lived in one biogeographic province, irrespective of their local environments.

Revision of Geologic Ages of Japanese Neogene Molluscan Faunas

Chronologic and geographic distributions of Japanese Neogene and Quaternary molluscan faunas are summarized in Fig. 1. The figure gives a revised version of my previous conclusions (Chinzei, 1978, Fig. 8).

The Ashiya fauna was formerly placed in the Early Miocene based mainly on its similarity of generic composition to Miocene and later faunas, as well as on some fragmentary information from accompaning planktonic fossils. Recent biostratigraphic studies of the Ashiya Group in northern Kyushu, the type area of the fauna, showed that most of the Group contains planktonic foraminifera and calcareous nannoplankton characteristic of the Oligocene (Tsuchi et al., 1983; Saito and Okada, 1984). According to these works the lower part of the Group is assigned to the lower Oligocene and the middle and upper parts to the upper Oligocene. Molluscan assemblages similar to those of the Ashiya Group are known from several localities on the Pacific coast of central and Southwest Japan. Except for the molluscs themselves there is no biostratigraphic nor radiometric age control. However, some of the assemblages may range into the Early Miocene as discussed later.

The cold water Asahi fauna of central Hokkaido has been distinguished from the early Middle Miocene Chikubetsu fauna mainly on differences in species composition, and has been assigned an Early Miocene age. However, the stratigraphic position of the Asahi fauna in the type area is very close to the overlying early Middle Miocene horizon (Uozumi, 1966; Sato, 1970). Also, some characteristic species of the fauna was recently found intermingled with the overlying early Middle Miocene fauna (see Chinzei, in this volume, p. 000). In this paper, I follow the opinion of Ogasawara et al. (1982) and others that the Asahi fauna may be placed in the early Middle Miocene.



Text-fig. 1. Succession and geographic distribution of Japanese Neogene molluscan faunas. Vertical columns shown in the figure indicate the principal stratigraphic sections in which the molluscan faunas were found (black part). *: planktonic foraminiferal zones (Tsuchi, ed., 1981). Areas of columnar sections: 1: Okinawa Islands; 2: Miyazaki area; 3: Mizunami area; 4: Kakegawa area; 5: Miura-Boso area; 6: Shimane area; 7: Fukui-Kanazawa area; 8: Toyama area; 9: Niigata area; 10: Ou Range; 11: Dewa Hills; 12: Oga Peninsula; 13: Northern Kanto area; 14: Sendai area; 15: Kadonosawa area; 16: Oshima Peninsula; 17: Hidaka area; 18: Chikubetsu area; 19: Tenpoku area.

Accordingly, the main part of the molluscan faunas formerly assigned to the Early Miocene have now been assigned to older or younger stratigraphic horizons. Thus results in a large Early Miocene hiatus in the molluscan succession of Japan.

The second major correction to my former synthesis is in the stratigraphic position of the middle Middle and Late Middle and Late Miocene Shiobara-Yama fauna of North Japan and the Japan Sea coast. I formerly thought that there was a barren of megafossils between the horizon of early Middle Miocene warm water molluscs, the Kadonosawa fauna, and that of the Shiobara-Yama fauna. This conclusion was drawn from some indirect evidences, for example that the fauna was known from sandy strata overlying Middle Miocene siliceous shale in the Ou Range of northern Honshu and in the San-in area of Southwest Japan.

Recent microbiostratigraphic evidence suggests that the shale in the Ou Range only represents a short interval of the early Middle Miocene, and that the mollusc-bearing beds themselves fall within the earlier half of the Middle Miocene (e.g., Okada, 1981). Occurrence of planktonic microfossils with molluscs in other areas also show that all the known horizons of the Shiobara-Yama fauna, including that of the Fujina Formation of San-in area (Nomura, 1984) may be assigned to the middle Middle Miocene. In some areas the Shiobara-Yama molluscs are found immediately above the early Middle Miocene Kadonosawa fauna.

Thus, the existence of a large faunal break has become apparent in the Late Miocene of Honshu Island, particularly in the areas of the Japan Sea coast. The faunal break correspond to the horizon of Late Miocene siliceous sediments ubiquitously distributed in the Japan Sea coast areas, and to a hiatus or horizon of low sedimentation rate found within the shale (Niitsuma, 1978). Offshore molluscan species comparable to those of the Yama fauna are only known from some Late Miocene mudstone in norhtern Hokkaido, and have been called the Wakkanai fauna.

Early Miocene Phase

The Ashiya fauna in north Kyushu has been regarded to represent the Early Miocene phase of the faunal succession in the Neogene of Japan (e.g., Chinzei, 1978). However, as discussed above, the type section of the fauna was now assigned to Oligocene based on up-dated biostratigraphy of planktonic microfossils. No other occurrence of molluscs which are evidently Early Miocene is known in Japan.

The Ashiya fauna in the Ashiya Group is characterized by *Glycymeris cisshuensis. Dosinia chikuzenensis, Pitar matsumotoi, Venericardia subnipponica, Acila ashiyaensis, Angulus maximus* and others. The fauna is thought to be subtropical. In the Miyazaki area of south Kyushu, the upper part of the Nichinan Group yields molluscs common to the Ashiya fauna, such as, *Glycymeris cisshuensis, Acila ashiyaensis, Angulus maximums* and some others, in association with some planktonic foraminifers characteristic to Oligocene to Early Miocene (Shuto, 1963). Also, some molluscs of the Ashiya elements have been known from the basal part of the Hikokubo Group in the Chichibu Basin, central Japan (Kanno, 1960). The group has been placed at around Blow's (1969) N.7 zone (Tsuchi, ed., 1981). These occurrences of the Ashiya elements suggest a possibility that the stratigraphic range of the fauna extends upwards to Early Miocene.

The Early Middle Miocene Phase

Neogene transgression began in the early Middle Miocene in the Japanese Islands. In most parts of Southwest Japan, marine sediments of this age lie directly upon Mesozoic or Paleozoic sedimentary and granitic rocks. In North Japan, the sediments overlie terrestrial or partly aquatic volcanic rocks of early Miocene or older ages that are generally called Green Tuff.

The early Middle Miocene sediments mainly consist of shallow marine sandy and muddy facies containing abundant molluscs and other fossils. The molluscan fauna is characterized by the predominance of tropical and subtropical species, most of which occur only in this horizon. The warm water species are distributed as far north as central Hokkaido, to the present latitude of 44°N. Microbiostratigraphic and radiometric data suggest that sediments containing this warm water fauna fall within the range of the N.8 and N.9 zones, about 16.5 to 15 Ma ago. A cold water fauna of this age is known only in northern and eastern Hokkaido.

The warm water fauna of this horizon has been called the Kadonosawa fauna (Otuka, 1939). The fauna has also been called the Yatsuo or the Yatsuo-Kadonosawa fauna. Yatsuo is a local name in Toyama, central Japan, where the occurrence of tropical molluscs was first noticed in the Kurosedani Formation (Oyama, 1950). The cold water fauna of this age is named the Chikubetsu fauna (Uozumi, 1962). Both warm and cold faunas are composed mainly of shallow marine molluscan associations ranging from intertidal to upper sublittoral facies.

A strictly tropical molluscan fauna is found in Southwest Japan, mainly in the Japan Sea coast areas and in the Setouchi Province, an inland marine basin passing through the central part of Southwest Japan. They are not know along the Pacific coast except for Tanegashima Island in nothern Ryukyus, and southern Kyushu. The tropical elements appear in both intertidal and sublittoral associations. An intertidal association found in the inner bay muddy sand is composed of the bivalves *Geloina stachi, G. yamanei, Anadara daitokudoensis,* the gastropod *Telescopium schencki, Cerithidea yatsuoensis, Littorinopsis miodelicatura, Ellobium yatsuoensis* and other species. Generic composition of the association is quite similar to that of present-day mangrove swamp communities (Oyama, 1950; Itoigawa, 1978; Tsuda et al., 1981, 1984), and the sediments contain pollen of a mangrove flora (e.g., Yamanoi et al., 1980). Sublittoral sandy associations in the Setouchi Province are typically composed of *Dosinia suketoensis, Katelysia nakamurai, Tapes siratoriensis, "Vasticardium" ogurai, Soletellina minoensis, Crassostrea gravitesta* and many other species (Itoigawa, 1971; Itoigawa and Nishikawa, 1976), although species composition varies considerably among localities. This association includes species thought to be tropical, such as *Globularia nakamurai, Rimella toyamaensis, Volema osawanoensis, Tectus japonica, Turbo minoensis, Maoricardium mizunamiensis,* etc. (Itoigawa and Tsuda, 1984). At some localities, these molluscs are accompanied by the cephalopod *Aturia minoensis* (e.g., Kobayashi and Horikoshi, 1958). The generic composition of this early Middle Miocene tropical fauna in Southwest Japan is comparable to that of the present-day Philippine Islands or further south (Horikoshi, 1981; Tsuda et al., 1984).

Another intertidal association is found at nearby localities to the *Geloina – Telescopium* association, and is characterized by *Vicarya callosa japonica, V. yokoyamai, Vicaryella notoensis, Batillaria yamanarii, Anadara daitokudoensis, Saxolucina khatail, Cyclina japonica* or *C. lunulata* and some others. This type of intertidal association occurs as far north as northern

Honshu.

The early Middle Miocene Kadonosawa fauna in North Japan is composed principally of the intertidal *Vicarya* spp. – *Anadara daitokudoensis* association, and sublittoral *Dosinia nomurai* – *Anadara ninohensis* association. The *Dosinia nomurai* – *A. ninohensis* association contains *Tapes siratoriensis, Glycymeris cisshuensis, Meretrix arugai* and other bivalves, along with some gastropods (refer to Chinzei, in this volume, p. 000). A pectinid association composed mainly of *Nanaochlamys notoensis, Cryptopecten yanagawaensis, Chlamys arakawai, Placopecten akihoensis,* and *Kotorapecten kagamianus,* is known from several localities in northern Honshu (e.g., Masuda, 1962). The Kadonosawa fauna in North Japan is considered to represent subtropical conditions. It lacks mangrove swamp species and other strictly tropical elements, although most of its species are known in Southwest Japan in association with some tropical species. The intertidal association is distributed in northern Honshu and southwestern Hokkaido: while the sublittoral elements appear in central Hokkaido. In central Hokkaido, the species of the Kadonosawa fauna are found intermingled with, or stratigraphically very close to cold water molluscs.

The early Middle Miocene molluscan fauna of northern and central Hokkaido differs strongly from the Kadonosawa fauna of northern Honshu by being composed of species of temperate or subarctic origin. In northern and central Hokkaido, different cold water molluscan faunas have been described and named separately. The Asahi fauna is known from the Horomui Formation, the basal part of the Neogene sequence in the Asahi area of the Ishikari Coalfield (Uozumi, 1962). It was once placed at the latest Early Miocene and treated as a distinct fauna representing cold water condition (Chinzei, 1978). In the type area, however, the upper part of the formation is contemporaneous with the horizon in which the early Middle Miocene Kadonosawa fauna appears (Uozumi, 1966; Sato, 1972). Also a comparable fauna in the Sankebetsu Formation of the Chikubetsu area has been recognized to be very close in species composition to that in the overlying Chikubetsu Formation (Ogasawara et al., 1982).

The sandy facies of the Sankebetsu and Chikubetsu Formations yields *Peronidia elongata, Spisula onnechiuria, Mercenaria chitaniana, Clinocardium* spp., *Tectonatica ezoana* and others. Many of these species are also found in the Asahi fauna. The Asahi and Sankebetsu faunas characteristically have *Mytilus tichanovitchi.* The fauna in the Chikubetsu Formation also contains *Macoma optiva, Anadara watanabei, Dosinia yamaguchie, Neptunea oomurai,* etc. Offshore taxa including *Portlandia tokunagain, P. watasei, Acila elongata* are found in the muddy facies of the Horomui Formation. All of these molluscs are thought to represent a narrow stratigraphic interval of the early Middle Miocene.

An association dominated by *Portlandia tokunagai* and other nuculanid bivalves are known in the offshore mud along the Pacific coast of central Honshu and the north. As the distribution of *P. tokunagai* continues to Sakhalin and Kamchatka (Gladenkov, 1973), the occurrence of this association suggest the presence of subsurface cold water tongue during this period (Fig. 3).

Middle Middle Miocene to Late Miocene Phase

Change from the early Middle Miocene fauna to that of the middle Middle Miocene seemed to occur within a very short interval in the Japan Sea coast areas. This is indicated by recent biostatigraphic studies discussed in the preceding section, as well as by the field observations.

At some localities in northern Honshu (e.g., Oga and Sugota areas, see Chinzei in this volume, p. 000), strata containing the warm water Kadonosawa fauna are continuous upwards to those which yield the temperate water Shiobara-type fauna. The stratigraphic interval between the two is in some places only 5 to 10 meters with no apparent change of lithology. The sharp change in faunal composition is recognized throughout the Japan Sea coast from northern Honshu to the Korean Peninsula. The horizon of the faunal change is located at about the upper part of N.9 of the planktonic foraminiferal zone, around 15 Ma ago.

On the Pacific coast of Southwest Japan, strata of this age are very restricted in distribution. There is a major Middle Miocene hiatus in this area, so that none of the Shiobara-Yama fauna or its warm water counterpart has been recognized.

The temperate water fauna of the middle Middle Miocene in North Japan and the Japan Sea coast areas has been named the Shiobara-Yama fauna. The name Shiobara was given to shallow marine and brackish water associations (Chinzei, 1963), while the Yama (Otuka, 1941) has been considered a deep water fauna. As will be discussed later, there is a sandy association widely recognized in northern Honshu, that is intermediate in character between the two types. The difference between the two types represents only a difference in habitats within the same faunal province.

The Shiobara type molluscan fauna is characterized by the association of *Anadara* and *Dosinia* found in muddy sand facies of shallow embayments. Other associations are also common; such as the *Crassostrea* and the *Mizuhopecten* – *Chlamys*, among the localities of the fauna.

The *Anadara* – *Dosinia* association is composed of the bivalves *Anadara ninohensis, Dosinia kaneharai, D. japonica, Mercenaria chitaniana, Laevicardium shiobarense, Protothaca tateiwai, Felaniella usta, Lucinoma annulata,* the gastropods *Neverita kiritaniana, Coraeophos iwakianus,* and some other minor species (Iwasaki, 1970). Among them, *Dosinia kaneharai, Protothaca teteiwai* and *Laevicardium shiobarense* are most characteristic, and indicative of the presence of the Shiobara type fauna. *Mizuhopecten paraplebejus* and *Chlamys kaneharai* are also characteristic of gravelly and sandy facies. The *Crassostrea* association is found in the intertidal mud or muddy sand facies in the innermost parts of embayments. *Crassostrea gigas* occurs as large oyster bank in the muddy facies, while in the sandy beds it forms smaller scale colonies.

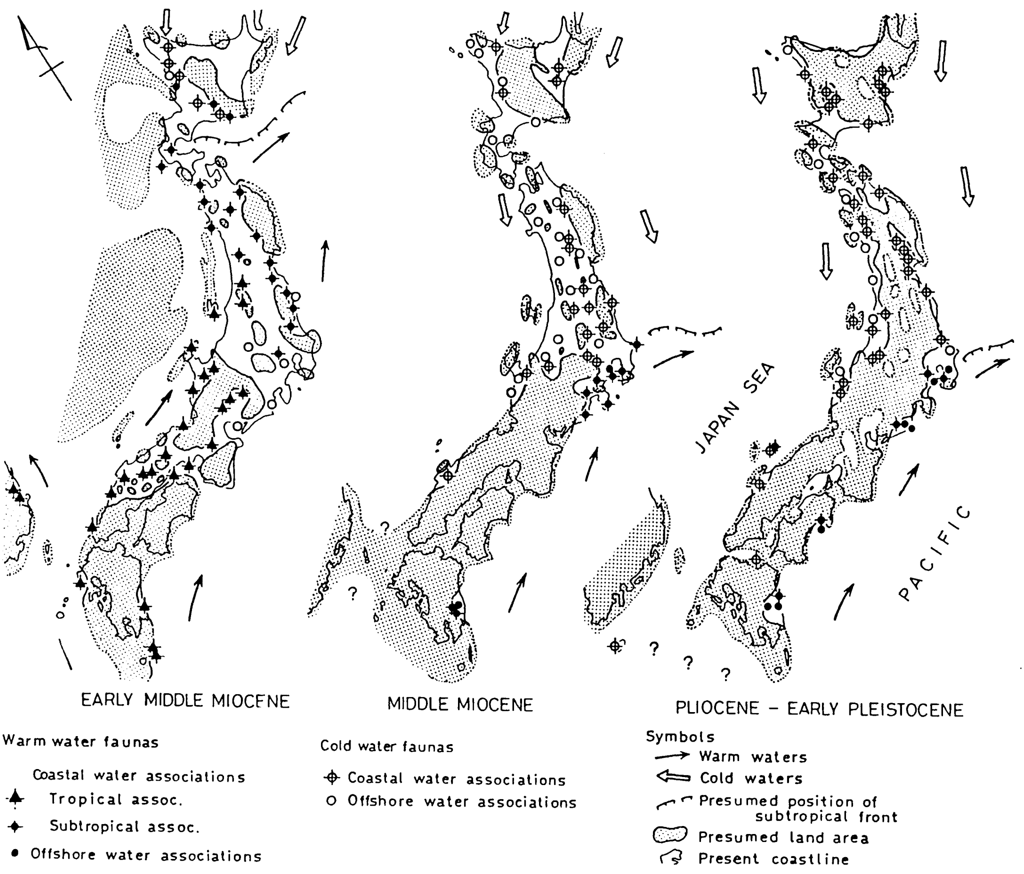
In northern Honshu, the shallow water Shiobara-type fauna lived along the coast of the mainland, the Kitakami-Abukuma massif along the Pacific, and adjacent row of islands, which was later upheaved as the Ou Range. The Atsunai-Togeshita fauna in the Late Miocene of Hokkaido was named and described by Uozumi (1962), and bears species in common with the Shiobara type fauna. It was as a whole thought to be the northern representative of the Shiobara fauna (Chinzei, 1978). Amano (1983) divided the fauna in the Togeshita area into Lower and Upper faunas. It is the Lower Togeshita fauna that is of the Shiobara type. The Upper Togeshita fauna is rich in living species and is thought to represent a later age. The Lower Togeshita fauna is composed of genera that also occur in the Shiobara type fauna, though there are few species in common between the two faunas. The Lower Togeshita fauna is particularly rich in such northern genera as *Clinocardium, Mercenaria,* and *Spisula.*

The molluscan fauna in the coeval offshore muddy facies was first noticed by Otuka (1941) and named the Yama fauna. The Yama type fauna is characterized by abundance of *Serripes* spp. (*S. yokoyamai, S. groenlandicus,* etc.) and large gastropods such as *Ancistrolepis mogamiensis* and *Neptunea* spp. They are usually associated with *Lucinoma acutilineatum* and

Conchocele bisecta, and sometimes with *Mya cuneiformis, Cultellus izumoensis, Panomya simotomensis,* etc.

In the Yama area, some Yama type taxa are found in sandstone together with the species characteristic of the Shiobara type, while a typical Yama type association is known from the underlying mudstone (Ogasawara, 1983b). Similarly, associations intermediate between the two faunal types have been recognized in fine-grained sandstone situated between shallow water sandstone and offshore mudstone facies. This intermediate association consists mainly of *Lucinoma acutilineatum, Serripes* spp., *Macoma optiva, Miyagipecten matsumoriensis, Panomya simotomensis* (e.g., Masuda, 1977), or of *Mizuhopecten kimurai, Panomya simotomensis, Venericardia siogamensis, Cultellus izumoensis* (e.g., Chinzei, 1982), and contains species of both Yama and Shiobara types as major or minor components. Conglomeratic sandstone in this intermediate facies yields a pectinid association characterized by *Mizuhopecten kimurai, M. ninohensis,* and *Kotorapecten tryblium.*

The stratigraphic range of the Shiobara-Yama fauna extends from the upper part of N.9 to probably N.15 of the planktonic foraminiferal zones in northern Honshu. On the Japan Sea coast of Southwest Japan, the uppermost known occurrence of the fauna is N.13 (Kaga area,



Text-fig. 2. Distribution of molluscan faunas and reconstructed paleogeography of Japan in the early Middle Miocene (16.5–15 Ma ago), Middle Miocene (15–10 Ma ago), and Pliocene and Early Pleistocene (5–1 Ma ago). (Revised from Chinzei, 1984)

Ogasawara et al., 1981). In Hokkaido, the Togeshita and the Wakkanai faunas occur mainly in the Late Miocene from N.13 to N.16 zones according to recent biostratigraphic correlations (Tanai, ed., 1982).

The Shiobara-Yama fauna, based on its geographic distribution, may represent the temperate fauna of this phase. The fauna is found in the Japan Sea coast areas, within southernmost occurrence in the Chichibu Basin, northwest of Tokyo (Kanno, 1960). *Chlamys kaneharai,* a representative species of the Shiobara type, is known in the Tanzawa Mountains, southwest of Tokyo, but not farther south.

In the late Middle Miocene (zone N.14), the warm water Sagara fauna (Tsuchi and Shuto, 1984) appeared along the Pacific coast of Southwest Japan. The Sagara fauna ranges through the Late Miocene and in places as young as N.19 zone of the Middle Pliocene. It is characterized by *Amussiopecten iitomiensis* and *Chlamys miurensis.* In the Miyazaki area of southern Kyushu, part of the fauna occur in muddy sandstone and is composed mainly of *A. iitomiensis, Paphia exilis, Crassatellites tenuiliratus, Joannisiella cummingi, Dosinia* spp., *Cardium* spp., *Clementia papyracea* and others (Shuto, 1960). The siltstone association of the same area consists of *Acila submirabilis, Limopsis obliqua, Glycymeris rotunda, Nemocardium samarangae, Ancilla otukai, Polinices reiniana.* Most of the species are now living in the lower sublittoral zone of the Pacific coast influenced by the warm Kuroshio water.

The fauna is considered to be subtropical based on its similarity of species and generic composition to the present-day Kuroshio fauna. The change from the early Middle Miocene Kadonosawa fauna to the Sagara fauna is not recorded because of the regional hiatus ranging from N.10 to N.14 zones in the Pacific coast areas of Southwest Japan.

Pliocene and Early Pleistocene Phase

For Pliocene and Early Pleistocene faunas, two provinces are recognized in the Japanese Islands. One is the Pacific coast of Southwest Japan, where the subtropical Kakegawa fauna occurs. The other consists of the Japan Sea coast and North Japan, which are the domain of the generally cold water Omma-Manganji fauna. The fauna locally ranges from temperate to subarctic in aspect. Extant Omma-Manganjian species occur in area dominated by the cold Oyashio current. A fauna named the Tatsunokuchi fauna (or Takikawa-Honbetsu fauna in Hokkaido), which is characterized by the presence of *Fortipecten takahashii,* is known on the Pacific coast of northern Honshu and central and eastern Hokkaido. The relationship between the Tatsunokuchi and the Omma-Manganji faunas will be discussed below.

Along the Pacific coast of Southwest Japan, the Sagara fauna is succeeded by the Kakegawa fauna, which ranges from Middle Pliocene to Early Pleistocene, N.19 to N.22 of the planktonic foraminiferal zones. It is characterized by the appearance of *Amussiopecten praesignis* in place of *A. iitomiensis* which was present in the Sagara fauna. Other species of the fauna are also different from the Sagara fauna.

The upper sublittoral sandy association of the Kakegawa fauna is peculiar in its abundance of extinct species, such as, *A. praesignis, Anadara castellata, Venericardia panda, Glycymeris totomiensis, Turritella perterebra, Umbonium suchiense, Babylonia elata,* and *Paradrillia dainichiensis.* These Kakegawa species occur with many species still living in the shallow water of Southwest Japan. The deeper-water Kakegawa facies are composed mostly of species now living in lower sublittoral to upper bathyal zones under the influence of the warm Kuroshio current (Chinzei, 1980). The lower sublittoral fine-grained sand association is composed mainly of *Venus foveolata, Glycymeris rotunda,* and *Nemocardium samarangae.* The lower sublittoral and upper bathyal muddy associations are dominated by the gastropods *Nassaria magnifica, Makiyamaia coreanica, Fulgoraria hirasei,* and *Lunatia plicispira,* together with *Limopsis tajimae, Neilonella coix, Malletia inaequilateralis,* and other bivalves. The Kakegawa fauna is known from Miyako and Okinawa Islands, and from Miyazaki, and Kakegawa areas. The fauna tends to appear earlier in the south, N.19 in Miyako and Miyazaki, N.21 in Kakegawa (Shuto, 1984).

The Kakegawa fauna is thought to be subtropical because its composition is comparable to the present-day subtropical fauna of the Pacific coast of Southwest Japan, which is under the strong influence of the warm Kuroshio current. The northernmost occurrence is in the southern Kanto region, south of Tokyo. Some of the characteristic species of the fauna occur as fossils in the western part of the Japan Sea coast as discussed later.

The cold water Omma-Manganji fauna is known from the Japan Sea coast areas and the Pacific coast of northern Honshu down to southern Kanto (Fig. 2). It is dominated by upper sublittoral sandy associations, with species compositions that differ from place to place. Some species occur at most localities, including *Turritella saishuensis, Anadara amicula, Mercenaria stimpsoni, Dosinia japonica,* and *Glycymeris yessoensis.* Of these species, *Turritella saishuensis* is especially characteristic and ubiquitous; it shows a temporal series of subspecies from *T. saishuensis motidukii,* through *T. saishuensis saishuensis* to *T. saishuensis etigoensis* (Kotaka, 1959, 1978).

The Omma-Manganji fauna also includes associations of offshore muddy facies characterized by the dominance of *Propebela candida, Rectiplanes sadoensis* and other turrid gastropods, *Buccinum* spp., *Ancistrolepis* spp., *Macoma calcarea, Nuculana robai, Serripes groenlandica, Conchocele bisecta,* etc. The species are found sporadically in grey siltstone.

As the Pliocene and lower Pleistocene strata of the Japan Sea coast areas accumulated during the last stage of filling of the Neogene basins, the offshore muddy fauna in the lower horizon was replaced upward by shallow water sandy associations. The age of appearance of the shallow water associations differs in places, and is earlier in the marginal areas and later in the central parts of the basin. The earliest appearance of the Omma-Manganji fauna was during the Early Pliocene in northeastern Honshu, as deduced from associated planktonic diatoms (Chinzei, 1982). The fauna is most common in the Late Pliocene and Early Pleistocene, between 2 and 1 Ma ago.

The uppermost marine strata on the Japan Sea coast frequently contain molluscs in gravel or coarse-grained sand. The fauna is characterized by the occurrence of *Astarte borealis, Mizuhopecten yessoensis, Glycymeris yessoensis, Chlamys cosibensis,* and others. The association is usually intermingled with species probably reworked from other facies. In some places it does not contain characteristic species of the Omma-Manganji fauna, and are thought to represent later ages, although they are not well dated.

Some species of the warm Kakegawa fauna have been reported from the Japan Sea areas in association with Omma-Manganjian shallow water sandy molluscs (e.g., Kanehara, 1940). The Kakegawa species are *Glycymeris nakamurai, Umbonium suchiense, Amussiopecten praesignis,* and others. *Amussiopecten praesignis* was reported by Okamoto and Honza (1978) from the sea bottom off the San-in district, southwestern Japan Sea. It was found in dredge samples with Omma-Manganji species such as *Anadara amicula* and *Mizuhopecten tokyoensis hokurikuensis.* Other warm water species, *Cryptopecten vesiculosus, Glycymeris pilsbryi,* *Endemoconus sieboldii, Oliva mustelina,* have also been reported from several localities along the Japan Sea coast (Ogasawara, 1981, 1983a). Ogasawara (1981) distinguished the fauna in the upper part of the Omma Formation, the zone of *Turritella saishuensis etigoensis,* from the Omma-Manganji fauna of the strict sense, and he named the Younger Ommaian fauna which is characterized by the dominance of warm water species living in the Kuroshio and its branch Tsushima current. As pointed out by Ogasawara, the occurrence of these species strongly suggests a connection between Japan Sea and the Pacific through Tsushima Straits during Early Pleistocene.

The embayments formed during the minor Pliocene transgression were inhabited by a fauna of brackish and shallow marine aspect, called the Tatsunokuchi fauna (or Takikawa-Honbetsu fauna in Hokkaido). The fauna is characterized by the hump-backed pectinids *Fortipecten takahashii* or *F. kenyoshiensis.*

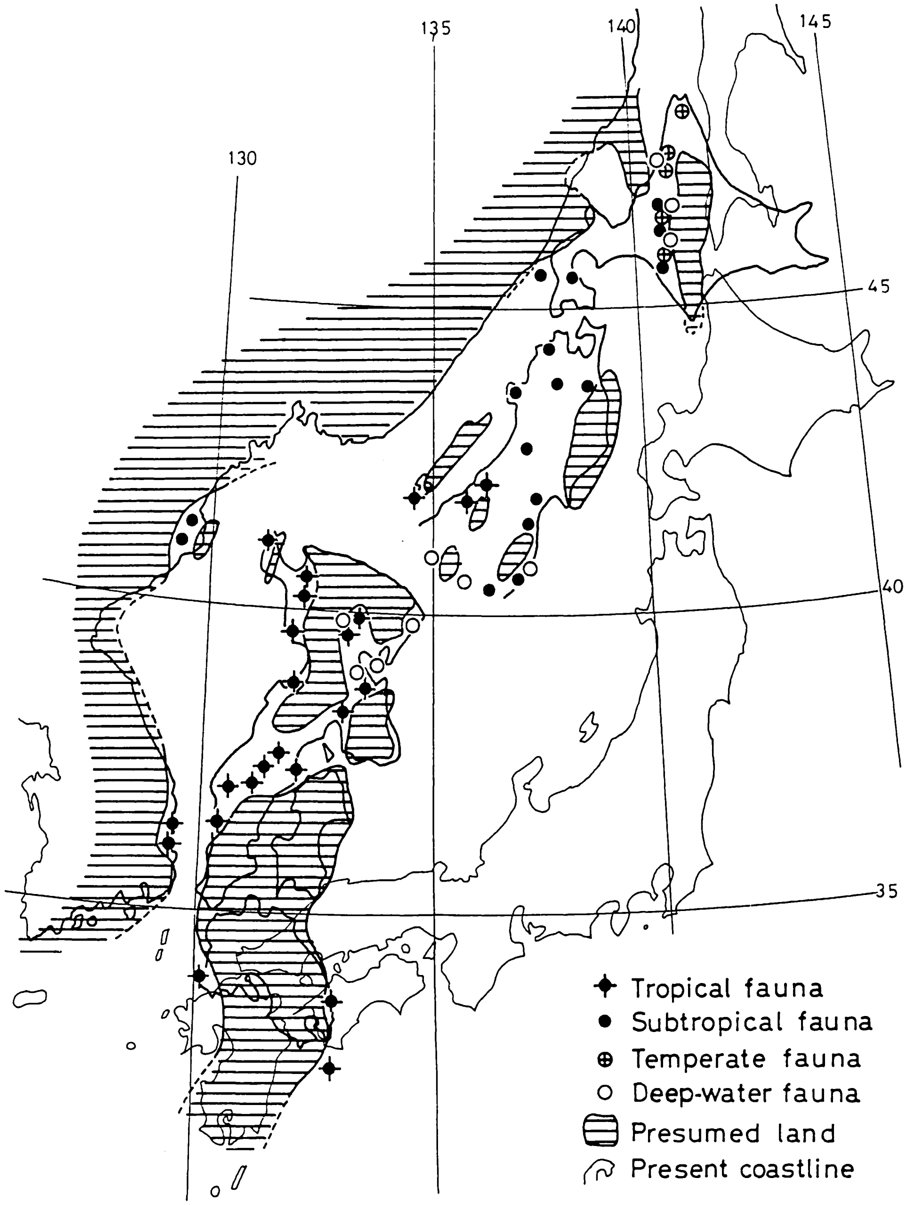
In northern Honshu, the distribution of the Tatsunokuchi fauna is confined to the Middle Pliocene of the Pacific coast, separated from the Japan Sea coast areas by the Ou Range, the backbone range of northern Honshu. In northern Honshu, the fauna is dominated by bivalves endemic to the fauna, such as *Pseudamiantis sendaicus, Anadara tatunokutiensis, Dosinia tatunokutiensis,* and others. These molluscs are found in the muddy sand facies representing shallow level bottom, and the association is in ecologically parallel relationship with the shallow muddy sand association of the Omma-Manganji fauna. The *Anadara* and *Dosinia* in each fauna are different species between the two. Also, *Turritella saisbuensis* in the Omma-Manganji fauna is replaced by *T. fortilirata* in the Tatsunokuchi fauna.

According to Uozumi et al. (1984), *Fortipecten takahashii* appeared in Hokkaido at about 6 Ma ago and found until 2 Ma ago. The species is widely distributed in central and eastern Hokkaido. The typical Omma-Manganjian associations occur above the horizon of *F. takahashii,* between 1.5 and 0.75 Ma ago (Uozumi et al., 1984). *Fortipecten takahashii* in Hokkaido is associated with both Tatsunokuchi and the Omma-Manganji species, such as, *Anadara amicula* and *Turritella fortilirata.* The biogeographic implication of this associated occurrence is uncertain. The segregation of species on both sides of northern Honshu might possibly be ascribed to a peculiar ecologic condition that prevailed in deep embayments along the Pacific coast of northern Honshu.

Discussion: A Short History of Japanese Neogene Molluscan Faunas

Recent biostratigraphic studies have shown that in the Japanese Islands, no remarkable molluscan fauna is known from sediments unequivocally assigned to the Early Miocene. Only some fragmentary occurrences of Ashiya type molluscs along the Pacific coast of Southwest Japan might represent a fauna of this age. The Early Miocene is represented mostly by terrestrial volcanic rocks in the Japan Sean areas. The Japan Sea side of Southwest Japan was a part of the Asian continent before the Middle Miocene, according to a recent paleomagnetic study of Paleogene and Early Neogene volcanic rocks (Otofuji and Matsuda, 1983). Most of Japan was thus thought to have emerged during Early Miocene time.

The great transgression and remarkable warming of marine climates during the early Middle Miocene are recognized as global phenomena (e.g., Shackleton and Kennett, 1975; Savin, 1977). The early Middle Miocene transgression and the dominance of warm-water faunas in Japanese sediments of this age are apparently related to these global phenomena. The north-



Text-fig. 3. Paleogeographic reconstruction of the Japanese Islands and the distribution of molluscan faunas during the early Middle Miocene, before the rotation of Southwest and Northeast Japan blocks. Reconstruction based on paleomagnetic studies (Torii et al., 1985 for Southwest Japan; Tosha, 1984 for Northeast Japan)

ward advancement of tropical and subtropical molluscs is recognized throughout northern Pacific region (Armentrout et al., 1984). A related paleogeographic change in the East China Sea and the Tsushima Straits areas was the opening of a seaway from the south, which allowed the warm Kuroshio current into the Japan Sea (Fig. 3).

The sharp switchover of the faunal aspects at around 15 Ma ago in the Japan Sea areas is one of the largest problems to be solved in the history of Japanese Neogene molluscan faunas.

The change from tropical and subtropical faunas to temperate faunas is very abrupt, and is hard to explain simply by the global tendency of climatic deterioration after the episodic warming. This suggests a remarkable geographic change around the Japan Sea. A clockwise rotation of Southwest Japan and resultant opening of the Japan Sea during the middle Middle Miocene have been inferred from paleomagnetic evidence. According to Torii *et al.* (1985), the rotation happened within a very short interval, probably between 15 and 14 Ma ago, at about the same time that the faunal change took place. They proposed a clockwise rotation of Southwest Japan with the pivot located in the northeastern part of the East China Sea. This might have closed the seaway at the Tsushima Straits, opened the Japan Sea to the north, and brought the Japan Sea fauna under the influence of cold, northern water. The sharp change in marine faunas of the Japan Sea areas may be reasonably explained by this catastrophic change of paleogeography combined with the effects of global climatic cooling.

In spite of the sharp change in marine climate, some shallow water Shiobara molluscan fauna were still dominated by genera originated from the south. The main genera in the sandy facies of the Shiobara-type, such as *Anadara, Dosinia, Laevicardium,* first appeared in the temperate region at this time. The Shiobara species of southern genera are considered to be identical to, or direct descendants of, species that first appeared in the early Middle Miocene. It seems reasonable to conclude that, during the early Middle Miocene period of marked warming, southern species invaded and colonized the coastal water of the Japan Sea and North Japan; then, with the change in marine climate, some taxa remained in embayments of these areas and adapted themselves to the cooler conditions. At the same time, some cold water genera, such as *Spisula* and *Clinocardium,* came down from the north, and mixed with or replaced some southern genera.

The interval of the Late Miocene was mostly barren of megafossils in the Japan Sea coast areas, which received major deposits of diatomaceous mud during this period. The mud preserved at least traces of activity of benthic animals that indicates a stagnant bottom environment (e.g., Ingle, 1981). The sedimentation rate was probably extremely slow; a hiatus has also been recognized in the mud.

Along the Pacific coast of Southwest Japan, an entirely new fauna, the Sagara fauna, invaded from the south in the Late Miocene. This was the second Neogene invasion of southern mollusks into Japanese waters. The generic composition of each association (such as upper sublittoral sandy association) is different from that of the early Middle Miocene, and bears a similarity to the present-day fauna in Kuroshio waters. The Sagara fauna was then succeeded by the Kakegawa fauna. The change from the Sagara to the Kakegawa fauna is probably related both to a third invasion of southern taxa and to evolutionary changes among Sagara species.

There is a major difference in species composition between the Shiobara fauna and the Omma-Manganji and Tatsunokuchi faunas. The genera also differ considerably, although *Anadara, Dosinia* and some other so-called Japonic elements, remained in the faunas of Pliocene and later ages. Only a few Shiobara elements, such as, *Polinices kiritaniana* and *Pseudamiantis,* appeared in the Tatsunokuchi fauna. This may indicate that during the Late Miocene stagnation of the Japan Sea, shallow water faunas also became impoverished. The appearance of the Plio-Pleistocene Omma-Manganji fauna in the Japan Sea perhaps resulted from a new immigration of the molluscan fauna from the north. Detailed taxonomic study of fauna and comparative study with northern faunas are needed to settle this question.

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LATE CENOZOIC MOLLUSCAN FAUNAS AND THEIR DEVELOPMENT IN SOUTHWESTERN JAPAN

By

Ryuichi TSUCHI

Introduction

Recent progress in defining the Neogene chronologic framework of Japan, including the Pleistocene, has been made by incorporating detailed biostratigraphy with new data on planktonic microfossils, radiometric dating, and magnetostratigraphy. This has resulted in more precise correlation of mollusc-bearing horizons and has also provided a more precise definition of the chronologic succession of benthic molluscan faunas (Tsuchi *et al.*, 1984). It is now possible to refine the distribution of molluscan faunas and species in time and space with reference to biohorizons of planktonic microfossils.

Based upon the above-mentioned biochronologic framework, the chronologic and geographic distributions of marine molluscan faunas, especially late Cenozoic faunas on the Pacific coast of central and southwestern Japan, are examined, and some implications for their origin and development are described.

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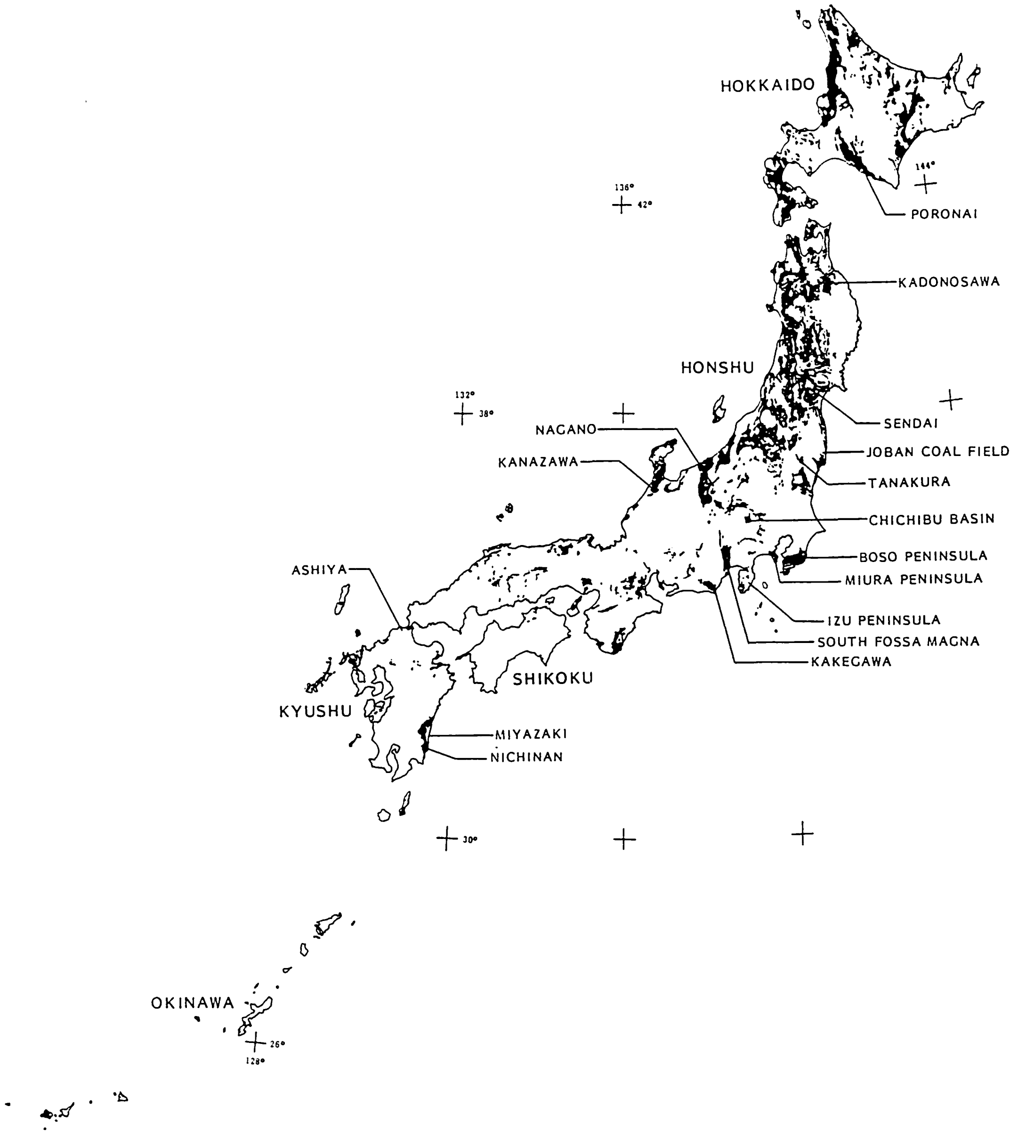
Late Cenozoic molluscan faunas in Japan and their distribution in time and space

A biochronologic division of Tertiary molluscan faunas in Japan was first outlined by Otuka (1939). Later, Chinzei (1978) synthesized ecologic and zoogeographic analyses of Neogene marine faunas. Some amendments based on a revised biochronologic framework were made by the author (Tsuchi and Shuto, 1984; Tsuchi *et al.*, 1984). A brief account of the chronologic and geographic distribution of late Cenozoic faunas is given below, with some new data recently obtained.

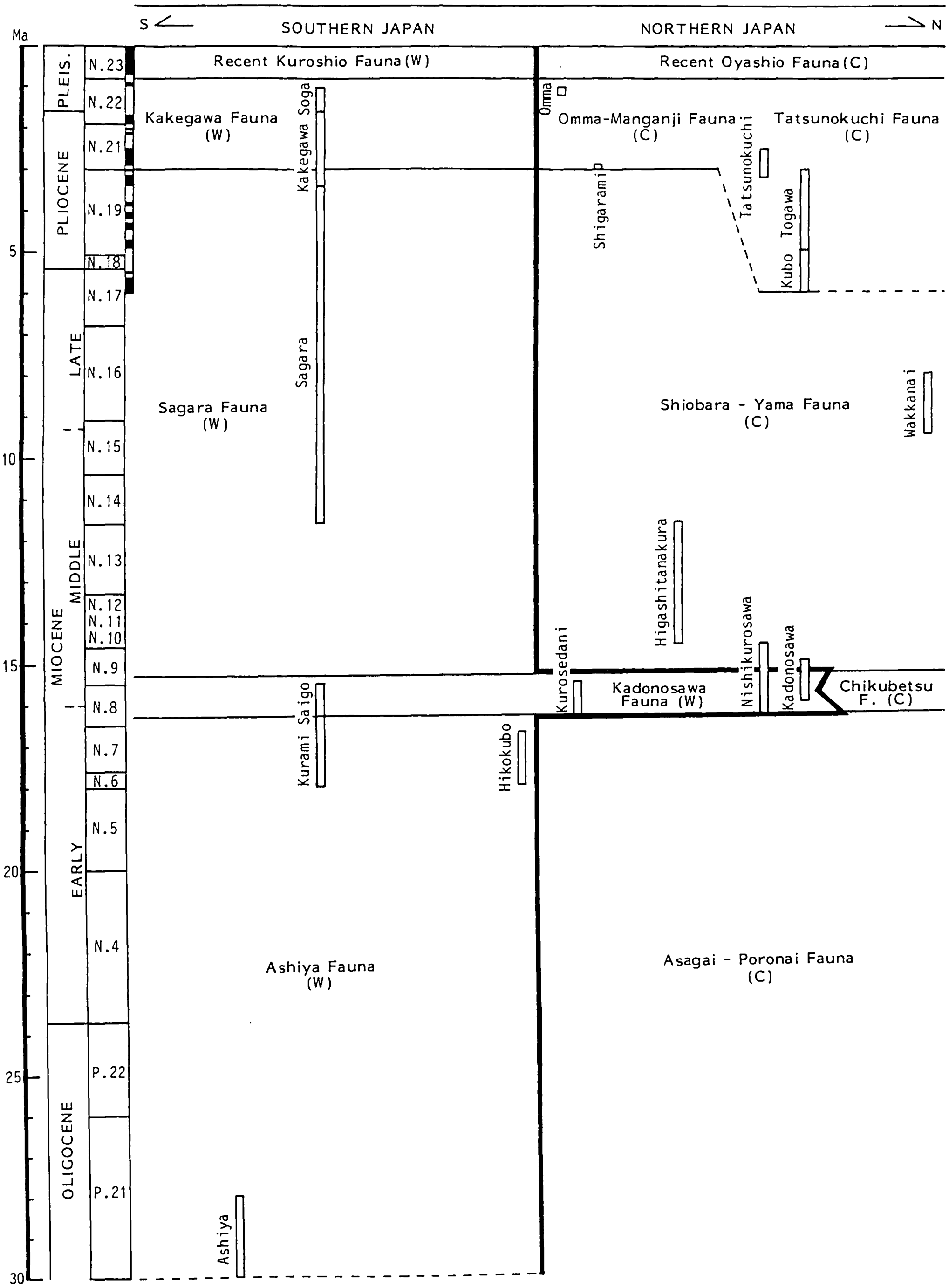
Late Cenozoic molluscan faunas in Japan can be grouped by age into four successive phases. Faunas in each phase are derived from two different water systems, namely, warm and cold; this division is also seen in the Recent faunas of the warm Kuroshio and the cold Oyashio currents.



Text-fig. 1. Index map showing the distribution of marine Neogene strata in Japan.

Ashiya and Asagai-Poronai faunas:

Molluscan faunas of the first phase are called Ashiya and Asagai-Poronai. The Ashiya fauna, taking molluscs of the Ashiya Group in north Kyushu as its type, is characterized by the appearance of many Neogene elements such as *Cultellus, Dosinia* and *Glycymeris* in the upper half of the group. The fauna is mainly a warm-water one, but includes some elements of the cold Asagai-Poronai fauna. The Ashiya Group is mostly included in Blow's planktonic foraminiferal zone P.21, of late Oligocene age. Principal members of the Ashiya fauna are also found in the upper part of the Paleogene Nichinan Group in estern Kyushu, and in the Hikokubo Group of the Chichibu Basin that is assignable to Zone N.6–7 of early Miocene age. Therefore, the Ashiya fauna can be regarded as ranging in age from late Oligocene to early Miocene.



Text-fig. 2. Late Cenozoic marine molluscan faunas in Japan and their distribution in time and space. (W) and (C) indicate warm and cold water faunas, respectively. The chronologic ranges of selected formations are also delineated.

The Asagai-Poronai fauna was named from molluscs of the Asagai Sandstone of the Joban coal field in central Honshu and from those of the Poronai Formation in central Hokkaido. The fauna is characterized by cold-water taxa and regarded as a cold-water equivalent of the Ashiya fauna. However, the stratigraphic range of the Asagai-Poronai fauna extends down to horizons of Eocene time lower than those of the Ashiya (Ibaraki, 1984; Kaiho, 1984).

Kadonosawa and Chikubetsu faunas:

Molluscan faunas of the second phase are called Kadonosawa and Chikubetsu. The Kadonosawa fauna was named from molluscs of the lower part of the Kadonosawa Formation in northeastern Honshu. The fauna is dominated by tropical and subtropical species such as *Vicarya, Vicaryella* and typical mangrove swamp dwellers including *Telescopium* and *Geloina.* This fauna is also associated with such larger foraminifers as *Lepidocyclina* and *Miogypsina,* and extends northward to southern Hokkaido. The range of the fauna seems to be limited to Zone N.8 and the basal part of N.9, of earliest middle Miocene age. The Chikubetsu fauna, a cold-water equivalent, is known only in northern Hokkaido. The Chikubetsu Sandstone of the Haboro area contains *Spisula onnechiuria* (Otuka), *Mya cuneiformis* (Böhm) and *Neptunia nomurai* Otuka.

Sagara and Shiobara-Yama faunas:

Molluscan faunas of the third phase are called Sagara and Shiobara-Yama. The Sagara fauna is found in the Sagara Group of the Kakegawa area and in correlative deposits on the Pacific side of central and southwestern Japan. The fauna ranges at least from Zone N.14 to N.19, of late middle Miocene to Pliocene age. The Shiobara-Yama fauna is the cold-water equivalent of the Sagara, and is found in central and northern Japan. The Higashitanakura Group in the Tanakura area of central Honshu, which contains typical Shiobara taxa, is included in the interval of Zone N.11–13, of middle Miocene age. The Wakkanai formation in northern Hokkaido, which contains Yama elements, is approximately correlative with Zone N.16 of early late Miocene age.

Kakegawa, Omma-Manganji and Tatsunokuchi faunas:

Faunas of the fourth phase are called Kakegawa, Omma-Manganji (or Omma-Manganjian) and Tatsunokuchi. The Kakegawa fauna is found in the Kakegawa and Soga Groups of the Kakegawa area and in correlative sequences on the Pacific side of central and southwestern Japan. The Kakegawa and Soga Groups, conformably lying on the Sagara Group, are assignable to Zone N.19–22 of Pliocene to early Pleistocene age. The Omma-Maanganji fauna, a cold-water equivalent of the Kakegawa, is found in the Omma Formation and in many other sequances on the Sea of Japan side. The Omma Formation is assigned to Zone N.22 of Pleistocene age, approximately at 1.2–1.0 Ma (Tsuchi *et al.,* 1985). An associated assemblage of the Kakegawa and the Omma-Manganji faunas from subsea outcrops in the southwestern Sea of Japan is assigned to an earliest Pleistocene age at 1.6–1.5 Ma (Tsuchi *et al.,* 1985). Horizons of the Shigarami fauna west of Nagano in central Honshu, containing taxa typical of the Omma-Manganji, can be assigned to the basal part of Zone N.21 of Pliocene age at about 3.0 Ma (Tsuchi *et al.,* 1985). Thus, the Omma-Manganji fauna seems to range from Pliocene to early Pleistocene, 3.0 to 1.0 Ma, or nearly the same as the Kakegawa fauna.

Some Omma-Manganji taxa found in the Kubo Formation of the Kadonosawa area in northeastern Honshu, which can be assigned to Zone N.17–18 of late Miocene to early Pliocene age, may suggest an earlier appearance of the fauna in northern Japan.

The Tatsunokuchi fauna, another cold-water equivalent of the Kakegawa fauna, is typically found in the Tatsunokuchi Formation near Sendai in northern Honshu. The fauna is known from northeastern Honshu and Hokkaido, sometimes in association with Omma-Manganji taxa, although the fauna is thought to be zoogeographically distinct from the Omma-Manganji. The Tatsunokuchi Formation can be assigned to Zone N.19–21 of Pliocene age.

The distribution in time and space of the above-mentioned late Cenozoic molluscan faunas in Japan is schematically summarized in Fig. 2. The microplanktonic time scale of the Neogene and the Pleistocene adopted here is that given by Tsuchi *et al.* (1984), and that of the Paleogene by Berggren *et al.* (in press).

The most pronounced bio-event of the Neogene is the predominance of warm-water molluscs in the earliest middle Miocene at about 16 Ma. This bio-event had a limited duration of about 1 Ma, during which tropical-subtropical shallow water species of the Kadonosawa fauna prevailed throughout the Japanese Islands, except northern Hokkaido. The Sagara and Kakegawa faunas are of ages subsequent to the above-mentioned Mid-Neogene climatic optimum; they also occurred during a time of temperature fluctuations accompanying global climatic deterioration, as delineated by Savin *et al.* (1975) and Douglass and Woodruff (1981).

Sagara and Kakegawa faunas and their equivalents

Neogene molluscs of the Kakegawa area on the Pacific coast of central Japan were first studied by Yokoyama (1923, 1926), and later in detail by Makiyama (1927, 1931). Based on these studies, Otuka (1939) named molluscs of the Kakegawa Group the "Kakegawa fauna", those of the preceding age the "Tuma-Tamari fauna" and those of the subsequent age the "Soga fauna". The molluscs were also examined by the auther (Tsuchi, 1961).

The Kakegawa area contains one of the classic Neogene sequences of Japan, in which marine strata are extensive, continuous, and consist of early and late Neogene deposits. The late Neogene sequence, lying unconformably on early Miocene strata, ranges in age from late middle Miocene to early Pleistocene, and is composed of open coastal sediments, with frequent intercalations of pyroclastic layers. Stratigraphically, the sequence consists of the Sagara, Kakegawa and Soga Groups, in ascending order (Tsuchi, 1961). Molluscs occur abundantly throughout the sequence, especially in nearshore shallow facies to the north, and less abundant deep water molluscs and rich planktonic foraminifers occur in finer sediments to the south. These three groups represent continuous sedimentation in the Kakegawa area. Many pyroclastic layers intercalated in the sequence are useful for the chronostratigraphic subdivision.

The chronostratigraphic succession of late Neogene molluscs of the Kakegawa area has been elucidated with reference to planktonic foraminiferal zones, datum levels, and key pyroclastic beds. (Tsuchi and Ibaraki, 1978). They are classified into following five stages in stratigraphic order:

5) Yuzanjian: The coexistence of Kakegawa relics with living species; the latter may amount to 90% of the assemblage. The whole Soga Group is included in this stage.

4) Kechienjian: The disappearance of some Kakegawa taxa and slight modification of

some others in their dimension. The upper part of the Kakegawa Group is assigned to this stage.

3) Suchian: The acme of the Kekegawa fauna. The mid-part of the Kakegawa Group is assigned to this stage.

2) Totomian: The initial appearance of a few Kakegawa taxa coexisting with Sagara relics. This is represented by the lower part of the Kakegawa Group.

1) Yuian; The fullest development of the Sagara fauna. The whole Sagara Group is included in this stage.

The Kakegawa fauna is thus defined as the molluscan fauna that flourished in the Kakegawa age and consists of taxa characteristically found in the Kakegawa Group. The Sagara fauna is also defined similarly. In early Kakegawa deposits, an association consisting of some forerunners of the Kakegawa fauna and Sagara relics can be found. In turn, the Soga fauna is considered to be an assemblage of Kakegawa relics with some forerunners of the Recent fauna of the warm Kuroshio current.

Sagara fauna and its equivalents:

In the Sagara Group, molluscs have been obtained from three horizons of the fossil locality Tsuchizawa in the base of the group, Ommagaya and Chokaiji in the middle of the group, where *Amussiopecten iitomiensis* (Otuka) and *Chlamys miurensis* (Yokoyama) occur together. Most molluscs from Hirugaya at the basal horizon of the Kakegawa Group consist of Sagara taxa, including *Amussiopecten iitomiensis, Chlamys miurensis, Spondylus* cf. *S. anacanthus* Mawe, *Oxyperas* cf. *O. aspersa* (Sowerby), and *Siphonalia* cf. *S. declivis* Yokoyama.

The Sagara fauna is an open coastal community and consists of the following four elements: 1) taxa allied to fossil species from tropical regions, such as *Amussiopecten iitomiensis,* 2) taxa allied to living tropical-subtropical species such as *Spondylus* cf. *S. anacanthus,* 3) cosmopolitan species or taxa allied living cold water species such as *Mercenaria chitaniana* (Yokoyama), and 4) Japonic endemic forms such as *Siphonalia* cf. *S. declivis.* Warm water element 1), 2) and 4) are dominant in the fauna. *Mercenaria chitaniana* is a species in common with the coldwater Shiobara-Yama fauna.

Equivalents of the Sagara fauna are known from several areas on the Pacific coast of central and southwestern Japan, just as in the case of the Kakegawa fauna. The Sagara equivalents occur in the Senhata Formation on the west coast of the Boso Peninsula (Ibaraki and Tsuchi, 1979), the Zushi Formation on the coast of the Miura Peninsula (Masuda, 1962), the Nishikoiso Formation near Oiso on the coast of Sagami Bay west of the Miura Peninsula (Ibaraki, 1978), the Harada Formation on the coast of the southeastern Izu Peninsula (Nomura and Niino, 1932; Ibaraki, 1976), the Shizukawa Group northeast of Kakegawa in the south Fossa Magna (Otuka, 1934; Ujiie and Muraki, 1976), the lower part of the Miyazaki Group in eastern Kyushu (Shuto, 1961), and in the Itoman horizon in the lower part of the Shimajiri Group of Okinawa Island (Tsuchi, MS). *Amussiopecten iitomiensis* has been obtained from all the above-mentioned areas. From the Tetokon horizon just below the Shinzato Tuff in the upper part of the Shimajiri Group, a well-preserved specimen of *Amussiopecten iitomiensis* has been found in association with planktonic foraminifer *Globorotalia tosaensis* Takayanagi and Saito, which is indicative of the Kakegawa age (Ibaraki, 1979). This Tetokon horizon is included in the Totomian Stage.

Otuka (1939) named the above-mentioned Sagara equivalents "Tuma-Tamari fauna". As the Tuma Mudstone represents only a part of the lower portion of the Miyazaki Group and the Tamari Silt is included in a part of the Sagara Group, the author calls them "Sagara fauna".

The Sagara fauna closely resembles the Kakegawa fauna in generic composition, but differs in species composition. Species of each fauna belong to the same genera are not necessarily closely allied. For example, *Amussiopecten iitomiensis* of the Sagara fauna is not considered to be the direct ancestor of *Amussiopecten praesignis* of the Kakegawa fauna, because of a distinct difference in the shape of their juvenile radial ribs. It is most probable that the Sagara fauna represents not a part of the Kakegawa fuana but a different one preceding the Kakegawa fauna. The Sagara fauna probably represents a northern oscillation of the ancient warm Kuroshio current that was distinct from that of the Kakegawa fauna.

Kakegawa fauna and its equivalents:

The Kakegawa fauna is also an open coastal community, consisting of littoral to archybenthal inhabitants, and lacking any embayment dwellers. However, characteristic species of the fauna are found abundantly in the main part of the Dainichi Sand, a marginal and littoral facies in the midpart of the Kakegawa Group. These are *Amussiopecten praesignis, Anadara castellata* (Yokoyama), *Venericadia panda* (Yokoyama), *Suchium suchiense* (Yokoyama), *Turritella perterebra* Yokoyama, and *Siphonalia declivis.*

The Kakegawa fauna is composed of the following five elements: 1) taxa allied to fossil species occurring in tropical regions, such as *Amussiopecten praesignis,* 2) taxa allied to living tropical species such as *Turritella perterebra,* 3) cosmopolitan taxa or taxa allied to living cold water species such as *Mercenaria yokoyamai* (Makiyama), 4) Japonic endemic species such as *Suchium suchiense,* and 5) taxa allied to living species on the adjacent coast such as *Glycymeris nakamurai* Makiyama. Among these, taxa of 1) and 2) can be regarded as tropical elements, which are prominent in the fauna. In later stages, species of elements 1), 2), and 3) become disappear and those of 4) and 5) evolved to Recent species. *Amussiopecten praesignis, Turritella perterebra* and *Mercenaria yokoyamai* disappear at the end of the Kakegawa age. Recent *Mercenaria stimpsoni* (Gould), allied to *M. yokoyamai* is common in northern Japan and the Sea of Okhotsk. The Recent species, *Suchium giganteum* (Lesson) and *Glycymeris albolineata* Lischke, both of which first appeared in the Yuzanijan Stage, are descendants of *S. suchiense* and *G. nakamurai,* respectively.

One of the characteristics of the Kakegawa fauna is an evolutionary acceleration during the late Kakegawa and Soga ages, which is demonstrated by *Suchium suchiense* and *S. giganteum* bio-series (Tsuchi, 1969). *Suchium suchiense* var. of the Totomian successively evolves to *S. giganteum* s.s. of the Yuzanjian through *S. suchiense* s.s. of the Suchian, to *S. suchiense subsuchiense* (Makiyama) and *S. giganteum naganumanum* (Otuka) of the Yuzanjian, during only two million years in the period from 3 Ma to 1 Ma. Such accelerated successional species are typically recognized in Japonic endemic forms. From planktonic foraminiferal evidence, the evolutionary acceleration recognized here seems to be related to a phased decline in seawater temperatures during the Kechienjian and Yuzanjian ages (Ibaraki, 1983).

Equivalents of the Kakegawa fauna are found in several areas on the Pacific coast of central and southwestern Japan. These include faunas of the Kurotaki Formation on the Boso Peninsula (Ohara and Takahashi, 1975; Ibaraki and Tsuchi, 1979), the Tonohama Group in southeastern Shikoku (Tsuchi, 1961; Tsuchi and Takayanagi, 1979), the upper part of the

Miyazaki Group in eastern Kyushu (Shuto, 1961), and the upper part of the Shimajiri Group in Okinawa Island (Noda, 1980; Tsuchi, MS). Specimens of *Amussiopecten presignis* have been found in all of these faunas, although the species composition varies with geographic location.

Notes on the living fauna on the coast of the Sagara-Kakegawa area

The Sagara-Kakegawa area is located on the Pacific coast of central Japan, and contains extensive sandy beach as well as the shallow shelf of the Sea of Enshu. The coast is strongly influenced by the warm Kuroshio current. The living molluscan fauna of the warm Kuroshio current on the coast of the Sea of Enshu has been studied by the author (Tsuchi, 1955, 1956, 1957), and was treated more generally by Kuroda and Habe (1952).

The depositional environment of the Dainichi Sand of the Kakegawa Group is thought to closely resemble that of the Sea of Enshu, where a medium-grained sand facies occurs extensively. Living molluscs of a littoral zone of the Sea of Enshu, ranging from a tidal flat to about 30 meters deep, comprise a typical open coastal community.

Principal species in this community are:

**Suchium giganteum* (Lesson)
**Suchium costatum* (Kiener)
**Babylonia japonica* (Reeve)
**Siphonalia signum* (Reeve)
Olivella japonica Pilsbry
Hastula diversa (Smith)
**Anadara satowi* (Dunker)
**Glycymeris albolineata* (Dunker)
Meretrix lamarckii Deshayes
**Cyclosunetta menstrualis* (Menke)
**Gomphina melanaegis* Römer
**Tentidonax kiusiuensis* (Pilsbry)
Chion semigranosus (Dunker)
Mactra chinensis Philippi
Paphia vernicosa (Gould)
**Dosinorbis bilunulata* (Glay)
**Callista chinensis* (Holten)
**Placamen tiara* (Dillwyn)

The generic composition of this living community is very close to that of the fossil assemblage of the Dainichi Sand. Many of the listed species, marking with an asterisk (*), are closely allied to fossil species of the Dainichi Sand; the latter, in turn, are ancestors of these living descendants. This relationship suggests that the Recent Kuroshio fauna may have been derived largely from the Kakegawa fauna.

Some implications for the origin and migration of the Sagara, Kakegawa and Recent Kuroshio faunas

The chronologic and geographic distribution of the Sagara and Kakegawa faunas can be delineated by the occurrences of their most characteristic species, *Amussiopecten iitomiensis* and *Amussiopecten praesignis,* respectively (Fig. 3). Generally speaking, an occurrence of a fossil molluscan species in a sequence is largely limited by various geologic conditions. Nevertheless, the distribution patterns of the above-mentioned characteristic species in time and space make spheroidal forms towards north, respectively. Specimens of *Amussiopecten praesignis* have been obtained from post-Kakegawa sediments in the southwestern Sea of Japan (Tsuchi, *et al.,* 1985) and from Okinawa Island (Tsuchi, 1975). Some tropical elements of the Kakegawa fauna appear earlier on Miyako Island than in the Kakegawa area (Shuto, pers. com.). These data indicate diachronous appearance and disappearance of tropical elements in the Kakegawa fauna. Northward migrations of *Amussiopecten iitomiensis* and *A. praesignis,* typical tropical elements of both faunas, culminated, respectively, in Zone N.17a and N.21a, approximately at 6 Ma and 2 Ma. These optimal ages correspond, respectively, to ages of the Chokaiji horizon of the Sagara Group and the acme of the Kakegawa fauna. The distribution patterns of the whole Sagara and whole Kakegawa faunas are considered to be about the same as those of their characteristic species.

The distribution patterns of the *Suchium suchiense* bio-series in the Kakegawa fauna and *S. giganteum* bio-series in the Recent Kuroshio fauna, both typically endemic species, are demonstrated in Fig. 4. These patterns are different from those of the tropical elements, and suggest that these endemic species made their evolutionary changes in the adjacent sea on the Pacific coast of central Japan.

From the distribution patterns of typical members of the faunas, it can be summarized that the Sagara and Kakegawa faunas originated mainly from respectively northward migrations of tropical forms, and partly from cosmopolitans and endemic forms of the preceding faunas. The Recent Kuroshio fauna, as above-mentioned, may have developed largely from the Kakegawa fauna.

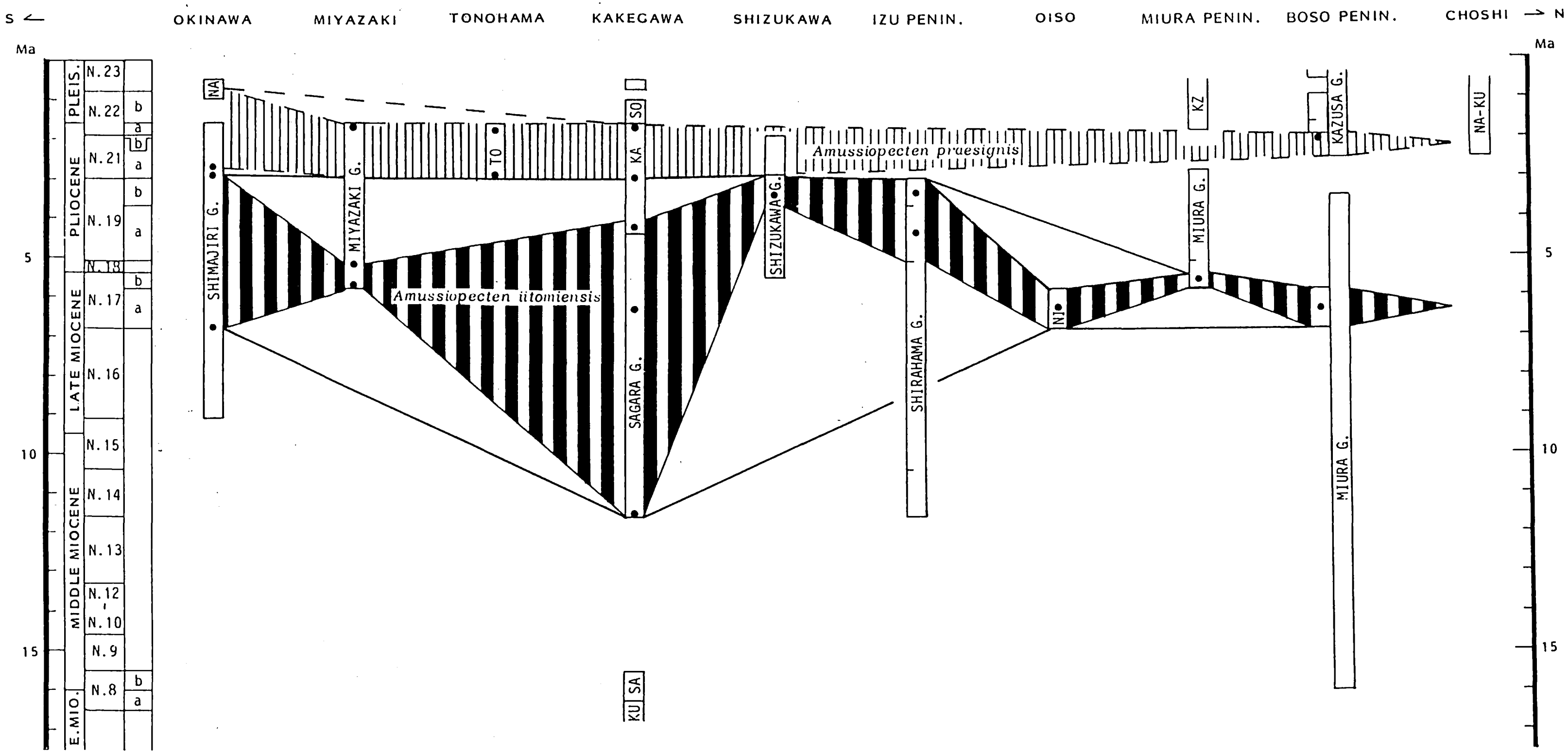
Concluding remarks

Using a late Cenozoic biochronologic framework based on planktonic microfossils, the distribution in time and space of marine molluscan faunas in Japan is schematically delineated in Fig. 2. Some previously unpublished data are included. The distribution and characters of the Sagara and Kakegawa faunas are examined in detail with reference to the Recent fauna.

The Sagara and Kakegawa faunas and their equivalents are mostly known from the Pacific coast of central and southwestern Japan. Characteristic species of the Kakegawa fauna are also known from the southwestern Sea of Japan.

The Sagara fauna is an open coastal community ranging in age from middle Miocene to early Pliocene, and bears a close resemblance to the Kakegawa fauna in generic composition, but largely different from it in species composition. The Sagara fauna represents a northward migration of tropical species accompanying the ancient warm Kuroshio current, and is distinct from the Kakegawa fauna.

The Kakegawa fauna is also an open coastal community of late Pliocene-early Pleistocene age, and is composed of five elements: 1) taxa allied to fossil tropical species, 2) taxa allied to living tropical species, 3) cosmopolitan taxa or taxa allied to living cold water species, 4) Japonic endemic taxa, and 5) taxa allied to living species in the adjacent sea. Among these, tropical elements are most prominent in the fauna. The fauna suggests a northward migration of tropical species. An evolutionary acceleration, manifested by the *Suchium suchiense* and

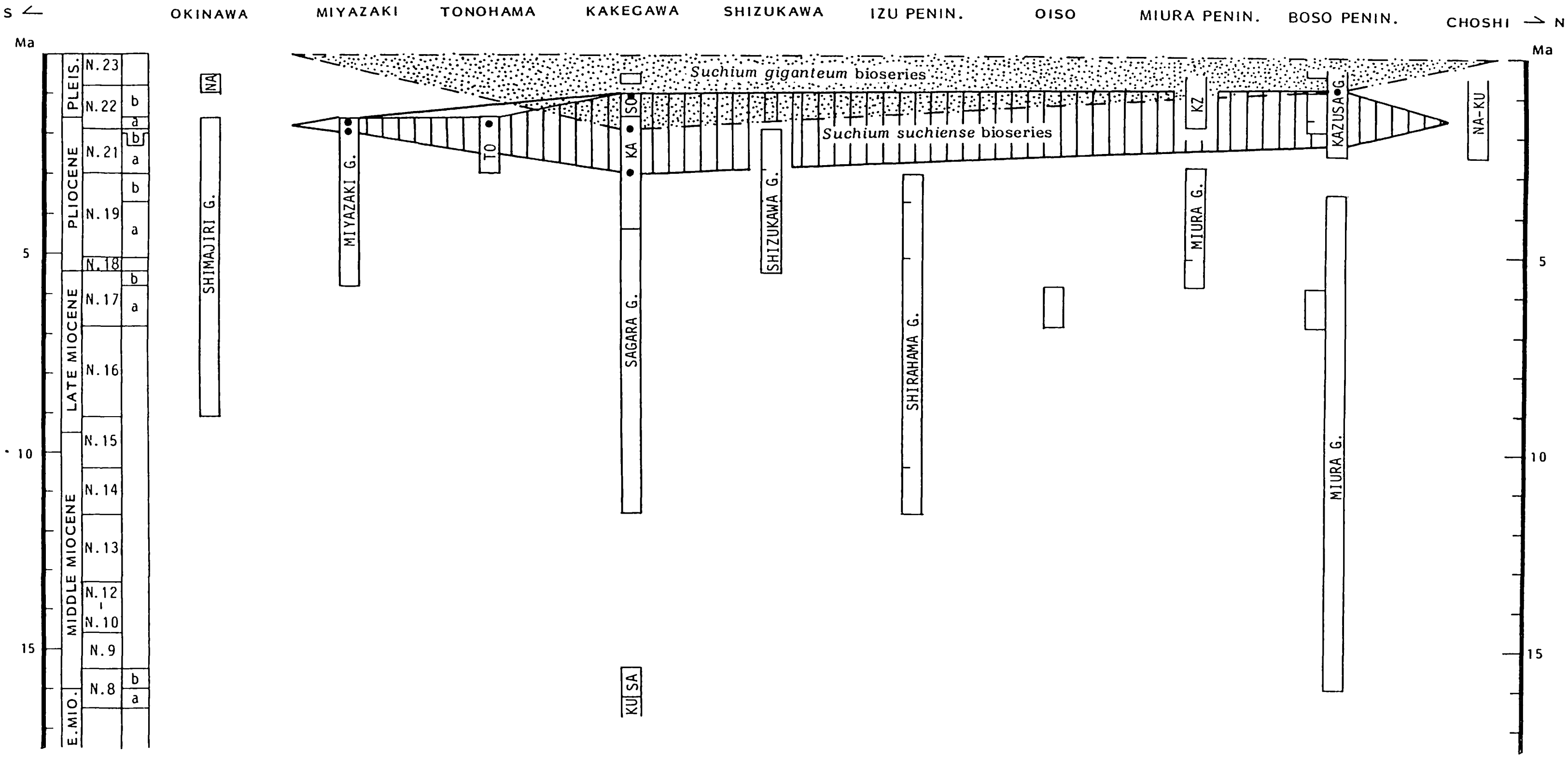


Text-fig. 3. The chronologic and geographic distribution of *Amussiopecten iitomiensis* and *A. praesignis*, characteristic species of the Sagara and Kakegawa faunas, respectively.

In the figure, chronologic ranges of respective late Cenozoic sequences on the Pacific coast of central and southwestern Japan and chronologic positions of the lowest and uppermost occurrences of the species in those sequences are fixed in assigned planktonic foraminiferal zones on the basis of contained or associated planktonic foraminifers. Ranges of the both species in respective sections are connected and hatched from south to north, respectively, and the lower and upper limits of their ranges are also smoothly outlined.

Further subdivisions (a, b) of some planktonic foraminiferal zones are made by utilizing additional datum levels.

Dots (•) indicate the chronologic positions of main fossil localities. G: Group. NA: Naha Limestone. TO: Tonohama Group. KA: Kakegawa Group. SO: Soga Group. NI: Nishikoiso Formation. KZ: Kazusa Group. NA-KU: Naarai and Kurahashi Formations.



Text-fig. 4. The chronologic and geographic distribution of the *Suchium suchiense* and *S. giganteum* bio-series, typical Japonic endemic species in the Kakegawa and Recent Kuroshio faunas, respectively.
Abbreviations are the same as in Fig. 3.

S. giganteum bio-series during the period from 3 Ma to 1 Ma, was probably accompanied by a phased dropping of seawater temperature. Such accelerated successional bio-series have been typically recognized among Japonic endemic species.

The chronologic and geographic distribution patterns of the Sagara and Kakegawa faunas, exhibited by their characteristic species, indicate northward migrations of tropical taxa culminating approximately at 6 Ma and 2 Ma, respectively. On the other hand, the distribution patterns of endemic taxa in the Kakegawa and Recent Kuroshio faunas suggest that those endemic species underwent evolutionary changes in the adjacent sea.

It is most probable, therefore, that the Sagara and Kakegawa faunas originated mainly from respectively northward migrations of tropical forms during their early phases, and partly from cosmopolitans and endemic texa of the preceding faunas. Because many living molluscs along the adjacent coast are closely allied to the Kakegawa species, the Recent Kuroshio fauna may have been derived largely from the Kakegawa fauna.

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TEMPORAL AND SPATIAL DISTRIBUTION OF MOLLUSCAN FAUNAS IN THE LATE CENOZOIC OF JAPAN

By

Junji ITOIGAWA

Introduction

In 1974, I proposed an idea of grade or order in molluscan fauna distribution in time and space on the basis of data obtained from the Miocene Mizunami Group (Itoigawa, 1974a, b). Thereafter, I have held this idea in my mind considering some supplementary data on the Setouchi Miocene Series (Itoigawa, 1983). This idea means theoretical synthesis of distribution of molluscan fauna in time and space. Three grades (I-high, II-medium, III-low) each in temporal and spatial distributions controlled by environmental factors and speciation are recognized.

Now, I check the idea on the basis of newly obtained data in wider and longer extensions in Cenozoic sequences in Japan, especially in the Miocene Setouchi Series, and try to revise the idea and to make a new proportion in line with the idea.

Prior to beginning the main discourse, three grades in environmental factors are shown, namely the first (I) is current (concerning sea water temperature), the second (II) is distribution of water mass (coastal or oceanic), and the third (III) is depth, bottom character, salinity and habitat etc.

I wish to express my hearty thanks to Dr. Kyotaka Chinzei of Kyoto University for discussion.

Temporal distribution of molluscan fauna in the Setouchi Miocene Series

a. Mizunami Group

The Miocene Mizunami Group distributed in central Honshu, Japan, is divided into several members and facies in four formations and summarized in three units, I, II and III (in ascending order) divided by two disconformities (Table 1) (Itoigawa, 1974c). Molluscan fauna consisting of five hundred and seventy species is recognized in the marine facies of the group (Itoigawa *et al.*, 1981).

Each member has different number of species (Table 2) and has representative assemblages. Comparison of constitution of each member is shown in Fig. 1. Common species, different species in different genus and different species in the same genus are examined and shown in percentage in two members which contact each other in above and below relation and in two members which do not contact each other but have a similar lithologic character. Relationship between the Tsukiyoshi and the Togari Members is the former and the one between the Kujiri and the Shukunohora Facies is the latter.

We can recognize three types of pattern in the relationship, namely, A, B and C, and the types A and B are divided each into two subtypes as shown by a and b, respectively. Each type

Table 1. Stratigraphy of the Mizunami Group.

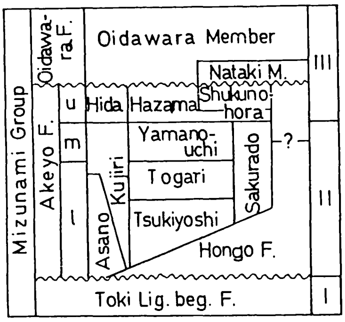
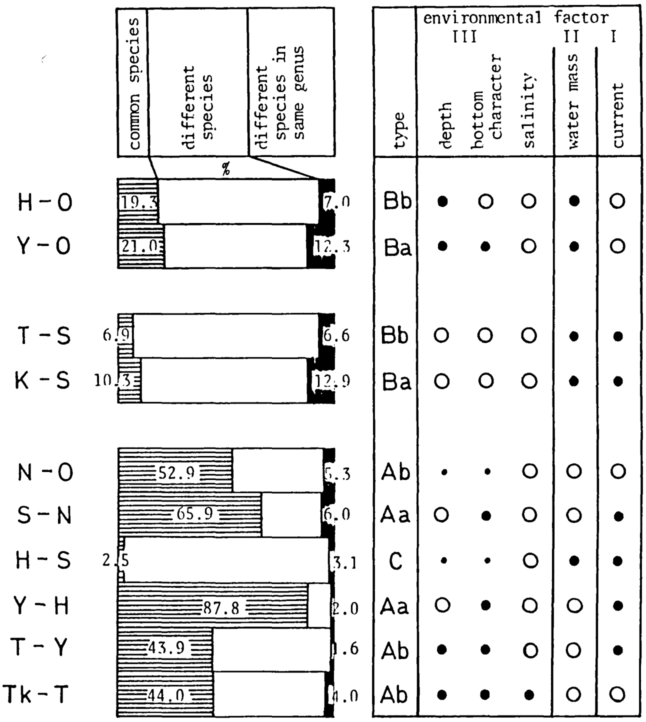


Table 2. Number of molluscan species of the Mizunami Group.

Formation	Number of species
the whole	570
Tsukiyoshi Member	63
Asano Facies	43
Kujiri Facies	130
Togari Member	75
Sakurado Facies	45
Yamanouchi Member	123
Hazama Member	49
Hida Facies	44
Shukunohora Facies	318
Nataki Member	252
Oidawara Member	57



Text-fig. 1. Comparison of species constitution among the members of the Mizunami Group. H: Hazama Facies, K: Kujiri Facies, N: Nataki Member, O: Oidawara Member, S: Shukunohora Facies, T: Togari Member, Tk: Tsukiyoshi Member, Y: Yamanouchi Member. Similarity in environments is shown in symbols. open circle: similar, black circle: rather different, black dot: different.

and subtype is seen in interrelation of the following members.

Type	Members or Facies
Aa	Yamanouchi – Hazama
	Shukunohora – Nataki
Ab	Tsukiyoshi – Togari
	Togari – Yamanouchi
	Nataki – Oidawara
Ba	Kujiri – Shukunohora
	Yamanouchi – Oidawara
Bb	Togari – Shukunohora
	Hazama – Oidawara
C	Hazama – Shukunohora

Type A characterized high percentage (over 40%) of the common species, especially type Aa over 65%, shows change in the constituting species between two members contacting in above and below relation. This feature is caused by change in environmental condition affected by the third (III) grade factors such as depth, bottom character and salinity. This phenomenon is easily understood because this case is common in geologic sequences controlled by transgression or regression. Type A relationship typically shows the third (III) or low grade change in temporal distribution of molluscan assemblages. Type C is characterized by occurrence of abundant different species and also shows change in the third grade.

Another feature is seen in Type B, especially in Ba which is characterized by the presence of the different species (over 12%) in the same genus. Type Bb has a little low percentage of the different species in the same genus. In the case of the Kujiri and Shukunohora Facies, I showed some examples which involve correlative but different species in *Glycymeris, Pillucina, Phacosoma, Mactra, Fabulina, Homalopoma, Turritella, Mitrella, Siphonalia, Coleophysis, Rhizorus* and so on (Itoigawa, 1974b).

As stated already, this type shows the second (II) or medium grade change affected by the second grade (water mass) or the first grade (current-water temperature) factors of environment.

And then, the first (I) or high grade change is assumed between molluscan faunas in Miocene, Pliocene and Recent. In this grade, it seems to be better to use "fauna" instead of "assemblage" as large-scaled grouping of molluscs. I already showed an example of this grade which is indicated by faunal correlation between the Miocene brackish bay fauna (so-called Potamid-Arcid fauna of Tsuda, 1965) and the living bay fauna (so-called continental coast fauna of Miyadi, Kuroda and Habe, 1953) (Itoigawa, 1974a). In this case, the third grade environmental factors are the same, but the second grade factor (current--temperature) is different between the both ages showing tropical (Miocene) and subtropical to temperate (living) conditions. Conclusive factors in the first grade change of temporal distribution are assumed to be speciation shown in bioseries and extinction. Migration may be related with the change in this grade, but is also related with the first grade change in spatial distribution. Then, the presence of influence of migration in this case is not clear.

b. Setouchi Miocene Series

There are many examples of changes in grade II and III in the Setouchi Miocene Series.

Some of them are shown in the following lines.

The Tsuzuki and the Iwamura groups have sequences shown by a cycle of sedimentation and have corresponding molluscan assemblages in them. Itoigawa (1956) recognized in the Tsuzuki Group four molluscan assemblages, *Protorotella–Anadara, Felaniella–Dosinia, Lucinoma–Acila* and *Nipponomarcia* assemblages in descending order. The succession of the assemblages represents faunal development which correlates with the cycle of sedimentation beginning from transgression and turning into regression. The Iwamura Group (the Mizunami Group in the Iwamura basin of Itoigawa, 1974c) and the Ichishi Group reveal the same phenomena found in the Tsuzuki (Shibata, 1978). In the case of the Bihoku Group, it is seen in the relationship between assemblages of the lower member (the *Vasticardium–Phacosoma*) and the upper member (the *Palliolum–Fissidentalium*) of the group. Change of the same pattern is recognized between the both assemblages (Itoigawa and Nishikawa, 1976).

Spatial distribution of the molluscan assemblages in the Setouchi Miocene Series

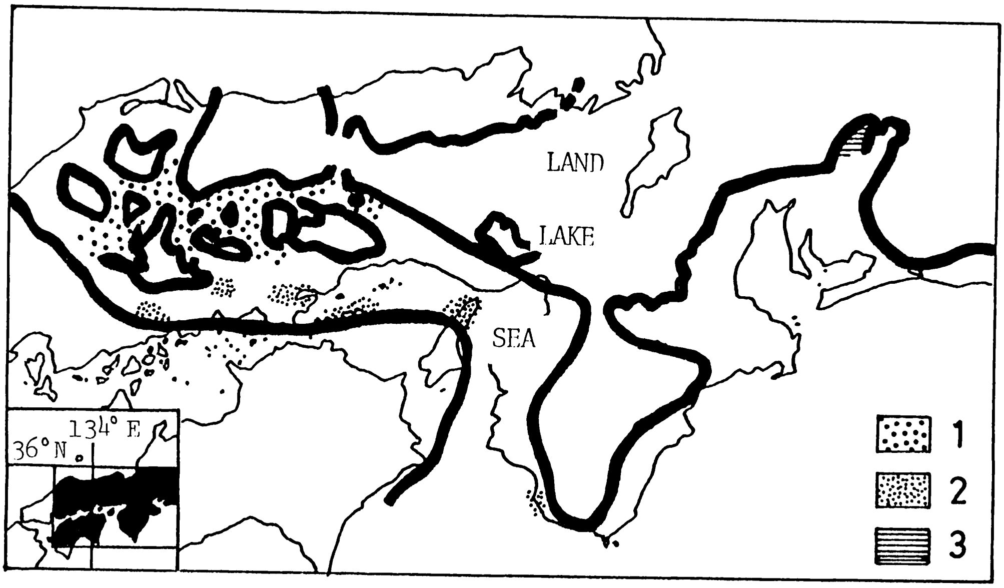
The pattern in the temporal distribution is easily recognized to be the same as that in the spatial distribution for the Setouchi Miocene Series. The Kujiri Facies occupies the lower part of the Akeyo Formation of the Mizunami Group and is correlative with the Togari Member. They are similar to each other in lithology but different in assemblage (Itoigawa *et al.*, 1981), the *Nipponamarcia* (Togari) and the *Glycymeris–Turritella* (Kujiri). Comparison of constitution between the both assemblages is as follows:

common species	48.5%
different species	49.5
different species in the same genus	2.3

This is similar to the pattern of Type Ab seen in the temporal change and shows the third grade change affected by the third grade factors of environment. This situation is the same for relationship between various members which stand side by side geographically. For example, the Hazama Member–the Hida Facies (the former has the *Macoma–Ennucula* assemblage and the latter has the *Cyclina–Phacosoma,* the *Phacosoma–Turreitella* and the *Macoma–Cyclocardia* assemblages) (Itoigawa *et al.,* 1981) and two facies (fine sandstone to siltstone and shelly limestone) of the lower Bihoku Group in the Tsuetate area of Okayama Prefecture which have *Saxolucina–Tateiwaia* and *Turbo–Chlamys* assemblages respectively (Itoigawa and Nishikawa, 1976) are in the same relationship.

The second grade change is presented in Fig. 2. This shows the paleogeography and distribution of molluscan assemblages in the Setouchi geologic province in the early Middle Miocene (15–16 Ma). We can distinguish three molluscan assemblages in the area. They are the *Vasticardium,* the *Mactra–Acila* and the *Cavilucina–Polinices* assemblages. The difference in the distribution of these three assemblages represents the difference in the second grade. Then, this pattern shows the second grade change in space.

The first grade change in spatial distribution is not recognized in the extension of the Setouchi Miocene Series. It will be discussed later for the larger extent of the Japanese Islands.



Text-fig. 2. Paleogeography and distribution of molluscan assemblages in the Setouchi geologic province in the early Middle Miocene (15 to 16 Ma). 1: *Vasticardium* assemblage, 2: *Mactra – Acila* assemblage, 3: *Cavilucina – Polinices* Assemblage.

Discussion

The third grade change in temporal and spatial distribution is commonly discovered in late Cenozoic and living molluscan faunas in Japan. Relationship between mangrove swamp and coral reef assemblages in present seas is a typical case in spatial distribution (Tsuda *et al.*, 1981).

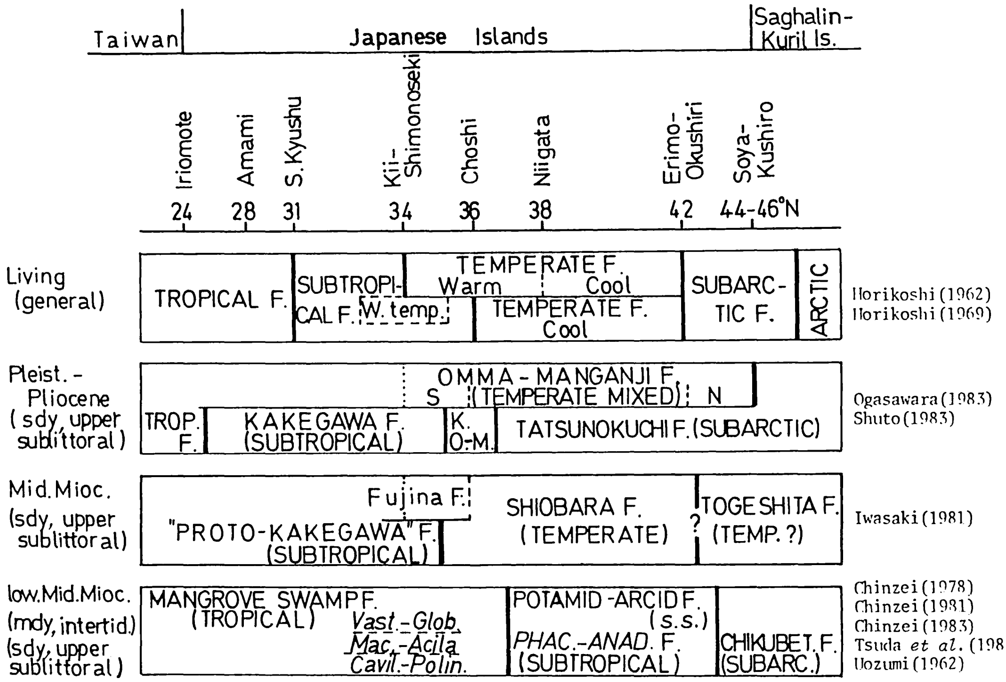
Chinzei (1981) showed lateral distribution of three associations (nearly equal to the assemblage in this paper) *Glycymeris rotunda– Venus foveolata, Nassaria magnifica* and *Limopsis tajimae* in the same horizon (T_3 horizon) of the Pliocene Kakegawa Group. The distribution is from the northwest to the southeast showing a deepening process of the sea from the upper to lower sublittoral zones. This is one of the third grade change in spatial distribution. Relation between so-called Shiobara and Yama type faunas (Iwasaki, 1981), correlative assemblages in sandy and muddy facies, shows the third grade spatial change in the Middle Miocene, too.

Change of the assemblages from I to IV recognized by Tsuda (1960) in the Middle Miocene Kurosedani fauna is equivalent to the third grade change in temporal distribution in general. The succession of the Higashi-innai Formation (Masuda, 1966) in the Middle Miocene is also the same.

The first and the second grade spatial changes are shown in Fig. 3. From the lower Middle Miocene to the living, faunal regions are recognized in each age.

There are some controlling factors for these divisions, but the first grade environmental factor, current, is predominant. Some divisions are ambiguous as the case of the Shiobara and the Togeshita faunas. The boundary between both faunas is possibly considered to be the first grade change.

The boundary of each grade is different. The boundary of the first grade change is not sharp as seen between the mangrove swamp fauna and the Potamid-Arcid fauna or between the



Text-fig. 3. The first and the second grades spatial change around the Japanese Islands from the Miocene to Recent. Solid line shows the boundary of the first grade.

latter and the Chikubetsu fauna in the early Middle Miocene. The Kanto type Omma-Manganji fauna (Ogasawara, 1983) existing between the Kakegawa fauna and the Tatsunokuchi fauna may show the second grade change. Similar feature of this kind of indistinct boundary is seen in muddy bottom environment in the lower sublittoral to bathyal zone of seas around the Japanese Islands from the Miocene to the present.

Chinzei and Iwasaki (1967), Chinzei (1978, 1984) showed the idea of "temporal parallelism". According to Chinzei (1984), this is indicated by "the existence of correlative associations of different ages and different species belonging to the same genus or ecologically allied genera".

This idea is similar to the first and the second grade changes in temporal distribution of my idea but is slightly different from both grades. In my opinion, the first grade change in temporal distribution is recognized when the second and the third grade environmental factors are the same.

"Temporal parallelism" occurs even when environmental factors of the second grade are different. Compared with the second grade change in my idea, temporal extension is large in the "temporal parallelism". Speciation is insignificant in the second grade change.

There is a fundamental difference in both ideas, namely, difference in the idea of speciation. Chinzei explained that species of the southern genera in the Middle Miocene Shiobara type fauna are considered to be the same, or direct descendent of the species that appeared in the early Middle Miocene Kadonosawa fauna, and the southern elements in the warm early Middle Miocene remained in the same areas and adapted themselves to the cold condition of the Middle Miocene.

Table 3. Three grades in spatial and temporal change of molluscan assemblage.

		grade	first (I) (high grade)	second (II) (medium grade)	third (III) (low grade)
change in distribution of assemblage	temporal	main cause	speciation extinction (migration)	change in environmental condition	
				grade I (current) grade II (water mass)	grade III (depth, bottom character salinity, habitat etc.)
		order of time range	10^7-10^6 years	10^6 y	10^5 y–
		grade in geologic formation	group	formation	member
	spatial	main cause	change in environmental condition		
			grade I (and II)	grade II (and I)	grade III
		order of distance	10^3-10^2 km	10^2-10 km	10 km
		grade in geologic formation	supergroup–group	group–formation	member–facies

I have no conclusive evidence for this speciation by adaptation. This is concerned with speciation and migration. These are basic problems in zoogeography, and will be dealt with in the future.

Tsuchi (1976) recognized bioserial change in some molluscan genera in the Kakegawa Group. Species differentiation is visible in the time range of about 4 to 0.5 Ma. These occur in *Amussiopecten, Glycymeris, Suchium, Turritella* and *Nassaria* under the same environmental conditions (sandy bottom, upper sublittoral zone, subtropical region–influence of the proto-Kuroshio current). This fact may be effective for the interpretation of the first grade change in temporal distribution.

I again represent in Table 3 the revised idea of grade in change of fossil molluscan assemblage. It might still be incomplete and can be revised with new data.

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PART II

ORIGIN AND MIGRATION OF SOME MOLLUSCAN TAXAS

The present part contains five papers on origin and migration of some Cenozoic molluscan taxa in the Japanese Islands. Included are studies of the arcids by H. Noda, the glycymerids by A. Matsukuma, the pectinids by K. Masuda, the turritellids by T. Kotaka and the pteropods by S. Shibata. These molluscan taxa are some of the most useful ones for deciphering Cenozoic paleogeographic and geologic events in region.

Noda discusses the origin of Neogene *Anadara,* especially *Hawaiarca,* which is known from the Pliocene to Recent in the Japanese Islands, from the Oligocene to Recent in the Indo-Pacific to Australian regions, from the Eocene to Pliocene in the East Coast of North America (including the Caribbean Sea) and from the Oligocene and Miocene in the West Coast of North America. He also suggests that *Hawaiarca* may be phylogenetically intermediate between *Arca* and *Anadara.* Noda further notes that the Japanese *Hawaiarca* immigrated into Japanese waters from the south in the Early Pliocene, but that Paleogene *Hawaiarca* are presently so confused with other arcid genera that their biogeographic history is unclear.

Matsukuma relates the origin of glycymerid bivalves including 17 living and about 40 fossil species from the Japanese Islands and adjacent waters. He recognizes three components among living Japanese species: (1) the tropical Indo-Pacific elements, (2) the warm temperate Japanese–Korean endemic elements, and (3) cool temperate and subarctic East Asian elements. He points out that Japanese Recent species are descended from Neogene glycymerids that were warm water inhabitants.

Masuda describes and illustrates comprehensively the pattern on migration of Neogene pectinids in the northern Pacific region, based on numerous species in and around the Japanese Islands. He points out that the Early Miocene pectinids in the Japanese Islands are immigrants from the Mediterranean region through Southeast Asia and also from the "Pacific Basin" area, and that few genera migrated to subsequently western North America in the late Middle to Late Miocene. Masuda also notes that the Pliocene warm water pectinids of Japan immigrated from the Southeast Asian region as well as from the "Pacific Basin" area, whereas the temperate water elements descended from the endemic Miocene pectinids and from cool and cold water species that immigrated from the northern Pacific region.

Kotaka describes two Paleogene turritellid genera of Kyushu, Japan, one of which could have originated in the Celebes Islands, Indonesia and then dispersed one stock towards Kyushu and the Ryukyus through Taiwan and the Philippines, and a second stock towards the Australia and New Zealand region during Latest Cretaceous or Earliest Paleogene time. He emphasizes that the migratory pattern of some Paleogene turritellids is very similar to that of certain groups of Indo-Pacific and Indo-European cidarid echinoids. He also notes that one of the Neogene turritellid bioseries might have originated in the Southeast Asian region and immigrated into Japanese waters during the Miocene and Pliocene along with some southern genera of Bivalvia.

Shibata describes two remarkable events that took place in the Cenozoic pteropod fauna of Central Japan during Miocene time. The first event was disappearance of most Early and Middle Miocene taxa and the first appearance of some Late Miocene and warm modern taxa. The second event was disappearance of the majority of Miocene taxa and appearance modern warm water elements.

It is very likely that several molluscan taxa immigrated into Japanese waters during Early Paleogene and Early Neogene times from southern regions, including the southern hemisphere. The Early Miocene molluscan fauna especially is characterized by an abrupt increase in the introduction of new molluscan genera. Subsequently, some molluscan genera immigrated into the Japanese waters from adjacent regions and, at the same time, some other taxa emigrated to the West Coast of North America through Sakhalin and Kamchatka during late Middle to Late Miocene time. During Pliocene time, relatively few taxa immigrated into Japan. It is evident that the historical changes in migratory paleozoogeographic patterns described by the authors mentioned above agree well with the climatic changes during Neogene time in the western Pacific.

(Koichiro MASUDA)

ORIGIN AND MIGRATION OF *ANADARA*
— ESPECIALLY THE GENUS *HAWAIARCA* (Bivalvia) —

By

Hiroshi NODA

Introduction

The main purpose of the present article is to discuss the origin and migration of *Anadara* in relation to *Hawaiarca.*

The first appearance of *Anadara* s.s. and its relation to possible ancestral taxa have long been debated. Several species have been described in *Anadara* s.s. from Paleogene fauna in Europe, the U.S.A. and the Caribbean regions. *Anadara* s.l. species radiated quickly during the Neogene. The Paleogene to Recent *Hawaiarca* appears to be intimately related to the genus *Anadara* s.s. Worldwide species of *Hawaiarca* and their inferred relationships to the origin of *Anadara* s.s. are described herein.

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Taxonomic discussion on *Hawaiarca*

The genus *Hawaiarca* was proposed for the modern species, *Hawaiarca rectangula,* dredged at the depth of 49–176 fathoms in Alenuihaha Channel between the islands of Hawaii and Maui, and described by Dall, Bartsch and Rehder in 1938 (Pl. 3, figs. 3–5). Along with this original description, another new species, *H. alia* was also proposed; it has been collected from a depth of 25–50 fathoms along the northern coast of Hawaii. Following this proposal of the genus and species, there were no further records of modern and fossil *Hawaiarca* species except from the neighborhood of Japan.

The genus *Hawaiarca* was originally defined as follows;

> "Shell small, rectangular, with the umbones anterior to the middle. The exterior is marked by heavy, decidedly elevated, almost flattend, and almost vertical-sided, radiating ribs and concentric cords, the latter render the ribs strongly nodulose, the nodules having their long axes parallel with the concentric sculpture. Periostrucum thin, translucent. Edge of shell scalloped. Ligamental area narrow; the posterior part much longer than the anterior, marked by a number of grooves. Hinge narrow, toothed throughout its entire length".

Additional morphological characters are provided herein. The most characteristic features of *Hawaiarca* are a medial sulcus (medial depression) extending from near the umbo to the middle part of the ventral margin, narrower or finner radial ribs on this ventral sulcus in comparison with those of the anterior and posterior sides, ribs sometimes bifrucated and with interstitial riblets on an around the medial depression, and a smooth or nearly smooth inner ventral margin at the depression. External radial ribs and inner crenulation are similar to those of *Anadara* except for those of medial depression. The external radial ribs are rather stout and flat-topped, 25–35 in general number without internal secondary riblets except on the medial sulcus. Longitudinal bifurcation on ribs is not very distinct except only for the ventral margin and medial depression. The genus *Hawaiarca* was once questionally considered to be synonymous with *Barbatia* as was *Nipponarca* by Cox *et al.* (1969). However, *Hawaiarca* has more distinct *Anadara*-like radial ribs and a small number of radial ribs with nodulous fine radial ribs. *Scapharca* has a medial depression but only in its young stage and no smooth nor nearly smooth ventral inner margin at the portion of medial depression. *Hawaiarca* does not reach the size of *Anadara* and *Scapharca. Hawaiarca* has no posterior depression with keel from the beak to posterior ventral corner, as does *Arca,* though the shell form is trapezoidal elongated. *Anadara* and *Scapharca* have smoothly rounded external profile but no smooth nor nearly smooth internal ventral margin at the medial depression.

Some European genera such as *Pectinatarca* Sacco, 1898 and *Soldania* Stephani and Pantanell, 1878, the American genus *Jacksonarca* Harris and Palmer, 1946, and the Australian genus *Miratacar* Iredale, 1939 are very similar to *Hawaiarca* in the shape of radial ribs, shell form and inner ventral features. Cox *et al.* (1969) considered all of those genera except for only *Pectinatarca* are synonymous with *Barbatia* Gray, 1842. The morphological features of *Hawaiarca* are very characteristic but are also common to or intermediate with those of *Anadara, Scapharca, Barbatia* as shown in Table 1. This shows *Hawaiarca* is intermediate between Arcinae and Anadarinae.

The genus *Hawaiarca* was originally described in the family Arcidae Lamarck, 1808 by Dall *et al.* in 1938. However, Reinhart (1935) had already proposed dividing the family Arcidae into Arcinae and the new subfamily Anadarinae. His proposal was three years prior to the establishment of *Hawaiarca* by Dall *et al.* So the subfamilial assignment of *Hawaiarca* has remained in dispute since that time.

Table 1. Morphological comparison between Hawaiarcinae, Arcinae and Anadarinae.

	Arcinae	Hawaiarcinae	Anadarinae
Shell form	Elongate to trapezoidal	Elongate to trapezoidal	Subrounded to ovate
Shell convexity	Rather flat	Rather flat	Inflated to swollen
Radial ribs	Numerous, narrow with nodes, riblets	Flat-topped, rather stout, about 25–35 in number	Regularly spaced, flat-topped, 25–35, in number
Medial depression	Present	Present	Usually absent
Medial finer radial ribs	Present	Present	Not present
Ligamental area	Irregular, narrow to wide	Usually narrow	Usually wide, triangular
Ligamental grooves	Usually present but irregular	Usually few	Present in chevron shape
Inner crenulations	Fine or smooth	Present but smooth at medial depression	Always present, spaced according to radial ribs
Posterior keel	Present to not present	Not present	Present to not present
Hinge structure	Perpendicular to oblique	Mostly perpendicular	Mostly perpendicular

When Reinhart (1943) summarized the Mesozoic and Cenozoic Arcidae of the Pacific Slope of North America, he mentioned only that *Hawaiarca* somewhat resembles *Anadara* but is difficult to recognize outside of the Hawaiian Island and is not present in the Pacific Slope Fauna. Hawaiarcan species rather commonly occur in Japanese Pliocene formations and modern seas (Masuda and Noda, 1976, Noda, 1966, 1983) but have been classified into Arcinae, even though those Hawaiarcan species resemble *Anadara* in morphological features, as treated by Vokes (1980). *Hawaiarca* was placed as a subgenus *Anadara* within the subfamily Anadarinae by Woodring (1973), who first mentioned that several species described under different names from Miocene formations in the Panamic Province were identifiable as *Hawaiarca*. As shown in Table 1, *Hawaiarca* shares many characteristics with Arcidae but is intermediate in some of its important morphological features between *Barbatia* or *Arca* (both typical genera of Arcinae) and *Anadara* or *Scapharca* (both typical genera of Anadarinae).

In addition to the presence of morphological features common to Anadarinae and Arcinae, the geological and geographical distributions of *Hawaiarca* are also significant for describing the origin and migration of genus *Anadara*. From the evidences mentioned above, Hawaiarcinae as a new subfamily in the Family Arcidae is proposed herewith based upon the type genus *Hawaiarca* Dall, Bartsch and Rehder, 1938.

In this new subfamily, *Hawaiarca, Nipponarca* Habe, 1951 and *Miratacar* Iredale, 1939 are included. Allied genera in Europe and Caribbean genera mentioned above will be discussed in a forthcomming paper.

Many papers previously published deal with several species which could be assigned to *Hawaiarca*, as discussed below.

Recognition of Hawaiarcan species

According to the type specimens and descriptions named under the different names, it become clear that many Hawaiarcan species are distributed worldwide, ranging from Eocene to Recent. (Text-fig. 1).

1) Caribbean Province

Around the Caribbean Sea, including the Panamic Province (Woodring, 1966), several species identified with *Hawaiarca* in the present sense, were described from the Eocene to Miocene formations as mentioned below:

Eocene species: Clark (*in* Clark and Durham, 1946) described the two new species *Anadara* (*Anadara*) *carmensis* and *Anadara* (*Anadara*) *olssoni* from the Eocene Fauna Zone B and Zone C, respectively from near El Carmen, Boliver, Colombia. These are the earliest specimens named under *Anadara* s.s. This Zone B was considered to be correlative with the Talara Formation of Peru, the Bartonian age in Europe, and with the lower portion of the Jackson Formation in the southern U.S.A. by Olsson (1930). The Zone C is also considered to be correlative with the Saman Sandstone and Chira Shale of Peru; the former is of the Late Eocene age and the latter of Early Oligocene age according to Olsson (1930).

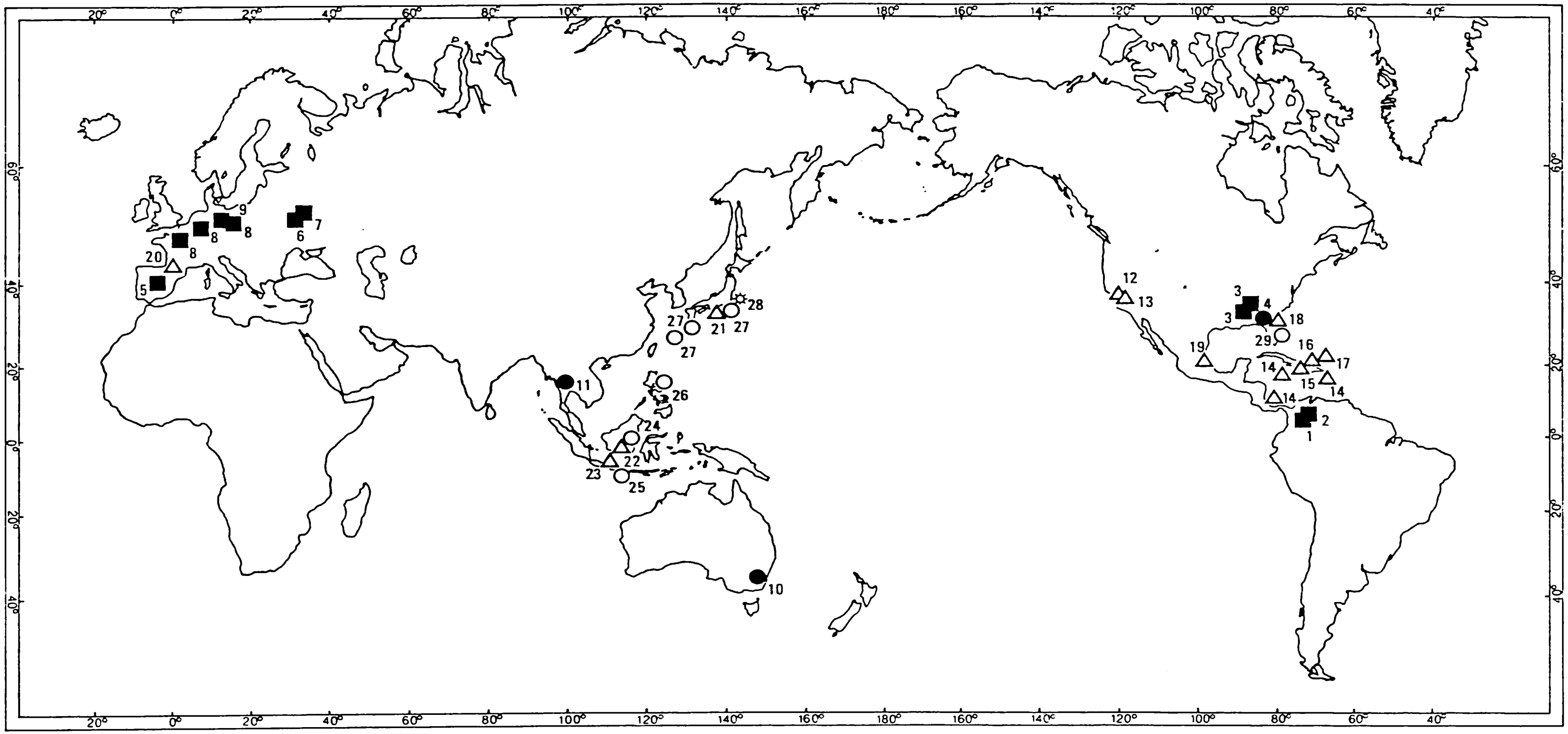
However, both species resemble each other and are referred to *Hawaiarca* because they have elongated shells with 25–30 *Anadara*-like flat-topped radial ribs and rather stout shells. Each species has medial depression and finer radial ribs on the depression, together with bifurcated ribs on the middle part of the ventral margin. The latter features are not characteristic of *Anadara* or *Scapharca,* but are typical features of *Hawaiarca.* This show that Hawaiarcan species clearly were present during the Eocene in the Caribbean Province.

Moreover, there are another species assigned to *Hawaiarca* herein which were described under the name of *Arca* with comments that the species were allied to *Barbatia* or intermediate between *Barbatia* and *Arca. Arca rhomboidella* Lea, 1833 (Pl. 3, fig. 1) described from the Eocene Clainbornian is a rather well known species in the southern part of the U.S.A. (Lea, 1833, Harris and Palmer, 1946, Sheldon, 1916). Its common features with *Hawaiarca* are rather stout radial ribs with a medial depression and narrower or finer radial ribs on the medial sulcus. The number of radial ribs is slightly larger (about 40) than those of the Colombian Eocene species mentioned above. However, the inner ventral margin at the medial depression becomes smooth, so that *A. rhomboidella,* including *Barbatia* (*Scapharca*?) *rhomboidella* of Harris and Palmer (1946), are easily transferred to *Hawaiarca* and consered to be a primitive form of the genus *Hawaiarca.*

Barbatia ludoviciana Harris, 1919 along with *Hawaiarca rhomboidella,* was also described from the same Eocene Clainbornian, but the former species is distinguished from the latter by having a distinct ventral opening, and narrow and numerous radial ribs.

Oligocene species: Some Oligocene species were already discussed by Schenck and Reinhart in 1938, but species once considered to be Oligocene *Anadara* are now considered to be of Miocene age because the Aquitanian was treated at the time as Upper Oligocene. However, there still several Oligocene species that are placed in *Hawaiarca* according to their morphological features, as noted below.

Arca invidiosa was described from the Lower Oligocene Red Bluff Formation in Mississippi, U.S.A. by Casey in 1903 (Pl. 3, fig. 13), and was first illustrated by Schenck and Rein-



Text-fig. 1. Geological and geographical distribution of Hawaiarcan species. Number corresponds with species name in Table 2.

Table 2. Geological and geographical distribution of Hawaiarcan species.

Province / Age	Indo-Pacific			Pacific Ocean, USA	Caribbean	North Europe	Mediterranean
	Australia	S-E Asia	Japan				
Recent	*H. wendti* *H. w. michaelis*		*H. uwaensis*	*H. rectangula* *H. alia*			
Pleistocene			*H. uwaensis* (28)				
Pliocene		*H. uwaensis*(26) *H. terhaari*(25) *H. nannodes*(24)	*H. uwaensis* (27)		*H. teriphera* (29)		
Miocene	⇧	*H. oostinghi* (23) *H. nannodes* (22)	*H. sp.* (21) *H. japonica*	*H. mediaimpressa*(12) *H. submontereyana*(13)	*H. veracruzuana* (19) *H. mikkula*(18) *H. guajatica* (17) *H. yaquensis* (16) *H. y. berryi* (15) *H. jamaicaensis* (14)	⇧	*H. burdigalina* (20)
Oligocene	*H. intercluthrata* (10)	·*H. sp. A.*(11)			*H. invidiosa* (4)	*H. sulcicosta* (8) *H. speyri*(9)	
Eocene					*H. olssoni*(2) *H. carmensis* (1) *H. rhomboidella* (3)	*H. appendiculata s.s.* (7) *H. a. sokolovi* (6)	*H. boschi*(5)

hart in 1938, who considered that *Arca delicatula* (described from the Lower Oligocene Vicksburgian Limestone in Mississippi) was a small form of *Arca invidiosa. Arca invidiosa* is surely identical with *Hawaiarca* by having an elongated trapezoidal shell form with 28 *Anadara*-like flat-topped radial ribs, distinct medial sulcus from the umbo to ventral margin, and a smooth inncer ventral margin at the ventral depression. These are no another Hawaiarcan species in the Oligocene of Caribbean Province, but it is very interesting to note that *Arca mississippiensis* Conrad, 1848 (non *Byssoarca mississippiensis* Conrad, 1848), sometimes called *Arca lesueri* Dall, 1898, dominantly occurs in the Vicksburg Beds, Lower Oligocene Vicksburgian in Mississippi, and is almost identical with *Anadara* or *Scapharca.* Schenck and Reinhart (1938) once considered it to be *Scapharca.* As Eames (1967a, b) said that *Anadara* s.s. is restricted in the Neogene and does not occur in the Paleogene, the record of *A. mississippiensis* should be checked again.

Miocene species: There are several Hawaiarcan species formerly placed in different genera such as *Barbatia* and *Arca* from Middle Miocene formations in the Caribbean Province.

Arca (*Arca*) *yaquensis berryi,* which was originally described from the Middle Miocene Bowden Formation in Jamaica by Woodring in 1925 (Pl. 4, figs. 5, 6) is well identified with *Hawaiarca* because of its trapezoidal shell form with a contracted medial part, narrower radial ribs on the sulcus, compared with those of the anterior and posterior sides, and a smooth surface along the internal margin of medial depression. Moreover, the species has secondary radial ribs on the medial depression. This species occurs in association with *Barbatia* (*Dilvarca*) *donacia* (Dall) according to Woodring (1925, p. 48–49, pl. 5, figs. 10–11), although Woodring's figures do not match the original description of *Scapharca* (*Scapharca*) *donacia* of Dall

(1898), which is rather common in Caribbean Miocene formations. Woodring (1925) described this species as follows;

> "The umbo of most right valves bears a shallow narrow groove. Toward the ventral margin, this groove broadens and slightly emarginates the base. On the left valve the groove is absent or obscure. The ribs (4 to 6) in the groove, and in a corresponding position on left valves, are narrower and flatter than the others."

These features, especially the medial depression with finer and secondary radial ribs on this depression, and 24 flat-topped *Anadara*-like radial ribs are enough to identify the species with *Hawaiarca. Scapharca donacia* of Dall (1898) as mentioned above, has no medial sulcus and narrower or finer medial ribs, so the species is easily distinguished from the Woodring's *Barbatia donacia.* The latter species is given the new name *Hawaiarca jamaicaensis,* proposed herein (Pl. 4, fig. 7). The speciemen of Woodring (1925) shown in his figs. 10–11 of plate 5 very much resembles the Eocene Hawaiarcan species, *H. carmensis* and the late Eocene to Early Oligocene species, *H. olssoni,* as mentioned above.

Arca yaquensis Maury, 1917a which was originally described from the Lower Miocene Bluffs 2 and 3, Cercado de Mao Zone I, Rio Cana at Camito, Santo Domingo (Pl. 4, figs. 8, 9, 18) is identical with *Hawaiarca* by having a small elongated shell form, a medial depression from umbo to ventral margin with *Anadara*-like flat-topped radial ribs. *Scapharca cibaoica,* also newly described from the same beds by Maury (1917a) has some resemblance with *Hawaiarca* by its *Anadara*-like radial ribs and medial depression, but its inequilateral shell form is far from that of Hawaiarcan species.

Arca (*Scapharca*) cf. *donacia* Dall described from the Upper Oligocene Quebradrillas Limestone in Puerto Rico by Hubbard (1920, p. 105, pl. 15, figs. 6–7) is well identified with *Hawaiarca jamaicaensis,* n.n. in having a similar shell form, 27 *Anadara*-like flat-topped radial ribs with a medial depression. *Hawaiarca jamaicaensis* was distributed in the Caribbean Sea Late Oligocene to Middle Miocene. *Barbatia* cf. *bonaczyi,* also described from the same locality of the above species in Puerto Rico by Hubbard (1920, p. 106, pl. 14, fig. 4), but which is different from the specimen illustrated by Maury (1917a) under the same species name from Santo Domingo, has a medial depression, and narrower and finer radial ribs on the depression compared to the anterior and posterior sides, but it has a greater number of radial ribs and finer radial ribs crossing the growth lines. So this species remains for future study.

Arca (*Scapharca*) *quajatica* Sheldon and Maury (*in* Maury, 1920), described from the Upper Oligocene Quebradillas Limestone in Puerto Rico (Maury, 1920), has a medial depression extending from near the umbo to ventral margin, with 27–28 narrow and flat-topped radial ribs, and narrower or finer radial ribs on the medial depression. The species is well identified with *Hawaiarca,* as already mentioned by Woodring (1973). From the Middle Miocene Aquequezquite Formation of Vercruz, Mexico, in the western marginal part of the Panamic Province, *Anadara* (*Rasia*) *veracruzana* was originally described by Perrilliat in 1976 (Pl. 4, fig. 7). The species has a medial depression with 30–33 distinct *Anadara*-like radial ribs and a smooth medial internal ventral margin at the depression. Species with such morphological features are common in *Hawaiarca.*

Arca (*Scapharca*) *mikkula* Gardner, 1926 described from the Miocene Chipola Formation of the Alum Bluff Group in Florida, U.S.A. has a narrow medial depression with *Anadara*-like radial ribs and is identical with *Hawaiarca.*

Pliocene species: Only one species, *Arca triphera* Dall, originally described from the Pliocene Marls of the Caloosahatchee River, Florida, U.S.A., in 1898 (Pl. 4, fig. 12) is Pliocene *Ha-*

waiarca species. The species has elongated subquadrate shell form, 38 *Anadara*-like radial ribs, narrower and finer radial ribs on the medial depression with a smooth surface along its inner ventral margin.

Several paleontological papers have treated modern species together with the fossil arcids in the Caribbean Province, but there are no Pleistocene and Recent species identical with *Hawaiarca.*

2) Pacific Ocean side of the United States of America

Along the long Pacific Ocean sea coast of the United States, thick Cenozoic sediments are well developed, although there are no fossil or modern species of *Hawaiarca,* as mentioned by Reinhart in 1943. Among the many species of *Anadara* and/or *Arca* described from the Cenozoic formations in the Pacific Ocean sea coast area, the following two species are referred to *Hawaiarca.* They are *Arca mediaimpressa* s.s. and *Arca mediaimpressa submontereyana,* both species described from the Lower Miocene San Ramon Formation in California by Clark in 1918. The formation at that time was considered to be Oligocene but Addicott (1967) revised the age to Early Miocene based upon the molluscan fauna. *Arca mediaimpressa* s.s. has 27–29 *Anadara*-like stout and flat-topped radial ribs (Pl. 4, fig. 17). However, as already mentioned by Schenck and Reinhart (1938), the species has "slight umbonal depression extends from top of beak halfway to ventral margin". The external surface of the species mostly seems to be like *Anadara* or *Scapharca,* but the radial ribs on the medial part are slightly finer than those of their anterior and posterior sides which is common in *Hawaiarca* but not in *Anadara* nor *Scapharca.* Since the type specimen of *Arca mediaimpressa submontereyana* of Clark (1918) was very poorly preserved, Addicott (1973, p. 23–24, pl. 1, figs. 6–7, 16–17) illustrated the well preserved specimens under the name of *Anadara* (*Anadara*) *submontereyana* from the Middle Miocene Temblor Formation in California. This specimens show the very characteristic features of *Hawaiarca,* shown by a medial depression with 21–25 *Anadara*-like flat-topped distinct radial ribs. However, both specimens mentioned above mostly allied to *Anadara* and/or *Scapharca* in having the stout radial ribs and similar shell form with rather inflated shell form.

The unnamed species *Anadara* sp. C of Reinhart (1943) which was re-illustrated by Hickman (1969, pl. 1, figs. 16–18) under the name of *Anadara* n. sp. is known from the Eugene Formation in Oregon. The Eugene Formation was considered to be of Oligocene age by Reinhart (1943), Hickman (1969) and others. The specimen is poorly preserved but the re-illustration by Hickman (1969) shows that it very much resembles *Anadara,* by having a smoothly swollen shell form with flat-topped, sometimes bifurcated radial ribs with no ventral sulcation or irregularity of sculpture. After the specimen was discovered from the Eugene Formation by Schenck and Reinhart in 1938, there have been no subsequent finds, so a more detail examination of its geological occurrence is necessary. No other Hawaiarcan species are known from this area.

3) Northern Europe Area

In the northern part of Europe, there are several species identified with *Hawaiarca.*

Arca sulcicosta Nyst, 1836 is rather commonly known from the Oligocene to Lower Miocene formations in Belgium, Germany, Austria and Holland according to Schenck and Reinhart (1938) and Eames (1967c). The species was once considered to be *Barbatia* by Eames (1967c) because of its distinct median depression. This species (Pl. 3, figs. 6, 7) has wide variation in shell form but usually has continuous medial depression from umbo to ventral margin, narrower or finer radial ribs on the medial depression, flat-topped low radial ribs about 27–33 in number, with bifurcation on the middle ventral border, and a rather wide ligamental area with chevron shaped grooves like those *Anadara.* The species has also smooth internal ventral margin at the internal depression, so the species is well identified with *Hawaiarca.*

Arca sulcicosta var. *carmensis* Koenen, 1893 which is considered to be synonymous with the former species, was described from the Lower Oligocene formation in Germany and is also referred to *Hawaiarca* by having a medial depression, narrower radial ribs on the medial depression and a smooth inner ventral margin at the depression.

Anadara (*Rasia*) *nederlandica* Eames, 1967a from the Oligocene of Holland, is also allied to *Hawaiarca* species but is difficult to decide its generic assignment until well preserved specimens can be examined. No another species identifiable to *Hawaiarca* are recorded from this area.

4) Mediterranean Province

Only a few species could be identified with *Hawaiarca* from Eocene and Miocene in this province.

Eocene species: Only one species questionably identified herewith *Hawaiarca* was illustrated by Staid-Staad (1964) from the Eocene Biarritziense Formation to west of Vich, Spain under the name of *Arca* (*Acar*) *boschi,* n.sp. The species is elongated trapezoidal in form with *Anadara*-like radial ribs and ventral depression with narrower radial ribs. This species is only questionably assigned to *Hawaiarca,* because the inner ventral features are uncertain, but this species may be the lowest occurrence of *Hawaiarca* in this province if the species is correctly referred to *Hawaiarca.*

Miocene species: Among the numerous anadarid species in the Mediterranean Province, only one species could be referred to *Hawaiarca. Arca burdigalina* Mayr, 1861 which was originally described from the Middle Miocene Burdigalien in France has 28–30 radial ribs with medial depression, and smooth and narrower internal ventral margin at the medial depression. The radial ribs on the medial depression become finer and narrower than those of the anterior and posterior sides. The species resembles somewhat young specimens of *Pectinatarca pectinata* and *Soldania mytiloides,* but the size and inner ventral features are different from the latter two species. *Hawaiarca burdigalina* is well illustrated by Cossmann and Peyrot (1912) under the name of *Arca* (*Pectinatarca*) *burdigalina* and said to occur in the Aquitanian to Burdigalien. No other species identified with *Hawaiarca* was discovered from this area.

5) Australian Province

In the Australian Province, the southeastern part of the Indo-Pacific Province, only one fossil species is identified with *Hawaiarca* herein. *Anadara interclathurata* which was originally described from the Jan Juc Formation (Janjukian, Upper Oligocene) in Victoria, Australia by Ludbrook in 1965 (Pl. 4, figs. 10, 11) is referred to *Hawaiarca.* The species has 22–24 rather strong *Anadara*-like radial ribs, medial depression from umbo to ventral margin, narrower radial ribs on the depression, smooth inner ventral margin along the depression, and *Anadara*-like ligamental area. One paratype specimen (Ludbrook, 1965, pl. 4, figs. 9–10) appears to be a typical form of *Hawaiarca* and resembles the Caribbean species in the shell form and radial ribs. The formation after the description of the species was re-examined for the age determination by foraminifers, and it was correlated to be Miocene by Eames (1967c).

Recent species: Iredale proposed a new genus and a new subspecies, *Miratacar wendti michaelis,* collected from Michaelmas Cay in the Great Barrier Reef Expedition, in 1939. This subspecies may be identical with *Arca wendti* Lamy (1907a, b, p. 45–47, pl. 1, figs. 11–13) which is rather widely distributed in the Indo-Pacific to Australian provinces as mentioned by Prashad (1932). This species has a trapezoidal elongated shell form with a medial depression, flat-topped radial ribs about 20–25 in number, finer radial ribs on the medial depression and a smooth inner ventral margin at the medial depression. This species by the features mentioned above is referred to *Hawaiarca.*

6) Indo-Pacific Province

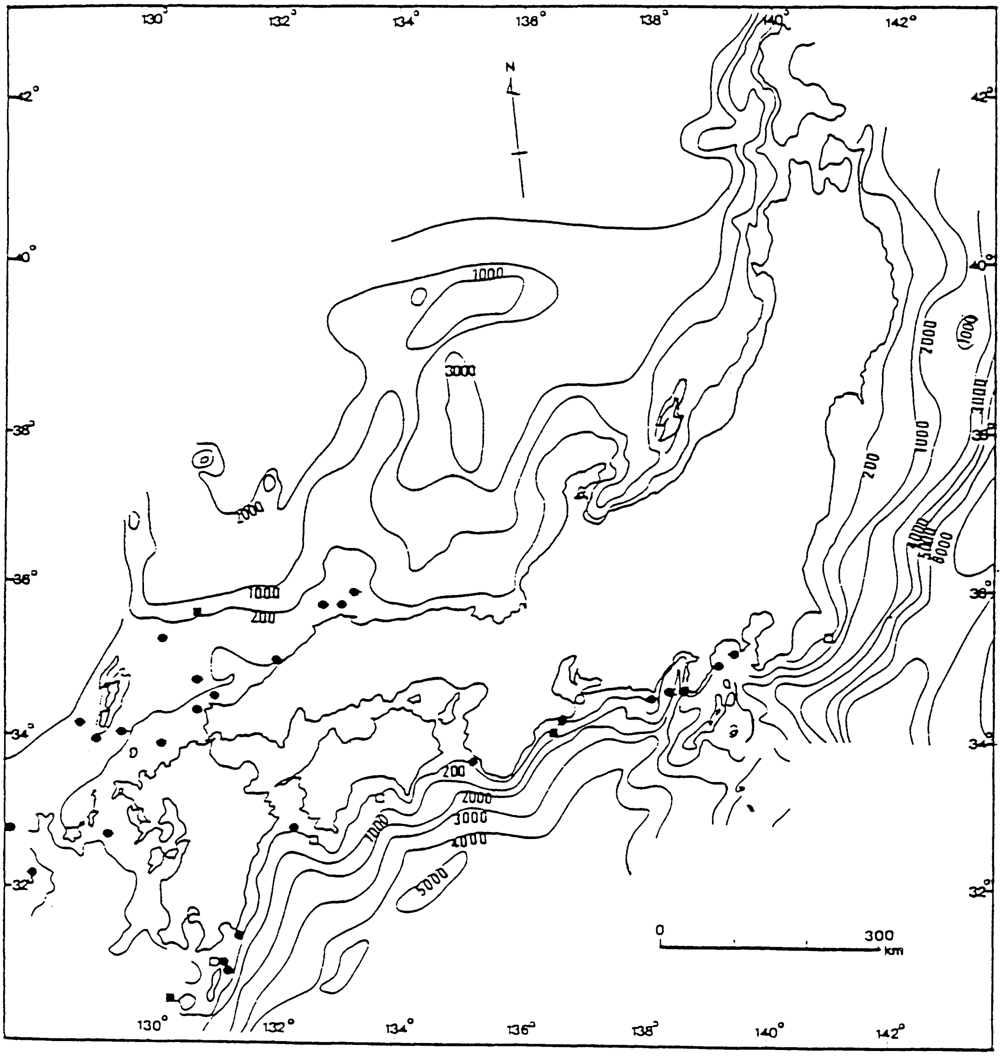
Miocene species: Itoigawa *et al.* (1981) and Taguchi (1983) reported *Nipponoarca* sp. from the Middle Miocene Akeyo Formation, Gifu Prefecture, central part of Japan and *Nipponarca japonica,* n. sp. from the Middle Miocene Yoshino Formation in Okayama Prefecture, southwestern part of Japan, respectively. Both species have an elongated shell form with *Anadara*-like flat-topped radial ribs, finer radial ribs on the medial depression and a smooth ventral inner margin of the medial depression. These features are characteristics of *Hawaiarca* and the both species are probably conspecific. The Miocene species *Arca metabiostrigata* described from Burma by Noetling (1909) and allied species which are probably referred *Hawaiarca* are mentioned in the following section.

Beet (1941) described *Arca* (*Barbatia*) *oostinghi* from the Late Miocene Menkrawitschichten (Neogene f_3 of Leupold and Vlerk, 1931) in East Borneo. The species is well identified with *Hawaiarca* in having an elongatedly trapezoidal shell form, 29–31 *Aradara*-like flat-topped radial ribs with finer or narrower radial ribs on the medial depression, and a smooth and narrow internal ventral margin of the depression. Other Miocene species are not known from this province but *Arca nannodes,* discussed below under the name of *Hawaiarca* occurred from the Miocene to Pliocene in Burma and Java.

Pliocene species: Habe (1951) first recognized the genus *Hawaiarca uwaensis* originally described from the Pliocene Takanabe Formation in Miyazaki Prefecture, southern Kyushu by Yokoyama (1928) under the name of *Arca uwaensis.* The species has elongatedly trapezoidal shell form, 17–28 flat-topped radial ribs, medial depression from umbo to ventral margin, narrower and finer radial ribs on the depression, and smooth and narrow inner ventral margin at the portion of medial depression. The species is well identical with *Hawaiarca* as stated by Habe (1951). *Hawaiarca uwaensis* is distributed in the southwestern part (Pl. 3, figs. 10–12) of Japan (Masuda and Noda, 1976, Noda, 1980, 1983, 1984) and ranging up to Recent (Text-fig. 2).

Arca nannodes Martin originally described from the Pliocene of Timor (1887) is well referred to *Hawaiarca* in having medial depression with 25–26 *Anadara*-like flat-topped radial ribs, narrower ribs on the medial depression, and narrow and slightly smooth inner ventral margin at the depression. According to Vlerk (1931), this species ranges from the Miocene to Pliocene in Java. Noetling (1901) described this species from the Miocene *Arca theobaldi* Zone in Burma.

Recent species: Habe (1951, 1977) mentioned that there are two living *Hawaiarca* species in Japan; *H. uwaensis* ranging from Pliocene and *H. yamamotoi* described from off Fukue,



Text-fig. 2. Distribution of the modern species *Hawaiarca uwaensis*, compiled from data of Habe (1958) and Horikoshi (1982).

○ = Shallower than 50m; ● = shallower than 200m;

□ = Shallower than 400m; ■ = shallower than 500m.

northern Kyushu by Sakurai and Habe (*in* Habe, 1961). However, the latter species could be refer to *Barbatia* because its finer beaded and much number of radial ribs. Modern species of *H. uwaensis* is mostly recorded at the depth of 50–200 m (Noda, 1983 and Text-fig. 2).

Notes on *Nipponarca*

The genus *Nipponarca* was originally proposed by Habe in 1951 based upon the modern type species *Arca bistrigata* Dunker. This species is known commonly in the Pleistocene Narita Formation (Pl. 3, fig. 14) and its correlative formations in the Kanto district, central Japan and is known from the shallow sea of southwestern Japan (Habe, 1977). The species has a medial depression with flat-topped radial ribs being sometimes bifurcated and beaded, finer radial ribs on the medial depression, a wide ligamental area with chevron shaped ligamental grooves, and a smooth inner ventral margin at the medial depression. The morphological features are very similar with those of *Hawaiarca.* The present writer inclines to conclude that both genera are synonymous, since the type species *A. bistrigata* is distinguished from type species *Hawaiarca uwaensis* in having a higher and more swollen shell form, more distinct ventral sulcus, distinct bifurcated radial ribs, wide ligamental area and more widely smooth inner ventral margin of sulcus. Based upon this recognition, there are several fossil species which are described under the different names and will be discussed below.

The probable earliest species of *Nipponarca* was collected from the Oligocene Okmintag Sandstone in Burma by the late Yuji Bando of Kagawa University. The species has 27–28 flat-topped radial ribs being bifurcated except at the anterior and posterior ends of the shell, the medial depression from umbo to ventral margin becoming wider on the marginal part, a low triangular ligamental area and small but perpendicular teeth; its inner features are unknown. The species is treated herein as *Hawaiarca* sp. A. (Pl. 4, fig. 18).

Noetling (1901) described *Arca bistrigata* and *Arca metabiostrigata* from the Miocene *Arca theobaldi* Zone in Burma but both species are very difficult to identify with *Arca bistrigata* or its allied species, and also with *Hawaiarca.* However, *Arca bistrigata* described by Martin (1887, 1901) and the associated species *Arca sinuata* Martin (1887) from the Pliocene of Java have characteristics very similar to "*Nipponarca*", in their dichotomous radial ribs on the medial part to swollen posterior part and in a medial depression with finer radial ribs. *Arca bistrigata* is distributed from the Late Miocene to Recent (Pl. 3, figs. 16, 17) in Southeast Asia up to southern part of Japan. Another modern species, *Arca signata* Dunker, illustrated by Lamy (1907b), and *A. fisheri* Lamy (1907b) are also included in the definition of "*Nipponarca*" of the *Arca bistrigata* group. From the shell size and degree of the bifurcation of radial ribs, the *A. bistrigata* group is recorded from the Oligocene shown by *Hawaiarca* sp. A in Burma to Recent, mentioned above as ranging in Southeast Asia to southern Japan.

Consideration of the origin of *Anadara*

For a long time, the Neogene *Anadara* s.s. was considered to have originated from some genus of Mesozoic arcid or barbatid by Cox *et al.* (1969) and Noda (1966) but there was big morphological gap. However, *Anadara* s.s. is accepted to have developed in a burst of worldwide species radiation during Neogene time, and Paleogene occurrences of *Anadara* s.s. were all questioned by Eames (1967b). However, *Hawaiarca* is herein inferred to be the ancestral form of Neogene *Anadara* s.s. and also of *Scapharca,* because *Hawaiarca* has intermediate morphological features of Anadarinae and Arcinae as shown in Table 1, and also occurs at earlier geological horizons than *Anadara* and *Scapharca.* The smooth inner ventral margin along only on the portion of medial depression suggests that their living habitats are nearly same with those of *Barbatia* or *Arca,* and its flat-topped and stout radial ribs and ligamental area and also teeth arrangement are mostly similar with those of *Anadara* or *Scapharca.* The umbonal sulcus in *Scapharca* is recognized only in immature stage but its function in the early stage of life history is a meaningful relationship with *Hawaiarca.*

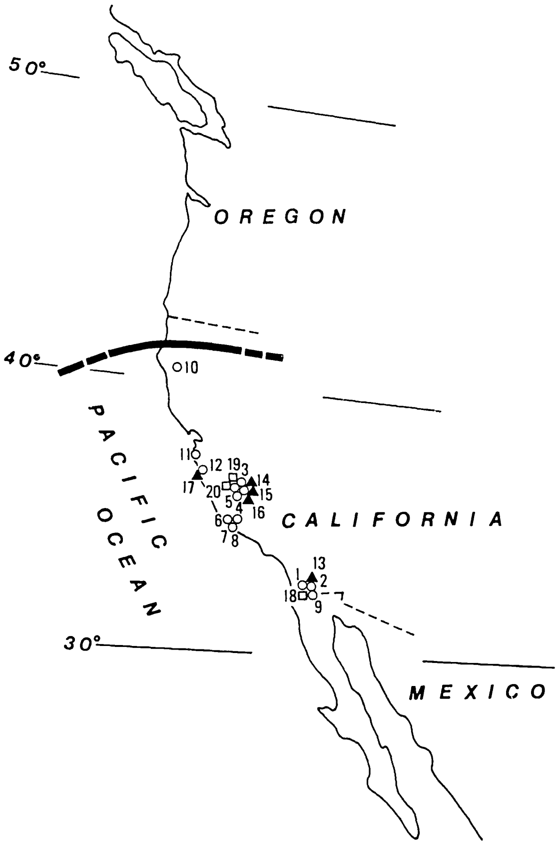
Although *Scapharca* is treated as a full genus by some malacologists but it is classified as a subgenus of *Anadara* (Noda, 1966).

As mentioned above, there are a few species identified with *Anadara* or *Scapharca* from

Oligocene formations that should be more closely examined, and which could be ancestral or primitive forms of Neogene *Anadara* or *Scapharca.*

So, before the distinct worldwide development of the genus *Anadara* s.s. at the beginning of the Neogene, the genus *Hawaiarca* had already appeared in the Caribbean Province from the Middle Eocene and Late Eocene as shown by *Hawaiarca rhomboidella, H. carmensis* and *H. olssoni.* The first species is considered to be a most primitive Hawaiarcan species because in having barbatid-like external sculptures and hinge structures being far form Neogene *Anadara* or *Scapharca.* And the latter two species are well referred to *Hawaiarca* in having external and internal features to be more close to those of *Anadara* or *Scapharca.* This indicates that the primitive and slightly advanced Hawaiarcan species were recorded from the Middle Eocene to Late Eocene in Caribbean Province, although sporadic Late Eocene Hawaiarcan species such as *Hawaiarca appendiculata* (Pl. 4, figs. 15, 16) and *H. appendiculata sokolovi* (Pl. 4, figs. 13, 14) from the Ukraina (Zelinskaya *et al.,* 1968) and *H. boschi* from Spain (Staid-Staad, 1964) were recorded. The abundant development of genus *Anadara* s.l. in the Early to Middle Miocene has been described in the West Coast of the United States (*e.g.,* Reinhart, 1943), North Europe (*e.g.,* Schaffer, 1910), Mediterranean Province (*e.g.,* Mayer, 1868, Cossmann and Peyrot, 1912), and Indo-Pacific Province (Vrendenburg, 1928, Noda, 1966). However, Hawaiarcan species in the Caribbean Province, including the southern part of U.S.A. and the east coast of Mexico during the Early to Middle Miocene, are especially dominant in comparison with other provinces. The Miocene species *H. jamaicaensis* from Jamaica and Puerto Rico resembles the Eocene species *H. carmensis* which may show the phylogenetic relationship in the Caribbean Province.

The genus *Anadara* s.l. is widely distributed in shallow sandy bottoms and reached its maximum development in the Early to Middle Miocene but Hawaiarcan species have never become a dominant group among arcid associations. The original ancestral Hawaiarcan species might have appeared in the Caribbean Province and become rather dominant in the Early to Middle Miocene in the province and also have spread or migrated out to northern Europe through the Atlantic Ocean in the Middle or Late Eocene. *Hawaiarca speyri* became rather common species in the northern part of Europe in the Oligocene to Early Miocene. The species most resembles "*Nipponoarca*" *bistrigata* and also *Hawaiarca appendiculata* and its subspecies *H. appendiculata sokolovi,* recorded from the Late Eocene in the Ukraina. Hawaiarcan species in Europe and Mediterranean provinces are not common in Paleogene to Lower Miocene faunas and almost disappeared from the areas after the Middle Miocene. Hawaiarcan species however, have been common in the Indo-Pacific Province from Pliocene to Recent times. Except for species in the Southeast Asia and Japan, the only Pliocene species *Hawaiarca triphera* is known from the East Coast of the U.S.A. So it seems that Hawaiarcan species including "*Nipponarca*" species reached their maximum development in the Caribbean Province during the Early to Middle Miocene. In the both sides of the U.S.A., anadarid species since they had distinctly developed at the Early to Middle Miocene, have been decreased in number of species from Late Miocene to Pliocene. Post Pliocene age, anadarid species had been completely disappeared from the northwest coastal area of the U.S.A. (Text-fig. 3). This will support that warm water origin Hawaiarcan species could migrate up to middle California from the Caribbean Province through the Panama Sea-Way being open at the Early to Middle Miocene shown by *Hawaiarca mediaimpressa* and *H. submontereyana* but after that there are no evidences for any Hawaiarcan species to cross the northern high latitude (Text-figs. 3–4) and no any Hawaiarcan species



○*Anadara trilineata trilineata* (Conrad)

1. Santa Barbara (= San Diego Form.); Conrad, 1857, Grant and Gale, 1931, Reinhart, 1943, Moore, 1968, 1983, Hertlein and Grant, 1972.
2. San Bernardino Base and Meridian; Hertlein and Grant, 1972.
3. San Joaquin Form.; Woodring *et al.*, 1940, Alexander, 1974.
4. Etchegoin Form.; Eldridge and Anderson, 1907.
5. Fernando Form.; Hall, 1958, Howard, 1935.
6. Sisquoc Form.; Woodring *et al.*, 1950.
7. Foxen Mudstone; Woodring *et al.*, 1950.
8. Careaga Sandstone, Woodring *et al.*, 1950.
9. Wilson's Ranch; Weaver, 1943.

?10. Pullan Form.; Faustman, 1964.

11. Merced Form.; Arnold, 1908.
12. Purisima Form.; Reinhart, 1943, Schenck and Keen, 1950.

▲*Anadara trilineata canalis* (Conrad)

13. Santa Barbara (= San Diego Form.); Conrad, 1857, Osmont, 1905.
14. Etchegoin Form.; Arnold, 1909, Arnold and Anderson, 1910, Woodring *et al.*, 1940.
15. San Joaquin Form.; Woodring *et al.*, 1940.
16. Fernando Form.; Arnold and Anderson, 1907.
17. Purisima Form.; Reinhart, 1943, Moore, 1983.

□*Anadara trilineata calcarea* (Grant and Gale)

18. San Diego Form.; Grant and Gale, 1931, Reinhart, 1943, Hertlein and Grant, 1972, Moore, 1983.

?19. Etchegoin Form.; Alexander, 1974.

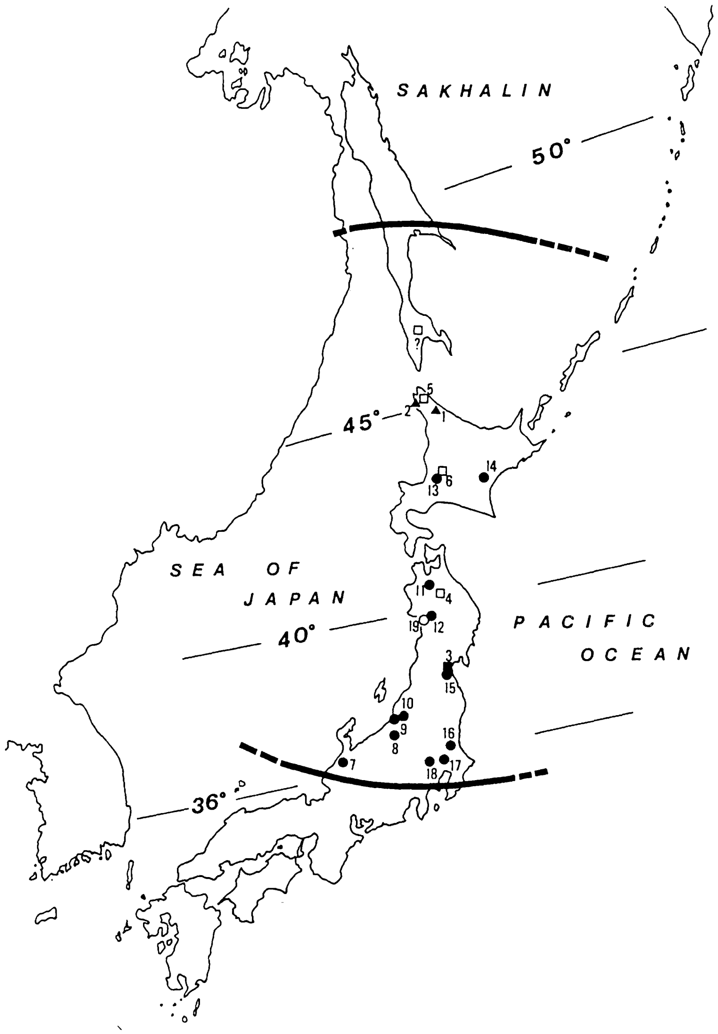
?20. San Joaquin Form.; Woodring *et al.*, 1940.

Text-fig. 3. Distribution of *Anadara trilineata* and its subspecies, representative Pliocene species in U.S.A.

are recorded along the northwest coast of U.S.A.

In the Indo-Pacific and Australian Provinces, the oldest Hawaiarcan species is the Junjucian *Hawaiarca interclathrata* from southern Australia, which resembles with the Caribbean Miocene species, *H. jamaicaensis,* and *H.* sp. from Oligocene of Burma. *Hawaiarca nipponica* and *H.* sp. from the Middle Miocene in Japan are the lowest Hawaiarcan species in Japan but they are taxonomically far from the Japanese Pliocene Hawaiarcan species, *H. uwaensis.* Because of the scarce distribution of Hawaiarcan species in intervening provinces, it is difficult to confirm relationships with the Panamic fauna (Ladd, 1960).

"*Nipponarca*" *bistrigata* from the Late Miocene in Southeast Asia, resembles European species that have bifurcated radial ribs, such as *Hawaiarca speyri* and *H. appendiculata* and its subspecies. So the migration route of "*Nipponarca*" might have been *via* the Mediterranean, because only one or two Hawaiarcan species were recorded from the west coast of the U.S.A., since there was sea-pass way from Panama Province to Pacific Ocean at the beginning of the Neogene or Latest Oligocene (Woodring, 1966) and no other Hawaiarcan species.



▲*Anadara uozumii* Noda

1. Shibiutan Form.; Fujie, 1958, Noda, 1966.
2. "Yuchi" Form.; Noda, MS.

■*Anadara tatunokutiensis* (Nomura and Hatai)

3. Tatunokuti (=Tatsunokuchi) Form.; Nomura and Hatai, 1936, Noda, 1966, Masuda and Ogasawara, 1981.

□*Anadara tatunokutiensis nagawaensis* Chinzei

4. Togawa Form.; Chinzei, 1961.
5. Toikanbetsu Form.; Noda, 1966.
6. Horokaoshirarika Form.; Noda, MS.

?. Maruyama Form.; Zhidokova *et al.*, 1968.

●*Anadara amicula elongata* Noda

7. Omma Form.; Kanehara, 1935, Hatai and Nisiyama, 1939, Kaseno, 1961, Kaseno and Matsuura, 1965, Noda, 1966, Ogasawara, 1977, Masuda and Ogasawara, 1981, Matsuura *et al.*, 1984.
8. Higashigawa Form.; Noda, 1966*.
9. Nishiyama Form.; Noda, 1966*.
10. Haizume Form.; Noda, 1966*.
11. Higashimeya Form.; Iwai, 1959, 1965.
12. "Futatsui Neogene deposits"; Chinzei, 1973.
13. Horokaoshirarika Form.; Noda, 1966.

?14. Chiyoda Form.; Oka and Akamatsu, 1979.

15. Dainenji Form.; Noda, 1966*.
16. Kume Form.; Noda and Amano, 1976.
17. Kazusa Group; Aoki and Baba, 1982.
18. Kanzawa Form.; Noda and Ito, MS.

○*Anadara amicula rotunda* Noda

19. Sasaoka Form.; Takayasu, 1961, Noda, 1966, Honda, 1978, Masuda and Ogasawara, 1981, ? Shimamoto, 1984.

Text-fig. 4. Distribution of some Japanese Pliocene cold water anadarid species and the limitation. (* indicates no illustration and ? shows questionable identification).

Concluding remarks

For a long time, the genus *Anadara* was thought to have evolved from a Mesozoic arcid or barbatid. However, *Hawaiarca* is herein considered to be the ancestor of *Anadara* s.s. and also of *Scapharca. Hawaiarca,* type genus of Hawaiarcinae, n. subfam. is intermediate in morphology and functional features of *Anadara* (Type of Anadarinae) and *Arca* (Type of Arcinae). Hawaiarcan species have been recognized from the Middle Eocene in the Caribbean Province and widely distributed in the Early to Middle Miocene, especially in the Caribbean Province. However, the Hawaiarcan species have decreased since the Late Miocene and almost disappeared in the Pliocene except for the Indo-Pacific Province. Modern species of *Hawaiarca* and "*Nipponarca*" have flourished in the Indo-Pacific Province. Hawaiarcan species are all adapted to live in outer-shelf depths of about 50–200m but "*Nipponarca*" species are found in shallower depths, as were Paleogene to Early Miocene Hawaiarcan species. The original Hawaiarcan species that was ancestral to *Anadara* might have appeared in the Caribbean Province in the Middle Eocene, and its larvae could have dispersed to northern Europe in the Late Paleogene. During the Late Paleogene and Early Miocene, Hawaiarcan species occurred almost worldwide, and were the stock from which Neoegene anadaran species evolved. Anadaran species proliferated during the Early to Middle Miocene but Hawaiarcan species were no dominant among them. Hawaiarcan species, including "*Nipponarca*" species now flourished only in the Indo-Pacific Province. This developmental history of Hawaiarcan species is also seen in the history of Japanese *Anadara*. Japanese *Anadara* and *Scapharca* were mostly dominant in the Middle Miocene (*e.g., Anadara kakehataensis/A. makiyamai* Zone of Noda, 1966) similarly abundant and diverse Anadarans also occurred at about the same time or slightly earlier than that of Japanese one, in the U.S.A. (*e.g.,* Vaquerous to Temblor) and Europe (Egerien to Eggenburgien or Aquitanian to Burdigalien). Most Middle Miocene Anadarid species, especially Hawaiarcan species immigrated from southern tropical seas along with other molluscs. Some Hawaiarcan species even ranged as far north as southern Hokkaido. However, according to the decrease of temperature at Late Miocene, many Anadaran species that originated in the south evolved into endemic species in Japan. By the second major marine transgression of the Pliocene, several Anadaran species that originated in tropical seas to the south newly migrated to southwestern Japan together with *Hawaiarca uwaensis.* The northern Anadarid species of Japan are characterized by species with bifurcated radial ribs. Such species also developed in Japan during the Miocene to Pliocene might have no interrelation with species from the west coast of America, because there are no Anadaran species in the Pliocene of western U.S.A. And the Pliocene species in the west coast lived only as far as north as northern California (Text-fig. 3). Moreoever, the Japanese characteristic Pliocene Anadaran species are almost restricted as far north as middle part of Saghalien (Karafto), U.S.S.R. (Text-fig. 4).

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Plate 3

Explanation of Plate 3

Figs. 1–2. *Hawaiarca rhomboidella* (Lea, 1833)
Claiborne Eocene Clainborne, Alabama, U.S.A., Paleont. Res. Inst. no. 1460, (ca. x 1.2).

Figs. 3–5. *Hawaiarca rectangula* Dall, Bartsch and Rehder, 1938
Type specimen of *Hawaiarca,* Recent, Off Alenuihaha Channel between Hawaii and Maui in 49–176 fathoms, USNM no. 173222, (ca. x 5).

Figs. 6–7. *Hawaiarca sulcicosta* (Nyst, 1836)
Grimittingen Oligocene to Early Miocene in Vienna, (ca. x 0.8).

Figs. 8–9. 18 *Hawaiarca yaquensis* (Maury, 1917)
Miocene Bluff 2, Cercado de Mao, Santo Domingo, type specimen, USNM 483684, (ca. x 2.5).

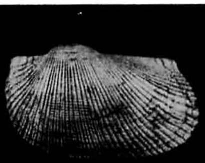
Figs. 10–12. *Hawaiarca uwaensis* (Yokoyama, 1928)
Pliocene Shinzato Formation, Okinawa Prefecture. IGUT no. 11015, (ca. x 4).

Fig. 13. *Hawaiarca invidiosa* (Casey, 1903)
Oligocene Vicksburg Formation, Mississippi, U.S.A., type specimen, USNM no. 480121, (ca. x 1.3).

Fig. 14. *"Nipponarca" bistrigata* (Dunker, 1866)
Pleistocene Narita Formation, Chiba Prefecture, IGUT no. 11016, (ca. x 1)

Fig. 15. *"Nipponarca" miikensis* (Noda, 1966)
Recent Miike, Fukuoka Prefecture, IGPS no. 23559 (Holotype), (ca. x 1)

Figs. 16–17. *"Nipponarca" bistrigata* (Dunker, 1866)
Recent, Penang, IGUT no. 11017, (ca. x 1).



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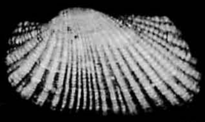

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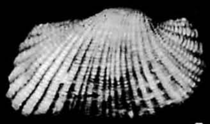

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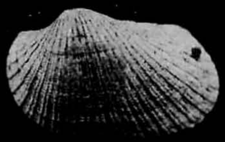

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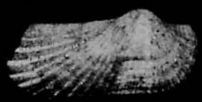

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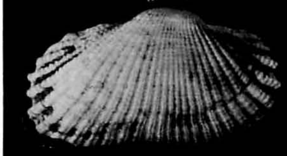

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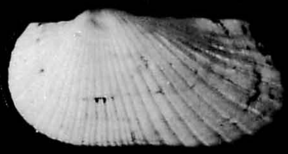

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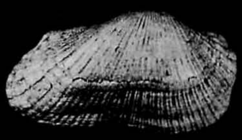

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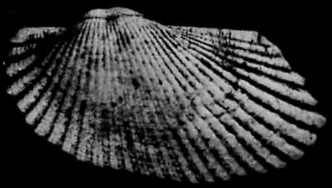

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Plate 4

Explanation of Plate 4

Figs. 1–4. *Hawaiarca jamaicaensis,* n.n.
Middle Miocene Bowden Formation, Jamaica, reproduced from Woodring, 1925. Holotype. USNM no. 352759, (ca. x 4).

Figs. 5–6. *Hawaiarca yaquensis berryi* (Woodring, 1925)
Middle Miocene Bowden Formation, Jamaica, reproduced from Woodring. USNM no. 352742, (ca. x 2).

Figs. 7–9. *Hawaiarca veracruzana* (Perrilliat, 1976)
Middle Miocene Aguequexquite Formation, Mexico, (ca. x 1).

Figs. 10–11. *Hawaiarca intercluthrata* (Ludbrook, 1965)
Oligo-Early Miocene Jan Juc Formation, Southern Victoria, Australia, reproduced from Ludbrook, 1965. (Paratype), (ca. x 1)

Fig. 12. *Hawaiarca triphera* (Dall, 1898)
Pliocene Caloosahatchee Formation, Florida, U.S.A., (ca. x 1.8). Reproduced from Dall (1898).

Figs. 13–14. *Hawaiarca appendiculata sokolovi* (Klucznikov, 1958)
Upper Eocene in Ukraina, USSR., Reproduced from Zelinskaya *et al.,* 1968, (ca. x 2).

Figs. 15–16. *Hawaiarca appendiculata appendiculata* (Sowerby, 1821)
Upper Eocene in Ukraina, USSR., Reproduced from Zelinskaya *et al.,* 1968, (ca. x 1).

Fig. 17. *Hawaiarca mediaimpressa* s.s. (Clark, 1918). Lower Miocene San Ramon Formation, California, U.S.A. Topotype specimen, (ca. x 1).

Fig. 18. *Hawaiarca* sp. A.
Oligocene Okmintag Formation in Burma. IGUT no. 11018, (ca. x 1.5). Collected by late Prof. Yuji Bando, Kagawa University.


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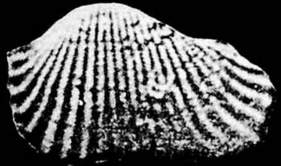
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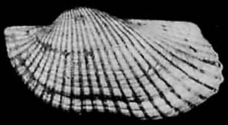
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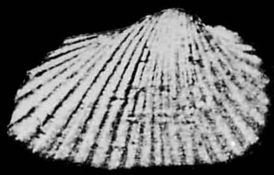
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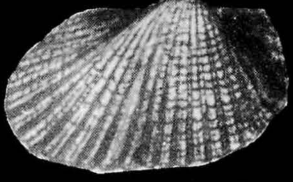
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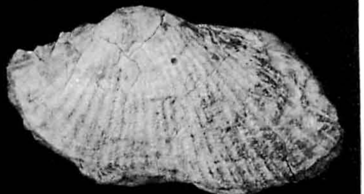
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CENOZOIC GLYCYMERIDID BIVALVES OF JAPAN

By

Akihiko MATSUKUMA

Introduction

The bivalve mollusk family Glycymerididae is a large and important one, especially in sandy bottom faunas. Glycymeridids are characterized by possessing a duplivincular ligament and an arched hinge-plate with taxodont teeth and crenulated ventral margin. The earliest known species are of Early Cretaceous age. Living species of the Glycymerididae are mainly upper subtidal, sandy bottom-dwellers from an open coast, in tropical and temperate waters. Glycymeridid fossils are very common in Cenozoic shallow water sediments. As many as 800 species, including about 50 living species, are placed in this family (Boss, 1971). In Japan there are 18 living and about 40 Cenozoic species, including a few subarctic species, several Indo-West Pacific tropical species and a number of East Asian endemic species.

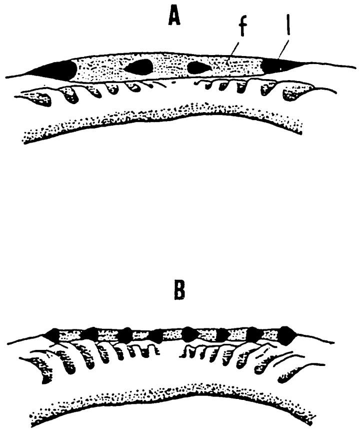
Glycymeridids are ideal for the study of phylogenetical classification and speciation among open coast mollusks. They satisfy the following conditions: (1) abundance both in living and fossil states, (2) ease of observation for studying general biology, and (3) relatively simple inferred evolutionary lineages.

Acknowledgements: I wish to express my sincere thanks to Professors Tamio Kotaka, Tsugio Shuto, Takashi Okutani, Koichiro Masuda, Hiroshi Noda, and Tadashige Habe, and to Drs. Louie Marincovich, Kiyotaka Chinzei, Kenshiro Ogasawara and Seiichiro Matsui for criticism of the manuscript, as well as for fruitful discussions on the subject. For the loan of specimens I am indebted to the following institutions: Tohoku University (IGPS); Miyagi University of Education; Saito Ho-on Kai Museum (SHM); Akita University; Niigata University; the University of Tsukuba (IGUT); the University Museum, the University of Tokyo (UMUT); St. Paul (Rikkyo) University (SPU); Shinshu University (SU); Mizunami Fossil Museum (MFM); Hiroshima University; Kyoto University (UK); Zoölogisce Museum, Humboldt-Universität, Berlin (ZMHU); and, Kyushu University (GK). This study is a part of a doctoral thesis in paleontology at Kyushu University, and was financially supported by the Ministry of Education, Culture and Science, Japanese Government.

Taxonomic Characters and Subdivision of the Glycymerididae

A number of authors have done taxonomic studies of the family Glycymerididae (Lamy, 1912; Marwick, 1923; Chapman & Singleton, 1925; Kanno, 1956; Tashiro, 1971), but its classification is still complicated mainly due to differing interpretations of their simple shell form. In order to consider evolutionary trends and phylogenetic subdivisions of the family, it is necessary to understand some of the most useful taxonomic characters of the Glycymerididae. They are the following:

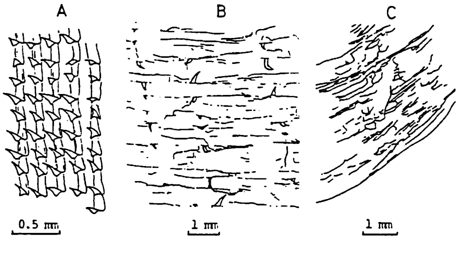
Ligament. The Glycymerididae have an external duplivincular ligament. Both anterior and posterior dorsal borders of the ligamental area are always occupied by tanned lamellar layers which are elastic under tensional stress. In early ontogeny the duplivincular ligament, with an outermost lamellar layers and a fibrous layer, is apparently identical with a ligament of



Text-fig. 1. Subventral view of ligament. A: *Glycymeris albolineata* (Lischke). B: *Glycymeris yessoensis* (Sowerby). f: fibrous layer. l: lamellar layer.

Limopsidae. The ligament of Glycymerididae is amphidetic or occasionally strongly prosodetic. The ligament is more constant in shape than the Arcidae, although some species show infraspecific variations such as reversed-W shaped chevrons and ripply chevrons in *Tucetona sibogae* Matsukuma, 1982 and *Glycymeris pilsbryi* (Yokoyama, 1920). The ligamental area of the Glycymerididae is usually deeply grooved by chevrons in all ribbed species and in some species with smooth outer surfaces. In the ribbed species their lamellar layer is situated in the ligamental groove. Some Japanese living species such as *Glycymeris vestita* (Dunker, 1877), *G. albolineata* (Lischke, 1872) and *G. reevei* (Mayer, 1868) have a smooth ligamental area. Some Japanese Cenozoic species, *e.g. Glycymeris cisshuensis* Makiyama, 1926, also has a smooth ligamental area. In these species the lamellar layer is imbedded in the fibrous layer, which is elastic under compressional stress. The presence of a grooved or smooth ligamental area is consistent within a species.

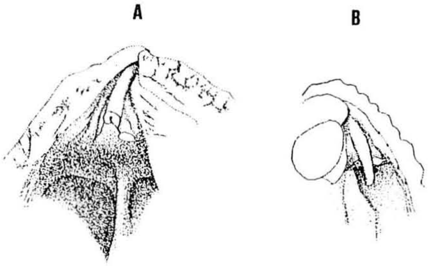
Periostracum. There are two major types of periostraca: a recurved, hairy periostracum and a filmy periostracum. The periostraca of strongly ribbedd species, *e.g. Tucetona auriflua* (Reeve, 1843) and *T. pectunculus* (Linnaeus, 1758), are filmy, and almost all species with smooth outer surface have hairy periostracum. The hairy periostracum has sharply pointed barbs which bend to beak. A radial row of the barbs is inserted in each fine radial striae (periostracal striation) on the outer shell surface. In *Glycymeris rotunda* (Dunker, 1882) and *G. imperialis* Kuroda, 1934 the radial rows of barbs are situated in the distantly spaced periostracal striations.



Text-fig. 2. Periostracum of Glycymerididae. A: Periostracal hairs of *Glycymeris vestita* (Dunker). B: Distantly spaced periostracal hairs of *Glycymeris rotunda* (Dunker). C: filmy periostracum of *Tucetona flabellata* (T.-Woods).

Crenulations. Although Nicol (1945) and Kuroda *et al.* (1971) noted that Glycymerididae occasionally have a smooth ventral margin, the border is always crenulated and this is one of the most important characteristics of the family. Except *Melaxinaea vitrea* (Lamarck, 1819), from northern Australia, every species of Indo-Pacific Glycymerididae has crenulations with two shoulders along both the anterior and posterior sides. Crenulations with two shoulders are called primary crenulations (Matsukuma, 1980), and these exactly correspond with interspaces between ribs in strongly ribbed species and white lines or interspaces between low rounded costae in smooth species. Only a few species, *e.g. Melaxinaea vitrea* (Lamarck, 1819), has crenulations without shoulders. Crenulations without any shoulders are called secondary crenulations (Matsukuma, 1980) and are intercalated between the primary crenulations. In a local population of the Glycymerididae frequency counts of ventral crenulations usually show normal distributions. In *Glycymeris vestita* (Dunker, 1877), *G. fulgurata* (Dunker, 1877) and *G. pilsbryi* (Yokoyama, 1920) the number of crenulations apparently becomes larger in cooler water populations.

Ornamentation. In Glycymerididae radial ornamentations such as ribs, ridges, rounded costae and periostracal striations are more conspicuous than concentric ornamentation such as riblets and growth striae. Concentric riblets are somewhat prominent in the umbonal regions of *Glycymeris rotunda* (Dunker, 1877) and *G. yessoensis* (Sowerby, 1889). Radial ribs of *Tucetona* species are very prominent; they are neither bifurcated nor intercalated and are called primary ribs (Matsukuma, 1980). Some *Melaxinaea* species have divided primary ribs and intercalated secondary ribs. *Glycymeris pilsbryi* (Yokoyama, 1920) has striated sharp ridges. A transverse section of the ridges shows a concave, nearly equilateral triangle. Almost all species with hairy epidermises have low, rounded costae which are densely striated by the regularly spaced periostracal striations. All the primary ribs, sharp ridges and rounded costae strictly correspond with interspaces between the inner ventral crenulations.



Text-fig. 3. Anus of Glycymerididae. A: Fixed anus of *Glycymeris vestita* (Dunker). B: Protruded anus of *Tucetona shinkurosensis* Hatai, Niino & Kotaka.

Anus. There are two distinctly different locations of the anus in Glycymerididae. *Glycymeris vestita* (Dunker, 1877), *G. fulgurata* (Dunker, 1877), *G. albolineata* (Lischke, 1872), *G. reevei* (Mayer, 1868) and *G. yessoensis* (Sowerby, 1889) have an anus attached to the postero-dorsal part of the posterior adductor muscle. However, *Tucetona pectunculus* (Linnaeus, 1758), *T. hanzawai* (Nomura & Zinbo, 1934), *T. shinkurosensis* Hatai, Niino & Kotaka, 1952, *Glycymeris rotunda* (Dunker, 1882), *G. imperialis* Kuroda, 1934 and *G. pilsbryi* (Yokoyama, 1920) have an anus protruding into the posterior mantle cavity and free from the posterior adductor muscle.

Nicol (1956) divided living members of the Glycymerididae in to two groups, the *Glycymeris* (*s.s.*) group and the *Tucetona* group. He pointed out that the former contains tropical and temperate species with a few subarctic northern Pacific species, while the latter contains tropical species. The strongly ribbed *Tucetona* group is more narrowly distributed and occurs mainly in the Indo-Pacific region, whereas the smooth-shelled *Glycymeris* (*s.s.*) group is cosmopolitan. Habe (1977) erected the subfamily Melaxinaeinae based on split-ribbed species, *Melaxinaea labyrintha* Iredale, 1930. Species placed in Melaxinaeinae by Habe (1977) have strong ribs covered by a filmy periostracum, a grooved ligamental area and a protruded anus. These characters also occur in the *Tucetona* group. More recently, Nicol & Jones (1984) proposed the subgenus *Bellaxinaea* for Eocene-Recent species of the tropical western hemisphere. *Bellaxinaea* is characterized by primary ribs that are regularly divided with age and secondary ribs intercalated between the primary ribs. *Bellaxinaea* closely resembles *Melaxinaea* Iredale, 1930 of the Indo-Pacific region. Nicol & Jones (1984) placed *Bellaxinaea* in the genus *Tucetona* Iredale, 1931. In this paper I recognize Melaxinaeinae Habe, 1977 in preference to the *Tucetona* group of Nicol (1956); however I transfer *Tucetilla* Iredale, 1939 to Glycymeridinae. A summary of classification and abridged diagnoses of the Glycymerididae

Table 1. Living species of the Glycymerididae from Japan and their taxonomic characters.

	Ligamental area	Periostracum	Periostracal striation	Anus	Outer surface
Glycymeris reevei	Smooth	Hairy	Dense	Fixed	Smooth
albolineata	Smooth	Hairy	Dense	Fixed	Smooth
vestita	Smoth	Hairy	Dense	Fixed	Smooth
fulgurata	Smooth	Hairy	Dense	Fixed	Smooth
livida	Smooth	Hairy	Dense	Fixed	Smooth
rotunda	Grooved	Hairy; Filmy	Scattered	Protruded	Smooth
imperialis	Grooved	Hairy; Filmy	Scattered	Protruded	Smooth
munda	Grooved	Hairy	Scattered	Protruded	Smooth
yessoensis	Grooved	Hairy	Dense	Fixed	Smooth
habei	Grooved	Hairy	Dense	?	Smooth
shutoi	Grooved	Hairy	Dense	?	Smooth
pilsbryi	Grooved	Hairy	Scattered	Protruded	Ridged
Tucetona auriflua	Grooved	Filmy	(Absent)	?	Ribbed
pectunculus	Grooved	Filmy	(Absent)	Protruded	Ribbed
hanzawai	Grooved	Filmy	(Absent)	Protruded	Ribbed
shinkurosensis	Grooved	Filmy	(Absent)	Protruded	Ribbed
sibogae	Grooved	Filmy	(Absent)	?	Ribbed

Table 2. Stratigraphic occurrence of taxonomic characters in the Glycymerididae.

Age	Cretaceous		Tertiary			
Characters	Lower	Upper	Paleogene	Neogene		
Surface ornamentation	A: low costae	A	A	A	A	A
		A': narrow ridges	?	A'	A'	A'
			a: strong ribs	a	a	a
			a': split ribs	a'	a'	a'
Periostracum	B: dense hairs	B	B	B	B	B
				B': scattered hairs	B'	B'
			b: filmy	b	b	b
Ligament	C: amphidetic	C	C	C	C	C
			c: prosodetic	c	c	c
Ligamental area	D: grooved	D	D	D	D	D
			d: smooth	d	d	d
Shell size	E: small	E	E	E	E	E
			e: large	e	e	e

are given as follows:

Family Glycymerididae Newton, 1922:

Subfamily Glycymeridinae Newton, 1922: Outer surface nearly smooth, or ornamented with narrow ridges; periostracum hairy.

Genus *Glycymeris* Costa, 1778: Periostracum hairy; ligament amphidetic or prosodetic; ligamental area grooved or smooth; anus fixed or protruding.

Subgenus *Glycymeris* (*s.s.*): Outer surface smooth; periostracum hairy, dense or scattered; ligament amphidetic; ligamental area deeply or shallowly grooved; anus fixed or protruding.

Subgenus *Veletuceta* Iredale, 1939: Outer surface ornamented with low, rounded costae; periostracum hairy, dense; ligament amphidetic; ligamental area smooth; anus fixed.

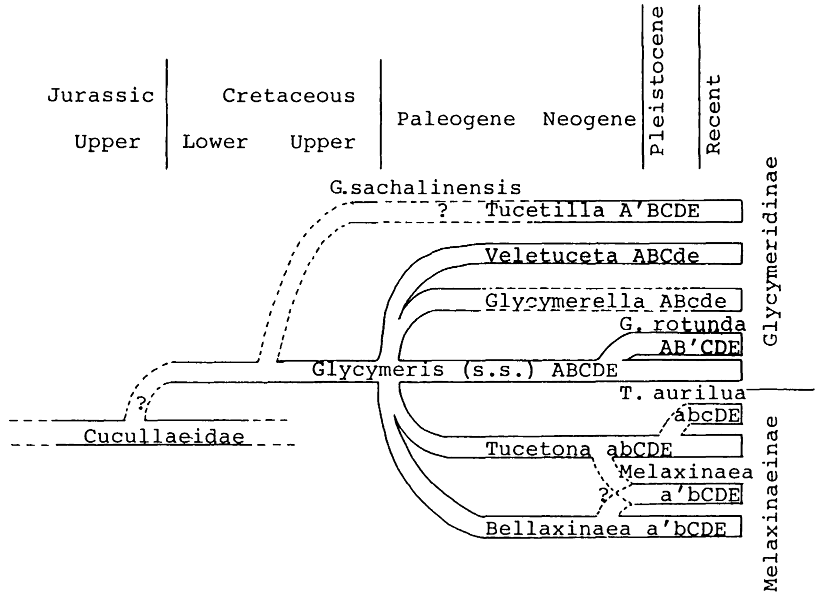
Subgenus *Tucetilla* Iredale, 1939: Outer surface ornamented with narrow ridges; periostracum hairy, dense; ligament amphidetic; ligamental area grooved; anus protruding.

Subgenus *Tucetonella* Habe, 1961: Outer surface smooth; periostracum hairy, scattered; ligament amphidetic; ligamental area grooved; anus protruding.

Subfamily Melaxinaeinae Habe, 1977: Outer surface ornamented with strong ribs; periostracum filmy; ligament amphidetic or prosodetic; ligamental area grooved; anus protruding.

Genus *Tucetona* Iredale, 1931: Outer surface ornamented with primary ribs; periostracum filmy; ligament amphidetic or prosodetic; ligamental area grooved; anus protruding.

Genus *Melaxinaea* Iredale, 1930: Outer surface ornamented with divided primary ribs and intercalated secondary ribs; periostracum filmy; ligament amphidetic; ligamental area grooved; anus protruding.



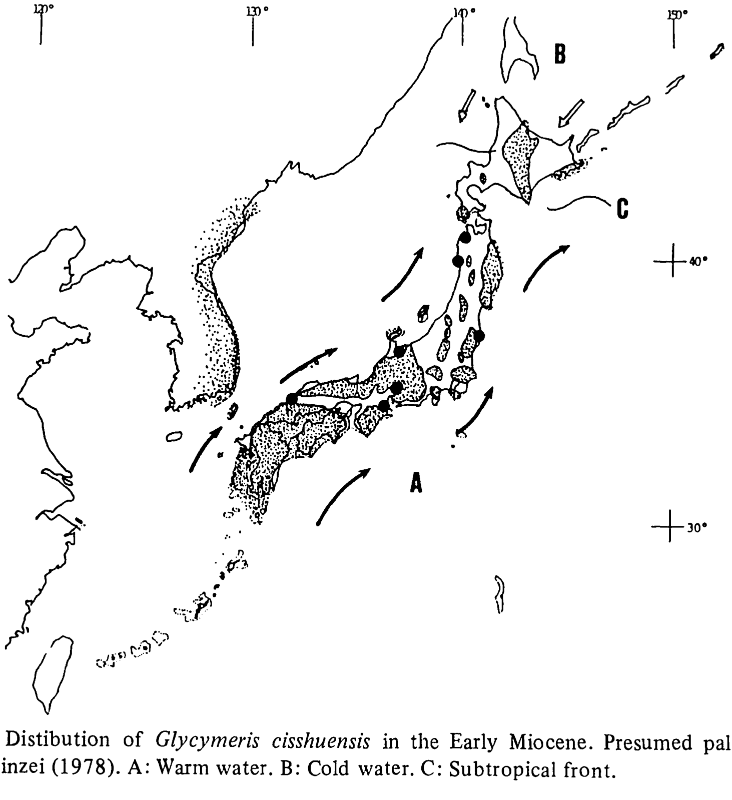
Text-fig. 4. Classification of Glycymerididae. For explanation of symbols (A, a, ...) see Table 2.

Bathymetric Distribution

Species of Glycymerididae distinctly differ from Arcidae and Limopsidae in their more limited bathymeric and geographic distribution. A number of limopsid species are recorded from deep-sea basins. For example, *Limopsis galatheae* Knudsen, 1970 was collected from 4360–5160 m, in the central and eastern Atlantic. However, in general glycymeridid species are limited to shallow waters and not found in the bathyal, abyssal and hadal zones (Nicol, 1956).

Most Japanese species live in a sandy bottom of the subtidal zone, usually less than 30 m deep, and their shells are commonly found as beach drift. The following species are inhabitants of the subtidal zone: *Glycymeris albolineata* (Lischke, 1872), *G. vestita* (Dunker, 1877), *G. fulgurata* (Dunker, 1877), *G. imperialis* Kuroda, 1834, *G. yessoensis* (Sowerby, 1889), *G. habei* Matsukuma, 1984, *G. shutoi* Matsukuma, 1981, *G. reevei* (Mayer, 1868), *Tucetona auriflua* (Reeve, 1843) and *T. pectunculus* (Linnaeus, 1758). The species *Glycymeris pilsbryi* (Yokoyama, 1920), *Tucetona sibogae* Matsukuma, 1982 and *T. shinkurosensis* Hatai, Niino & Kotaka, 1952 live in coarse sand with shells in the upper shelf zone at depths of about 60–190 m, and *Glycymeris rotunda* (Dunker, 1882) is a sandy-muddy bottom dweller in the upper shelf zone at about 50–250 m.

Japanese fossil species usually occur with subtidal sandy bottom associations. For example, *Glycymeris cisshuensis* Makiyama, 1926 is a main component of the *Glycymeris-Pitar* association (Shuto & Shiraishi, 1971) in the Early Miocene Ashiya Fauna and *Anadara-Dosinia* association of the Middle Miocene Kadonosawa Fauna (Chinzei & Iwasaki, 1967; Chinzei, 1981) and



Text-fig. 5. Distibution of *Glycymeris cisshuensis* in the Early Miocene. Presumed paleogeography after Chinzei (1978). A: Warm water. B: Cold water. C: Subtropical front.

the Late Miocene Shiobara Fauna (Chinzei & Iwasaki, 1967; Iwasaki, 1970, 1981). Only a few species, such as *Glycymeris derelicta* (Yokoyama, 1928), *G. nipponica* (Yokoyama, 1920) [= *G. rotunda* (Dunker, 1882)] and *G. okinawaensis* Noda, 1980 [= *G. rotunda*], are considered to be a sandy-muddy bottom dweller of the upper shelf zone (Chinzei, 1959; Noda, 1980). According to Chinzei (1959) *G. derelicta* is commonly found in the offshore silty sand facies of the Pliocene Kubo Formation in Iwate Prefecture, northeastern Honshu. *Glycymeris nipponica* from the Pliocene Nojima Formation of Kanagawa Prefecture, central Honshu, was collected along with the following sandy-muddy bottom dwellers of the upper to lower shelf zone: *Crenulilimopsis oblonga* (Adams, 1860), *Cryptonatica janthostomoides* (Kuroda & Habe, 1949), *Trophon echinus* (Dall, 1907), *Fulgoraria kamakuraensis* Otuka, 1949 and *Fissidentalium yokoyamai* Makiyama, 1931.

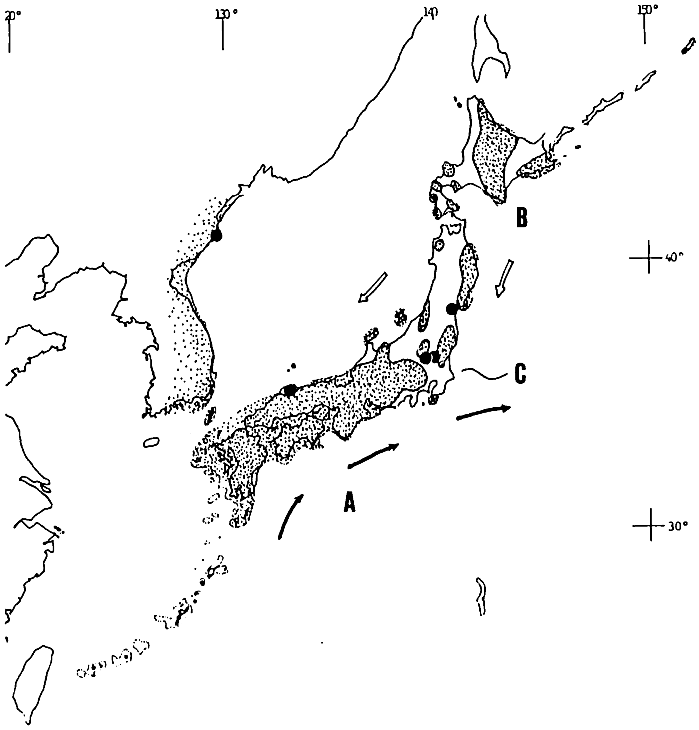
Paleozoogeographic and Stratigraphic Distribution

Shuto (1977) pointed out that the Indo-West Pacific paleozoogeographic province during the Middle Miocene was subdivided into three subprovinces, namely, Taiwan-Japan, Indonesia-Philippines and Indo-Burma. A little less than ten percent of the taxa of the Taiwan-Japan subprovince were present in the Indonesia-Philippines subprovince, and the figure was similar or lower for the younger Neogene time (Shuto, 1977).

Several fossil species of Glycymerididae have been described from Cenozoic strata of the Indo-West Pacific region. Vredenburg (1928) described *Tucetona sindiensis* [= *T. lima* (D'Archiac & Haime, 1853)] from the Miocene of Pakistan and *T. gwadarensis* from the Pliocene of Pakistan. The following ribbed species have been described from this region: *Tucetona angusanana* (Martin, 1922) (Middle Miocene, Java), *T. gembacana* (Martin, 1885) (Pliocene, Java), *T. teshi* (Altena & Beets, 1945) (Middle Miocene, Java) and *Melaxinaea laticardo* (Altena & Beets, 1945) (Middle Miocene, Java). *Tucetona teshi* and *T. gembacana* resemble *T. auriflua* (Reeve, 1843) by having prosodetic ligaments, but differ by having more numerous ribs. *Melaxinaea laticardo* has a compressed shell with a straight dorsal margin and divided ribs and is possible synonym of *M. planata* (G. & H. Nevill, 1874) from the Andaman Sea and the Philippines. The following species lack prominent ribs on the outer surface: *Glycymeris puruensis* (Martin, 1915) (Eocene, Java), *G. rembangensis* Pannekoek, 1936 (Middle Miocene, Java), *G. junghuhni* (Martin, 1879) (Neogene, Java), *G. martini* Finlay, 1927 (Pliocene, Java), *G. priangensis* Altena & Beets, 1945 (Middle Miocene, Java) and *G. bonneti* (Cossmann, 1923) (Pliocene, French India). Fischer (1927) recorded *G. reevei* (Mayer, 1868) from the Pliocene of Indonesia and *G. bonneti* apparently resembles *Glycymeris* (*Tucetilla*) *crebrelirata* (Sowerby, 1889), but all other species clearly differ form fossil and living species of the Taiwan-Japan subprovince.

One Eocene species, *Glycymeris altoumbonata* Nagao, 1928, has been reported from the Doshi Formation of northern Kyushu, southwest Japan. According to K. Masuda (1984, personal communication) the Eocene Miyara Formation in Ishigaki Island, Ryukyu Islands, yields strongly deformed specimens of *Glycymeris*. Kanno & Chung (1975) recorded a well-inflated, medium-sized *Glycymeris* from the Eocene of Taiwan as *G. altoumbonata*. The Taiwanese species differs from *G. altoumbonata* by having smooth ligamental area, and may be identical with *G. cisshuensis* Makiyama, 1926 from the Oligo-Miocene in Kyushu.

Two Oligocene species, *Glycymeris cisshuensis* and *G. nakosoensis* Hatai & Nisiyama,



Text-fig. 6. Distribution of *Glycymeris cisshuensis* in the early Middle Miocene. Presumed paleogéography after Chinzei (1978). A: Warm water. B: Cold water. C: subtropical front.

1949, have been recorded from Kyushu and northern Honshu (Nagao, 1928; Hatai & Nisiyama, 1949; Kamada, 1962; Mizuno, 1964).

Japanese glycymeridid bivalves apparently flourished in Miocene time. The warm water Ashiya Fauna associated with *G. cisshuensis* lived during in the Early Miocene in the Kyushu and Chugoku Districts, western Japan. According to Chinzei (1978), in Middle Miocene time the convergence between warm and cold currents, the subtropical front, was most probably located as far north as central Hokkaido. In that time *G. cisshuensis* was occurred with the subtropical shallow water Kadonosawa Fauna (Chinzei, 1981, 1983), and was widely distributed from Kyushu to northern Honshu, or even Hokkaido. Middle Miocene sediments of Hokkaido are said to yield *G. cisshuensis* (S. Uozumi and K. Chinzei, 1984, personal communication). The genus *Tucetona* mainly consists of tropical species. Three *Tucetona* species, *i.e. T. nozokiensis* (Hatai & Nisiyama, 1951). *T. osawanoensis* Tsuda, 1959 and *T. chichibuensis* Hirayama, 1973, have been reported from the Middle Miocene of central to northern Honshu. In Late Miocene time shallow water sediments reappeared in northern Honshu and along the Japan Sea coast (Chinzei, 1978). The subtropical front at that time was likely located around the Boso Peninsula, central Honshu. At this time glycymeridid species were associated with the shallow, cold-water Shiobara Fauna (Chinzei & Iwasaki, 1967; Iwasaki, 1970). I think that *Glycymeris ksuzukii* Oinomikado, 1938 and *G. vestitoides* Nomura, 1935 are synonymous with *G. cisshuensis* of the cold-water Shiobara Fauna. *Glycymeris uandiensis* Lautenschlaeger, 1952 from the Late Miocene Uandi Formation of Sakhalin apparently resembles *G. cisshuensis.* In Late Miocene time, *G. yessoensis* (Sowerby, 1889) ranged from central and northern Honshu through Hokkaido northward to Sakhalin and Kamchatka (Slodkewitsch, 1938; Ilyina, 1963; Krishtofovich, 1964; Zhidkova *et al.*, 1968; Iwasaki, 1970; Chinzei, 1978; Amano, 1983).

In Pliocene and Early Pleistocene times the subtropical front supposedly lay around the Boso Peninsula, similar to where it lies at the present time (Chinzei, 1978). Therefore, faunal characters and distribution at that time closely resemble those of the Recent molluscan fauna. The warm water Kakegawa Fauna is distributed along the Pacific coast from Kyushu to central Honshu (Makiyama, 1927; Tsuchi, 1955; Shuto, 1961; Chinzei, 1978, 1980). *Glycymeris nakamurai* Makiyama, 1927 [= *G. albolineata* (Lischke, 1872)] and *G. totomiensis* Makiyama, 1927 are associated with the Kakegawa Fauna. At that time the shallow, cold water Tatsunokuchi Fauna was distributed from northern Honshu to southern Hokkaido (Nomura, 1938; Hayasaka, 1956; Masuda & Ogasawara, 1981). *Glycymeris yamaguchii* Hayasaka, 1956 and *G. gorokuensis* Nomura, 1938 were associated with the Tatsunokuchi Fauna. The cold water Omma-Manganji Fauna (Ogasawara, 1981, 1983) prevailed along Japan Sea and Pacific coasts of central to northern Honshu (Masuda & Ogasawara, 1981; Ogasawara, 1983). *Glycymeris yessoensis* and *G. echigoensis* Kanehara, 1940 [= *G. albolineata*] were associated with the shallow water facies of the Omma-Manganji Fauna and *G. derelicta* (Yokoyama, 1925) and *G. convexa* Ozaki, 1954 were associated with the offshore facies (Ozaki, 1954; Chinzei, 1959, 1978; Ogasawara, 1983).

Zoogeographic Elements of Living Species and Their Origin

Living species of Glycymerididae are characteristically confind to warm waters and no species is found in the arctic. Although further field studies are expected, distributional patterns of the Indo-West Pacific species recorded here provide useful evidence for discussing the migration and speciation of the Glycymerididae. The Glycymerididae of Japan is much more diverse in subtropical southwestern and warm temperate central Japan than in cool temperate to subarctic northern Japan. The following three faunal components are recognized for Japanese species: (1) tropical Indo-Pacific element, (2) warm temperate Japanese-Korean endemic element and (3) cool temperate and subarctic northern East Asian element (Matsukuma, 1984).

Tropical Indo-Pacific element: This element is fairly common in Japanese molluscan faunas that include many species of Pectinidae, Pteriidae, Cypraeidae, Strombidae and Conidae. In Japan this element consists of the following ten species and subspecies: *Glycymeris shutoi* Matsukuma, 1981, *G. fulgurata* (Dunker, 1877), *G. livida* (Reeve, 1943), *G. habei* Matsukuma, 1984, *G. reevei* (Mayer, 1868), *Tucetona hanzawai hanzawai* Nomura & Zinbo, 1934), *T. auriflua* (Reeve, 1943), *T. sibogae* Matsukuma, 1982, *T. pectunculus pectunculus* (Linnaeus, 1758) and *Melaxinaea subpectiniformis* (Nomura & Zinbo, 1934). Further studies are required to confirm the occurrences of *G. habei, T. hanzawai hanzawai* and *M. subpectiniformis.* The members of this element in Japan occur in the Ryukyu Islands, southern coasts of Kyushu, Shikoku, the Kii Peninsula and the Izu Islands, and they are distributed widely throughout the tropical West Pacific. *Glycymeris reevei* is distributed from Indonesia across northeastern Australia and New Guinea as far east as New Caledonia, Tonga and the Eastern Caroline Islands. Both *G. livida* and *T. pectunculus pectunculus* range across the Malay Peninsula as far west as the Indian Ocean. Except for *T. hanzawai hanzawai,* members of this element have no fossil record, which suggests that they did not live in Japan before the Pleistocene. The geologic and giographic evidence suggests that most species of this element were brought in by the Kuroshio

Table 3. Species composition of Recent Glycymerididae of Japan.

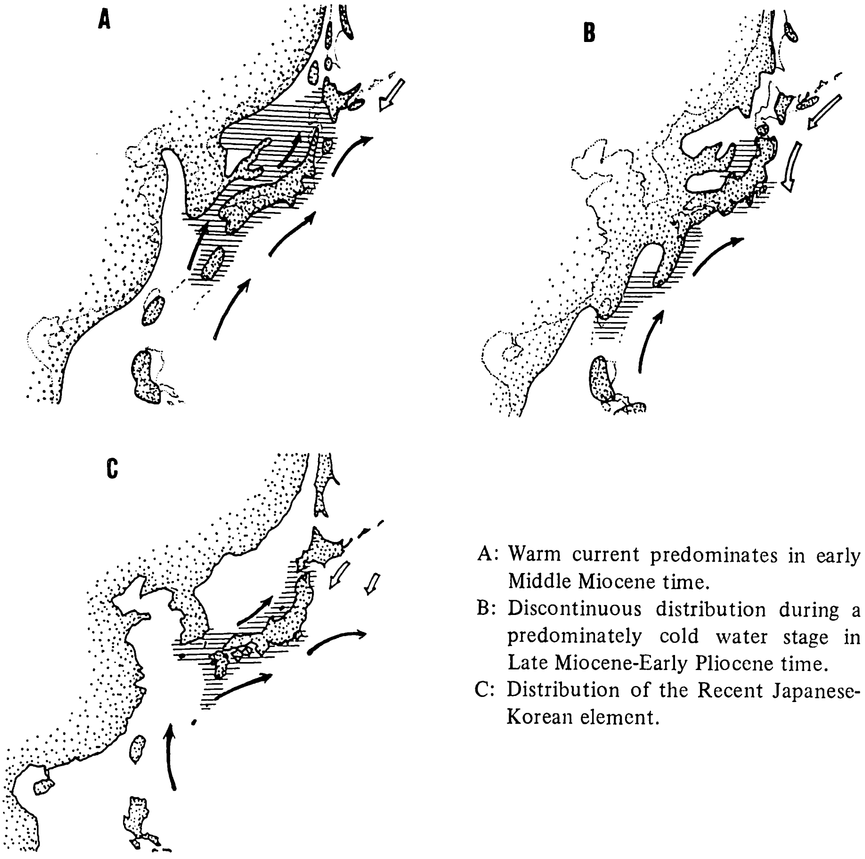
Subfamily / Zoogeographic element	Glycymeridinae	Melaxinaeinae	Total
	spp.	spp.	spp.
Subarctic	1 (8.3 %)	0 (0.0 %)	1 (5.6 %)
Japanese-Korean	6 (50.0 %)	1 (16.7 %)	7 (38.9 %)
Indo-West Pacific	5 (41.7 %)	5 (83.3 %)	10 (55.5 %)
Total	12 (66.7%)	6 (33.3 %)	18 (100 %)

Current in relatively recent times.

Temperate Japanese-Korean endemic element: This element is represented by open coast species of the East Asian endemic element and is common in the Japanese fauna (Sakai, 1940; Nisiyama, 1966, 1968). It is well known that a number of mollusks, *e.g. Nordotis madaka* Habe, 1979 (Ino, 1952) and *Batillus cornutus* (Lightfoot, 1786) (Okada & Fujita, 1933), belong to this Japanese-Korean element. In the Glycymerididae this element consists of the following seven species: *Glycymeris vestita* (Dunker, 1877), *G. albolineata* (Lischke, 1872), *G. rotunda* (Dunker, 1882), *G. imperialis* Kuroda, 1934, *G. munda* (Sowerby, 1903), *G. pilsbryi* (Yokoyama, 1920) and *Tucetona shinkurosensis* Hatai, Niino & Kotaka, 1952. Most species range southward to the Amami Islands and the southern coasts of the Korean Peninsula, and as far northeast as the southern part of Hokkaido along the Japan Sea coast and the Boso Peninsula in the Pacific coast. Some species, *e.g. G. albolineata* and *G. rotunda,* range to Tsugaru Strait and are found at around Hachinohe City on the Pacific coast of northern Honshu. The occurrence of this element coincide well with the distribution of the Kuroshio and Tsushima Warm Current.

A few investigators have discussed the origins of the East Asian endemic element, which includes the Japanese-Korean element of the Glycymerididae. Miyadi *et al.* (1953) pointed out that various Japanese embayment species or their closely related analog species are found in coastal areas of the mainland of China and Southern Asia. The Chinese coastal element was widely distributed from Japan to coastal areas of China in the Pleistocene and is now restricted to embayments in Japan, *e.g.* the Ariake Sea and Mikawa Bay. The hypothesis of relic endemism of the Chinese coastal element (Miyadi *et al.,* 1953) indicates a possible origin of some embayment species of Japan, such as *Trisidos kiyonoi* (Kuroda, 1929) and *Tegillarca granosa* (Linnaeus, 1758). However, it does not explain the origin of endemic Glycymerididae species found in open coast environments of Japan and along the southern coast of the Korean Peninsula.

Nishimura (1971, 1974, 1981) thought that Japanese initial endemic species consisted of the following three components: (1) endemic species derived from a tropical Indo-Pacific element, (2) endemic species derived from a northern Pacific element and (3) endemic species derived from a secondary speciation of the East Asian element. The Paleo-East China Sea and Paleo-Japan Sea were thought to be isolated seas for the development of Japanese endemic species derived from the Indo-Pacific element. According to Nishimura (1971) the tropical Indo-Pacific element brough by the Kuroshio arrived in the Paleo-East China Sea and Paleo-Japan Sea during an intergracial stage of Plio-Pleistocene time and was isolated in the Paleo-



A: Warm current predominates in early Middle Miocene time.
B: Discontinuous distribution during a predominately cold water stage in Late Miocene-Early Pliocene time.
C: Distribution of the Recent Japanese-Korean element.

Text-fig. 7. Inferred initial endemism of the Japanese-Korean element of the Glycymerididae. Solid arrow: Warm current. Open arrow: Cold current. Hatched area: Distribution of Japanese-Korean element.

East China Sea Gulf and Paleo-Japan Sea Lake during a glacial stage.

Tucetona shinkurosensis is the only endemic species of *Tucetona* and it has no fossil record. The geographic distribution of *T. shinkurosensis* suggests that this species may be an initial endemic species derived from the Pliocene-Recent speices *T. hanzawai* that occurs on submarine banks around the Izu Islands, the eastern extremity of subtropical waters around Japan. The Izu Islands are isolated from the southern coast of Honshu by depressions deeper than 200 m and the molluscan assemblage of the Izu Banks is an isolated fauna composed of species derived from warmer waters off of Kyushu and the Ryukyu Islands (Okutani, 1963). Larvae of *T. hanzawai* might have been carried by a warm current to the Izu Banks during the Pliocene and Pleistocene time. A population of *T. hanzawai* on the Izu Banks would be easily isolated from the southwestern Japanese population during a cold water period.

Glycymeris albolineata and *G. vestita* are very common in shallow warm-temperate waters around Japan. They first appeared in Upper Pliocene strata of central to southwestern Japan. Morphological characters, such as a dense, hairy periostracum, lamellar layers embedded in the fibrous layer and large shell size, indicate that they may be a descendant of the Oligo-Miocene species *G. cisshuensis* Makiyama, 1926, which was associated with the warm water Ashiya Fauna restricted to southwestern Japan in Oligocene to Early Miocene time. In early

Middle Miocene time *G. cisshuensis* was associated with the warm water Kadonosawa Fauna ranged as far north as northeastern Honshu, or Hokkaido. In Late Miocene time the subtropical front moved south and probably was located around the Boso Peninsula (Chinzei, 1978). During this period *G. cisshuensis* was found in the cold water Shiobara Fauna of Northern Korea and central Honshu, and some individual might have migrated as far as the Rhykyu Islands. Although further paleozoogeographic studies are required, I take a view that the southern populations became *G. vestita* in Late Miocene to Early Pliocene time around the Ryukyu Islands, because *G. vestita* was first recorded from the Pliocene of Miyazaki (Shuto, 1952) and Okinawa Prefectures and allied species, *G. formosana* (Yokoyama, 1928), was found in the Pleistocene of Taiwan (Yokoyama, 1928; Nomura, 1933). The northern populations might have become *G. albolineata* in the Japan Sea and along the Pacific coast of central Japan. The Pliocene species, *Glycymeris echigoensis* Kanehara, 1940 and *G. nakamurai* Makiyama, 1927, have large quadrate shells with embedded lamellar layers and conspicuous punctations on the outer surface and are forerunners of the Recent *G. albolineata* (Matsukuma, 1984).

Although the present study of Glycymerididae suggests that the idea of speciation hypothesized by Nishimura (1971, 1974, 1981) is applicable, with slight amendment, for the origin of *T. shinkurosensis,* it is not useful for explaining the origin of *G. albolineata* and *G. vestita.* The stratigraphic evidence suggests that living Japanese-Korean endemic species, such as *G. albolineata, G. vestita* and *G. munda,* first appeared in the Late Pliocene. Therefore, these species evolved in the Early Pliocene or earlier. The paleoecological evidence indicates that fossil glycymeridids are always found in the open coast associations and none of them is associated with an embayment molluscan fauna. Such a mode of occurrences indicates that most Japanese-Korean endemic species might have evolved from secondary speciation of the East Asia element within the open coast environment of Japan during Late Miocene or Early Pliocene time.

Cool temperate to subarctic northern East Asian element: Only one glycymeridid species, *G. yessoensis* (Sowerby, 1889), belongs to this element. Living *G. yessoensis* is found in the subtidal zone in Sakhalin, the Kuril Islands, southern Primorskii, the northeastern Korean Peninsula, and on Hokkaido, as far west as the Oki Islands of the Japan Sea, the Chugoku District of western Honshu. The distributional pattern is apparently not influenced by warm nor cold currents, but may reflect geologic history of the species. Stratigraphic evidence suggests that *G. yessoensis* first occurred in the Middle Miocene of Kamchatka and Sakhalin (Slodkewitsch, 1938; Ilyina, 1963; Zhidkova *et al.*, 1968) and it is commonly found in Late Miocene formations of Sakhalin, Hokkaido and northern Honshu. An north East Pacific, Pliocene-Recent species, *G. subobsoleta* (Carpenter, 1864), has a dense hairy periostracum, a grooved ligamental area and a fixed anus. These characteristics are common to *G. yessoensis. G. yessoensis* may be one of the relic species derived from ancestral species that was widely distributed around the northern Pacific in the Middle Miocene.

List of Japanese Glycymeridid Species

Fossil and living species of the Glycymerididae of Japan are summarized as follows:

Glycymeris (*Glycymeris*) *altoumbonata* Nagao, 1928. Eocene: Doshi F., Fukuoka (type-locality); [? Miyara F., Miyako Is. Oligocen: Yonryo Sandstone, central Taiwan (Kanno &

Chung, 1975)].

Glycymeris (*Glycymeris*) *chitanii* (Yokoyama, 1929). Miocene: Borsk F., Sakhalin (type-locality); Chokubetsu and Ishiizawa F., Hokkaido.

Glycymeris (*Glycymeris*) *convexa* Ozaki, 1954. Pliocene: Naarai F., Chiba (type-locality). Syn. *Glycymeris crassitesta* Ozaki, 1954, *ibid.*, no. 34, p. 15, pl. 8, figs. 1–2, Pliocene: Naarai F., Chiba.

Glycymeris (*Glycymeris*) *derelicta* (Yokoyama, 1928). Pliocene: Shiraiwa F., Niigata (type-locality); Kubo F., Iwate (Chinzei, 1959); Sasaoka F., Aomori (Matsui, 1981).

Glycymeris (*Glycymeris*) *gorokuensis* Nomura, 1938. Pliocene: Tatsunokuchi F., Miyagi (type-locality); Gobanshoyama F., Miyagi.

Glycymeris (*Glycymeris*) *habei* Matsukuma, 1984. Recent: Kochi (type-locality); Okinawa.

Glycymeris (*Glycymeris*) *imperialis* Kuroda, 1934. Pleistocene: Narita F., Chiba; Ninomiya F., Kanagawa; Tokyo F., Tokyo. Recent: Iwate; Miyagi; Ibaraki; Chiba; Kanagawa; Sagami Bay (type-locality); Shizuoka; Aichi; Wakayama; Yamagata; Niigata; Shimane; Fukuoka.

Glycymeris (*Glycymeris*) *izumoensis* Matsukuma & Okamoto (MS). Miocene: Fujina F., Izumo City, Shimane (type-locality).

Glycymeris (*Glycymeris*) *matumoriensis matumoriensis* Nomura & Hatai, 1937. Miocene: Nanakita F., Miyagi.

Glycymeris (*Glycymeris*) *matumoriensis ikezawensis* Tanaka, 1960. Miocene: Omi F., Nagano (type-locality); Aoki F., Nagano (Kuroda, 1931); Jyoyama Mudstone Mem., Yatsuo Gr., Toyama. [Karatou, Teshima and Shikai F., Kagawa (Saito, 1962)]. Syn. *Glycymeris crassa* Kuroda, 1931 (non Koch & Pallary in Pallary, 1900), Miocene Aoki F., Nagano; *Glycymeris ikusakensis* Tanaka, 1960, Miocene Omi F., Nagano; *Glycymeris ikezawensis kurodai* Matsukuma, 1979, new name for *G. crassa* Kuroda.

Glycymeris (*Glycymeris*) *minochiensis* (Yokoyama, 1925). Miocene (or Pliocene): Shigarami F., Nagano (type-locality). Pliocene: Minagawa F., Niigata.

Glycymeris (*Glycymeris*) *minoensis* Itoigawa, 1955. Miocene: Kubohara F. (type-locality), Nataki and Yamanouchi F., Gifu; Togane F., Shimane.

Glycymeris (*Glycymeris*) *osozawensis* Kanno, 1956. Pliocene: Akebono F., Yamanashi (type-locality).

Glycymeris (*Glycymeris*) *rotunda* (Dunker, 1882). Pliocene: Koshiba (Yokoyama, 1920) and Nojima F., Kanagawa; Hosoya Silt Member, Kakegawa Gr., Shizuoka; Tonohama and Nobori F., Kochi; Takanabe and Tsuma Mem., Miyazaki Gr., Miyazaki; Shinzato F., Okinawa (Noda, 1980). Pleistocene: Zizodo and Semata F., Chiba (Yokoyama, 1922); Miyata, Ninomiya, Kakio and Naganuma F., Kanagawa; Negoya F., Shizuoka; Omma F., Ishikawa; Sogippo F., Korea. Recent: Shiribeshi, Hokkaido to East China Sea (Japan Sea coast); Hachinohe, Iwate; Boso Peninsula to Miyakojima Is., Okinawa (Pacific coast). Syn. *Pectunculus nipponicus* Yokoyama, 1920, Pliocene Koshiba F., Kanagawa; *Pectunculus yamakawai* Yokoyama, 1922, Pleistocene Semata F., Chiba; *Glycymeris okinawaensis* Noda, 1980, Pliocene Shinzato F., Okinawa.

Glycymeris (*Glycymeris*) *shutoi* Matsukuma, 1981. Recent: Amami Is., Kagoshima (type-locality); Okinawa; Philippines.

Glycymeris (*Glycymeris*) *snatolensis* Slodkewitsch, 1934. Pliocene: Kavran Ser., Kamchatka (type-locality); Yuchi F., Hokkaido (Masuda *et al.*, 1981).

Glycymeris (*Glycymeris*) *subcostata* Matsukuma & Okamoto (MS). Miocene: Ginzan F., Yamagata; Matsue F., Matsue City, Shimane (type-locality).

Glycymeris (*Glycymeris*) *totomiensis* Makiyama, 1927. Pliocene: Dainichi F., Shizuoka (type-locality); Takanabe Mem., Miyazaki Gr., Miyazaki. Pleistocene; Soga F., Shizuoka.

Glycymeris (*Glycymeris*) *yamaguchii* Hayasaka, 1956. Pliocene: Ishiguma (type-locality) and Iwasawa (Kamada & Hayasaka, 1959) F., Fukushima.

Glycymeris (*Glycymeris*) *yanagawaensis* Matsukuma (MS). Miocene: Yanagawa Mem., Date F., Fukushima (type-locality).

Glycymeris (*Glycymeris*) *yessoensis* (Sowerby, 1889). Miocene: Etolon F., Kamchatka; Sertúnai, Uandi, Nutovo and Maruyama F., Sakhalin; Togeshita and Onisuka F., Hokkaido; Ginzan F., Yamagata; Kubota and Kamitoya F., Fukushima. Miocene (or Pliocene): Shigarami F., Nagano (Yokoyama, 1925). Pliocene: Shibetsugawa and Tomikawa F., Hokkaido; Daishaka, Narusawa, Totezawa, Kanita and Hamada F., Aomori; Sasaoka and Shibikawa F., Akita; Kannonji F., Yamagata; Ota, Haizume, Nishiyama, Minagawa and Sawane F., Niigata; Himi F., Toyama; Omma F., Ishikawa; Yamadahama and Sukegawa F., Fukushima. Pleistocene: Nopporo F., Hokkaido; Katanishi F., Akita; Narita, Semata, Zizodo, Naruto, Mandano, Sanuki and Nagahama F., Chiba; Tokyo, F., Tokyo; Miyata F., Kanagawa. Recent: Vostok near Uladiostok; Uladimir Bay, USSR; Hamgyong Namdo and Kogendo, northern Korea. Southern Sakhalin to Oki Islands, Shimane (Japan Sea coast); Kunashiri and Shikotan Islands, Hokkaido to Boso Peninsula (Pacific coast). Syn. *Pectunculus yamasakii* Yokoyama, 1925, Miocene (or Pliocene) Shigarami F., Nagano.

Glycymeris (*Veletuceta*) *albolineata* (Lischke, 1872). Pliocene: Tentokuji F., Akita; Ota (Kanehara, 1940), Shiotani, Kawaguchi and Natachi F., Niigata; Ishiguma F., Fukushima; Dainichi F., Shizuoka (Makiyama, 1927); Ananai and Konomine F., Kochi; Takanabe Mem., Miyazaki Gr., Miyazaki. Pleistocene: Sanuki and Jizodo F., Chiba; Soga F., Shizuoka. Recent: Okushiri Is., Hokkaido to Nagasaki and southern coast of Korean Peninsula (Japan Sea coast); Boso Peninsula to Tokunoshima Is., Kagoshima (Pacific coast). Syn. *Glycymeris nakamurai* Makiyama, 1927, Pliocene Dainichi F., Shizuoka; *Glycymeris echigoensis* Kanehara, 1940, Pliocene Ota F., Niigata.

Glycymeris (*Veletuceta*) *cisshuensis* Makiyama, 1926. Oligocene: Yoshinotani and Kyuragi F., Saga; Funatsu F., Nagasaki. Miocene: Mankodo F., North Korea (type-locality); Tanosawa F., Aomori (Nomura, 1935); Nanakita F., Miyagi; Nishikurosawa F., Akita; Kubota F., Fukushima; Itahana F., Gumma (Oinomikado, 1938); Kurosedani F., Toyama Prefecture; Kujiri Facies, Mizunami Gr., Gifu (Itoigawa & Shibata, 1975); Kaisekizan F., Mie; Matsue, Fujina and Togane F., Shimane; Yamaga F., Yamaguchi; Sakamizu (Nagao, 1928), Waita and Yamaga F., Fukuoka; Ainoura, Itanoura and Kakinoura F., Nagasaki; Nichinan Gr., Miyazaki. Syn. *Glycymeris cisshuensis compressa* Nagao, 1928, Miocene Yamaga F., Fukuoka; *Glycymeris vestitoides* Nomura, 1935, Miocene Tanosawa F., Aomori; *Glycymeris ksuzukii* Oinomikado, 1938, Miocene Itahana F., Gumma; *Glycymeris ikebei* Itoigawa & Shibata, 1975, Miocene Mizunami Gr., Gifu.

Glycymeris (*Veletuceta*) *fulgurata* (Dunker, 1877). Recent: Hachijojima Is. to Taiwan.

Glycymeris (*Veletuceta*) *livida* (Reeve, 1843). Recent: Amami Is., Kagoshima; Taiwan; Indonesia; Mozambique.

Glycymeris (*Veletuceta*) *nakosoensis* Hatai & Nisiyama, 1949. Oligocene: Iwaki F., Fukushima (type-locality).

Glycymeris (*Veletuceta*) *reevei* (Mayer, 1868). Recent: Kochi to Okinawa; Taiwan; Philippines (type-locality); Indonesia; New Guinea; Queensland, Australia; Truk, Micronesia; Tonga; New Caledonia. Syn. *Axinaea fringilla* Angas, 1872, Torres Strait; *Axinaea hanleyi* Angas, 1879, type-locality unknown; *Veletuceta cotinga* Iredale, 1939, Queensland.

Glycymeris (*Veletuceta*) *vestita* (Dunker, 1877). Pliocene: Takanabe Mem., Miyazaki Gr., Miyazaki; Nakoshi F., Okinawa. Pleistocene: Semata and Narita F., Chiba; Tokyo F., Tokyo; Miyata F., Kanagawa; Toshima Gr., Aichi. Recent: Okushiri Is., southern Hokkaido to Kyushu and southern coast of Korean Peninsula (Japan Sea coast); Fukushima to Okinawa (Pacific coast).

Glycymeris (*Tucetilla*) *hirayamai* Matsukuma (MS). Miocene: Hiranita F., Chichibu City, Saitama (type-locality).

Glycymeris (*Tucetilla*) *pilsbryi* (Yokoyama, 1920). Pliocene: Haizume F., Niigata; Konomine F., Kochi; Shinzato F.,Okinawa; Sumagui F., Philippines. Pleistocene: Sanuki, Mandano, Jizodo, Semata and Narita F., Chiba; Miyata F., Kanagawa; Ryukyu Limestone, Amami Is.; Toukoshan F., Taiwan. Recent: Tsugaru Strait to Kyushu and southern coast of Korean Peninsula (Japan Sea coast); Aomori to Okinawa and Taiwan (Pacific coast). Syn. *Glycymeris amamiensis* Kuroda, 1930, Recent, Amami Is.

Glycymeris (*Tucetonella*) *munda* (Sowerby, 1903). Pliocene: Minagawa and Haizume F., Niigata. Pleistocene: Miyata F., Kanagawa; Ryukyu Limestone, Amami Is. Recent: southern coast of Korean Peninsula and Kyushu (Japan Sea coast); Boso Peninsula to Kagoshima. Syn. *Glycymeris* (*Tucetonella*) *planicostata* Habe, 1961, Recent, Nagasaki.

Tucetona auriflua (Reeve, 1843). Recent: Amami and Ryukyu Is.; Philippines (type-locality); Indonesia. Syn. *Glycymeris mindoroensis* Smith, 1916, Philippines.

Tucetona chichibuensis Hirayama, 1973. Miocene: Hiranita F., Saitama (type-locality).

Tucetona hanzawai hanzawai (Nomura & Zinbo, 1934). Pleistocene: Ryukyu Limestone, Amami Is.; Yoshida Shell Bed, Kagoshima. Recent: Wakayama; Nagasaki; Kumamoto; Okinawa.

Tucetona hanzawai granulicostata Matsukuma (MS). Pliocene: Shinzato F., Okinawa (type-locality).

Tucetona nozokiensis (Hatai & Nisiyama, 1951). Miocene: Okawa F., Yamagata (type-locality); Nataki F., Gifu.

Tucetona osawanoensis Tsuda, 1959. Miocene: Kurosedani F., Toyama (type-locality).

Tucetona pectunculus pectunculus (Linnaeus, 1758). Recent: Okinawa; Philippines; Palau Is., Gulf of Thailand; Indonesia; Queensland, Australia; Andaman Sea; Sri Lanka; India. Syn. *Cardium amboinense* Gmelin, 1791, Indonesia; *Pectunculus subauritus* Lamarck, 1819; *Pectunculus pectiniformis* Lamarck, 1819, India; *Tucetona extra* Iredale, 1939, Queensland.

Tucetona shinkurosensis Hatai, Niino & Kotaka, 1952. Recent: Izu (type-locality) and Bonin Is.

Tucetona sibogae Matsukuma, 1982. Pleistocene: Ryukyu Limestone, Amami Is. Recent: Wakayama; Luzon Is., Philippines; Moluccas, Indonesia (type-locality).

Melaxinaea subpectiniformis (Nomura & Zinbo, 1934). Pleistocene: Ryukyu Limestone, Amami Is. (type-locality).

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Plate 5

Explanation of Plate 5

Figs. 1–3, 5–6, 11–12. *Glycymeris albolineata* (Lischke, 1872)

1–2: *G. albolineata* forma *echigoensis* Kanehara, 1940. NSMT-Mo59990, Pliocene Ota Formation, Niigata Prefecture. L 49.5 mm.

3: NSMT-Mo59358, Fukuoka Prefecture. L 73.4 mm.

5–6: GK.L4373, Pliocene Toriyama Formation, Miyazaki Prefecture. L 78.8 mm.

11: *G. albolineata* forma *nakamurai* Makiyama, 1927. NSMT-Mo59991, Pliocene Dainichi Formation, Shizuoka Prefecture. L 74.6 mm.

12: *G. albolineata* forma *nakamurai* Makiyama, 1927. Holotype of *G. nakamurai*, UK-JC200206, Pliocene Dainichi Formation, Shizuoka Prefecture. H 72.1 mm.

Fig. 4. *Glycymeris vestita* (Dunker, 1877)

Holotype, ZMHUB 101919, Japan. L 49.1 mm.

Figs. 7–8. *Glycymeris cisshuensis* Makiyama, 1926

Holotype, UK-CC100201, Miocene Mankodo Formation, Hamgyong Pukdo, North Korea. L (66 mm).

Figs. 9–10. *Glycymeris nakosoensis* Nomura & Hatai, 1948

Holotype, IGPS coll. cat. no. 72502, Oligocene Iwaki Formation, Fukushima Prefecture. L 23.6 mm.

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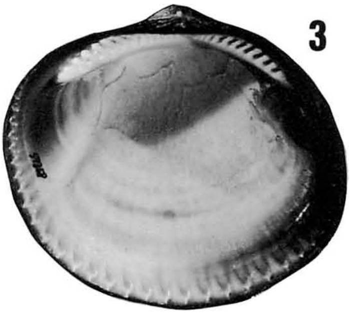

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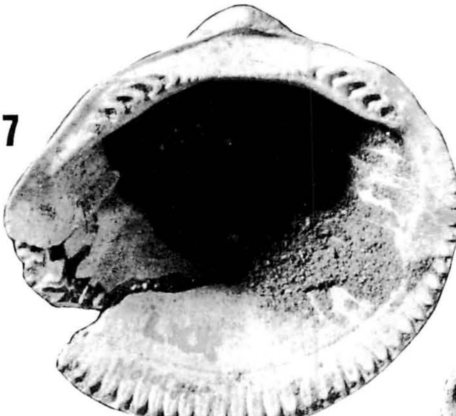

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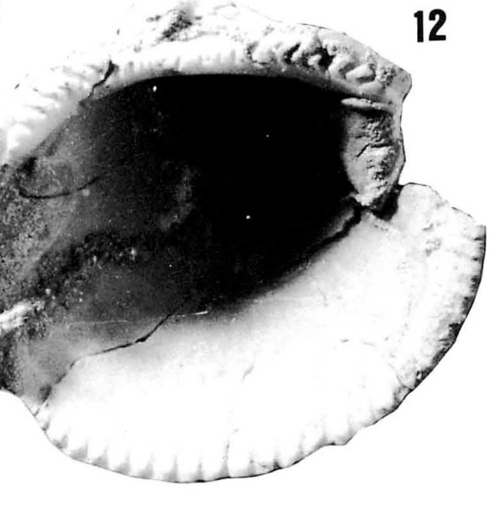

Plate 6

Explanation of Plate 6

Fig. 1. *Tucetona shinkurosensis* Hatai, Niino & Kotaka, 1952
NSMT-Mo62364, Hyotanse Bank, Izu Islands. L 14. 8 mm.
Figs. 2–3. *Tucetona hanzawai granulicostata* Matsukuma (MS)
NSMT-Mo59967, Pliocene Shinzato Formation, Okinawa Prefecture. L 14.6 mm.
Fig. 4. *Tucetona osawanoensis* (Tsuda, 1959)
Holotype, UK-JC 1400005, Miocene Kurosedani Formation, Toyama Prefecture. H 19.7 mm.
Fig. 5. *Tucetona chichibuensis* Hirayama, 1973
Holotype, SPU1618, Miocene Hiranita Formation, Saitama Prefecture. L (16 mm).
Fig. 6. *Glycymeris minoensis* Itoigawa, 1955
Holotype, UK-JC 1300001, Miocene Kubohara Formation, Gifu Prefecture. L 26.1 mm.
Fig. 7. *Glycymeris okinawaensis* Noda, 1980
[= *G. rotunda* (Dunker, 1882)]. NSMT-Mo60628, Pliocene Shinzato Formation, Okinawa Prefecture. L 30.6 mm.
Figs. 8–9. *Glycymeris convexa* Ozaki, 1954
NSMT-Mo58920, Pliocene Naarai Formation, Chiba Prefecture. L 30.9 mm.
Fig. 10. *Glycymeris matumoriensis ikezawensis* Tanaka, 1960
SU210, Miocene Omi Formation, Nagano Prefecture. L 50.0 mm.
Fig. 11. *Glycymeris totomiensis* Makiyama, 1927
Holotype, UK-JC200204, Pliocene Dainichi Formation, Shizuoka Prefecture. L 33.5 mm.
Fig. 12. *Glycymeris kannoi* Matsukuma, 1979
NSMT-Mo61299, Miocene Akashiba Formation, Fukushima Prefecture. L 38.6 mm.
Fig. 13. *Glycymeris yamaguchii* Hayasaka, 1956
Holotype, IGPS coll. cat. no. 77373, Pliocene Ishiguma Formation, Fukushima Prefecture. H 48.3 mm.
Fig. 14–15. *Glycymeris rotunda* forma *nipponica* (Yokoyama, 1920)
NSMT-Mo59549, Pliocene Nojima Formation, Kanagawa Prefecture. L 25.9 mm.
Fig. 16. *Glycymeris matumoriensis matumoriensis* Nomura & Hatai, 1937
Paratype, SHM2631, Miocene Nanakita Formation, Miyagi Prefecture. L 52.2 mm.
Fig. 17. *Glycymeris minochiensis* (Yokoyama, 1925)
Holotype, UMUT-CM22652, Miocene (or Pliocene) Shigarami Formation, Nagano Prefecture. L (60 mm).

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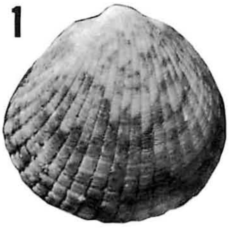

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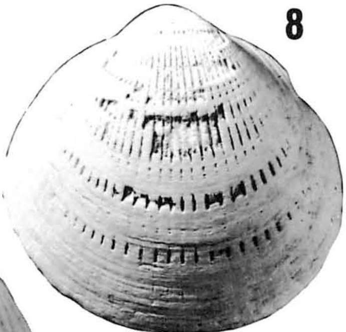

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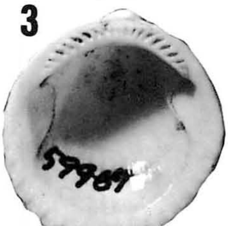

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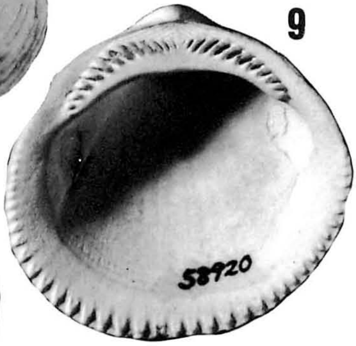

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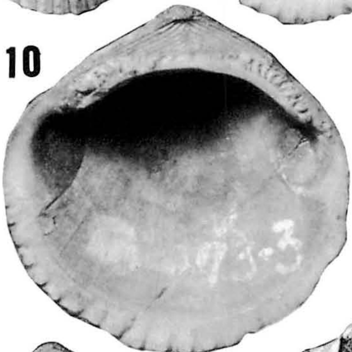

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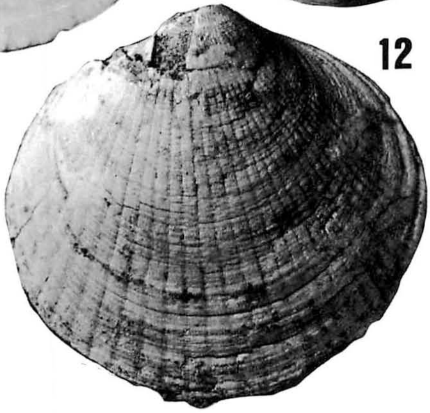

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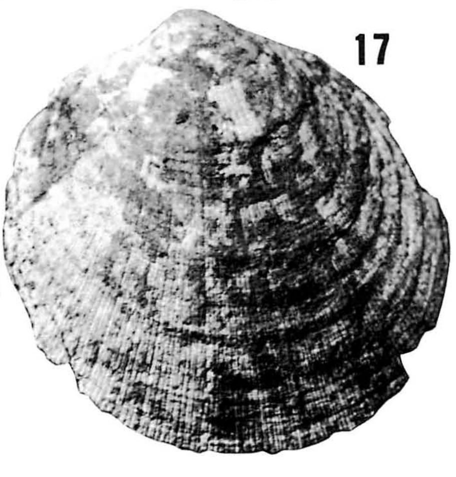

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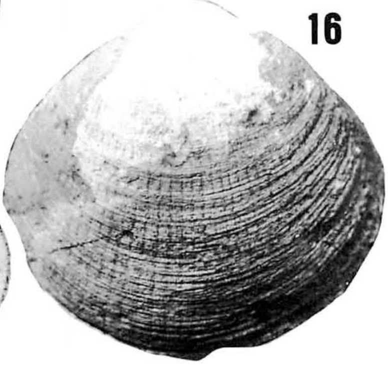

15

NOTES ON ORIGIN AND MIGRATION OF CENOZOIC PECTINIDS IN THE NORTHERN PACIFIC

by

Kôichirô MASUDA

Introduction

Many species of pectinids have been described from Tertiary and Quaternary formations in the Northern Pacific region, where Cenozoic pectinids are the largest single group of fossil marine molluscs. Also, pectinid shells are usually rather well preserved in strata even when the majority of the associated shells are represented as molds or casts. Therefore, pectinid fossils are useful in age determination and correlation of nearshore Tertiary marine strata, especially because of their rather short geologic range and wide geographical distribution (Masuda, 1973 B, 1978; Addicott, 1974, 1981).

Among Cenozoic pectinids of the Northern Pacific region *Patinopecten, Mizuhopecten, Fortipecten, Yabepecten, Nanaochlamys, Swiftopecten, Amussiopecten, Amusium, Comptopallium,* etc. are considered to be very important for interregional correlation between Eastern Asia and Western North America. These genera are also significant for addressing problems of origin and migration because of their sometimes wide but still locally limited geographical distribution and their more or less restricted geologic ranges.

In the present article remarks on some important pectinids in the Northern Pacific region are given and aspects of their origins and migration are discussed.

Acknowledgments

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Remarks on Some Pectinids of the Northern Pacific

1. *Patinopecten* and *Mizuhopecten*

Many species of the genus *Patinopecten* have been described from Cenozoic formations in the Japanese Islands, Sakhalin and Kamchatka as well as from the West Coast of North America. However, according to the writer's study (Masuda, 1963) it became evident that most species of the *Patinopecten* group in Japan differ from the true *Patinopecten* of the West Coast of North America, and should be placed in different genus. Thus, the writer proposed a new genus, *Mizuhopecten*, for most of the species of so-called *Patinopecten* of Japan, with a type species of *Pecten yessoensis* Jay, a common Recent scallop of the Northern Pacific.

From a study of the *Patinopecten* on the West Coast of North America, the writer (Masuda, 1971 A) pointed out that among the species described from the West Coast, *Patinopecten bakeri* (Hanna and Hertlein), *Patinopecten bakeri diazi* Durham and *Patinopecten marquerensis* Durham from Pliocene formations in Baja California (Durham, 1950 A) should be removed from *Patinopecten* and placed in the genus *Leopecten*. Moreover, the writer pointed out that *Patinopecten* (*Mizuhopecten*) *skonunensis* MacNeil (1967) described from the Skonun Formation, British Colombia cannot be referred to *Mizuhopecten* but to *Patinopecten* (s. s.). Also, *Patinopecten* n. sp. illustrated by Addicott (1966) from the Montesano Formation, Washington represents a new species of *Mizuhopecten* (Masuda, 1971 A), and *Fortipecten mollerensis* MacNeil (1967) described from the Unga Conglomerate Member of the Bear Lake Formation, Alaska should be removed from *Fortipecten* and placed in *Mizuhopecten* (Masuda, 1978).

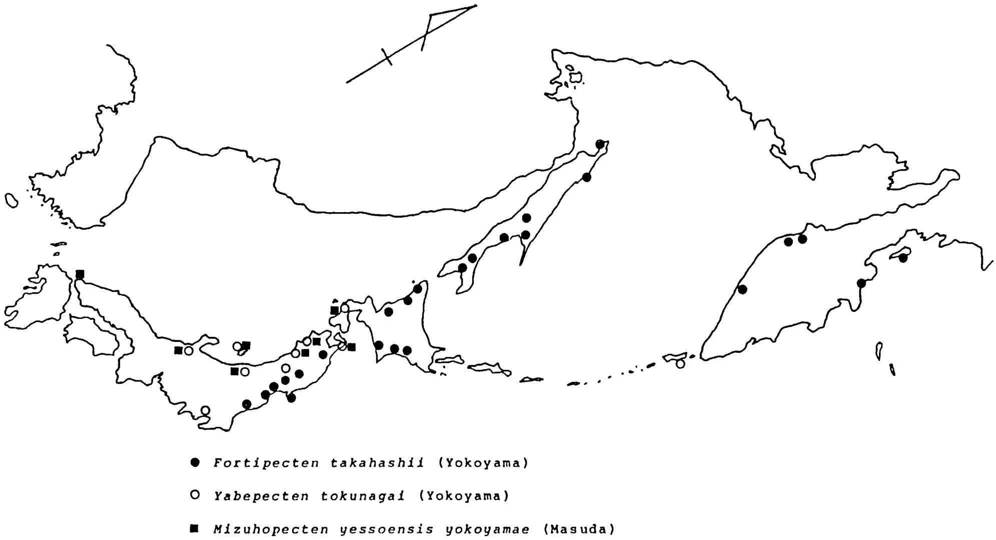
The genus *Mizuhopecten* known from the Tertiary formations in the Japanese Islands is very abundant specifically and individually, but there are only two species, *M. tokyoensis* (Tokunaga) and *M. yessoensis* (Jay), known in the Pleistocene and only one species, *M. yessoensis*, from the Recent seas of Northern Japan. And it seems probable that the majority of the *Patinopecten* species recorded from Sakhalin and Kamchatka should be allocated to the genus *Mizuhopecten*, and that true *Patinopecten* does not occur in the Western Pacific. Therefore, it is evident that the appearance of *Mizuhopecten warreni* Masuda (1971 A) in the Late Miocene Montesano Formation of Washington and *Mizuhopecten mollerensis* (MacNeil, 1967) in the Late to Middle Miocene Unga Conglomerate of Alaska, both resulted from eastward migration from the Western Pacific region.

As already noticed by the writer (Masuda, 1971 A), from the paleontological data it can be concluded that *Mizuhopecten* might have been originally a warm water inhabitant in the Late Oligocene to Early Miocene in the Japanese Islands. Even though changes in marine environmental conditions from the Oligocene to Recent have greatly changed the generic composition of marine faunas, *Mizuhopecten* evidently became adapted to different environmental conditions. However, a result of gradually changing environmental conditions only *Mizuhopecten yessoensis* (Jay) survived to the Recent while but other *Mizuhopecten* species became extinct.

Similarly, the genus *Patinopecten* ranges from the Middle Miocene to Recent of the West Coast of North America, and was especially abundant during the Neogene, but it contains only one Recent species, *Patinopecten caurinus* (Gould), which lives north of San Francisco Bay (Masuda, 1971 A). Consequently, it is considered that a result of the gradual changing of environmental conditions from the Tertiary to Recent only *Patinopecten caurinus* could survive to the Recent while other species became extinct at the end of the Tertiary. The changes in environmental conditions from the Tertiary to Recent in the Japanese Islands coincide well with those in the West Coast of North America (Durham, 1950 B; Masuda, 1962 B, 1963, 1971 A, 1973 B; Addicott, 1969).

2. *Fortipecten*

Pecten takahashii Yokoyama (1930), the type species of *Fortipecten*, is of particular interest because of its very large, thick shell, peculiar shell form, restricted geologic range and rather



Text-fig. 1. Geographic distribution of some Pliocene pectinids in the Northern Pacific.

wide geographical distribution. Since *P. takahashii* was described from the Pliocene Maruyama Formation, South Sakhalin, it has frequently been recorded from the Pliocene formations of Northern Japan, Sakhalin and Kamchatka, and it has been considered to be one of the most important Pliocene pectinids in the Northern Pacific region (Fig. 1).

In 1940 Yabe and Hatai established the subgenus *Fortipecten* based upon *P. takahashii* and then Hatai and Nisiyama (1952) raised *Fortipecten* to the generic ranking, as do most recent authors. Later, Chinzei (1960) described *Pecten* (*Fortipecten*) *kenyoshiensis* from the Pliocene Togawa Formation, Aomori Prefecture and Kotaka and Noda (1967) described *Fortipecten kuroishiensis* from the Middle Miocene Ogawara Formation, Aomori Prefecture.

On the other hand, several species of *Fortipecten*, including *takahashii* and *kenyoshiensis*, have been recorded from Pliocene formations of Sakhalin and Kamchatka (Khomenko, 1931; Slodkewitsch, 1938; Illyina, 1963; Krishtofovich, 1964; Zhidkova *et al.*, 1968; Sinelinikova, 1975), and *Fortipecten hallae* (Dall) (MacNeil *et al.*, 1943; Durham and MacNeil, 1967) and *F. mollerensis* MacNeil (1967), which is now referred to *Mizuhopecten*, have been described from Alaska.

As far as now known, the oldest species of *Fortipecten* is *kuroishiensis* described from the Ogawara Formation, Aomori Prefecture. Judging from morphological characters it appears that *kuroishiensis* branched off from the *Mizuhopecten* stock in the Middle Miocene and became extinct at the end of the Middle Miocene, but its descendants reached their maximum flourishing in the Pliocene. Therefore, it is evident that very wide occurrences of *Fortipecten* in the Circum North Pacific region reflect the north- to northeastward migration from the Japanese Islands. All species of *Fortipecten* became extinct in the Pliocene.

3. *Yabepecten*

Pecten tokunagai Yokoyama (1920) described from the Pliocene Koshiba Formation, Kanagawa Prefecture is particular interest because of its broad range of morphologic characters and rather restricted geologic range, and because it has been referred at times to *Pecten,* *Amussiopecten* or *Patinopecten.* Based upon the type specimens the writer (Masuda, 1962 A) pointed out that *Pecten plebejus* Yokoyama (1926) described from the Pliocene Sawane Formation, Niigata Prefecture is a synonym of *Pecten tokunagai. Pecten tokunagai* was designated as the type species of *Yabepecten* when this genus was established by the writer (Masuda, 1963).

As far as now known, *Yabepecten tokunagai* is only known from Pliocene formations in the Japanese Islands and Kurile Islands (Masuda, 1963, 1978, 1980; Zhidkova *et al.*, 1972) (Fig. 1). It represents an important element of the Omma-Manganzi fauna (Masuda, 1962 A; Masuda and Ogasawara, 1981), but pectinids related to *tokunagai* are not known in Miocene and Pliocene faunas of the Japanese Islands.

Masuda and Addicott (1970) pointed out that *Pecten* (*Amusium*) *condoni* Hertlein (1925) from the Montesano Formation of western Washington is probably assigned to *Yabepecten* and not *Amusium.* As the Montesano Formation yielding *Yabepecten condoni* (Hertlein) and *Mizuhopecten warreni* Masuda is now considered to be Late Miocene in age (Addicott, 1969, 1981), it seems likely that the occurrence of *Yabepecten condoni* in the Montesano Formation is a result of migration from the Northern Pacific or Arctic into the eastern North Pacific, probably during the Late Miocene. Also, it is evident that the presence of *Yabepecten tokunagai* in the Pliocene formations ranging from the Kurile Islands to Central Honshu resulted from southwestward migration from the Northern Pacific.

4. *Amussiopecten*

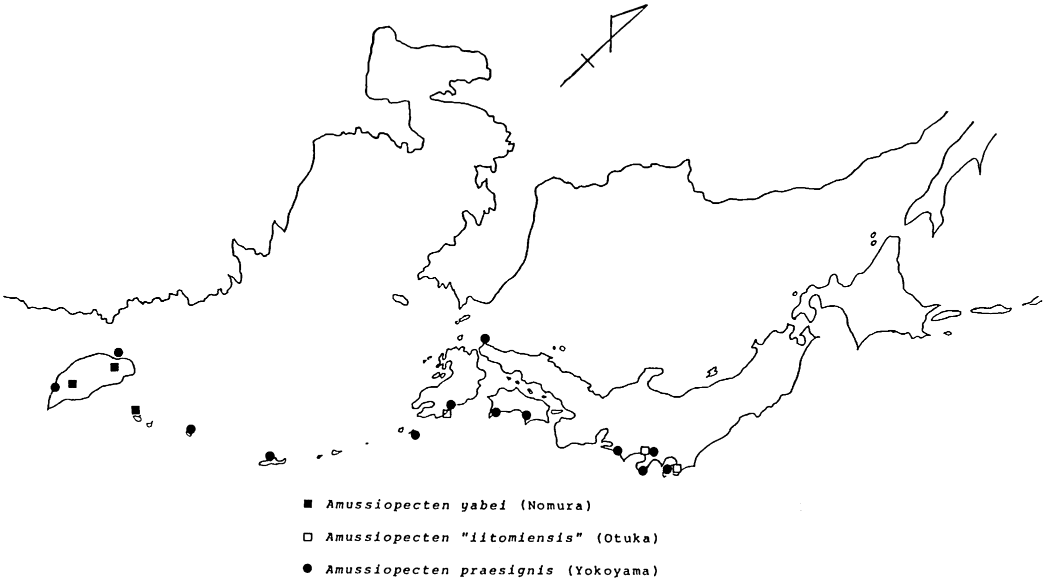
The genus *Amussiopecten*, established as a subgenus of *Pecten* and based upon *Pecten burdigalensis* Lamarck, is an important pectinid in Europe, but it has frequently been confused with related pectinids.

Amussiopecten has frequently been described from various Paleogene and Neogene formations in South and Central Europe, the Mediterranean Region, Iran, East Africa, Madagascar, Southeast Asia and East Asia (Martin, 1909; Deprét et Roman, 1912; Cox, 1927, 1939; Eames and Cox, 1956). However, *Amussiopecten* species were not known from either North or South America until the present writer described several species of *Amussiopecten* from the Oligocene and Miocene formations along the West Coast of North America, Central America, the West Indies and northern South America (Masuda, 1971 B).

Among the Cenozoic pectinids of the world the genus *Amussiopecten* is one of the most important and significant, particularly from the viewpoint of its worldwide but locally limited geographical distribution and restricted geologic range.

Some Oligocene species of *Amussiopecten* are known from Europe, Iran, Puerto Rico and Antigua Island in the West Indies, Venezuela and Mexico (Masuda, 1971 B), and numerous species have been described from the Early to Middle Miocene formations around the world. Though all species of *Amussiopecten* in Europe, North and East Africa, Southeast Asia, North, Central and South America became extinct at the end of the Middle Miocene, some species in Southeast Asia and East Asia were able to survive to the end of the Early Pliocene.

The first known appearance of *Amussiopecten* in the Japanese Islands is in the Early Miocene Yaeyama Group of Iriomote-jima in southern part of Okinawa Prefecture. A Middle to Late Miocene species of *Amussiopecten* has been described from the Shizukawa Formation, Yamanashi Prefecture (Otuka, 1934; Akiyama, 1957), Tsuma Formation, Miyazaki Prefecture (Shuto, 1955) and Inagozawa Formation, Chiba Prefecture (Masuda, 1962 A), and the Pliocene



Text-fig. 2. Geologic and geographic distribution of *Amussiopecten* in the Japanese Islands.
Amussiopecten yabei (Nomura); Early Miocene
Amussiopecten "iitomiensis" (Otuka); Middle to Late Miocene
Amussiopecten praesignis (Yokoyama); Early Pliocene

Amussiopecten is known from the Southern Pacific borderland (Masuda, 1962 B) (Fig. 2). From the accounts given above it is evident that *Amussiopecten* in East Asia expanded its geographic range northwards with time and became extinct at the end of the Early Pliocene.

Kanno and Chang (1973) pointed out that *Amussiopecten* migrated from the Gulf of Mexico through the Mediterranean Region to East Asia. However, as it is very questionable whether *Pecten okalanus* (Dall) described from the Eocene Ocla Limestone, Florida can be referred to the genus *Amussiopecten*, further investigations are necessary to settle the problem.

In general, the decrease in number of species through geological time are related to changes in oceanographic environmental conditions, as pointed out in the cases of *Mizuhopecten* and *Patinopecten*. Therefore, it can be concluded that environmental conditions in East Asia and Southeast Asia did not change extremely during the late Tertiary and have been more stable than those of other areas from the Miocene to Early Pliocene.

5. *Amusium*

The genus *Amusium* is characterized by its large, circular, rather thin, smooth shell, small, angulated auricles and distinct, paired internal ribs. Also, as the shell color of right and left valves are usually considered to be important criteria for classification of the recent species (Habe, 1964), specific identification of fossil shells is very difficult, because the shell colors are usually not preserved.

Many species of fossil *Amusium* have been described from the Mediterranean Region, East Africa, Pakistan, India, Southeast Asia, East Asia, North America, Central America, the West Indies and northern South America, and also some Recent species are known from the tropical to subtropical areas of the Indo-Pacific, the Gulf of Mexico and the Caribbean Sea. As a few species of *Amusium* described from Paleogene formations in West Indies and Central America have not been confirmed, it seems probable that the geologic range of *Amusium* is from the Early Miocene to Recent (Hertlein, 1969).

In the Japanese Islands the first appearance of *Amusium* is in the Late Miocene Tonogori Member of the Honjogawa Formation (Shuto, 1960), but the genus is unknown from Early to Middle Miocene formations. Pliocene *Amusium* is known from the Shimajiri Group, Miyako-jima, Okinawa Prefecture (Sato, Masuda and Shuto, 1986) and also a few species or subspecies are known from the Recent seas surrounding the southern Japanese Islands (Habe, 1964). Because Early Miocene *Amusium* has been described from the Mediterranean Region, East Africa, Pakistan and India, it is thought that the first appearance of *Amusium* in the Late Miocene of Japanese Islands is a result of migration from the Mediterranean Region *via* Southeast Asia. Also it is evident that the occurrences of living *Amusium* in New Guinea, New Caledonia and North Australia (south to New South Wales) are a result of eastward migration from Southeast Asia.

The occurrences of fossil and living *Amusium* are nearly the same as those of *Amussiopecten* stated on the earlier pages. Therefore, it may be that environmental conditions in East Asia and also in the Gulf of Mexico and Caribbean Sea were more stable than those of other areas from the Early Miocene to Recent.

Among Cenozoic pectinids the *Amusium* group is considered to be very important and significant for interregional correlation and for studying migration patterns, because of their world wide geographical distribution. However, because fossil species of *Amusium* have frequently been confused with each other, further study is needed to clarify their taxonomic relations.

6. *Pecten* (s. s.)

In the Japanese Islands, Taiwan and Philippines there are five fossil and living species of the genus *Pecten*, that is, *albicans, excavatus, naganumanus, puncticulatus* and *sinensis* (Dickerson, 1922; Habe, 1977). Among them *naganumanus* is known from Pliocene to Pleistocene formations distributed from the Philippines to Japanese Islands, *albicans* ranges from the Pliocene to Recent, and the other species are living. *Pecten* (*Notovola*) sp. illustrated by Kanno (1960) from the Nenokami Sandstone, Saitama Prefecture, Central Japan has not been verified.

Comprehensive studies on the genus *Pecten* (s. s.) in New Zealand have been made by Fleming (1957). He subdivided the *Pecten* (s. s.) group into the *Pecten benedictus* and *Pecten jacobaeus* groups, which might have originated in the Mediterranean Region during the Miocene, and pointed out that these two groups migrated to New Zealand and Australia by different routes. Furthermore, he subdivided the *Pecten* (s. s.) group in the Western Pacific into *Pecten excavatus* Anton in the southern area and *Pecten albicans* (Schröter) in the northern area, and concluded that *excavatus* of the *benedictus* group migrated from the Mediterranean Region *via* Southeast Asia, and that *Pecten aletes* Hertlein of the *jacobaeus* group in the West Coast of North America extended its geographic range westwards to the Japanese Islands and gave rise to *albicans*. However, as *Pecten albicans* in the Japanese Islands is quite different morphologically from *Pecten aletes* described from the Pliocene of California, it is evident that the first appearance of *Pecten naganumanus* and *P. albicans* in the Pliocene formations of the Philippines, Taiwan and Japan are the result of migration from the Mediterranean Region *via* Southeast Asia.

7. *Nanaochlamys* and *Swiftopecten*

Nanaochlamys Hatai and Masuda (1953), based upon *Pecten notoensis* Yokoyama (1929) from the Miocene Nanao Formation, Ishikawa Prefecture, Central Japan is considered to be a biostratigraphically very important and significant genus among Japanese Miocene pectinids because of its characteristic morphological features, restricted geologic range and rather wide geographical distribution.

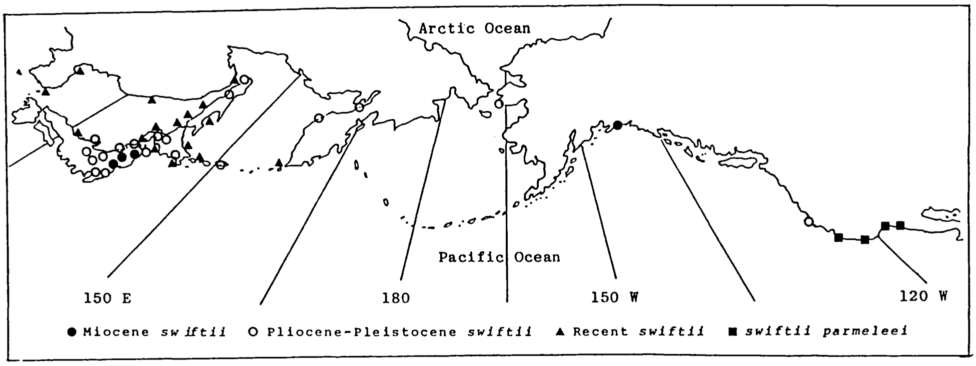
Nanaochlamys notoensis otutumiensis (Nomura and Hatai, 1937) described from the Miocene Otsutsumi Formation, Miyagi Prefecture, Northeast Honshu is distinguished from *notoensis notoensis* by its large shell, prominent radial ribs which bifurcate on the upper part of the shell and then divided into several radial threads by shallow longitudinal furrows, three to five intercalary threads between radial ribs, a few fine intercalary threads between bifurcated radial riblets of the right valve, and by the left valve having prominent radial ribs divided into three to five radial threads by shallow longitudinal furrows and primary prominent intercalary ribs divided into a few radial threads. However, juvenile *notoensis otutumiensis* has surface sculpture quite similar to that of juvenile *notoensis notoensis*, though with growth the surface sculpture in the adult stage becomes considerably different. The surface sculpture in the younger stage of *notoensis notoensis* is retained in the adult stage in *notoensis otutumiensis*, but the adult surface sculpture of the former is not observed in that of the latter. Moreover, *notoensis otutumiensis* occurs from a horizon higher than that of *notoensis notoensis*. Consequently, it is inferred safely that *notoensis notoensis* is ancestral to *notoensis otutumiensis* (Masuda, 1960).

Judging from the associated molluscan fauna it is thought that *notoensis notoensis* was a warm water inhabitant, whereas the fauna associated with *notoensis otutumiensis* mainly comprises rather temperate water elements. Therefore, it is evident that *notoensis notoensis* became extinct probably owing to the diverse environmental conditions at the end of the Early Miocene, and that *notoensis otutumiensis* branched off from *notoensis notoensis* at that time. But *notoensis otutumiensis* became extinct due to the onset of rather cool water conditions in the late Middle Miocene. Thus, it can be considered that the factors controlling the evolutional changes in the *notoensis* group probably due in part to differences of environmental conditions.

Although Sinelinikova (1975) has recorded a few species of the genus *Nanaochlamys* from Miocene and Pliocene formations in Kamchatka, judging from the descriptions and figures the writer is inclined to consider that all species of *Nanaochlamys* by Sinelinikova should be referred to the genus *Chlamys*. Also, recently Moore (1984) referred *Pecten nutteri* Arnold, described from the Pliocene of California, to the genus *Nanaochlamys*, but according to the writer's study of the type specimens preserved in the collections of Stanford University it is evident that *nutteri* should be referred to the genus *Chlamys*.

Up to the present time pectinids related to the *Nanaochlamys* group have not been n recorded from Oligocene or Early Miocene formations in Southeast Asia.

On the other hand, *Swiftopecten* Hertlein (1935), based upon *Pecten swiftii* Bernardi, a common Recent scallop in Northern Japan, is closely related with *Nanaochlamys* (Masuda, 1960, 1972) The morphological characters of surface sculpture in the adult stage of *swiftii* are very similar to those of the younger stage of the above mentioned *notoensis notoensis* and *notoensis otutumiensis*. Consequently, the relations existing between *notoensis notoensis* and *notoensis otutumiensis* also may be applied to the case of *swiftii*, because *swiftii* occurs from a horizon higher than that of *notoensis notoensis*.



Text-fig. 3. Geographic distribution of Recent and fossil *Swiftopecten*.

The oldest occurrence of *Swiftopecten swiftii* is in Middle Miocene formations of Northern Japan, where it is rather rare. In time this species gradually increased its dominancy with the increase of cool water conditions from the Middle Miocene to Recent (Masuda, 1959 A, 1960, 1972, 1978). And as pointed out already by the writer (Masuda, 1960) it seems that *Swiftopecten swiftii* branched off from *Nanaochlamys notoensis* in the early Middle Miocene. The first occurrence of *Swiftopecten* in the West Coast of North America is known from the Yakataga Formation in Alaska (MacNeil, 1967; Kanno, 1971), and the Yakataga Formation is considered to be no older than the Middle Miocene formations yielding *swiftii* in the Japanese Islands. Therefore, it is thought that the occurrence of *Swiftopecten* along the West Coast of North America is a result of its eastward migration from Asia to North America.

Swiftopecten swiftii extended its distribution to Northern California probably in the Early Pliocene and *swiftii parmeleei* (Dall), ranging from Central to Southern California, branched off from the *swiftii swiftii* stock as a result of its southward migration followed by localization and adaptation in the Middle Pliocene, and it became extinct at the end of the Middle Pliocene. But *swiftii swiftii* was able to survive into the Pleistocene in Alaska and became extinct probably at the end of the Pleistocene.

8. *Chlamys cosibensis* (Yokoyama)

Chlamys cosibensis (Yokoyama, 1911) described from the Pliocene Koshiba Formation, Kanagawa Prefecture, Central Japan has frequently been recorded from the Miocene to Pliocene formations in the Japanese Islands and adjacent areas. Also Yokoyama (1925, 1926) described two species very close to *cosibensis*, that is, *Pecten turpiculus* from the Shigarami Formation, Nagano Prefecture and *Pecten heteroglyptus* from the Sawane Formation, Niigata Prefecture, Central Japan.

Chlamys cosibensis has frequently been considered to be a synonym of *Chlamys etchegoini* (Anderson) and *Chlamys nutteri* (Arnold), both described from Pliocene formations in California (Grant and Gale, 1931; Otuka, 1935; Slodkewitsch, 1938; Ilyina, 1963; Krishtofovich, 1964).

Cosibensis and its related species were reviewed by the writer (Masuda, 1959 B), based upon the specimens collected from various localities in the Japanese Islands, and the writer concluded that the *cosibensis* group can be subdivided into *cosibensis cosibensis, cosibensis hanzawae, cosibensis turpicula* and *cosibensis heteroglypta.* However, as the results of the writer's subsequent study of *cosibensis* group (Masuda, 1973 A), based upon numerous specimens from the Japanese Islands, Korea, Kamchatka and Alaska, it became evident that the *cosibensis* group should be subdivided into *cosibensis cosibensis* and *cosibensis hanzawae,* and the morphological characters of the so-called *turpicula* and *heteroglypta* were considered to be mere morphological variations of *cosibensis cosibensis*. The ancestral form of *cosibensis cosibensis* is considered to be *cosibensis hanzawae*, which is known from the Early Miocene formations of Northern Japan.

Moreover, as pointed out by the writer (Masuda, 1959 B, 1973 A), it is evident that the Californian species such as *Chlamys etchegoini* and *C. nutteri* are quite different from *cosibensis cosibensis*. Also *cosibensis cosibensis* has hitherto frequently been confused with *Swiftopecten swiftii* (Bernardi) but its differences from *Swiftopecten* have already pointed out by the writer (Masuda, 1972).

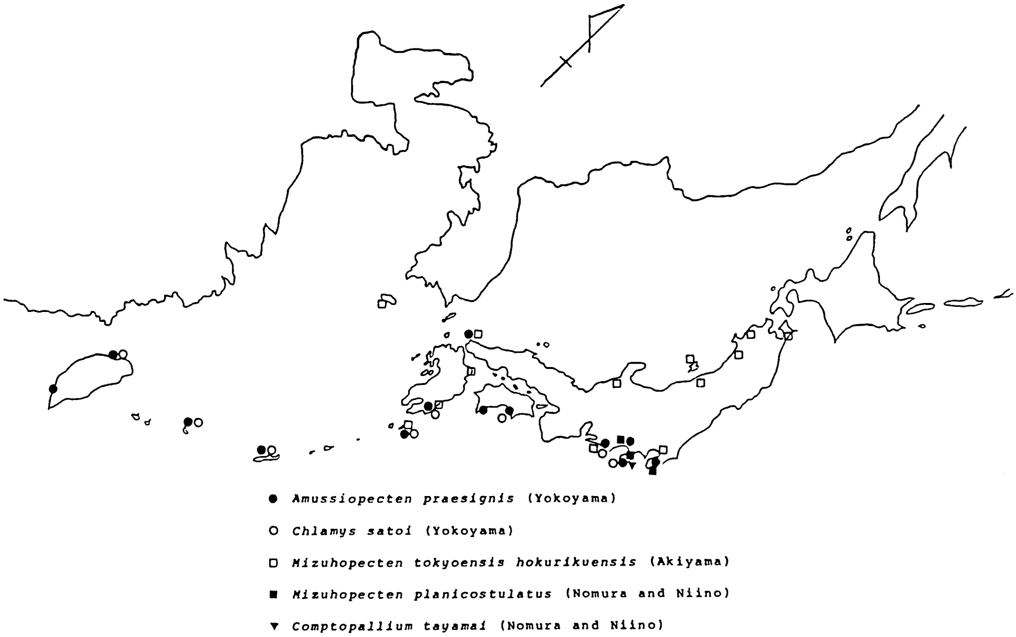
The first appearance of *cosibensis cosibensis* is in the Middle Miocene formations of the Northern Pacific region, and its associated molluscan fauna mainly consists of temperate water elements. In time *cosibensis cosibensis* increased its dominancy in association with an increase of cool water conditions from the Middle Miocene to Pliocene, and spread its geographical distribution from the Japanese Islands *via* Kamchatka to Alaska. Consequently, it is evident that the occurrences of *cosibensis cosibensis* from Alaska and Kamchatka are a result of its northeastward migration from the Japanese Islands.

9. *Mizuhopecten planicostulatus* (Nomura and Niino) and *Comptopallium tayamai* (Nomura and Niino)

Among the species of *Mizuhopecten* described from Neogene formations in the Japanese Islands, *Mizuhopecten planicostulatus* (Nomura and Niino, 1932), described from the Pliocene Shirahama Formation, Izu Peninsula, Shizuoka Prefecture, Central Japan, is of particular interest because of its very restricted geologic range and geographical distribution in association with some very characteristic molluscs such as *Amussiopecten praesignis* (Yokoyama), *Chlamys satoi* (Yokoyama), *Chlamys shirahamaensis* (Nomura and Niino), *Comptopallium tayamai* (Nomura and Niino), *Perotrochus yabei* (Nomura and Niino), *Strombus luhuanus* Linnaeus, etc. Among these, *Amussiopecten praesignis* and *Chlamys satoi* are representatives of the Kakegawa fauna that is distributed in the southern part of the Japanese Islands.

Comptopallium tayamai (Nomura and Niino) is of particular interest because of its peculiar morphology and it can be distinguished from other pectinids by its weakly inflated, oblique, higher shell which has about 17 stout radial ribs with numerous, fine radial threads, and by its nearly equal-sized triangular auricles with wide and shallow byssal notch.

From the accounts given above, it is interesting to note that the molluscan fauna of the Shirahama Formation can be referred to the Kakegawa fauna based upon the presence of the *Amussiopecten praesignis* assemblage (Masuda and Ogasawara, 1981). However, *Mizuhopecten planicostulatus* is known from the Shirahama Formation in the environs of the Izu Peninsula and from the Kurotaki Formation of the Boso Peninsula, Chiba Prefecture, and its distribution forms a remarkable contrast with that of *Mizuhopecten tokyoensis hokurikuensis*, (Akiyama) known from Pliocene formations distributed from Taiwan to Hokkaido (Fig. 4). *Comptopallium tayamai* is known only from the Shirahama Formation. Thus, it is evident that the molluscan fauna of the Shirahama Formation and its equivalent formations in the environs of the Izu Peninsula is different from the true Kakegawa fauna from the viewpoint of its pectinid



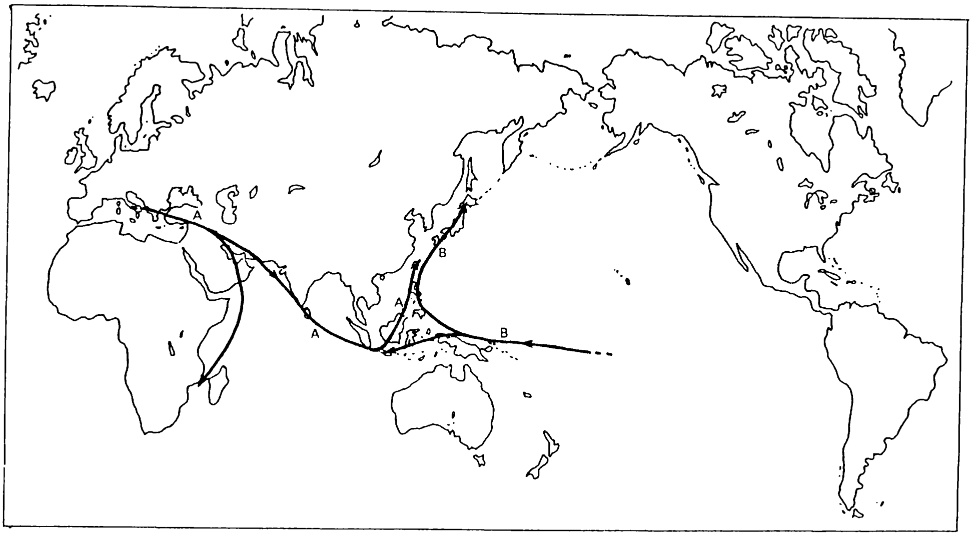
Text-fig. 4. Geographic distribution of some Pliocene pectinids in the Southern Pacific borderland.

assemblage. That is to say, the pectinid fauna of the Shirahama Formation and its equivalent formations consists of some pectinids of the *Amussiopecten praesignis* assemblage and other pectinids, such as *Mizuhopecten planicostulatus, Comptopallium tayamai, Chlamys shirahamaensis*, etc., which are probably different from the former in origin.

Concluding Remarks

As already pointed out by the writer (Masuda, 1962 B), there were two periods of remarkable development of Pectinidae in the Tertiary of the Japanese Islands. These two periods were marked by abrupt increases in numbers of genera and subgenera plus extreme individual variability and species differentiation, and occurred in the late Early Miocene and Pliocene. Such remarkable developments are also recognized in the Pectinidae of the West Coast of North America (Arnold, 1906; Addicott, 1974, 1981).

In the Central to Northern Japanese Islands, the Early Miocene pectinids were abundant in species and individuals, showed a wide variety of sculpture and possessed a rather restricted chronological distribution. They are mainly represented by the *Nanaochlamys notoensis* assemblage that can be traced from Central Honshu to Hokkaido (Masuda, 1962 B; 1978). In Southern Japan only *Amussiopecten yabei* (Nomura, 1933), which can be traced southwards to Taiwan, has hitherto been known from an Early Miocene fauna (the Yaeyama Group of the Ryukyu Islands). As known at present *Amussiopecten* has its oldest representatives in Paleogene formations of the Mediterranean Region (Masuda, 1971 B). Thus, it is evident that the occurrence of *Amussiopecten yabei* from the Yaeyama Group of the Southern Ryukyu Islands is a result of migration from the Mediterranean Region *via* Southeast Asia to the Japanese Islands. However, as there are no pectinids that are related to the *Nanaochlamys notoensis*



Text-fig. 5. Early Miocene expansion of geographic ranges by pectinids of the Western Pacific. Arrows represent diagrammatically the inferred invasion but not necessarily the route. A: *Amussiopecten*. B: *Nanaochlamys notoensis* assemblage.

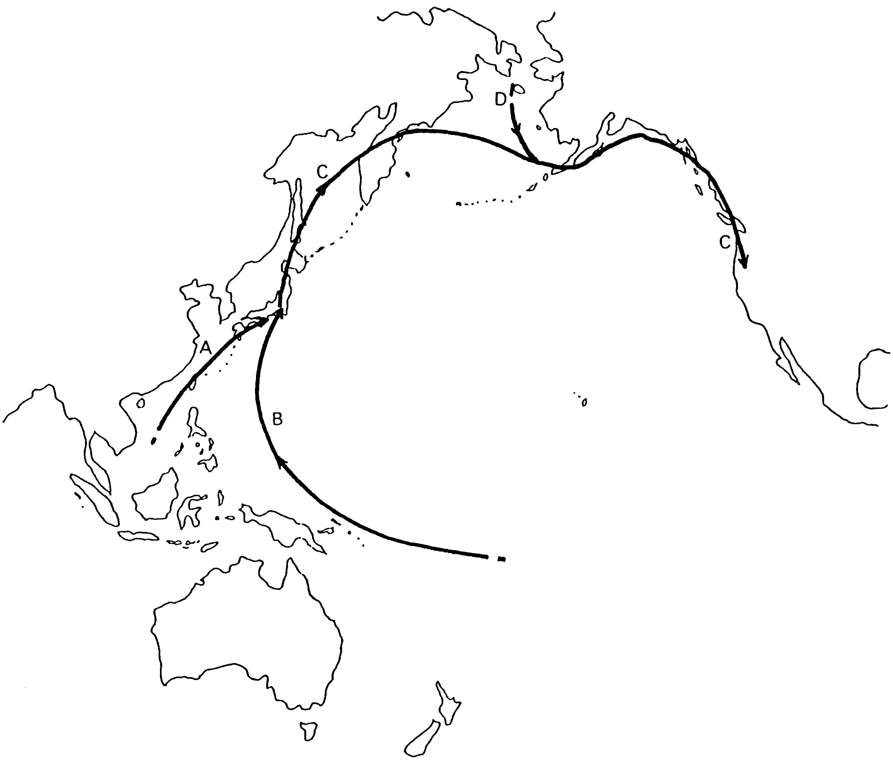
assemblage in the Paleogene or Early Miocene formations in Southeast Asia, the oldest representatives of the *Nanaochlamys notoensis* assemblage may have lived outside of Southeast Asia, probably in the central southern Pacific.

Ladd (1960) discussed the origin of the Pacific Islands molluscan fauna and concluded that many elements of the "Indo-Pacific Fauna", generally believed to have spread from Indonesia, may have originated among the islands in the "Pacific Basin" during the Cretaceous and Tertiary. Therefore, the writer's above mentioned view on the origin of the *Nanaochlamys notoensis* assemblage gives support to Ladd's hypothesis (Fig. 5).

So far as can be judged from the associated fauna in the Japanese Islands, it is thought that the deposition of the Early Miocene formations occurred under the influence of warm thermal conditions, and in general it is inferred that the water temperature gradually decreased from the Early to latest Neogene in the Circum Pacific Region (Durham, 1950 B; Masuda, 1963, 1971 A; Addicott, 1969).

The seas in which the Middle to Late Miocene formations were deposited had temperate thermal conditions in Central to Northern Japan, but it is evident that warm thermal conditions prevailed in Southern Japan (Chinzei, 1978). The Middle to Late Miocene pectinid fauna in the Japanese Islands became more varied as shown by three pectinid assemblages (Masuda, 1962 B), namely the *Amussiopecten akiyamae* assemblage, the *Miyagipecten matsumoriensis* assemblage, and the *Mizuhopecten kimurai* (s. s.) assemblage. The *Miyagipecten matsumoriensis* assemblage changes southwards gradually to the *Amussiopecten akiyamae* assemblage. The *Amussiopecten akiyamae* assemblage of the Southern Japanese Islands then expanded its range to Central Japan. That is to say, these two assemblages are geographical ones, but the *Miyagipecten matsumoriensis* and *Mizuhopecten kimurai* (s. s.) assemblages, which are thought to be descendants of the *Nanaochlamys notoensis* assemblage, represent different ecological conditions in the same sedimentary province (Masuda, 1962 B, 1973 B).

On the other hand, some pectinids such as *Mizuhopecten, Swiftopecten* and *Chlamys cosi-*



Text-fig. 6. Middle to Late Miocene expansion of geographic ranges by pectinids of the Western Pacific. A: *Amussiopecten*. B: *Miyagipecten*. C: *Mizuhopecten*. C: *Swiftopecten* and *Yabepecten*.

bensis expanded their range to the West Coast of North America *via* Sakhalin and Kamchatka, as shown by the occurrences of *Mizuhopecten warreni* from the Montesano Formation in Washington (Addicott, 1966; Masuda, 1971 A), *Mizuhopecten mollerensis* and *Chlamys cosibensis* from the Unga Conglomerate Member of the Bear Lake Formation in Alaska (MacNeil, 1967; Masuda, 1973 A; 1978), and also *Swiftopecten swiftii* from the Yakataga Formation in Alaska (MacNeil, 1967; Kanno, 1971; Masuda, 1972) (Fig. 6).

Also, as pointed out in earlier pages, it is evident that the genus *Amusium* migrated northwards to the Japanese Islands from Southeast Asia, probably in the Late Miocene or Early Pliocene, and that some species of *Amusium* dispersed southeastwards from Southeast Asia to New Guinea, New Caledonia and North Australia, probably in the latest Tertiary.

The Pliocene pectinids are represented by the *Amussiopecten praesignis* assemblage in the Southern Pacific borderland, the *Yabepecten tokunagai* assemblage in the Japan Sea borderland and Kanto region, and the *Fortipecten takahashii* assemblage in the Northern Pacific borderland (Masuda, 1962 B). Among them the *Fortipecten takahashii* assemblage can be traced from the southern part of Northeast Honshu through Sakhalin to Kamchatka, and the *Yabepecten tokunagai* assemblage can be traced to the Kurile Islands. However, because the remarkable expansion of *F. takahashii* (generally believed to have branched off from *F. kuroishiensis*), is not exactly synchronous with that of the development of the *Y. tokunagai* assemblage, there are some mixed pectinid faunas in the Northern Pacific region.

The first appearance of *Yabepecten* is in the Late Miocene Montesano Formation in

Text-fig. 7. Pliocene expansion of geographic ranges by pectinids of the Western Pacific. A: *Amussiopecten praesignis* assemblage. B: *Comptopallium tayamai* assemblage. C: *Fortipecten takahashii* assemblage. D: *Yabepecten tokunagai* assemblage.

Washington (Addicott, 1981) and it is inferred safely that *Yabepecten condoni* probably migrated from the Northern Pacific or Arctic Ocean along the West Coast of North America. The occurrence of *Yabepecten tokunagai* in Pliocene formations of the Japanese Islands and Kurile Islands probably resulted from its southwestward migration from the Northern Pacific (Fig. 7). However, further investigation is necessary to settle this problem, because no data are known from Kamchatka and Alaska.

Also it appears that the Shirahama Formation, which evidently was deposited during warm thermal conditions, contains a mixture of the *Amussiopecten praesignis* assemblage from the Kakegawa fauna (which ranged from Taiwan to Central Japan) and another pectinid assemblage. The latter assemblage is believed to have migrated northwards to the Izu Peninsula from a source area in Southeast Asia different from that of the Kakegawa fauna (Fig. 7). However, as the fossil molluscan fauna in the "Pacific Basin" is not well known at present, further investigation is necessary to settle the problem.

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Plate 7

Explanation of Plate 7

(Natural size)

Figs. 1, 2, 3, 4, 5. *Nanaochlamys notoensis* (Yokoyama)

1, 2. Loc.: Kita-Akaishi, Sendai City, Miyagi Prefecture. Moniwa Miocene.

3, 4. Loc.: Kaigarabashi, Imagane-cho, Setana-gun, Hokkaido. Imagane Miocene.

5. Loc.: Iwaya, Nanao City, Ishikawa Prefecture. Nanao Miocene.

Fig. 6. *Nanaochlamys notoensis otutumiensis* (Nomura and Hatai)

Loc.; Otsutsumi, southwest of Miyatoko, Taiwa-cho, Kurokawa-gun, Miyagi Prefecture. Otsutsumi Miocene.

Fig. 7. *Swiftopecten swiftii* (Bernardi)

Loc.: Tominaga, Wakimoto-cho, Oga City, Akita Prefecture. Shibikawa Pleistocene.


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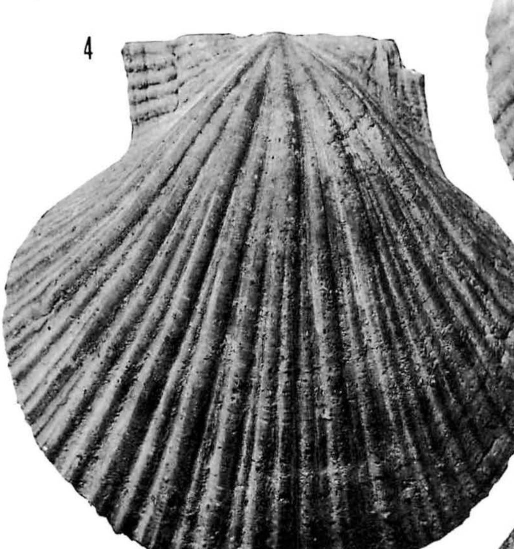
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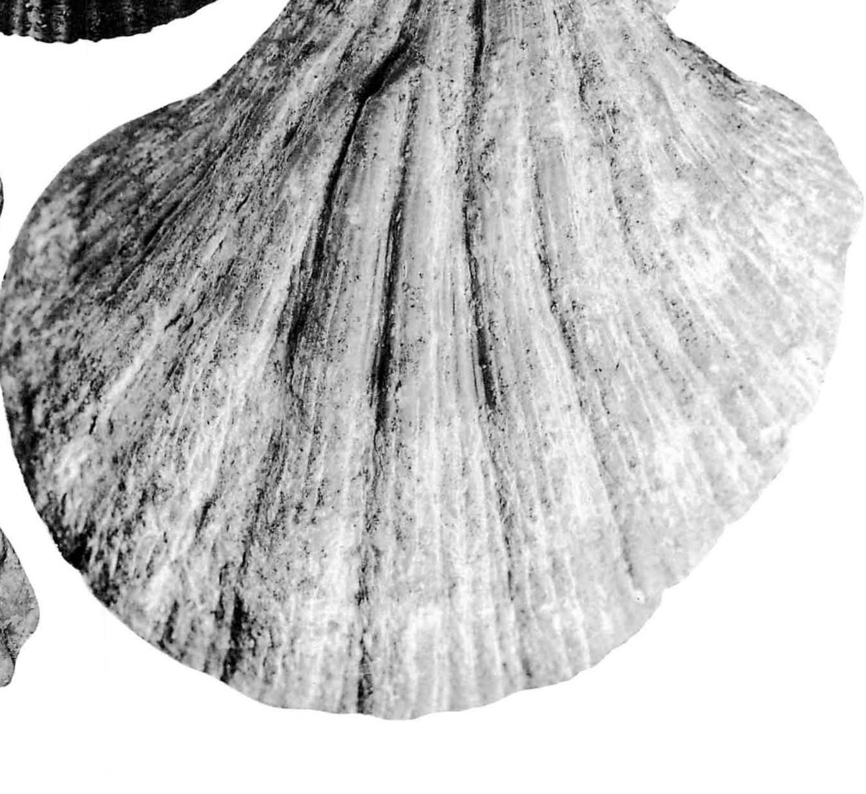
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Plate 8

Explanation of Plate 8

(Natural size)

Figs. 1, 2, 3. *Swiftopecten swiftii* (Bernardi)
  1. Loc.: Kurosawa, Akita City, Akita Prefecture. Sasaoka Pliocene.
  2, 3. Loc.: Crescent City Wharf, Del Monte County, California. "Wildcat" Pliocene.
Fig. 4. *Nanaochlamys notoensis otutumiensis* (Nomura and Hatai)
  Loc.: Nagamine, Ninohe City, Iwate Prefecture. Suenomatsuyama Miocene.
Fig. 5, 6, 7. *Yabepecten tokunagai* (Yokoyama)
  Loc.: Chikagawa, Mutsu City, Aomori Prefecture. Hamada Pliocene.
Fig. 8. *Fortipecten takahashii* (Yokoyama)
  Loc.: Kawauchi, Sendai City, Miyagi Prefecture. Tatsunokuchi Pliocene.
Fig. 9. *Miyagipecten matsumoriensis* Masuda
  Loc.: Sabusawa, Miyazaki-cho, Kami-gun, Miyagi Prefecture. Utsuno Miocene.

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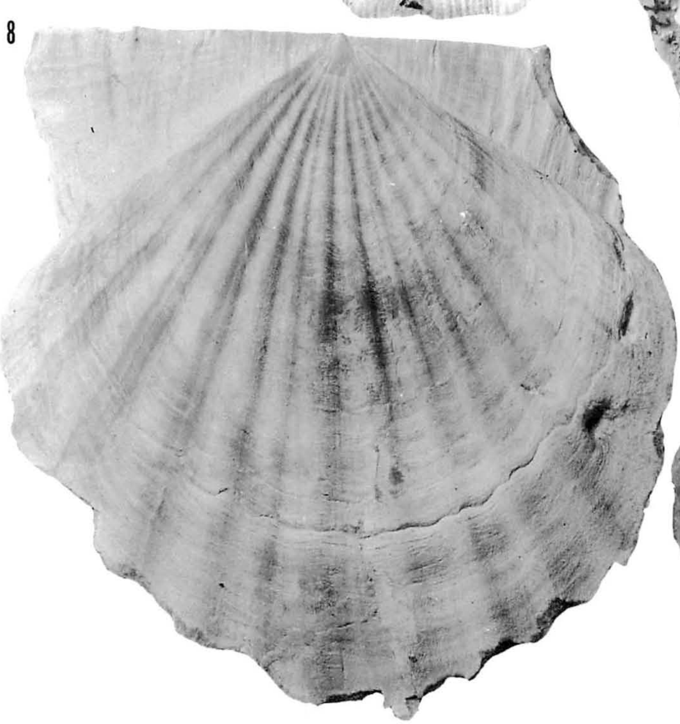

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Plate 9

Explanation of Plate 9

(All figures in natural size unless otherwise stated)

Fig. 1. *Mizuhopecten yessoensis* (Jay) x 4/5
Loc.: Kaigarazawa, Kuromatsunai-cho, Suttsu-gun, Hokkaido. Setana Pliocene.
Fig. 2. *Mizuhopecten warreni* Masuda
Loc.: West Fork of the Wishkah River, Grays Harbor County, Washington. Montesano Miocene.
Fig. 3. *Pecten albicans* (Schröter)
Loc.: Shinagawa, Tokyo Metropolis. Tokyo Pleistocene.
Fig. 4, 5. *Chlamys cosibensis hanzawae* Masuda
Loc.: Ukibuta, Higashi-Yuri-machi, Yuri-gun, Akita Prefecture. Sugota Miocene.
Fig. 6, 7, 8. *Chlamys cosibensis* (Yokoyama)
6. Loc.: Kitatoyotsu, Oshamanbe-cho, Yamakoshi-gun, Hokkaido. Setana Pliocene.
7. Loc.: Fudosawa, Showa-mura, Minami-Aizu-gun, Fukushima Prefecture. Matsuzakatoge Miocene.
8. Loc.: Chikagawa, Mutsu City, Aomori Prefecture. Hamada Pliocene.


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Plate 10

Explanation of Plate 10

(Natural size)

Fig. 1. *Amussiopecten praesignis* (Yokoyama)
Loc.: Nakoshi, Haneji-mura, Kunisaki-gun, Okinawa Prefecture. Nakoshi Pliocene.
Fig. 2. *Amusium pleuronectes okinawaensis* Masuda, Sato and Shuto
Loc.: Piseoganzaki, Miyako-jima, Okinawa Prefecture. Shimajiri Pliocene.
Fig. 3. *Chlamys satoi* (Yokoyama)
Loc.: Shimajiri, Miyako-jima, Okinawa Prefecture. Shimajiri Pliocene.
Fig. 4. *Chlamys shirahamaensis* (Nomura and Niino)
Loc.: Nagata, Shimoda City, Shizuoka Prefecture. Shirahama Pliocene.
Figs. 5, 6. *Comptopallium tayamai* (Nomura and Niino)
Loc.: Same as above. Shirahama Pliocene.
Fig. 7. *Mizuhopecten planicostulatus* (Nomura and Niino)
Loc.: Ichiyama near Yugashima, Amagi-Yugashima-cho, Tagata-gun, Shizuoka Prefecture. Shirahama Pliocene.

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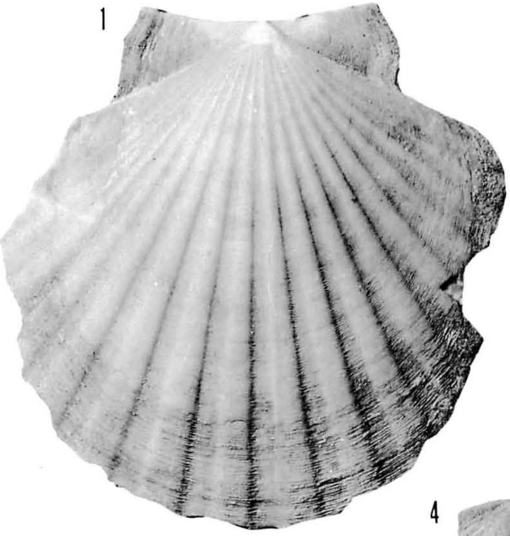

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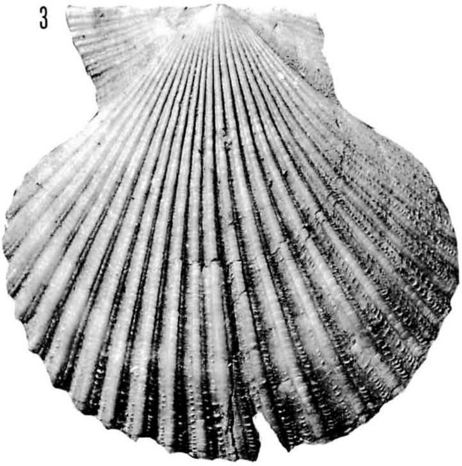

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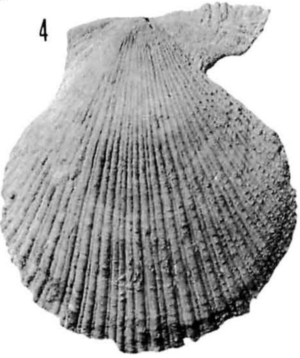

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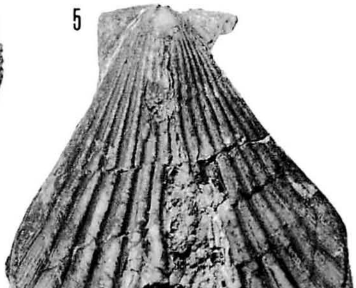

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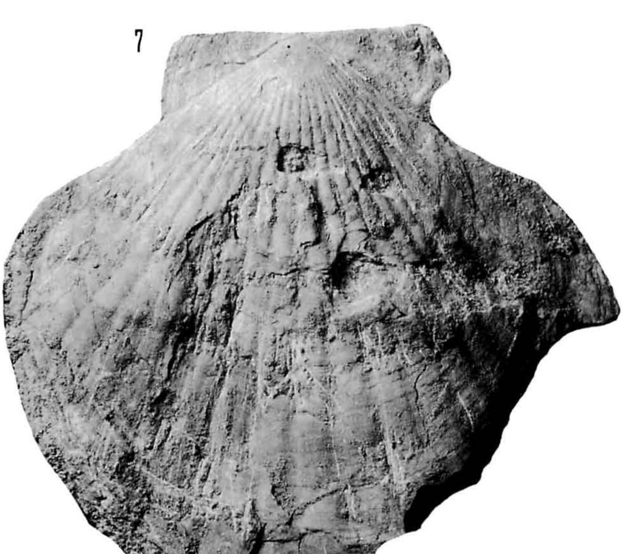


6

ORIGIN AND MIGRATION ROUTES OF JAPANESE TURRITELLID GASTROPODS

By

Tamio KOTAKA

Introduction

The generic name *Turritella* was first introduced into the Japanese marine molluscan literature by C. T. Menke in 1828 based on the living species *Turritella* (*Kurosioia*) *fascialis* Menke, 1828, which was collected from probablly Chijiwa Bay, off Nagasaki, Nagasaki Prefecture, Kyushu. Since then, more than 50 species and subspecies of fossil and living turritellas have been described from the Japanese Islands and adjacent waters.

At present, these species are classified into five genera and seven subgenera of the family Turritellidae. These divisions roughly correspond to phylogenetic bioseries as shown in Table 1.

Table 1. Japanese Turritellid Gastropods

- Family TURRITELLIDAE Woodward, 1851
  - Subfamily Turritellinae, Woodward, 1851
    - Genus *Turritella* Lamarck, 1799
      - Subgenus *Turritella* Lamarck, 1799
        - 2 Species (Miocene – Pleistocene)
      - Subgenus *Neohaustator* Ida, 1952
        - 21 Species (Miocene – Recent)
      - Subgenus *Kurosioia* Ida, 1952
        - 4 Species (Miocene – Recent)
      - Subgenus *Hataiella* Kotaka, 1959
        - 10 Species (Miocene – Recent)
      - Subgenus *Idaella* Kotaka, 1959
        - 1 Species (Miocene)
      - Subgenus *Nipponocolpus* Kotaka, 1959
        - 1 Species (Recent)
      - Subgenus Incertae Sedis
        - 7 Species (Createaceous & Paleogene)
    - Genus *Tropicolpus* Marwick, 1931
      - 1 Species (Oligocene)
    - Genus *Colpospira* Donald, 1900
      - Subgenus *Acutospira* Kotaka, 1959
        - 4 Species (Eocene)
  - Subfamily Pareorinae Finlay & Marwick, 1937
    - Genus *Mesalia* Gray, 1907
      - 3 Species (Miocene – Recent)
  - Subfamily Orectospirinae Habe, 1955
    - Genus *Orectospira* Dall, 1907
      - 3 Species (Oligocene, Pliocene & Recent)

Eight bioseries or phylogenetic groups are recognized in the family Turritellidae in Japan: the Eocene *Acutospira* Bioseries in Kyushu and the Ryukyus, the Miocene-Pliocene *Turritella* (s.s.) Bioseries mainly in SW Japan, the Miocene *Hataiella* and *Idaella* Bioseries in SW Japan, the Pliocene-Recent *Kurosioia* Bioseries, the Miocene-Recent *Naohaustator fortilirata* Bioseries in NE Japan and Hokkaido, the Pliocene-Recent *Neohaustator saishuensis* Bioseries in the borderland of the Sea of Japan and the Pliocene-Recent *Neohaustator nipponica* Bioseries in Kanto and NE Japan. Although the ancestral taxa or origins of some bioseries cannot be found, due to fairly rapid diversification caused by isolation or endemism, the ancestral forms of some bioseries can be traced back based on morphologic characteristics, ontogeny and inferred phylogeny.

The writer, here, would express his deep appreciation to Dr. Louie Marincovich, Jr. of the United States Geological Survey, Menlo Park, California for his critical reading of the manuscript. Thanks are also due to the Ministry of Education, Science and Culture of the Japanese Government for their financial support during the study.

Mesozoic turritellid species in Japan

In order to determine whether the origin of Japanese Cenozoic turritellids is recorded in the Pre-Tertiary deposists of Japan, the writer investigated the Mesozoic species of the genus "*Turritella*"

The geologic history of the turritellids in Japan started with the appearance of *Turritella yaegashii* described by Nagao (1934) from the Lower Cretaceous Hiraiga Formation of the Pacific coast of Miyako district, Iwate Prefecture, NE Japan. Otuka (1938) afterward proposed the name *nagaoi* for *Turritella* (?) sp. of Nagao (op. cit.) from the same locality as of *Turritella yaegashii.* Matsumoto (1938) also recorded two turritellid species, *Turritella goshorana* and *Turritella* sp. from the Middle Cretaceous Gosyonoura Group of Kumamoto Prefecture, Kyushu. Nagao (1939) again proposed a new species, *Turritella sorachiensis,* from the Upper Cretaceous Trigonia Sandstone, the Upper Cretaceous of Sorachi district, Ishikari Coal Field, Hokkaido. Among these Mesozoic taxa, *Turritella nagaoi* Otuka and *Turritella* sp. of Matsumoto have very slender spire outlines and seemed to be nerineid species to the writer.

The present writer can discern no direct phylogenetic relationships between Cretaceous and Early Cenozoic turritellids of Japan, judging from shell outlines and surface ornamentation. It is most likely that the Cenozoic turritellas of Japan immigrated into the Japonic (Paleo-zoogeographic) Province from adjacent regions.

Origin of Paleogene turritellids in Japan

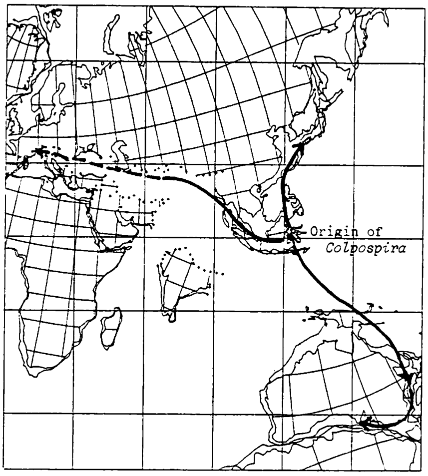
1. *Colpospira* (*Acutospira*) Bioseries

Beets (1950) proposed a revised classification of the Late Cretaceous and Early Eocene turritellas previously classified as one taxon, *Turritella krooni* Dollfus from SW and Central Celebes. He subdivided *T. krooni* into three subspecies based on their stratigraphic ranges, ontogenetic development and phylogeny, and recognized following bioseries or phylogenetic group of species: *Turritella krooni krooni* Dollfus (Upper Cretaceous Mororo Formation) ⟶ *T. krooni batukuensis* Beets (Lower Eocene TA Bed) ⟶ *T. krooni kalosiensis* Beets (Upper Eocene TB Bed?). Beets emphasized that the phylogenetic trend of the bioseries was expressed by progressive increase in the density and strength of secondary spiral cords.

The sepcies and its subspecies seem to the writer to be probably assigned to the genus *Colpospira,* which was first established in Australia based on a Recent form. The genus ranges from Eocene to Recent in Australia, and from Eocene to Oligocene in New Zealand. These species are similar to the writer's species of *Acutospira* judging from the features of the spiral ornamentation and the shape of growth-lines, which can be seen in the description and illustrations presented by Beets.

Kotaka (1959, 1982, etc.) described and proposed the *Acutospira* Bioseries based on specimens from Eocene deposits in Kyushu and on Ishigaki-jima Island, the Ryukyus. This bioseries is also expressed by progressive increase in the density and strength of secondary spiral cords, in accord the "*Turritella*" *krooni* Bioseries of Beets. The *Acutospira* Bioseries is as follows: *Colpospira* (*Acutospira*) *yabei* Kotaka (Lower Eocene Shiratake Formation, Kagoshima Prefecture) ⟶ *C.* (*A.*) *tashiroi* Kotaka (Upper Eocene Iojima Formation, Nagasaki Prefecture) ⟶ *C.* (*A.*) *kotakai* MacNeil (Upper Eocene Miyara Formation, Ishigaki-jima Island).

Judging from the similar spire outlines, the arrangement of knife edged spiral cords, and also the similarities in phylogenetic trend and age relationship between both bioseries, it is most probable that they are quite closely related to each other. In other words, the *Acutospira* Bioseries probably had its origin in or around Celebes and immigrated into S Japan during Latest Cretaceous or Earliest Cenozoic time through the Philippines (No data at present), and Taiwan (Oral information of S. Kanno, Joetsu University of Education, 1984).

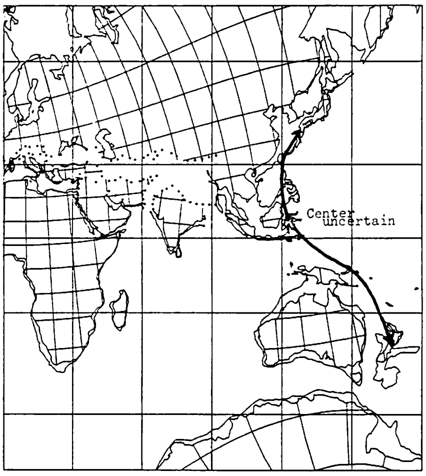


Text-fig. 1. Origin and migration route of *Colpospira*. Paleogeography adopted from Smith & Briden (1977), Map 5, 60 Ma.

2. *Tropicolpus sakitoensis* Nagao

The genus *Tropicolpus* was first established in New Zealand on *Turritella albolapis* Finlay from the Oligocene deposits of New Zealand (Marwick, 1931), and has been recorded only from New Zealand.

Although only one species of the genus *Tropicolpus* is known from the Upper Oligocene Itanoura Formation, Nagasaki Prefecture, the type species of the genus, *Tropicolpus albolapis* (Finlay) (Marwick, 1957) has a strong relationship with *sakitoensis* in general morphology, especially in the concave shaped whorl profile and the development of multispiral ornamentation.



Text-fig. 2. Migration route of *Tropicolpus*. Paleogeography adopted from Smith & Briden (1977), Map 4, 40 Ma.

Tan (1971) recorded *Turritella* aff. *sakitoensis* Nagao from the Eocene deposits in association with the specimens of *Nummulites*, and his illustrations indicate strong affinity with the species, and this also serves to support the presumable route of migration of the genus. The genus *Tropicolpus* may have been also originated from the Malayan region and invaded into Japan through Taiwan during Oligocene time.

Origin of Neogene turritellids in Japan

1. Subgenus *Turritella* s.s.

The genus *Turritella* was proposed by Lamarck in 1799 based on *Turbo terebra* Linné, which lives in the Indo-Pacific region and is especially widely distributed in SE and S Asian waters. According to Shuto (1973, 1978) who reviewed the biostratigraphy of the SE Asian Neogene formations based on molluscan fossils collected from the region during the last half century, more than 27 species including subspecies distributed in five genera of the family Turritellidae have been recorded from the strata of Late Eocene to Pleistocene age. Among these, five species are still living in SE Asian waters, and eight species and subspecies are classified into the subgenus *Turritella* s.s.

Two species of the subgenus are known from Miocene deposits of the Paleo-Setouchi sedimentary province in SW Japan (*Turritella kiiensis* Yokoyama) and the Pliocene Miyazaki Group in Kyushu, the Pliocene Tonohama Group in Shikoku and the Pliocene Kakegawa Group in Shizuoka Prefecture (*Turritella perterebra* Yokoyama).

The stratigraphic interval between these two species is fairly large, so it is very difficult to be sure of a direct relationship between them. But both species always occur in association with tropical and/or subtropical molluscan species, which may suggest an origin in the Indo-Pacific region.

2. *Turritella* (*Kurosioia*) *fascialis* Bioseries

Ida (1952) established a new subgenus *Kurosioia* based on a Pleistocene species of Shizuoka Prefecture. Probable lineage of this bioseries can be expressed in the following way and is mainly based on ontogenetic development of spiral ornamentation: *Turritella* (*Kurosioia*) *filiora* Yokoyama (Pliocene-Pleistocene Byoritsu-Myaoli Group, Taiwan) ⟶ *T.* (*K.*) *kurosioia* Ida (Lower Pleistocene, Shizuoka Prefecture) ⟶ *T.* (*K.*) *fascialis naganumaensis* Otuka (Upper Pleistocene Naganuma Formation, Kanagawa Prefecture) ⟶ *T.* (*K.*) *fascialis* Menke (living in the embayments along the Pacific- and the Sea of Japan coasts in Central and SW Japan).

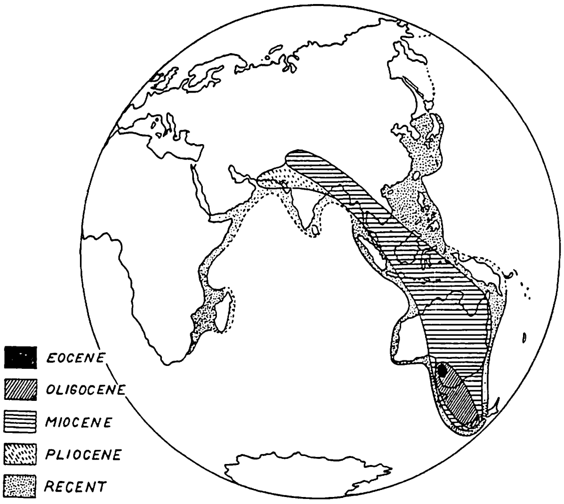
Ida (op. cit.) also described the Miocene species *T.* (*K.*) *neiensis* from Toyama Prefecture, but direct relationship with the bioseries cannot be traced because of the fairly distant age relationship.

Shuto (op. cit.) classicified six species into this subgenus, among them, *Turritella* (*Kurosioia*) *cingulata* (Sowerby), which seem to be closely related to Japanese *Kurosioia.*

3. *Turritella* (*Hataiella*) *sagai* Kotaka

This species is known from a fairly limited stratigraphic interval in Miocene deposits of the central Honshu, Japan, and is closely related to the type species of the subgenus, *T.* (*H.*) *s-hataii* Nomura.

Some genera and species of the Japanese Cenozoic turritellid just mentioned above have their origin in the Indo-Pacific or SE Asian region. Recently, L. Marincovich, Jr. collected many turritellid specimens from Miocene strata of Alaska Peninsula, his specimens seem to have a



Text-fig. 3. Approximate limits of distribution of *Goniocidaris* at successive interval during the Cenozoic. Cited from Fell (1954).

very close affinity with *sagai.* Although this might suggest that the descendant species of *sagai* and its allied ones have emigrated into the Alaska Peninsula during Middle Miocene time from Japan, detailed systematic study of specimens should be necessary.

Other Evidence supporting Turritellid Migration Routes

1. Migration of *Goniocidaris*

Fell (1952), in his monograph on "Tertiary and Recent Echinoidea of New Zealand: Cidaridae," focused on the biostratigraphy and zoogeography of the taxa, and tried to decipher "Origin and Migration Routes", "Paleozoogeography" and "Tertiary Climates of Australasia".

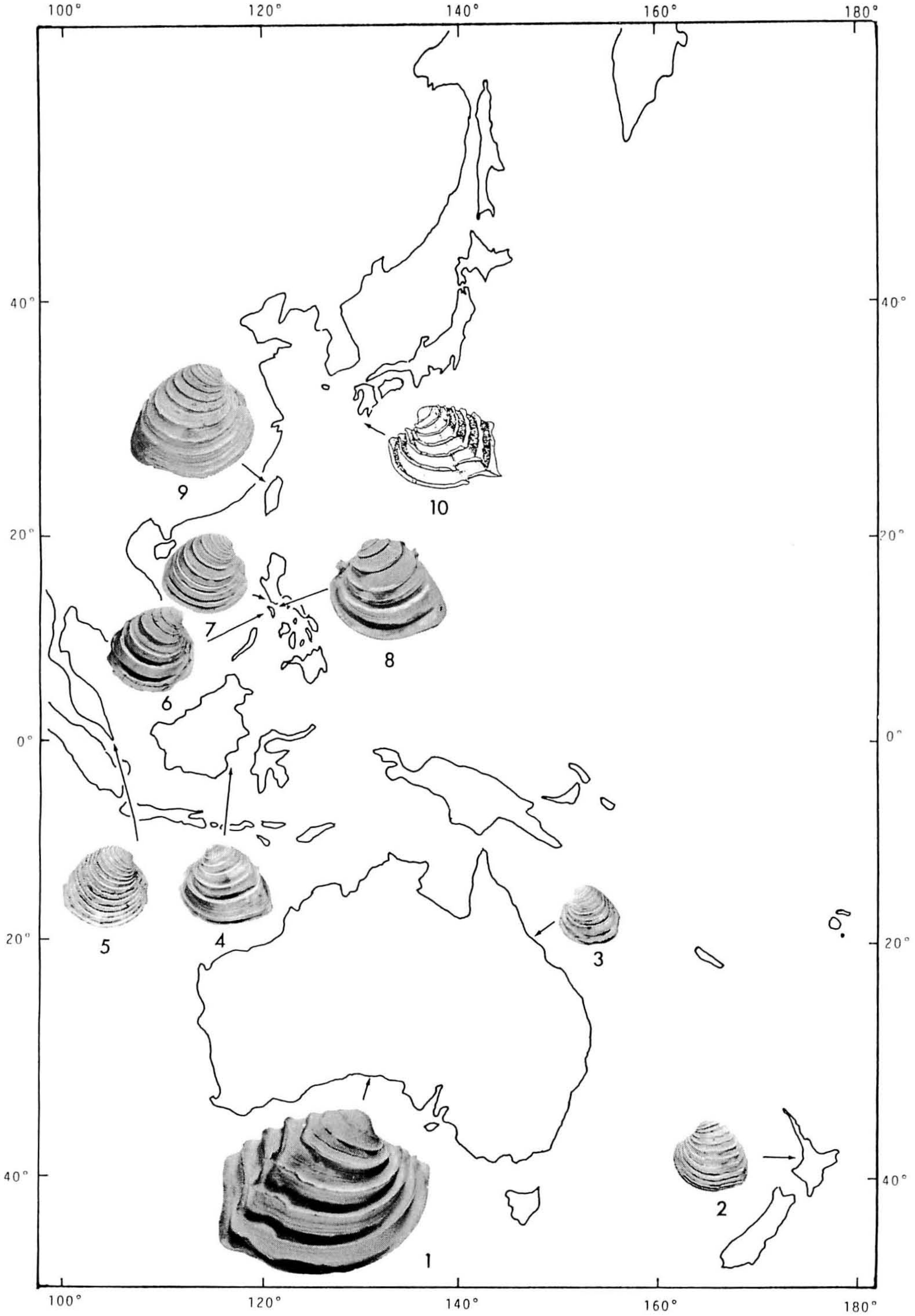
Text-fig. 3 in his monograph shows the distribution limits of *Goniocidaris* at successive intervals during the Cenozoic and also indicates faunal exchange between the Indo-Pacific and Australasian regions, i.e., the northern- and southern-hemisphere during Cenozoic.

2. Immigration of the Southern Genus *Bassina*

The southern genus *Bassina* has a history extending from the Early Cenozoic to the present in the Australasian region (New Zealand, Australia and adjacent small islands). The only Japanese species of the genus, *Bassina* (*Callanaitis*) *hiraseana* (Kuroda) is known from the sea of S Japan. Even though Japan and Australia are situated at a distance, the Japanese Recent species, *hiraseana,* is almost identical with the Australian Recent species, *Callanaitis disjecta* (Perry), except for differences in shell size and position of the umbo.

Fleming (1962), in his paper on the relation between speciation and isolation, mentioned that movements of temperate organisms between northern- and southern-hemisphere must have been difficult because the equitorial tropical belt was very wide before being restricted by Pleistocene cooling.

Kotaka (1977) described *Bassina* (*Callanaitis*) *hayasakai* from a shell mound in Taiwan, and pointed out that there were some common morphologic characteristics, (e.g., a fold on the dorsal margin of the shell) shared by *hayasakai* and the subtropical bivalve genera *Chione* and *Placamen.* During the course of his study on the northern *Bassina,* he found several species with morphologic characteristics similar to those of *Bassina,* but which had hitherto been



Text-fig. 4. Map showing distribution of Recent species of *Bassina* in the W Pacific. Cited from Kotaka (1977).

classified into the genera *Chione* and *Placamen* in Miocene to Recent of the SE Asian region. Therefore, he concluded that during the migration of *Bassina* from south to north, some members of the genus become adapted in subtropical seas and also developed slight change in morphology.

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P.S.

Since this paper was submitted to the Editorial Board, the writer received the following papers:

1) Kanno, S. et al. (1985): New discovery of *Colpospira* (*Acutospira*), Gastropoda, from Taiwan and Philippines. *Proc. Japan Acad.*, **61** (B), 348–351.
2) Marincovich, L., Jr. & Kase, T. (1986): An occurrence of *Turritella* (*Hataiella*) *sagai* in Alaska: Implications for the age of the Bear Lake Formation. *Bull. Nat. Sci. Mus.*, C, **12** (2), 61–66.

Plate 11

Explanation of Plate 11

Vertical bar on the left side of each figure indicates 10 mm, otherwise in natural size.

Fig. 1. *Colpospira* (*Acutospira*) *krooni batukuensis* (Beets)
Lower Eocene, SW Celebes. Reproduced from Beets (1950).
Fig. 2. *C.* (*A.*) *krooni kalosiensis* (Beets)
Upper Eocene, SW of Central Celebes. Reproduced from Beets (1950).
Fig. 3. *C.* (*A.*) *tashiroi* Kotaka
IGPS coll. cat. no. 77748-1, Eocene, Kumamoto Prefecture.
Fig. 4. *C.* (*A.*) *yabei* Kotaka
IGPS coll. cat. no. 36182-1, Eocene, Nagasaki Prefecture.
Fig. 5. *Turritella* (*Turritella*) *kiiensis* Yokoyama
IGPS coll. cat. no. 72897-2, Miocene, Toyama Prefecture.
Fig. 6. *T.* (*T.*) *kiiensis* Yokoyama
IGPS coll. cat. no. 77650-2, Miocene, Okayama Prefecture.
Fig. 7. *Tropicolpus sakitoensis* (Nagao)
IGPS coll. cat. no. 36200-1, Oligocene, Nagasaki Prefecture.
Fig. 8. *Trop. sakitoensis* (Nagao)
IGPS coll. cat. no. 36200-32, Oligocene, Nagasaki Prefecture.
Fig. 9. *Turritella* (*Hataiella*) *sagai* Kotaka
IGPS coll. cat. no. 72877-1, Miocene, Gifu Prefecture.
Fig. 10. *Turritella karatsuensis* Nagao
IGPS coll. cat. no. 36132, Oligocene, Nagasaki Prefecture.
Fig. 11. *Turritella* (*Turritella*) *kiiensis* Yokoyama
IGPS coll. cat. no. 77727-3, Miocene, Wakayama Prefecture.
Fig. 12. *T.* (*T.*) *perterebra* Yokoyama
IGPS coll. cat. no. 6183-6, Pliocene, Shizuoka Prefecture.
Fig. 13. *T.* (*T.*) *perterebra* Yokoyama
IGPS coll. cat. no. 92196, Pliocene, Shizuoka Prefecture.
Fig. 14. *Turritella* (*Kurosioia*) *kurosio* Ida
IGPS coll. cat. no. 77651, Pleistocene, Shizuoka Prefecture.
Fig. 15. *T.* (*K.*) *filiora* Yokoyama
IGPS coll. cat. no. 15135, Pliocene, Okinawa Prefecture.
Fig. 16. *T.* (*K.*) *fascialis* Menke
IGPS coll. cat. no. 19719, Recent, Chiba Prefecture.


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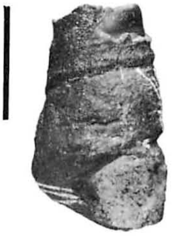
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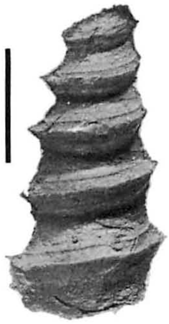
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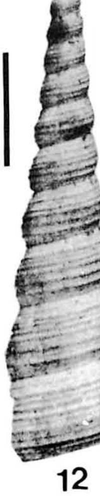
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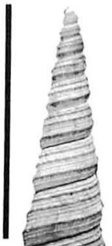
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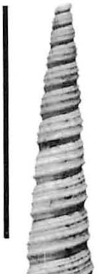
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16

DEVELOPMENT OF THE LATE CENOZOIC PTEROPOD FAUNA IN CENTRAL JAPAN

By

Hiroshi SHIBATA

Introduction

In recent years a considerable amount of information has been published on late Cenozoic pteropod assemblages from central Japan by a few workers, including Shibata (1977; 1979; 1980; 1984), Shibata and Ishigaki (1981), Ujihara and Shibata (1982) and Shibata and Ujihara (1983). These works include data from many localities which are stratigraphically situated in the latest Early (late Langhian) and early Middle Miocene, the Pliocene and the Pleistocene. Such information is still increasing. During current work I made small collections of pteropods from Cenozoic sediments of three areas, the Miocene of Tsuyama, Okayama Prefecture, the Miocene and Pliocene of Shimobe, Yamanashi Prefecture and the Pleistocene of Kanazawa, Ishikawa Prefecture. In addition to these collections, vast pteropod collections were systematically made by Atsushi Ujihara during the past three years throughout the late Cenozoic sequence of the Boso Peninsula, Chiba Prefecture, and fairly large collections were made by Eiji Taguchi during the past five years from the Miocene of Tsuyama. The Boso Peninsula collections include the first pteropods from the middle and late Middle and Late Miocene in central Japan, and provide the longest succession of pteropod assemblages in this region.

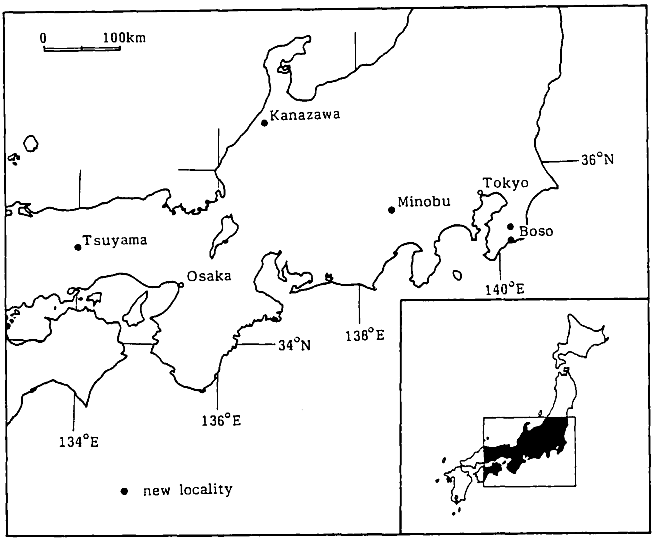
This paper presents new data on pteropod assemblages from the four areas abovementioned, and discusses historical changes in the pteropod fauna of central Japan during the late Cenozoic with reference to the origin of the modern pteropod fauna of Japan. This discussion is based on both new and previously published data. The systematic paleontology of late Cenozoic pteropods from this region has been given by Shibata (1983; 1984) and Shibata and Ujihara (1983).

Acknowledgments

I thank Mr. Atsushi Ujihara of Nagoya University for allowing me to study collections of pteropods made by him from the Boso Peninsula. Mr. Takehisa Ishigaki of Yamanashi University provided some pteropod specimens from Shimobe and data on planktonic foraminiferal assemblages from some localities in Shimobe and the Boso Peninsula for this study. Mr. Eiji Taguchi supplied collections of pteropods made by him from Tsuyama. Dr. Tadashige Habe of Tokai University generously provided dredge samples from the Pacific off Iriomote-jima, Okinawa Prefecture.

New data

New data obtained from the Boso Peninsula, Shimobe, Tsuyama and Kanazawa (Text-fig. 1) are summarized below.



Text-fig. 1. General location of new collecting localities in central Japan.

Boso Peninsula–Different stratigraphic classifications have been proposed by several workers for the thick Cenozoic sequence of this area. The classification of Oda (1977) is followed here to show the stratigraphic position of pteropod occurrences.

Pteropods were collected from 24 localities in the Miocene Sakuma Group and from a single locality in the overlying Pliocene Kiyosumi Formation of the Toyo-oka Group in the Kamogawa District. Of the former, two collecting localities are situated in the Kinone Formation, and the others in the overlying Amatsu Formation. The Plio-Pleistocene Kazusa Group of the Yoro-gawa area has yielded pteropods at more than 200 localities, which are stratigraphically scattered throughout the entire group except for its basal part, the Kurotaki Formation. A list of pteropods by formation is shown in Table 1. For the Amatsu Formation, however, the pteropod content of minor stratigraphic intervals is given in the list since the Amatsu includes a thick sequence that spans much of the Neogene, and the pteropod content notably changes vertically within it. These intervals are defined on the basis of ten distinct stratigraphic marker tuffs designated by Nakajima and others (1981).

According to Oda (1977), correlation of each formation with the planktonic foraminiferal zones of Blow (1969) is as follows. The Kinone Formation is correlated with the N. 8 zone, the Amatsu Formation ranges from the N. 9 to the N. 17 zone, the Kiyosumi Formation is placed within the interval between the N. 18 and N. 19 zones, and the Kazusa Group is correlated with the N. 21 and N. 22 zones. The boundary of the last two zones occurs within the Ohara Formation. The pteropod bearing intervals within the Amatsu Formation are correlated with following zones by comparison between them and the sampling section indicated by Oda on the basis of characteristic marker tuffs; the interval between Km3 and Am4 with the N. 10–N. 13 zones, the interval between Am14 and Am19 with the N. 14–N. 16 zones, the interval between Am20 and Am29 with the N. 16–N. 17 zones, the interval between Am33 and Am44 with the N. 17 zone, the interval between Am44 and Am53 with the N. 17 zone and the interval between Am73 and Am98 with the N. 18–N. 19 zones.

Shimobe–Pteropods were recovered from four localities in the Cenozoic sequence in and

Stratigraphic units (Oda, 1977) and marker beds (Nakajima and others, 1981) / Heteropods and pteropods	Sakuma Group							← Toyo-oka Group Kazusa Group											
		Amatsu Formation																	
	Kinone For.	Kn3 – Am4	Am14 – Am19	Am20 – Am29	Am33 – Am44	Am44 – Am53	Am73 – Am98	Kiyosumi For.	Katsuura For.	Namihana For.	Ohara For.	Kiwada For.	Otadai For.	Umegase For.	Kokumoto For.	Kakinokidai For.	Chonan For.	Mandano For.	Kasamori For.
Atlanta sp.														■	■			■	
Carinarja galea Benson									■					■	■				
—— sp.				■															
Limacina inflata (d'Orbigny)													■	■	■	■			
—— *trochiformis* (d'Orbigny)												■	■	■					
—— spp.												■	■	■		■			
Creseis acicula f. *acicula* Rang								■					■	■		■			
—— *virgula* f. *conica* Eschscholtz												■	■						
Styliola subula (Quoy and Gaimard)					■		■					■		■				■	
Hyalocylix striata (Rang)											■	■	■		■				
Vaginella katoi Shibata	■	■	■																
—— cf. *lapugyensis* Kittl				■	■	■													
—— sp.	■																		
Clio cuspidata (Bosc)										■		■							
—— *pyramidata* f. *lanceolata* (Lesueur)				■	■	■			■	■	■	■	■	■	■	■	■	■	■
—— *balantium* (Rang)															■				
—— *balantium* (Rang) forma												■		■					
—— *itoigawai* (Shibata) ?			■	■	■														
—— sp.1			■	■	■														
—— sp.2					■														
Cuvierina columnella f. *columnella* (Rang)													■		■			■	
—— *columnella* f. *urceolaris* (Mörch)				■															
Diacria trispinosa f. *trispinosa* (Blainville)						■	■		■	■		■		■	■				
—— *trispinosa* f. *major* (Boas)											■	■	■	■	■			■	
—— *quadridentata* f. *costata* (Pfeffer)											■	■	■	■		■	■		
—— *sangiorgii* Scarsella					■														
Cavolinia globulosa (Rang)					■							■	■						
—— *gibbosa* (Rang)																		■	
—— *longirostris* f. *longirostris* (Blainville)						■	■		■	■	■	■	■	■	■	■	■	■	
—— *longirostris* f. *angulosa* (Gray)												■							
—— *tridentata* cf. f. *tridentata* (Niebuhr)									■		■	■		■					
—— *tridentata* cf. f. *teschi* Spoel									■	■	■	■	■	■	■	■		■	
—— *tridentata* subsp.						■	■	■											
—— *uncinata* f. *uncinata* (Rang)												■	■		■				
—— *inflexa* f. *labiata* (d'Orbigny)									■			■	■	■	■	■		■	
—— *audeninoi* Vinassa de Regny				■	■	■													
—— *audeninoi* var.	■		■																

Text fig. 2. List of pteropods and heteropods collected from the late Cenozoic of the Boso Peninsula.

around Shimobe. One locality is situated in the Yamaho Mudstone and Tuff Member of the Nishiyatsushiro Group. One of the remaining localities is in the Hara Mudstone Formation of the Shizukawa Group, and the others in the Akebono Conglomerate Formation of the same group. *Limacina* sp., *Vaginella katoi* Shibata, *Clio itoigawai* (Shibata), *Clio* sp. 1, *Clio* sp. 2 and

Cavolinia audeninoi Vinassa de Regny are represented in the collection from the Yamaho Mudstone and Tuff Member. In addition to them, *Carinaria* sp., a heteropod species, was collected from this locality. Among the pteropods, *Vaginella katoi* Shibata is the most abundant species. Pteropod assemblages from the other localities are very meager. *Clio* sp. 3 and *Cavolinia audeninoi* Vinassa de Regny were recovered from the locality in the Hara Mudstone Formation. Collections from the Akebono Conglomerate Formation consist of *Hyalocylix striata* (Rang), *Clio pyramidata* forma *lanceolata* (Lesueur) and *Diacria trispinosa* forma *trispinosa* (Blainville).

According to Ishigaki (personal communication), the planktonic foraminiferal assemblage associated with the Yamaho pteropods includes *Globigerinoides quadrilobatus saccurifer* (Brady), *Globigerinoides subquadratus* Brönnimann, *Globoquadrina altispira* (Cushman and Jarvis), *Globorotalia peripheroronda* Blow and Banner, *Globorotalia siakensis* (LeRoy), *Orbulina suturalis* Brönnimann and *Praeorbulina glomerosa circuralis* (Blow), being probably assigned to the N. 9 zone. The collecting locality in the Hara Mudstone Formation is situated in the stratigraphic interval assigned to the N. 19 zone by Ujiié and Muraki (1976), and the Akebono Conglomerate Formation has been correlated with the N. 20 zone by them.

Tsuyama–Pteropods were found at eight localities in the Takakura Formation of the Katsuta Group of the Tsuyama basin. They consist of six species, *Limacina* sp., *Vaginella depressa* Daudin, *Vaginella* cf. *rotundata* Blanckenhorn, *Clio itoigawai* (Shibata), *Clio* sp. and *Cavolinia audeninoi* Vinassa de Regny var. Of them, *Vaginella* cf. *rotundata* Blanckenhorn is the most common species. The Takakura Formation has been assigned to the early Middle Miocene age by Shibata and Itoigawa (1980).

Kanazawa–Kaseno and Matsuura (1965) reported *Cavolinia longirostris* (Blainville) and *Cavolinia uncinata* (Rang) from the Onma Formation in Kanazawa. Collection at both a previously known locality and a new one in the formation has yielded the following additional species; *Limacina lesueuri* Souleyet, *Creseis virgula* forma *constricta* Chen and Bé, *Hyalocylix striata* (Rang) and *Cuvierina columnella* (Rang). The Onma Formation is placed in the early Pleistocene (Tsuchi and Working group, 1981).

Furthermore, additional information has been obtained from two localities previously described. One additional species, *Vaginella rzehki* Kittl was discovered from locality Icl of Shibata (1977) in the Miocene Ichishi Group, Mie Prefecture. It constitutes the first record of the occurrence of the species in Japan. *Diacria quadridentata* forma *quadridentata* (Blainville) and *Atlanta fusca* Souleyet, a heteropod, have been added to the list of pelagic molluscs reported by Shibata and Ujihara (1983) from the middle Pleistocene Semata Shell Bed, Chiba Prefecture.

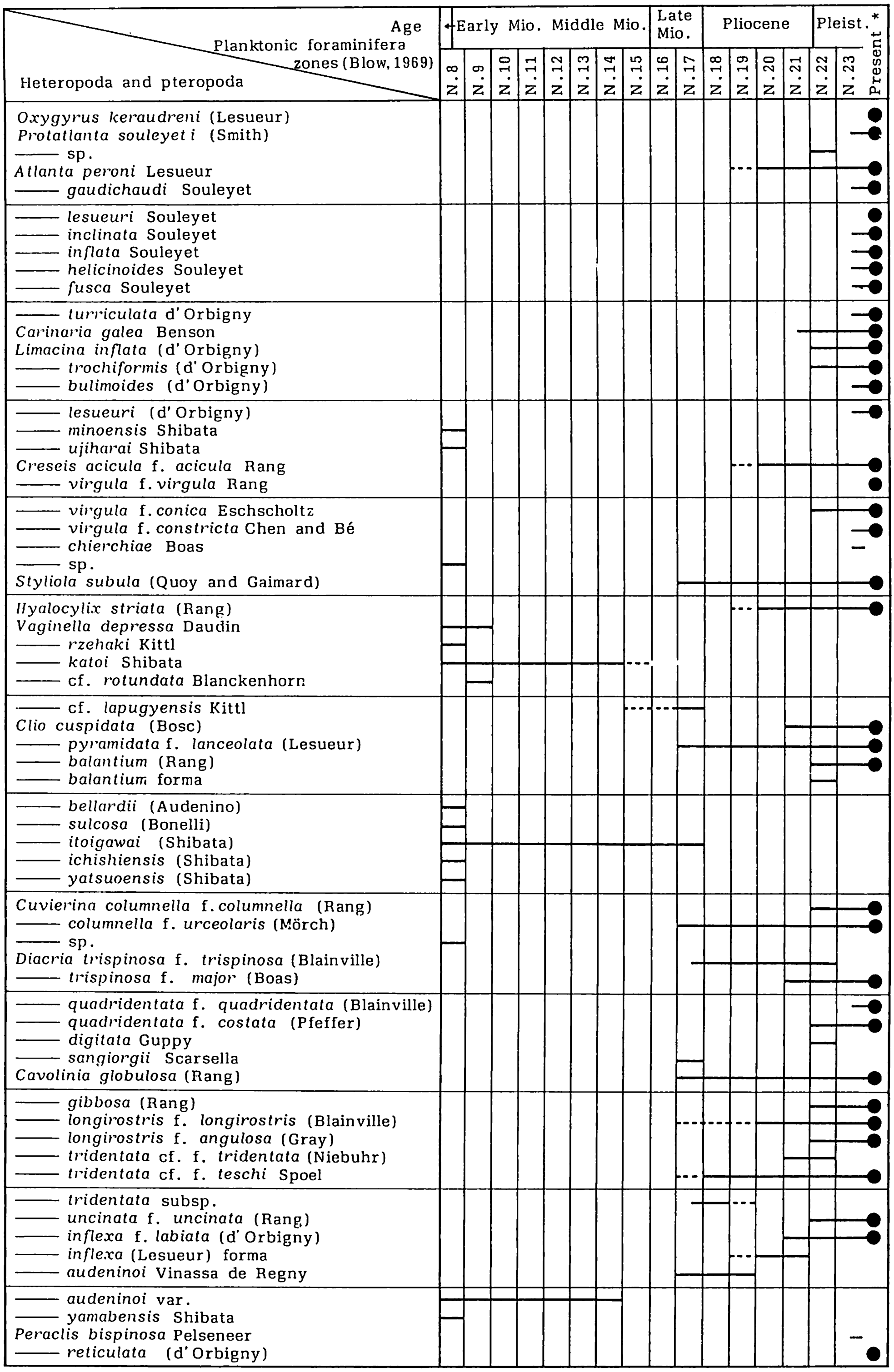
Vertical Changes

Late Cenozoic pteropod assemblages of central Japan are classified into three general groups differing in their percentage content of modern taxa as well as in species composition: (1) assemblages consisting entirely of extinct taxa, (2) assemblages with various proportions of modern and extinct taxa, and (3) assemblages consisting entirely or mostly of modern taxa. The majority of extinct taxa found in assemblages of the third group differ from their closest modern allies below the subspecies level.

Representatives of the first group are the assemblages from the Joyama Mudstone Member of the Hokuriku Group, Toyama Prefecture, the Mitsugano Tuffaceous Shale and Sandstone Member of the Ichishi Group, the Saigo Mudstone Member of the Saigo Group, Shizuoka Prefecture and the Shikiya Siltstone Formation of the Kumano Group, Wakayama Prefecture. Constituent taxa differs from their closest modern allies at the genus or species level, and most of them occur exclusively in assemblages of this group. *Vaginella depressa* Daudin, *Vaginella katoi* Shibata, *Clio bellardii* (Audenino), *Clio itoigawai* (Shibata) and *Cavolinia audeninoi* Vinassa de Regny var. are common and characteristic elements. The oldest assemblages of this group are found in the Masago Member of the Kurami Group, Shizuoka Prefecture which has been assigned to the N. 8 zone by Ibaraki (1981) and the Mitsugano Tuffaceous Shale and Sandstone Member referred to the same zone by Shibata and Ishigaki (1981). The assemblage from the stratigraphic interval between Am14 and Am19 in the Amatsu Formation of the Boso Peninsula is the youngest assemblage of this group. Thus, the distribution range of assemblages of the first group is from the N. 8 zone to the N. 14–N. 16 zones.

Assemblages of the second group are represented by those of the stratigraphic intervals between Am20 and Am29, Am33 and Am44, and Am44 and Am53 in the Amatsu Formation. All are within the N. 17 zone. *Vaginella* cf. *lapugiensis* Kittl, *Clio pyramidata* forma *lanceolata* (Lesueur), *Cavolinia audeninoi* Vinassa de Regny and *Cavolinia globulosa* (Rang) are common components. Modern forms found in these assemblages are *Styliola subula* (Quoy and Gaimard), *Clio pyramidata* forma *lanceolata* (Lesueur), *Diacria trispinosa* forma *trispinosa* (Blainville) and *Cavolinia longirostris* forma *longirostris* (Blainville) all of which are living in warm waters of the Kuroshio current surrounding Japan. Most of the extinct elements occur only in the assemblages of the second group, but a few are found in some assemblages of the first group, and some in those of the third group. The assemblage from the Hara Mudstone Formation of the Shizukawa Group which contains *Cavolinia audeninoi* Vinassa de Regny may be referred to this group, and this may extend the distribution range of this group up to the N. 19 zone. The presence of the modern taxa indicates that assemblages of the second group represent the germinal stage of the modern warm water pteropod fauna of Japan.

The assemblages of the Kakegawa Group, Shizuoka Prefecture, the Kazusa Group and the Semata Shell Bed are typical of the third group. Among those, common components are *Hyalocylix striata* (Rang), *Stylioda subula* (Quoy and Gaimard), *Clio pyramidata* forma *lanceolata* (Lesueur), *Diacria trispinosa* forma *trispinosa* (Blainville), *Cavolinia longirostris* forma *longirostris* (Blainville) and *Cavolinia tridentata* cf. forma *teschi* Spoel. Extinct taxa include *Clio balantium* (Rang) forma, *Diacria digitata* Guppy, *Cavolinia tridentata* cf. forma *tridentata* (Niebuhr) and *Cavolinia inflexa* forma. The assemblage of the main part of the Sagara Group, Shizuoka Prefecture or the assemblage of the interval between Am73 and Am98 is the stratigraphically lowest assemblage of this group. The former has been assigned to the N. 16–N. 18 zones (Shibata and Ishigaki, 1981), and the latter is in the N. 18–N. 19 zones. The assemblage of the late Pleistocene Hiradoko Shell Bed, Ishikawa Prefecture is the stratigraphically highest one. Assemblages older than the early Pleistocene often contain a few of the extinct forms, the majority of which differ from modern forms below the subspecies level. These assemblages seem to represent the past pteropod fauna most comparable to the modern one. On the other hand, middle and late Pleistocene pteropod assemblages contain no extinct forms, consisting exclusively of modern warm water forms. The assemblage of the Semata Shell Bed includes very diversified pteropod taxa in which most of modern warm water pteropods of Japan are found. A similar situation exists in the associated heteropod assemblage. The middle and late



* Dredge samples from the Pacific off Iriomote-shima (24°22'65N, 123°35'7E)

Text-fig. 3. Stratigraphic distribution of pteropods and heteropods in central Japan.

Pleistocene pteropod fauna of central Japan seem to be comparable in every respect to the modern pteropod fauna of warm water regions of Japan.

The three groups described above represent faunas of three successive periods, and there are remarkable faunal differences between them. This suggests the occurrence of two major faunal changes during the late Cenozoic; one in the early or middle Late Miocene and one near the Miocene/Pliocene boundary.

Discussion

Published data on late Cenozoic pteropod assemblages from other regions worldwide are limited. Italy is the only area with abundant data, allowing us to interpret changes in the past pteropod fauna. The following seem to be noteworthy for relating faunal events between Italy and central Japan: (1) a faunal break similar to the second event seen in central Japan is recognizable in the stratigraphical distribution of pteropods in Italy (Dieci, 1961) at the Messinian/Piacenzian boundary, (2) modern taxa which appear earliest in Italy indicated by Bellini (1905) and Dieci (1961) coincide, for the most part, with those which show the earliest appearance in central Japan, and (3) recent studies of Sirna (1968), Robba (1971; 1977), Pavia and Robba (1979) and D'Alessandro and Robba (1980) indicate that all taxa except one found in late Cenozoic faunas older than the late Messinian are extinct taxa. These facts may suggest that two events seen in central Japan are worldwide ones, which seems to be reasonable as most pteropods are cosmopolitan.

Elsewhere in Japan the only late Cenozoic pteropod records are of one species from the Miocene Yanagawa Shell-Beds of Fukushima Prefecture (Nomura and Zinbo, 1935), one species from the Miocene of Oki islands, Shimane Prefecture (Okubo and Takayasu, 1979), one species from the Miocene Kawabaru Member of the Koyu Formation, Miyazaki Prefecture and several species from the Pliocene Yonabaru and Shinzato Members of the Shimajiri Group, Okinawa Prefecture (Noda, 1972). The Miocene pteropods from Fukushima and Shimane Prefectures seem to be referable to either *Cavolinia audeninoi* Vinassa de Regny (a characteristic taxon of the second group) or to its variety (a characteristic taxon of the first group). The Pliocene assemblages from Okinawa Prefecture are composed of both modern and extinct forms, and is comparable to the assemblages of the third group.

The stratigraphic distribution of pteropods in central Japan (Text-fig. 2) shows a sudden decrease of taxa in the early Middle Miocene (near the Langhian/Serravallian boundary) and a paucity of taxa in the interval between the early Middle Miocene and the Late Miocene. This may be due to inadequate sampling to some degree. In addition, it may be due to a global decrease of pteropods in this interval to a certain degree, because a similar situation is suggested by their stratigraphic distribution in Italy (Robba, 1971; 1977; D'Alessandro and Robba, 1980).

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PART III

Faunal Characteristics of Cenozoic Molluscs in Japan

This part of the volume is subdivided into three sections by subjects: e.g., geographic areas, ages and/or faunal characteristics. The first section is composed of the papers of K. Tsuda, J. Itoigawa and T. Yamanoi; T. Ozawa, T. Nakagawa and K. Takeyama; J. Itoigawa and H. Shibata; K. Chinzei. The papers of K. Takayasu; and K. Amano form the second one. And the third section is of T. Shuto; S. Uozumi, M. Akamatsu and T. Takagi; K. Ogasawara; and I. Kobayashi.

In all of these papers, the authors discuss aspects of the biostratigraphy, bioecology, biogeography, origin, migration and development of their respective faunas.

As mentioned in K. Chinzei's paper in Part I of this volume, tropical and subtropical environments developed at certain time during the Neogene in Japan. The authors of papers of the first part of Part III describe and discuss paleoenvironments inferred from faunas of the early Middle Miocene.

With special reference to the fauna associated with mangrove swamps in Central and Southwest Japan during the early Middle Miocene (N. 8–N. 9 or 16–15 Ma), Tsuda, Itoigawa & Yamanoi discuss the geographic distribution and paleoenvironments at that time. This ancient mangrove swamps which included tropical fossil mulluscs such as *Geloina, Telescopium* and others, and a characteristic fossil pollen flora is compared with Recent mangrove swamps in Southeast Asia and the southern Japan. These authors conclude that the mean air temperature around the Japanese Islands during early Middle Miocene was at least as high as that of Iriomote-jima Island (20° N. Lat.).

Ozawa et al. clearly analyze the molluscan fauna of the Uchiura Group and reconstruct the paleoenvironmental conditions and paleogeography of a part of southwestern Japan during early Middle Miocene time.

The molluscan fauna of the Setouchi Miocene Series in Southwest Japan is described by Itoigawa & Shibata. Eight hundred and eighteen species of fossil molluscs are found at many localities in the Setouchi geologic province and these are grouped into 28 basic assemblages. Among these, the *Batissa* and *Geloina* assemblages contain undoubted mangrove swamp taxa live in the tropical seas of that time. The *Cavilucina-Glycymeris* and *Vasticardium* assemblages are also the indicators of tropical sea environment. Paleogeography and paleoenvironment of the Setouchi province are discussed briefly in this paper.

Chinzei summarizes marine paleobiogeography in northern Japan during the early Middle Miocene, as an update of his previous works. Four areas are recognized in northern Japan from Hokuriku in the south to Hokkaido in the north: tropical-, subtropical-, mixed- and subarctic-area, respectively. He also places the early Middle Miocene subtropical front at the northern limit of the Oshima Peninsula, Hokkaido.

Following the four papers just mentioned, Takayasu and Amano describe and discuss the so-called Miocene Shiobara-Yama fauna. These faunas are significant in the development of faunas in Japan as a link between the ancestral Kadonosawa and descendant Pliocene faunas.

Based on the mode of fossil occurrence, Takayasu deciphers interspecific relationship within the fauna of the Izumo Group. He recognizes six molluscan assemblages in the Miocene of the San-in district, which is thought to be the southwesternmost limit of distribution of the

Shiobara-Yama faunas. He also describes rapid diversification of the molluscan fauna from the Izumo Group is response to the great diversity of paleoenvironments available in the area. Takayasu further summarizes the cold water molluscan funa of the Fujina Formation and contrasts it with the warm water faunas of under- and overlying strata.

In Hokkaido, faunas correlative with the Shiobara-Yama faunas are known as the Atsunai-Togeshita faunas. According to Amano, so-called Atunai-Togeshita faunas may be subdivided into two faunas, the Lower Togeshita-Atsunai fauna and Upper Togeshita fauna, which he assigns to the Middle and Late Miocene, respectively. Amanc also concludes that the Upper Togeshita fauna might be ancestral to some Pliocene faunas, such as the Takikawa-Honbetsu fauna also in Hokkaido and the Omma-Manganzi fauna in Honshu.

Three other papers focus on Pliocene faunas in Japan as well as in the Southeast Asia and the northern Pacific region.

Origin and development of the well-known Plio-Pleistocene Kakegawa fauna is discussed by Shuto. He analyzes so-called Kakegawa fauna occurring from Shizuoka to Miyazaki, compares it with correlative faunas of Okinawa and Luzon Island (the Philippines), and tries to establish the geographic limit of the Kakegawa fauna. Shuto also describes changes in the species composition of the fauna as it gradually changed southward into a typical fauna. He concludes that species characteristics of the Kakegawa fauna might have descended from the tropical species in latest Miocene time.

Uozumi, Akamatsu and Takagi present data on the age-range of the major index fossil *Fortipecten takahashii*, which occurs widely in northern Japan, Sakhalin and Kamchatka. They conclude that the Takikawa-Honbetsu and Tatsunokuchi faunas have an age range of about 6 to 2 Ma and represent cold water conditions. These authors also emphasize that the *Fortipecten takahashii*-bearing Pliocene fauna might have been originated in Japan and emigrated towards the north or northeast to Sakhakin and Kamchatka, and perhaps as far as the Alaska Peninsula, during Early Pliocene time. They finally mention the stratigraphic relationship between formations yielding the Takikawa-Honbetsu fauna and the Setana fauna; the latter fauna contains significant elements of the Omma-Manganzian fauna of Ogasawara.

Ogasawara redefines the Omma-Mangazian fauna, based on comparisons with the Tatsunokuchi and Kakegawa faunas. He tries to establish new subdivisions of the Omma-Manganzi Faunal Province, namely the southern-, central-, northern-, Kanto-type- and tentative Kuril subprovinces. Based on these subdivisions, he analyzes the paleo-current system which influenced species dispersions at that time. Ogasawara also infers that there might have been two places of origin of the Omma-Manganzian fauna, the central part of the Sea of Japan and/or the Okhotsk Sea. The latter place might have been the northern limit of the Miocene Shiobara-Yama Faunal Province, and the study by Uozumi, Akamatsu and Takagi seems to support with this opinion Ogasawara finally suggests that emigration time of the fauna coincides with the opening of the Bering Strait before about 3 Ma.

In the final paper of this volume, Kobayashi provides details of the geochronology and biostratigraphy of the Pliocene and Pleistocene sequence in the Niigata sedimentary basin. He recognizes seven faunal assemblages during the interval of 3–1 Ma. Kobayashi concludes that an important faunal change took place during Late Pliocene time in the Niigata sedimentary basin, and that it was mainly related to an influx of warm water elements from the south.

(Junji ITOIGAWA and Kenshiro OGASAWARA)

MANGROVE SWAMP FAUNA AND FLORA IN THE MIDDLE MIOCENE OF JAPAN

By

Karyu TSUDA, Junji ITOIGAWA and Tohru YAMANOI

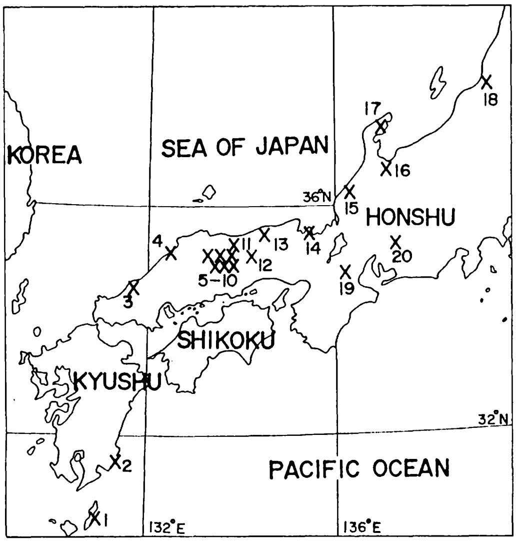
Introduction

In 1950, K. Oyama reported that he found the *Geloina-Telescopium* fauna among the Middle Miocene Yatsuo Group in Toyama Prefecture, and he pointed out that this fauna contains the species characteristic of the mangrove swamps which are found in recent tropical regions. This discovery was the event which aroused much interest among the schollars in those days who were studying the Japanese Neogene stratigraphy and fossils.

After that there have been successive discoveries of fossils of tropical molluscs in various parts of Japan, and also discoveries of red-colored beds. In this way, it has gradually become clear that the Honshu of Japan in the so-called Middle Miocene (N. 8–9, 16–15 Ma) were in tropical or subtropical condition.

In 1980, 30 years after Oyama's discovery of *Geloina-Telescopium* fauna, Yamanoi *et al.* reported that they found the pollen fossils of mangrove swamp plants, such as *Bruguiera* (cf. Rhizophoraceae, *Avicennia*), in Toyama Prefecture and in other places.

Side by side with these studies in Japan, in order to reconstruct the Middle Miocene paleoenvironments of Japan, we have been investigated the recent mangrove swamps in Indonesia, Singapore, Malaysia, New Caledonia, Hong Kong, Nansei Islands of Japan etc. We are still undertaking this study, and the final conclusion has not been established, therefore, we would record what we have been able to make clear until the present.



Text-fig. 1. Distribution of mangrove swamp molluscs in the middle Miocene and related recent species. The no. of fossil localities are same with table 1.

Through this investigation, we are indebted to several persons in Japan and abroad, they are Dr. T. Yokota of Toyama City, Mr. T. Saeki, an explorer/alpinist, Professor S. Sakai of Niigata University, Professor H. D. Tjia of the University of Kabansaan, Malaysia, Professor Pho Pho Wong of the University of Singapore to whom we would like to express our sincere appreciation for their collaborations in many ways.

Japanese Middle Miocene mangrove swamp molluscs

Since 1950, many geologists have reported the discoveries of mangrove swamp molluscs in various parts of

	Living distribution						Fossil locality																			
							Japan Sea side																		P. side	
	SE Asia	Taiwan	Okinawa	Amami	S Kyushu	Kii	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Batissa bihokuensis	→												x	x												
Rhizophrimurex capuchinus nagiensis	→																	x								
Telescopium schencki		→								x								(x)				x				
T. sp.		→					x	x												x	?					
Geloina stachi				→							(x)		x	x	x			(x)		x		x	x	x		
G. yamanei				→							x	x				x	x	x				x				x
G. sp.				→					x		x	x				x		x	x		x				x	
Terebralia itoigawai				→														x								
T. kakiensis				→														x								
T. sp.				→			x						x													x
Littorinopsis miodelicatula						→																x	x			
Ellobium yatsuoensis						→																x				

Text-fig. 2. Distribution of Japanese middle Miocene mangrove swamp molluscs.
The locality no. are same with those of fig. 2.

Japan. Table 1 and Fig. 1 indicate these discoveries. For the last few years, we have been studying the recent mangrove swamps in Bali, Java and Smatra of Indonesia, compare the mangrove fauna in the tropical areas and the molluscan and pollen fossils found in Japan.

As an acount of our observations in the areas just mentioned, we can point out that the following 11 genera could be the typical elements of the mangrove swamp molluscs:

Table 1. Localities and typical mangrove swamp molluscs of the Japanese middle Miocene.
G. Group, F: Formation, M: Member, Ge: *Geloina*, T: *Telescopium*, Tr: *Terebralia*, E: *Ellobium*, L: *Littorinopsis*.
The locality no. are same with those of Text-fig. 1.

	no.	locality	formation	Ge	T	Tr	B	E	L	literature
				mangrove mollusca						
Japan Sea side	1	Tanega-shima, Kagoshima	Kawachi F., Kukinaga G.		x	x				Iwasaki (1970), Itoigawa (MS)
	2	Nichinan, Miyazaki	Oyatori M., Nichinan G.		x					Shuto (1963)
	3	Hamada, Shimane	Toyota F., Masuda G.	x						Tsuru (1985)
	4	Nima, S.	Kawai F., Iwami G.		x					Okamoto *et al.* (1971)
	5	Kimita, Hiroshima	lower M., Bihoku G.	x						Okamoto *et al.* (1968)
	6	Shobara, H.	lower M., Bihoku G.	x						Okamoto and Terachi (1974)
	7	Tojo, H.	lower M., Bihoku G.	x		x	x			Itoigawa and Nishikawa (1976); Matsuoka (1979)
	8	Yuki, H.	lower M., Bihoku G.	x			x			*ibid.*
	9	Kawakami, Okayama	lower M., Bihoku G.	x						Itoigawa and Nishikawa (1976)
	10	Niimi, O.	lower M., Bihoku G.	x						Taguchi *et al.* (1979)
	11	Osa, O.	lower M., Bihoku G.	x						Itoigawa and Nishikawa (1976)
	12	Tsuyama, O.	Yoshino F., Katsuta G.	x	x	x				Taguchi (1981)
	13	Wakasa, Tottori	Entsuji M., Tottori G.	x						Yamana (1977)
	14	Maizuru, Kyoto	Uchiura G.	x	x					Itoigawa (MS)
	15	Ayukawa, Fukui	Kunimi F.	x	?					Azuma (MS)
	16	Yatsuo, Toyama	Kurosedani F., Yatsuo G.	x	x	x		x	x	Oyama (1950); Tsuda (1960)
	17	Suzu, Ishikawa	Higashi-innai F.	x						Okumura (1981)
	18	Asahi, Niigata	Iwafune F.	x						Tsuda (1965)
Pacific side	19	Geino, Mie	Himetani M., Suzuka G.	x						Shibata (1978)
	20	Mizunami, Gifu	Shukunohora M., Mizunami G.	x		x				Okumura (1983)

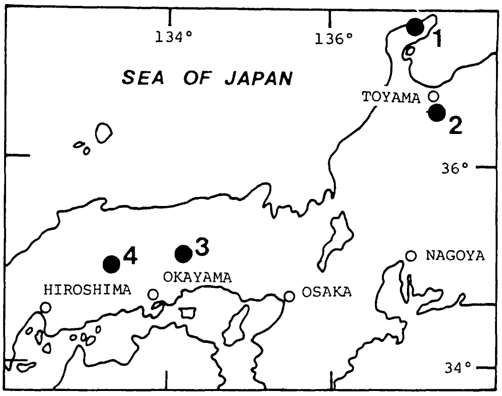
Isognomon, Geloina, Batissa,
Littorinopsis, Cerithidea, Cerithideopsilla,
Telescopium, Terebralia, Rhizophrimurex,
Ellobium, Pythia.

Species of these genera all live in the regions near the equator (0–10°N or S), such as in Singapore and/or Malaysia, but some of the genera are lacking in the regions of comparatively higher latitudes (20–25°N or S), such as New Caledonia, Hong Kong, Nansei Islands. For instance, in New Caledonia (20–22°S), there are mangrove swamps in many places, and we can find rich molluscan fauna, but we can not find any *Telescopium* specimens. In Hong Kong and Nansei Islands, a considerable number of genera are lacking.

In Japan, Middle Miocene sediments yielding these elements pointed above can not be found from a single locality, however, nearly the all elements are found in the Kurosedani Formation. As shown in Text-fig. 2, not so extensive though, all the elements shown above are found in the Middle Miocene formations in the central and southwestern parts of Honshu, Japan. This evidence suggests that the Middle Miocene mangrove swamp faunas in Japan are rather similar to those in tropical or subtropical areas. Fig. 2 shows the distribution pattern of the fossil elements of mangrove swamp fauna and related species.

Mangrove swamp plants

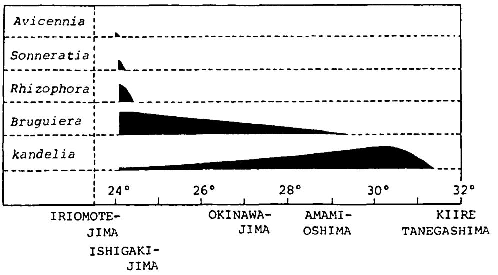
Since Yamanoi *et al.* (1980) reported the discovery of pollen of mangrove swamp plants, the genus *Sonneratia* and other elements of mangrove swamp plants have been recorded. Especially, 8 genera have recorded from the Kurosedani Formation, among these the pollen frequency of the genera *Sonneratia* and *Excoecaria* are



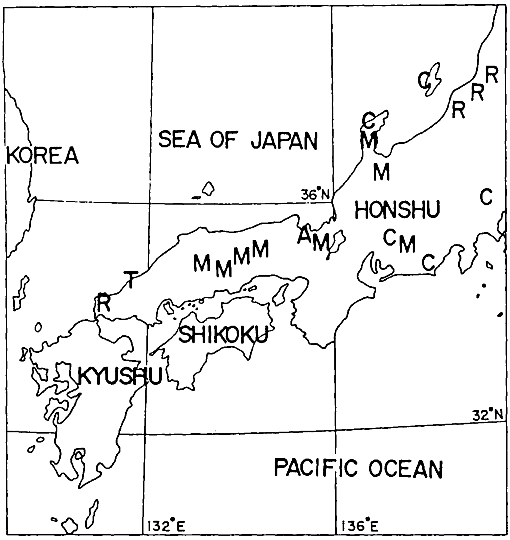
Text-fig. 3. Localities where the mangrove swamp plants were discovered.
1. Noto Peninsula (Higashi-innai formation), 2. South of Toyama (Kurosedani formation), 3. Tsuyama (Yoshino formation), 4. Northeast of Hiroshima (Bihoku group).

Table 2. Occurrence of the middle Miocene pollen fossils of mangrove swamp plants.
Black circle: abundant, White circle: common.
Locality no. are same with fig. 3.

	1	2	3	4
Excoecaria		●	○	
Rhizophora		○	○	○
Bruguiera		○	○	○
Ceriopus		○		
Sonneratia	○	●	○	
Scyphiphora		○		
Avicennia		○	○	○
Nypa		○		



Text-fig. 4. Distribution of recent mangrove plants in the Nansei Islands, Southern Japan.

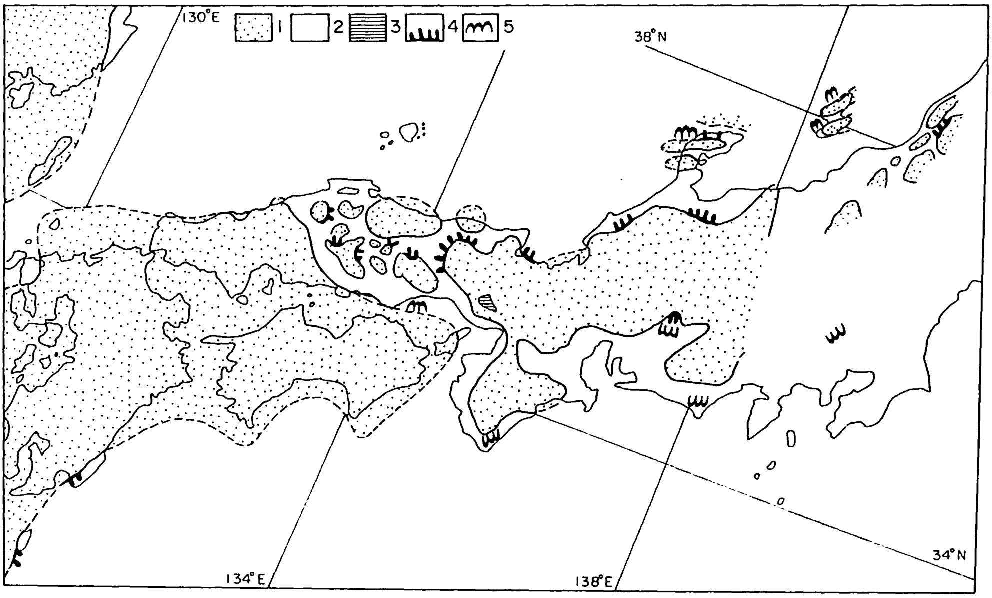


Text-fig. 5. Other evidences of tropical condition in the Japanese middle Miocene epoch.
C: coral reef, A: Indigenous *Aturia*, M: Molluscs, T: Turtle, R: Red colored beds.

sometimes higher than 50% of the total pollen number. In comparing with the pollen percentage of the Recent mangrove swamps in the tropical region, that of the Kurosedani is rather high, and this evidence suggests that the Kurosedani Formation has been accumulated in very similar environment to the Recent tropical mangrove swamps. The distribution pattern of the Recent pollens of mangrove plants is shown in Fig. 4. While, the distribution of these mangrove plants extends further north to more than 35°N. Lat., some of the mangrove genera can only reach to Iriomote-jima Island which situated in 24°N. Lat. The genera found in Iriomote-jima Island and those of fossil mangrove plants are most common, and the tropical elements living further south at present such as *Ceriopus* are also found in the island.

Other evidence of tropical envinronment

Judging from the facts mentioned above, the Japanese Islands, especially the southwestern



Text-fig. 6. Palaeo-geographical map of the Central and Southwestern Japan in the middle Miocene.
1: Land area, 2: Sea area, 3: freshwater area, 4: Mangrove swamp, 5: coral reef.

part, had been under the tropical environments during the Middle Miocene time. We can add the following evidences which support the tropical climatic conditions during that time around the Japanese Islands, these are;

1) Occurrences of several tropical molluscan genera now living in the waters around Taiwan (Formosa), the Philippine Islands and the areas further south in the Indo-Pacific region as shown in Tables 3 & 4.
2) Occurrences of red-colored bed which resulted from tropical weathering developed in several places in Niigata Prefecture.
3) Occúrrence of the tropical genera of fossil corals such as *Favia* and others are recored from several localities of the Miocene formations (Fig. 5).

Paleoenvironment during the Middle Miocene in Japan

Judging from the faunal and floral evidences and the existence of the red-beds, we can reconstruct paleogeography of the central and southwestern parts of Japanese Islands during the Middle Miocene time as shown in Fig. 6. As indicated in the figure, we can recognize several small islands in present Chugoku and San-in districts, coral reefs and mangrove swamps along the beaches and near shore shallow seas.

The thickness of sediments during that time varies from several meters to more than 1,000 meters, and the lithologic variation is from boulder conglomerate to fine grained sediments. And thick volcanic products are often intercalated in the stratigraphic sequences. It has long been generally accepted that the earliest Neogene transgression had been taken place during the Middle Miocene time in Japan. Therefore, rapid accumulation of sediments, especially the vast amount of boulder conglomerates suggests that there had been under violent erosions on land areas during that time. On the other hand, the red-bed intercalations indicate that the region had been suffered fairly strong lateritization. But judging from the fact that lateritization had not reached even toward the alluvial sediments in the present tropical regions, it is quite likely that the process of lateritization against the sediments should take a considerably long time. Therefore, we conclude that there had been

Table 3. Tropical genera of Japanese middle Miocene molluscs. Numerals show Locality No. B: Bihoku Group.

Isognomon (s.s.) *minoensis*	20
Perna oyamai	12
Placuna sp.	16
Maoricardium mizunamiensis	20
Vepricardium sp.	12
Katelysia sp.	19
Novaculina sp.	B
Aplymetis sp.	12
Phylloda sp.	16
Rissolina naomiae	17, 20
Melanoides sp.	B
Lyncina sp.	20
Laebistrombus sp.	20
Globularia nakamurai	12, 14
Cypraecassis sp.	20
Transtrafer sp.	20
Rimella toyamaensis	16
Volema osawanoensis	16
Pionoconus sp.	20

Table 4. Tropical species of Japanese middle Miocene molluscs. (Mainly after Horikoshi (1983))

Arca minoensis	20, B
Barbatia minoensis	20
Meretrix avugai	20, B
Tellinella osafunei	12
Turbo minoensis	20, B
Lunella sp.	20
'Nucella' tokishiensis	20
Babylonia toyamaensis	16, 20, B

some fairly long stable intervals from time to time during the epoch of violent crustal movements in the Middle Miocene of Japan.

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MIDDLE MIOCENE MOLLUSCAN FAUNA OF THE UCHIURA GROUP, WAKASA PROVINCE, SOUTHWEST JAPAN

By

Tomowo OZAWA, Tomio NAKAGAWA and Ken-ichi TAKEYAMA

Introduction

Since Oyama (1950) described the mangrove swamp molluscan association including *Geloina* and *Telescopium* from the Middle Miocene Yatsuo Group, Toyama Prefecture, much fossil and geologic evidence of tropical to subtropical environments in early Middle Miocene of Japan has been accumulated.

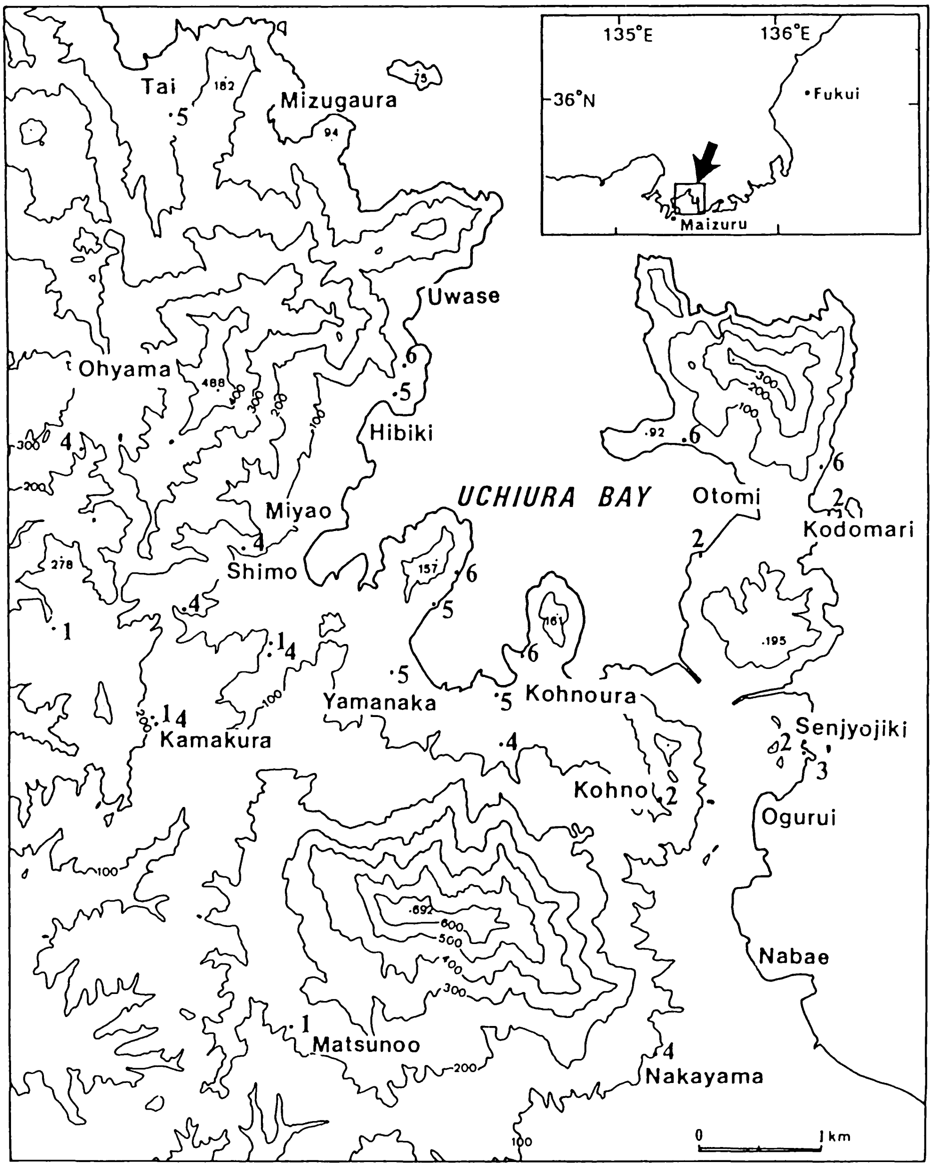
For example Tsuda, Hasegawa and Komatsu (1977) reported the occurrence of red-coloured beds in the Middle Miocene Tsugawa Formation, Niigata Prefecture. Yamanoi et al. (1980) discovered pollens of mangroves from the Middle Miocene *Geloina*-bearing beds in Southwest Japan.

The Uchiura Group on the western boarder of Fukui Prefecture is well known for marine beds yielding tropical and subtropical molluscan fossils of the age. Kobayashi and Horikoshi (1958) have described a semi-autochthonous occurrence of *Aturia* cf. *minoensis* and some tropical gastropods such as *Tectus (Rochia) japonicus, Globularia nakamurai, Turbo (Marmarostoma)* cf. *ticaonica* and *Conus (Plinoconus)* cf. *jenkinsi* from the group. Recently Yamana (1981) and Itoigawa (1981) reported the occurrence of *Geloina, Vicarya, Telescopium,* etc. which were the inhabitants of a mangrove swamp at that time.

Concerning the molluscan fauna of the Uchiura Group, no detailed study has, however, been done to this day. One of the present authors (T. N.) did a geologic study of the Uchiura Group during 1982 to 1983 for his graduation thesis at Fukui University, when he collected many molluscan fossils from the group. In making analyses of litho-facies and molluscan fossils, Nakagawa et al. (1985) clarified that the Uchiura Group had been deposited under shallow marine environments, supplied with the terrigenous materials from the main source area in the western and southwestern part of the basin. K. Takeyama, also one of the authors, made the paleoecological study of the molluscan fauna of the group during 1983 to 1984 for his Master thesis at Hyogo University of Teacher Education, when, with the senior author, he collected many interesting molluscan fossils.

The purpose of this paper is to present the characteristics of the molluscan fauna and to describe the paleoenvironments under which the Uchiura Group was deposited, based on a large number of molluscan fossils.

Before going further, the authors wish to express their hearty thanks to Professor Shizuka Miura of Fukui University, Professor Akira Tokuyama of Hyogo University of Teacher Education and Dr. Manzo Chiji, Director of Osaka Museum of Natural History, for their advice and continuous encouragement throughout the present study. Also, the authors extend their cordial thanks to Associate Professor Junji Itoigawa of Nagoya University for his kind suggestions on the molluscan taxonomy. Acknowledgements are also due to Mr. Kunio Araki of Maizuru City, Mr. Yoichi Azuma of Fukui Prefectural Museum and Mrs. Miyuki Umeda of Fukui Municipal Museum of Natural History for giving us the loan of molluscan collections for the present study. The authors' cordial thanks are due to Professor Albert John Chick of Hyogo University of Teacher Education who kindly read over the manuscript and refine sentence structure.



Text-fig. 1. Topographic map of the Uchiura area, Fukui Prefecture showing the main fossil localities of the Middle Miocene Uchiura Group. The numbers indicate localities where the molluscan associations mentioned in the text occur. 1. *Vicarya-Geloina*, 2. *Turbo (Marmorostoma)-Tectus (Rochia)*, 3. *Oxyperas-Katelysia*, 4. *Cyclina-Hiatula-Nipponomarcia*, 5. *Acila-Saccella* and 6. *Limatula-Propeamussium* association.

Geologic Outline of the Uchiura Group

The Uchiura Group is distributed in hill areas facing Uchiura Bay in the western part of Fukui Prefecture, forming a U-shaped basinal structure which opens to the north (Text-fig. 1). The group lies unconformably on the basement rocks of the Permo-Triassic formations of the Maizuru Belt and Late Mesozoic rhyolite, and is overlain by the Pliocene andesitic volcanics. The group is divided into the Shimo Formation and the Imadobana Formation in ascending order (Nakagawa et al., 1985 and Text-fig. 2).

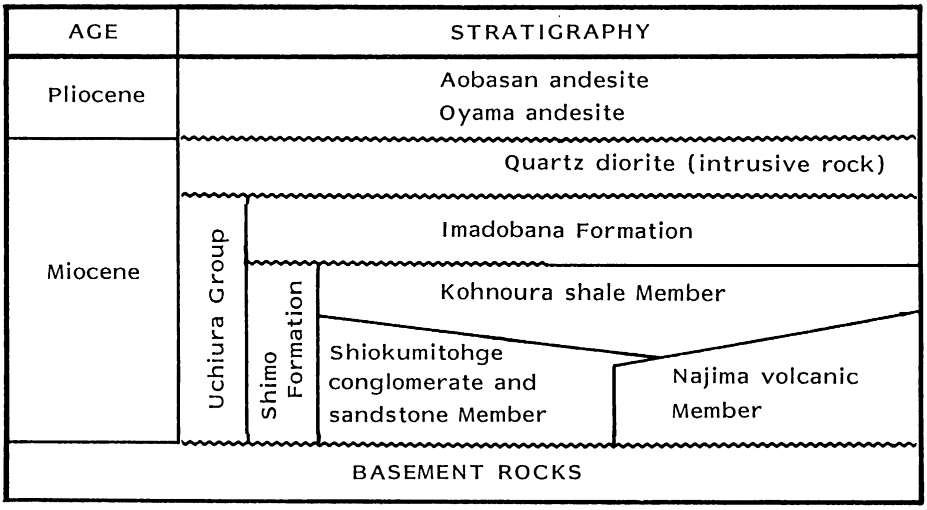
A brief description of each formation is presented first, since the formations have an intimate connection with the paleoecological study on which this paper is based.

The Shimo Formation can be divided into Shiokumitohge conglomerate and sandstone, Najima volcanic and Kohnoura shale members as shown in Text-fig. 2.

The Shiokumitohge conglomerate and sandstone Member unconformably covers the basement rocks with a basal conglomerate and is distributed in the southwestern part of the Uchiura area. This member, about 70 m thick, consists mainly of conglomerate and sandstone. The conglomerate and sandstone beds become thicker to the southwest and thins out northeastward. The sandstone and pebbly mudstone beds in the upper part of the member carry rich and varied molluscan fossils.

The Najima volcanic Member, about 50 m thick, lies unconformably on the basement rocks and is distributed in the eastern part of the area studied. It is composed mainly of andesitic lava, tuff breccia and tuff. All available evidence suggest that these volcanic rocks came from fissure-like vents and formed a volcanic island at the time of the deposition of the Shiokumitohge conglomerate and sandstone Member. Many hard bottom dwelling molluscs ocur from the pyroclastic rocks of this member. As is shown in Text-fig. 2, an interfingering relationship is observable between this member and the Shiokumitohge conglomerate and sandstone Member.

The Kohnoura shale Member, conformably overlying both the Shiokumitohge conglomerate and sandstone Member and the Najima volcanic Member, is extensively distributed in the



Text-fig. 2. Stratigraphy of the Uchiura area, Fukui Prefecture. The wavy line indicates unconformity. (Stratigraphic subdivision after Nakagawa et al., 1985) central part of the Uchiura basin. It consists mainly of massive black shale and grey siltstone with intercalations of sandy turbidite beds. Acidic and intermediate tuff beds named as U1 and U2 key tuff in ascending order are found in this member. In a number of localities, pelecypod and gastropod fossils occur from the siltstone and shale of the member. Some planktonic foraminifers including *Orbulina suturalis, Praeorbulina glomerosa* and *Globigerinoides sicanus* were found in the siltstone at a horizon near the U1 key tuff bed. Based on these index foraminiferal species, the lower part of the Kohnoura shale Member corresponds to the lower part of Blow's Zone N. 9 or early Middle Miocene in age (Nakagawa et al., 1985).

The Imadobana Formation, composed mainly of andesitic lava and its pyroclastic rocks, and rhyolite, is distributed in the northern part of the area studied. It conformably overlies the Kohnoura shale Member, although partial unconformity is observable in some localities. No fossils occur from the formation.

Litho- Facies and Mode of Fossil Occurrence

In the late Early Miocene age, the subsidence of the tectonic sedimentary basin was caused by normal faulting within the basement and the sedimentation of the Uchiura Group was initiated. Talus breccia from a fault scarp are observable along the north-south normal fault which forms the western boundary of the tectonic basin. Thus, the basin was surrounded by the Paleozoic and the Mesozoic basement rocks along its western, southern and southeastern margins. The basement rocks exposed in the southwestern part of the basin served as the main source area for the terrigeneous materials of the deposits, as the conglomerate and sandstone beds of the Shiokumitohge conglomerate and sandstone Member become thicker to the southwest and thin out northeastward. The imbricated structure, distribution and change in thickness of the conglomerate bed suggest that from the southwest a river had flowed into the bay at the time of the deposition of the member (Nakagawa et al., 1985).

The litho-facies varies considerably horizontally and vertically in the Uchiura Group. The following litho-facies are recognized horizontally in a stratigraphic level below the U1 key tuff bed (Text-fig. 3).

Conglomerate facies. – The facies is found in the southwestern corner of the basin. The well-rounded pebbles and cobbles are cemented with a coarse sandy matrix. This is considered to be a deposit in the mouth of a river.

Pebbly mudstone facies. – Along the basements, the dark grey, pebbly mudstone with plant remains is distributed narrowly in the southwestern part of the basin. Mature and immature shells of *Vicarya japonica* occur gregariously from this facies. *Geloina stachi, Scapharca daitokudoensis* and *"Striarca" uetsukiensis* with articulated valves occur sporadically from the mudstone. These molluscan fossils may represent an autochthonous assemblage. Judging from the molluscan association, the mudstone may be the deposits in a mangrove swamp.

Medium-grained sandstone facies. – The well-sorted, medium-grained sandstone is widely distributed in the western and southern part of the basin. The sandstone yields a large number of molluscan fossils. Several types of burrows are observable. Among them the burrows of the Ophiomorpha-type are conspicuous. Many articulated shells of pelecypods which lived on intertidal and subtidal sandy flats are found in life position.

Grey siltstone and black shale facies. – The facies is found in the central area of the embayment. It is characterized by the massive grey siltstone and black shale with thin interbeds of fine-grained sandstone. Molluscan fossils are found from the rock-facies. Dominant species are *Acesta* cf. *goliath, Acila submirabilis, Fissidentalium yokoyamai, Saccella miensis,* and *Patinopecten (Mizuhopecten) kimurai.* Most of the pelecypod species occur with articulated valves scattered in some restricted horizons in parallel with laminae.

Lappilli tuff and tuffaceous coarse-grained sandstone facies. – The facies is characterized by the volcanic breccia, lappilli tuff and tuffaceous coarse-grained sandstone. It is distributed in the eastern part of the Uchiura basin, surrounding the swell composed of the Najima volcanic Member. Hard-bottom dwelling gastropods occur abundantly from these rocks, although most of shells are broken and imperfectly preserved.

Lappilli tuff and tuffaceous sandstone facies. – It is characterized by sandy lappilli tuff and coarse-grained tuffaceous sandstone. The facies is narrowly distributed in the Senjojiki area in the eastern part of the Uchiura Basin. Some venerid pelecypods which lived on the subtidal sandy bottom are found in association with some pelecypod and a few gastropod species. Usually detached valves of these shells are arranged parallel to the bedding plane.

Massive black shale facies. – In the lower part of the Kohnoura shale Member, the grey siltstone and black shale overlapped rapidly the sandy facies of the Shiokumitohge conglomerate and sandstone Member and the Najima volcanic Member. In a stratigraphic level above the U1 key tuff bed, the monotonous, massive black shale with crystals of pyrite and carbonaceous matter occupied a larger part of the embayment. The rock is considered to have been deposited in a relatively deep depression which was dominated by stagnant water. Small nuclanid, pectinid and limid pelecypods occur sporadically from the rock-facies. Most of the pelecypod shells are found with articulated valves, suggesting that these are an autochthonous assemblage.

Molluscan Associations in the Uchiura Group

The molluscan fossils here identified in 42 localities are 129 species belonging to 109 genera, of which 58 species are gastropods, 67 pelecypods, 3 scaphopods and 1 cephalopod. In each locality the mode of fossil occurrence and the type of sediments that contain the fossils are carefully observed. Six types of molluscan association can be discriminated in the Uchiura Group, taking into consideration autochthonous individuals and individuals transported only a short distance within the limits of a habitat into consideration. As described below, each type of molluscan association is characterized by several dominant and characteristic species which lived in a particular sedimentary facies.

1. *Vicarya-Geloina* association. – This molluscan association is characterized by the elements of the mangrove swamp mud bottom community. Among molluscan species, *Vicarya japonica* Yabe and Hatai is the most dominant species. Other conspicuous species are *Scapharca daitokudoensis* (Makiyama), *"Striarca" uetsukiensis* Hatai and Nishiyama, *Geloina stachi* Oyama, *Littorinopsis miodelicatula* Oyama, *Vicaryella ishiiana* (Yokoyama), *Terebraria itoigawai* Taguchi, Osafune and Obayashi, *Tateiwaia yamanarii* (Makiyama) and *Chicoreus (Rhizophorimurex) tiganouranus* (Nomura). The association occurs in the pebbly mudstone in the upper part of the Shiokumitohge conglomerate and sandstone Member. The distribution of the association is narrow, being limited to the southwestern corner of the Uchiura basin.

2. *Turbo (Marmorostoma)-Tectus (Rochia)* association. – This association is composed mainly of rocky bottom dwellers. The main constituent species are *Turbo (Marmorostoma) ozawai* Otuka, *Tectus (Rochia) japonicus* Horikoshi, *Haliotis notoensis* Masuda, *"Tugali"*

Table 1. Distribution of representative molluscan species in the different litho-facies in the Shimo Formation.

The numbers indicate the total number of individuals collected from fossil localities shown in Text-fig. 1.

Abbreviations: 1. *Vicarya-Geloina* association, 2. *Turbo (Marmorostoma)-Tectus (Rochia)* association, 3. *Oxyperas-Katelysia* association, 4. *Cyclina-Hiatula-Nipponomarcia* association, 5. *Acila-Saccella* association, 6. *Limatula-Propeamussium* association; A. pebbly mudstone, B. tuffaceous coarse-grained sandstone, C. lappilli tuff and tuffaceous sandstone, D. fine-grained and medium-grained sandstone, E. siltstone and black shale, F. massive black shale.

Association	Species	Lithofacies					
		A	B	C	D	E	F
1	*Scapharca daitokudoensis* (MAKIYAMA)	8			1		
	"*Striarca*" *uetsukiensis* HATAI & NISHIYAMA	5			5		
	Geloina stachi OYAMA	6			1		
	Littorinopsis miodelicatula OYAMA	2					
	Vicarya japonica YABE & HATAI	173			15		
	Vicaryella ishiiana (YOKOYAMA)	30			4		
	Terebraria itoigawai TAGUCHI,OSAFUNE & OBAYASHI	6			1		
	Tateiwaia yamanarii (MAKIYAMA)	18			15		
	Chicoreus (Rhizophorimurex) tiganouranus (NOMURA)	13			7		
2	*Saccostrea* sp.		25	3		21	
	Haliotis notoensis MASUDA			4			
	Cellana depressa ITOIGAWA & SHIBATA		2				
	Tsugali notoensis MASUDA		2				
	Tectus (Rochia) japonicus HORIKOSHI		9				
	Turbo (Marmorostoma) ozawai OTUKA		47	8	3		
3	*Placopecten protomollitus* (NOMURA)			10			
	Venus sp.			11			
	Katelysia (Hemitapes) sp.			5			
	Oxyperas osawanoensis TSUDA			36			
	Cardilia sp.			1	2		
	Erosaria sp.			1			
	Olivella iwakiensis NOMURA & HATAI			1	7		
	Globularia nakamurai OTUKA			1	7	1	
	"*Conus*" *tokunagai* OTUKA			6	14		
4	*Phacosoma nomurai* (OTUKA)			5	13		
	Tapes (Siratoria) siratoriensis (OTUKA)			1	8		
	Ruditapes takagii (MASUDA)				85		
	Nipponomarcia nakamurai IKEBE				271		
	Cyclina japonica KAMADA			2	106		
	Hiatula minoensis (YOKOYAMA)				105		
	Solen sp.				12		
	Cultellus izumoensis YOKOYAMA				3		
	Panope tyugokuensis OTUKA				3		
	Polinices sp.				5		
	Neverita (Glossaulax) sp.				11		
	Murex sp.				10		
	Pugilina (Hemifusus) sazanami (KANEHARA)				9		
5	*Acharax tokunagai* (YOKOYAMA)					5	2
	Acila submirabilis MAKIYAMA				2	11	2
	Saccella miensis ARAKI					18	
	Yoldia (Cnesterium) sp.					7	2
	Patinopecten (Mizuhopecten) kimurai (YOKOYAMA)			2	5	10	
	Acesta cf. *goliath* (SOWERBY)					27	
	Lucinoma acutilineatum (CONRAD)					2	
	Fissidentalium yokoyamai (MAKIYAMA)			30		52	
	Liracassis japonica (YOKOYAMA)					8	
6	*Neilonella* sp.						4
	Delectopecten peckhami (GABB)						18
	Propeamussium tateiwai KANEHARA						17
	Limatula sp.						46

notoensis Masuda, *Cellana depressa* Itoigawa and Shibata and *Saccostrea* sp. The occurrence of this molluscan association is confined to the tuffaceous coarse-grained sandstone of the Najima volcanic Member and well sorted sandstone of the Shimokumitohge conglomerate and sandstone Member.

3. *Oxyperas-Katelysia* (*Hemitapes*) association. – In Senjojiki area, the lappilli tuff and tuffaceous sandstone of the Najima volcanic Member contains *Oxyperas osawanoensis* Tsuda, *Venus* sp., *Ketelysia* (*Hemitapes*) sp., *Placopecten protomollitus* (Nomura), *Fissidentalium yokoyamai* (Makiyama), *Conus tokunagai* Otuka, *Globularia nakamurai* Otuka, *Erosaria* sp., *Olivella iwakiensis* Nomura and Hatai and some other gastropod and pelecypod species. This molluscan association consists chiefly of dwellers of subtidal sand bottom facing an open sea.

4. *Cyclina-Hiatula-Nipponomarcia* association. – This molluscan association is found in the medium-grained sandstone facies in the upper part of the Shiokumitohge conglomerate and sandstone Member. It is characterized by a high diversity of species, and is dominated by *Nipponomarcia nakamurai* Ikebe, in association with *Cyclina japonica* Kamada, *Hiatula minoensis* (Yokoyama), *Ruditapes takagii* Masuda, *Phacosoma nomurai* (Otuka), *Clementia papyracea* (Gray), *Tapes (Siratoria) siratoriensis* (Otuka), *Cultellus izumoensis* Yokoyama, *Pugilina (Hemifusus) sazanami* (Kanehara) and many other molluscan species. The association consists mainly of sand bottom dwellers in the intertidal to subtidal zones of the embayment.

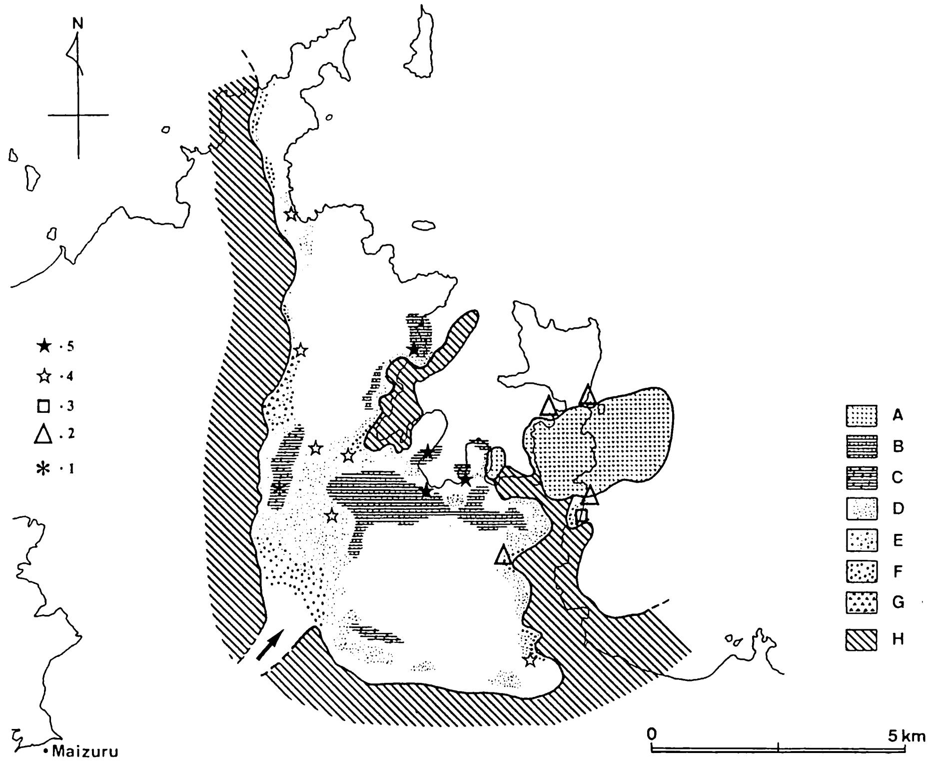
5. *Acila-Saccella* association. – The central part of the embayment is occupied by the grey siltostone and black shale of the Kohnoura shale Member. These rocks contain *Acesta* cf. *goliath* (Sowerby), *Acila submirabilis* Makiyama, *Saccella miensis* Araki, *Patinopecten (Mizuhopecten) kimurai* (Yokoyama), *Lucinoma acutilineatum* (Conrad), *Acharax tokunagai* (Yokoyama), *Yoldia (Cnestrium)* sp., *Fissidentalium yokoyamai* Makiyama, *Liracassis japonica* (Yokoyama), *Musashia* sp., *Fusinus* sp., etc. Among them, *Acila submirabilis* and *Saccella miensis* are conspicuous at every locality. *Patinopecten* (*Mizuhopecten*) *kimurai* is also known to occur in the *Cyclina-Hiatula-Nipponomarcia* association, and *Acila submirabilis* and *Acharax tokunagai* in the *Limatura-Propeamussium* association mentioned below. It is thus considered that this molluscan association occupied the bathymetric range intermediate between the *Cyclina-Hiatula-Nipponomarcia* association and the *Limatula-Propeamussium* association.

6. *Limatula-Propeamussium* association. – The monotonous black shale in the upper part of the Kohnoura shale Member is characterized by the presence of *Limatula* sp. and *Propeamussium tateiwai* Kanehara. They are associated with *Bathymalletia* sp., *Neilonella* sp., *Portlandia* sp., *Delectopecten peckhami* (Gabb), *Polynemamussium* sp., *Acharax tokunagai* Yokoyama, *Acila submirabilis* Makiyama, *Periploma* sp., *Fissidentalium* sp., etc. These molluscs were found to occur sporadically in the massive black shale at every locality. Besides these molluscs, *Linthia nipponica* Yoshiwara is common in the black shale. This molluscan association may present the mud bottom community in a relatively deep sea at the entrance of the embayment.

Judging from the zonal arrangement of the litho-facies, as well as the zonal change in molluscan associations, the sedimentary basin of the Uchiura Group can be restored as an embayment of a U-shape opening northward (Text-figs. 3, 4).

Based on all available evidence, the environment and distribution of the molluscan association in the restored bay at the time of the deposition of the lower part of the Shimo Formation may be presented as follows.

The western and southeastern sides of the bay were surrounded by mountainous areas. From the southwest, a river flowed into the bay, supplying it with terrigeneous materials from



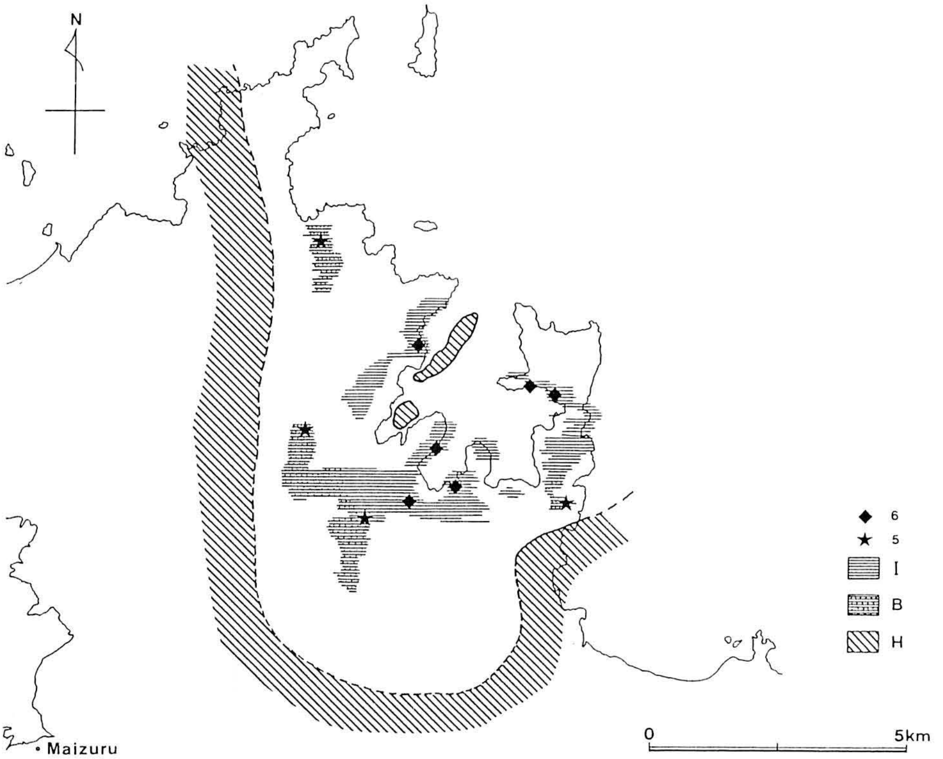
Text-fig. 3. Distribution of the molluscan association in a horizon below the U1 key tuff bed in the middle part of the Shimo Formation in the Uchiura Basin. The thick line indicates the presumed coastline. 1. *Vicarya-Geloina* association, 2. *Turbo (Marmorostoma)-Tectus (Rochia)* association, 3. *Oxyperas-Katelysia* association, 4. *Cyclina-Hiatula-Nipponomarcia* association, 5. *Acila-Saccella* association; A. andesite, B. grey silt and black mud, C. pebbly mud, D. sand, E. granule, F. gravel, G. talus breccia, H. land area.

the main sourse area in the southwestern part of the bay.

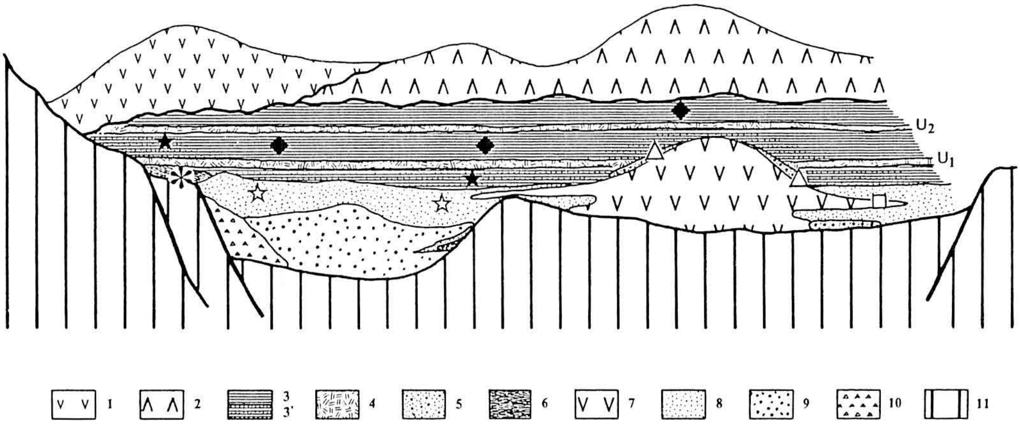
Mangrove forests developed in the mouth of the river. Molluscs of the *Vicarya-Geloina* association inhabited the mangrove swamps. Outside the area of the mangrove swamps, there occurred sandy tidal flats which continued as subtidal sandy bottoms. A large number of molluscan species which constitute the *Cyclina-Hiatula-Nipponomarcia* association lived on the sandy bottoms. In the central part of the bay, there was a depression dominated by muddy bottoms. The molluscs of the *Acila-Succella* association lived in the mud. In the central and southeastern part of the bay, there were islands and a headland consisting of volcanic rocks. The islands and headland were surrounded by rocky shores. Many rocky bottom dwelling molluscs of the *Turbo (Marmorostoma) – Tectus (Rochia)* association inhabited the shore. A small sand coast faced the open sea to the south of the headland. The molluscan species of the *Oxyperas-Katelysia* (*Hemitapes*) association lived on the subtidal sandy bottoms.

Discussion

The molluscan associations are arranged more or less zonally from the shore to the central area of the embayment in accordance with the zonal distribution of litho-facies (Text-figs. 3,4).



Text-fig. 4. Distribution of the molluscan associations in a horizon above the U1 key tuff bed in the upper part of the Shimo Formation in the Uchiura Basin. The thick broken line indicates the presumed coastline. 5. *Acila-Saccella* association, 6. *Limatula-Propeamussium* association; I. black mud, B. grey silt and black mud, H. land area.



Text-fig. 5. Schematic E-W section of the Uchiura Group and the stratigraphic distribution of the molluscan associations. (adopted from Nakagawa et al., 1985).
The figure is exaggerated vertically. 1. Oyama andesite, 2. Imadobana Formation, 3–10. Shimo Formation, 3. massive shale, 3′. siltstone and shale, 4. tuff, 5. volcanic breccia and sandy lappilli tuff, 6. pebbly mudstone, 7. andesite and its pyroclastic rocks, 8. sandstone, 9. conglomerate, 10. talus breccia, 11. basement rocks. Symbols of molluscan associations as in Text-figs. 3 and 4.

Similarly, the vertical change in the molluscan association corresponds well to the vertical change in the litho-facies. As is recognized in a number of the Middle Miocene formations in Southwest Japan, the sediments of the Uchiura Group become gradually finer upwards. Conforming with the change in litho-facies, the molluscan association changes from the members of the mangrove swamp community in the lower horizon to those of the offshore muddy bottom community in the upper horizons (Text-fig. 5). It is thus ascertained that the molluscan association is controlled strongly by the characteristics of the sediments in which the molluscs live. This conclusion agrees well with that of previous authors (ex. Chinzei and Iwasaki, 1967, Chinzei, 1973, etc.).

In the paleoecological study of the Japanese Neogene molluscan fauna, Chinzei and Iwasaki (1967) recognized four different molluscan assemblages in the early Middle Miocene Kadonosawa fauna, namely, the *Batillaria*, the *Ostrea*, the *Dosinia-Anadara* and the *Macoma-Lucinoma* assemblages from the shore to the central area of the embayment. In addition to these, Iwasaki (1970) added another assemblage, the *Telescopium-Geloina* assemblage which characterizes the inner-most area of an embayment at that time. The scheme of the distribution pattern of the molluscan assemblage was established mainly on the basis of the Kadonosawa basin in Northeast Japan. There existed some differences in the species composition of the assemblage between embayments in northern and southern Japan at that time.

The *Vicarya-Geloina* association of the Uchiura Group may roughly correspond to the *Telescopium-Geloina* and the *Batillaria* assemblages; the *Cyclina-Hiatula-Nipponomarcia* association to the *Ostrea*, the *Dosinia-Anadara* and a part of the *Macoma-Lucinoma* assemblages, judging from the composition of species.

A molluscan association nearly identical with the *Vicarya-Geloina* association found in the Uchiura Group is found in a number of the early Middle Miocene formations in the Southwest Japan; i. e., in the Oyama Formation of the Kamigo Group, Yamagata Prefecture (Nishida and Chihara, 1966), in the Iwafune Formation, Niigata Prefecture (Tsuda, 1965), in the Kurosedani Formation of the Yatsuo Group, Toyama Prefecture (Oyama, 1950, Tsuda, 1960), in the Higashi-Innai Formation, Ishikawa Prefecture (Masuda, 1966a, 1966b, 1967), in the Entsuji conglomerate and sandstone Member of the Tottori Group, Tottori Prefecture (Yamana, 1977), in the Yoshino Formation of the Katsuta Group, Okayama Prefecture (Taguchi, 1981), in the Lower Formation of the Bihoku Group, Hiroshima and Okayama Prefectures (Okamoto and Terachi, 1974, Itoigawa and Nishikawa, 1976, Okamoto et al., 1978, Taguchi et al., 1979), in the Himetani Formation of the Suzuka Group, Mie Prefecture (Shibata, 1978), in the Shukunohora sandsone Member of the Mizunami Group, Gifu Prefecture (Okumura, 1983) and in the Sakai Formation of Tanegashima Island, Kagoshima Prefecture (Hayasaka, 1969, Iwasaki, 1970). These molluscan associations represent the mangrove swamp mud-bottom community at the time around 15.5 Ma. Recently fossil pollens of mangroves were discovered from *Geloina*-bearing beds in Southwest Japan (Yamanoi et al., 1980, Tsuda et al., 1981).

It has thus become clear that at that time mangrove forest was found extensively in the southwestern part of Japan.

Knowledge of the hard-bottom molluscan association in the Kadonosawa-type molluscan fauna has untill now been insufficient. In this respect, the *Turbo (Marmorostoma)-Tectus (Rochia)* association found in the Uchiura Group seems to provide important data for the paleoecological reconstruction of the early Middle Miocene molluscan fauna of Japan.

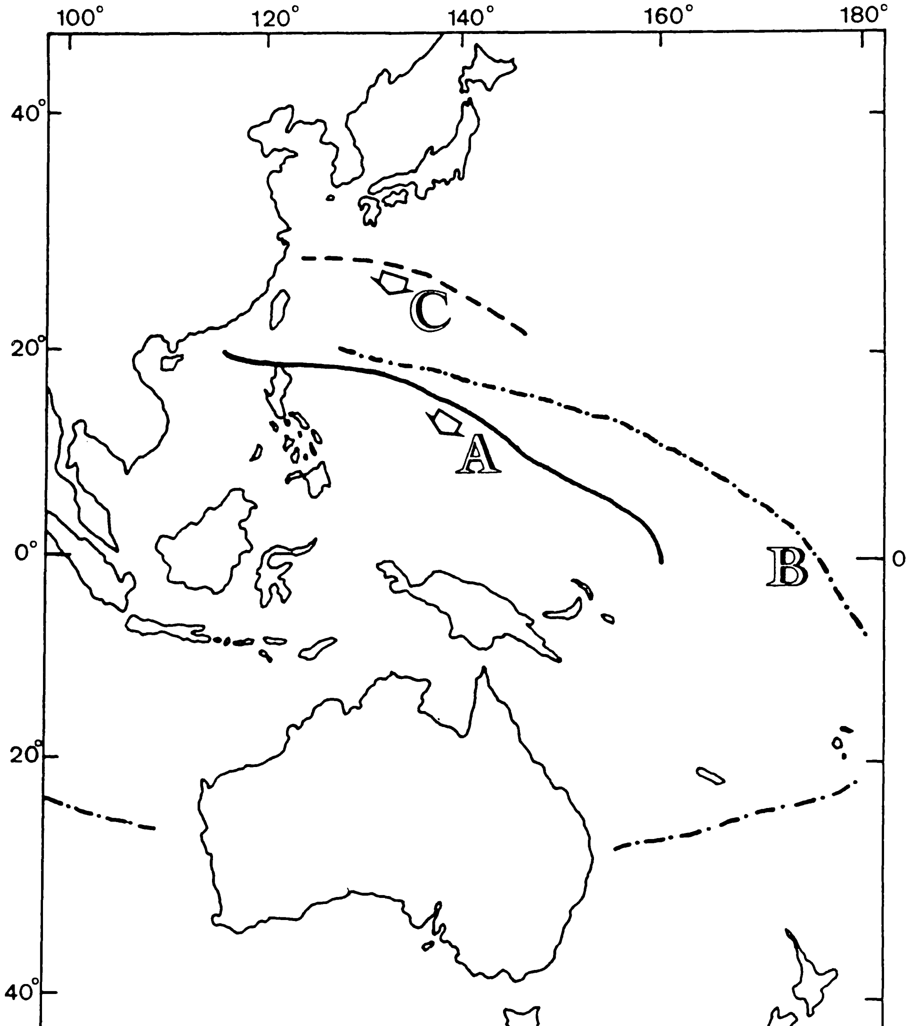
Hard-bottom dwelling molluscs occurred in several localities in the Higashi-Innai Formation of the Noto Peninsula (Masuda, 1966a) and the Shukunohora sandstone Member of the Oidawara Formation, Mizunami Group (Itoigawa, 1960). These molluscan species are, however, found in the conglomeratic sandy sediments as a transported assemblage. In the Uchiura Group, the molluscan association composed mostly of the hard bottom dwellers is known to occur in the tuffaceous coarse-grained sandstone of the Najima volcanic Member, indicating little transportation of shells after death.

The muddy bottom molluscan associations found in the Uchiura Group are closely related to the muddy bottom molluscan assemblages found in the Upper Member of the Bihoku Group (Itoigawa and Nishikawa, 1976), in the Oidawara mudstone Member of the Mizunami Group (Itoigawa, et al., 1974, Shibata, 1978) and in the upper part of the Kurosedani Formation of the Yatsuo Group (Tsuda, 1960).

Sixteen species among twenty-three molluscan species found in the Kohnoura shale Member of the Uchiura Group are also known to occur in the Upper Member of the Bihoku Group. The *Acharax-Neilonella* cf. *soyoae* assemblage in the Mizunami Group (Shibata, 1978) is characterized by *Acharax tokunagai, Neilonella* cf. *soyoae, Bathymalletia* sp., *Portlandia watasei, Polynemamussium* cf. *intuscostatum, Musashia* sp., *Periploma mitsuganoensis* and many other species. Most of the representative species of the assemblage are also found in the Kohnoura shale Member of the Uchiura Group. In specific composition, the *Acila-Saccella* association and the *Limatula-Propeamussium* association found in the Kohnoura shale Member resemble the *Saccella* assemblage and the *Malletia-Nuculana* assemblage, respectively, found in the Shidara, the Iwamura, the Tomikusa, the Awa, the Ichishi and the Morozaki groups in the First Setouchi Series in the eastern part of the Setouchi Geologic Province (Shibata, 1978). These molluscan assemblages represent off-shore mud bottom communities in the early Middle Miocene age of southwestern Japan.

Generally speaking, the molluscan fauna of the Uchiura Group resemble closely the Kadonosawa-type molluscan fauna in southwestern Japan which are represented well by the fauna of the Kurosedani Formation, Toyama Prefecture (Tsuda, 1960), the Higashi-Innai Formation, Ishikawa Prefecture (Masuda, 1966a, 1966b, 1967), the Tottori Group, Tottori Prefecture (Yamana, 1977), the Togane Formation, Shimane Prefecture (Tsuru, 1983), the Susa Group, Yamaguchi Prefecture (Okamoto et al., 1983), the Bihoku Group, Hiroshima and Okayama Prefectures (Okamoto and Terachi, 1974, Itoigawa and Nishikawa, 1976, Taguchi, Ono and Okamoto, 1979, etc.), the Katsuta Group, Okayama Prefecture (Taguchi, 1981, Taguchi et al., 1981), the Mizunami Group and its coeval groups in the eastern part of the Setouchi Geologic Province (Itoigawa, 1960, Itoigawa et al., 1974, Shibata, 1978, etc.) and the Kukinaga Group, Kagoshima Prefecture (Hayasaka, 1969, Iwasaki, 1970).

It is worthy to note that the molluscan fauna of the Uchiura Group contains the specific elements which characterise tropical and subtropical marine fauna. For example, *Geloina stachi* Oyama, *Littorinopsis miodelicatula* Oyama and *Chicoreus (Rhizophorimurex) tiganouranus* Nomura, the members of the mangrove swamp community of the Uchiura Group, are closely related to *Geloina coaxans* (Gmelin), *Littorinopsis carinifera* (Menke) and *Chicoreus (Rhizophorimurex) capucinus* (Lamarck), respectively. The latter three species are dwellers in the present-day mangrove swamps in Southeast Asia and its adjacent region. *Tectus (Rochia) japonicus* Horikoshi from the Uchiura Group resembles *Tectus (Rochia) niloticus* (Linné) distributed in the area south of the Amami Islands in the Ryukyu Archiperago. *Globularia nakamurai* Otuka from the Uchiura Group is closely akin to *Globularia fluctuata* (Sowerby), a



Text-fig. 6. Distribution range of some tropical molluscan species in the Western Pacific which are closely related to the fossil species found in the Middle Miocene Uchiura Group. A. *Turbo (Marmorostoma) brunneum* (Röding), *Globularia fluctuata* (Sowerby), *Rhizophorimurex capucinus* (Röding). B. *Littorinopsis carinifera* (Menke), *Cerithidea obtusa* (Lamarck). C. *Geloina coaxans* (Gmelin), *Katelysia hiantina* (Lamarck), *Oxyperas triangularis* (Lamarck), *Tectus (Rochia) niliticus* (Linné).

living species in the area south of the Philippines in the Indo-Western Pacific Region.

Judging from the marine bio-climatic zones of those living species related closely to the fossil species, the climatic condition of the Uchiura area at the time of the early Middle Miocene age may be inferred to have been equal to the present-day climatic conditions of the Philippines (Text-fig. 6). This inference may also be supported by the common occurrence of *Aturia* and such tropical sea turtles as *Lepidochelys* and *Chelonia* from the Uchiura Group.

The molluscan fauna of the Uchiura Group is also characterized by very high species diversity. In the fauna, most of the genera are represented by a single species.

It is well known that the species diversity in shallow marine molluscs is the highest in the tropical region and decreases gradually towards the high latitudes (Fisher, 1960). The high species diversity of the Uchiura molluscan fauna may indicate the tropical or subtropical nature of the fauna.

Compiling much geological and paleontological data on the warm climatic environments in the Middle Miocene age, Itoigawa (1978) discussed the paleoenvironment and paleobiogeography in the Middle Miocene age of Japan. He concluded that a subtropical climate was dominant over Southwest Japan at the time around 15.5 to 16 Ma.

Chinzei (1981) reconstructed the marine biogeography of Japan during the Miocene age based on benthic marine faunas. In this article, he concluded that in terms of the marine bioclimatic zones, Southwest Japan was tropical at the time around the early Middle Miocene age.

Horikoshi (1981) discussed the tropical marine fauna in the Western Pacific, and he arrived at a conclusion that, as inferred from the bio-climatic zone of those living species related closely to the fossil species, the climate in the early Middle Miocene age of southwestern Japan was as warm as that of the present Philippine Islands.

Our inference on the paleoclimate of the Middle Miocene age of Japan thus conforms to the inferences of previous authors.

To sum up, the Uchiura fauna characterized by such tropical and subtropical molluscs as *Geloina, Littorinopsis, Chicoreus (Rhizophorimurex), Turbo (Marmorostoma), Tectus (Rochia), Globularia, Conus, Katelysia (Hemitapes), Aturia,* will provide us with important data for the reconstruction of the paleoecology and paleobiogeography of the early Middle Miocene Kadonosawa-type molluscan fauna of Japan, as well as for a discussion of the origin and migration of Middle Miocene molluscs in Japan.

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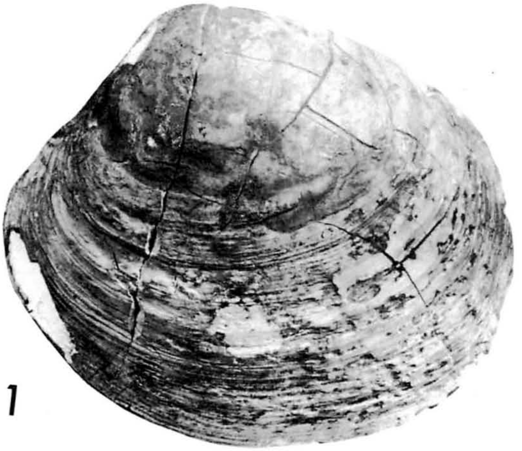
Plate 12

Explanation of Plate 12

Representative species of *Vicarya-Geloina* association

Fig. 1. *Geloina stachi* Oyama x 1.
Both valves, left lateral view, Loc. Shiokumitohge conglomerate and sandstone Member at Sasabe (Araki coll.).
Fig. 2. *Scapharca daitokudoensis* (Makiyama) x 1.
Both valves, left lateral view, Loc. ditto (Araki coll.).
Fig. 3. *Tateiwaia yamanarii* (Makiyama) x 2.4.
Apertural view, Loc. Shiokumitohge conglomerate and sandstone Member at Kamakura (Araki coll.).
Fig. 4. *Littorinopsis miodelicatula* Oyama x 2.3.
Back view, Loc. ditto (Araki coll.).
Fig. 5. *Terebralia itoigawai* Taguchi, Osafune and Obayashi x 1.6.
Apertural view, Loc. Shiokumitohge conglomerate and sandstone Member at Sasabe.
Fig. 6. *Nerita* sp. x 3.4.
Apertural view, Loc. Shiokumitohge conglometate and sandstone Member at Kamakura (Araki coll.).
Fig. 7. *Chiocoreus (Rhizophorimurex) tiganouranus* (Nomura) x 1.8.
Back view, Loc. ditto.
Fig. 8. *Vicarya japonica* Yabe and Hatai x 1.
Apertural view, Loc. Shiokumitohge conglomerate and sandstone Member at Northwest of Yamanaka.
Fig. 9. *Vicarya japonica* Yabe and Hatai x 1.
Back view, Loc. Shiokumitohge conglomerate and sandstone Member at Sasabe (Araki coll.).

Plate 12



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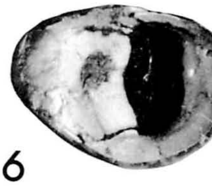

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Plate 13

Explanation of Plate 13

Representative species of *Turbo-Tectus* association

Fig. 1. *Turbo (Marmorostoma) ozawai* Otuka x 1.4.
Apertural view, Loc. Shiokumitohge conglomerate and sandstone Member at Ogurui.
Fig. 2. *Cellana depressa* Itoigawa and Shibata x 1.4.
Apical view, Loc. Najima volcanic Member at Senjojiki.
Fig. 3. *Haliotis notoensis* Masuda x 1.6.
Apical view, Loc. ditto.
Fig. 4. *Tectus* (*Rochia*) *japonicus* Horikoshi x 1.4.
Apertural view, Loc. Shiokumitohge conglomerate and sandstone Member at Ogurui (Holotype specimen, Fukui Municipal Museum of Natural History)

Representative species of *Oxyperas-Katelysia* association

Fig. 5. *Globularia nakamurai* Otuka x 0.8.
Apertural view, Loc. ditto.
Fig. 6. *Erosaria* sp. x 1.4.
Back view, Loc. Najima volcanic Member at Senjojiki.
Fig. 7. *"Conus" tokunagai* Otuka x 1.4.
Apertural view, Loc. Shiokumitohge conglomerate and sandstone Member at Ogurui.
Fig. 8. *Placopecten protomolitus* (Nomura) x 0.9.
Right valve, Loc. Najima volcanic Member at Senjojiki.

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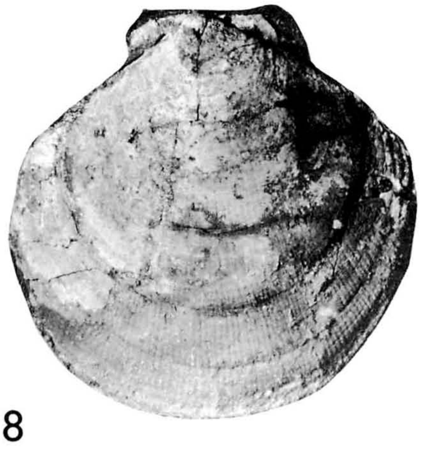

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Plate 14

Explanation of Plate 14

Representative species of *Oxyperas-Katelysia* association

Fig. 1. *Katelysia (Hemitapes)* sp. x 1.4.
Left valve, Loc. Najima volcanic Member at Senjojiki.
Fig. 2. *Oxyperas osawanoensis* Tsuda x 1.4.
Left valve, Loc. ditto.
Fig. 3. *Venus* sp. x 1.2.
Right valve, Loc. ditto.

Representative species of *Cyclina-Hiatula-Nipponomarcia* association

Fig. 4. *Hiatula minoensis* (Yokoyama) x 0.8.
Both valves, right lateral view, Loc. Shiokumitohge conglomerate and sandstone Member at Kamakura.
Fig. 5. *Cyclina japonica* Kamada x 1.
Left valve, Loc. ditto.
Fig. 6. *Ruditapes takagii*(Masuda) x 3.
Left valve, Loc. ditto.
Fig. 7. *Nipponomarcia nakamurai* Ikebe x 3.4.
Left valve, Loc. ditto.
Fig. 8. *Tapes (Siratoria) siratoriensis* (Otuka) x 1.
Right valve, Loc. Shiokumitohge conglomerate and sandstone Member at Northwest of Yamanaka.
Fig. 9. *Nitidotellina* sp. x 2.7.
Right valve, Loc. Shiokumitohge conglomerate and sandstone Member at Kamakura.
Fig. 10. *Diplodonta ferruginata* Makiyama x 3.
Right valve, Loc. ditto.


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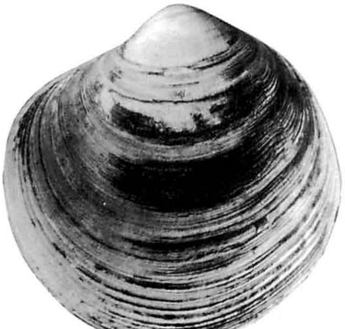
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Plate 15

Explanation of Plate 15

Representative species of *Cyclina-Hiatula-Nipponomarcia* association

Fig. 1. *Saxodomus* n. sp. x 1.
Right valve, Loc. Shiokumitohge conglomerate and sandstone Member at Kamakura (Araki coll.).
Fig. 2. *Olivella iwakiensis* Nomura and Hatai x 4.
Back view, Loc. ditto.
Fig. 3. *Macoma* sp. x 2.7.
Left valve, Loc. ditto.
Fig. 4. *Euspira meisensis* Makiyama x 1.5.
Back view, Loc. ditto.
Fig. 5. *Pugilina (Hemifusus) sazanami* (Kanehara) x 1.
Apertural view, Loc. ditto.
Fig. 6. *"Vasticardium" ogurai* (Otuka) x 2.
Right valve, Loc. ditto.

Representative species of *Limatula-Propeamussium* association

Fig. 7. *Delectopecten peckhami* (Gabb) x 3.
Right valve, Loc. Kohnoura shale Member at North of Yamanaka.

Representative species of *Acila-Saccella* association

Fig. 8. *Acila submirabilis* Makiyama x 2.3.
Left valve, Loc. Kohnoura shale Member at North of Yamanaka.
Fig. 9. *Saccella miensis* Araki x 2.3.
Both valves, Right lateral view, Loc. Kohnoura shale Member at Ogurui.
Fig. 10. *Acharax tokunagai* (Yokoyama) x 2.
Both valves, Right lateral view, Loc. Kohnoura shale Member at North of Yamanaka.


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MOLLUSCAN FAUNA OF THE SETOUCHI MIOCENE SERIES, SOUTHWEST JAPAN

By

Junji ITOIGAWA and Hiroshi SHIBATA

1. Introduction

Since the period of the pioneer works (Makiyama, 1924; Yokoyama, 1926), many studies have been made on fossil molluscs of the Setouchi Miocene series. Especially, after World War II, molluscan assemblage types have been recognized in association with paleoecological and paleoenvironmental syntheses such as in Itoigawa (1960) and Shibata (1970). These works are supported mainly by character of the molluscan fauna such as abundant occurrence of well-preserved specimens and various constituents of species which are useful for restoration of paloenvironments and for paleoecological or paleozoogeographical analysis.

About the molluscan fauna, we already tried to summarize and to generalize in part or general, and describe the molluscan assemblages and discuss paleoecological and paleozoogeographical meaning (Itoigawa, 1969, 1971, 1983; Itoigawa & Shibata, 1973, 1981; Shibata, 1978, Shibata & Itoigawa, 1981). In this paper, we review our previous works and to summarize the molluscan fauna including newly obtained data such as terrestrial and fresh water molluscs.

2. Localities and Stratigraphic Units

Fifty localities of fossil molluscs are recognized in the Miocene groups or formations (generalized as the Setouchi Miocene Series) distributed in the Setouchi geologic province, Southwest Japan (Fig. 1, Table 1). The province is divided near the Osaka Bay, into two parts, the eastern part (Loc. 1 to 20) and the western part (Loc. 21 to 50) on the basis of an appreciable difference in lithofacies and the molluscan fauna. Also the Series is divided stratigraphically into three units, I, II and III in ascending order.

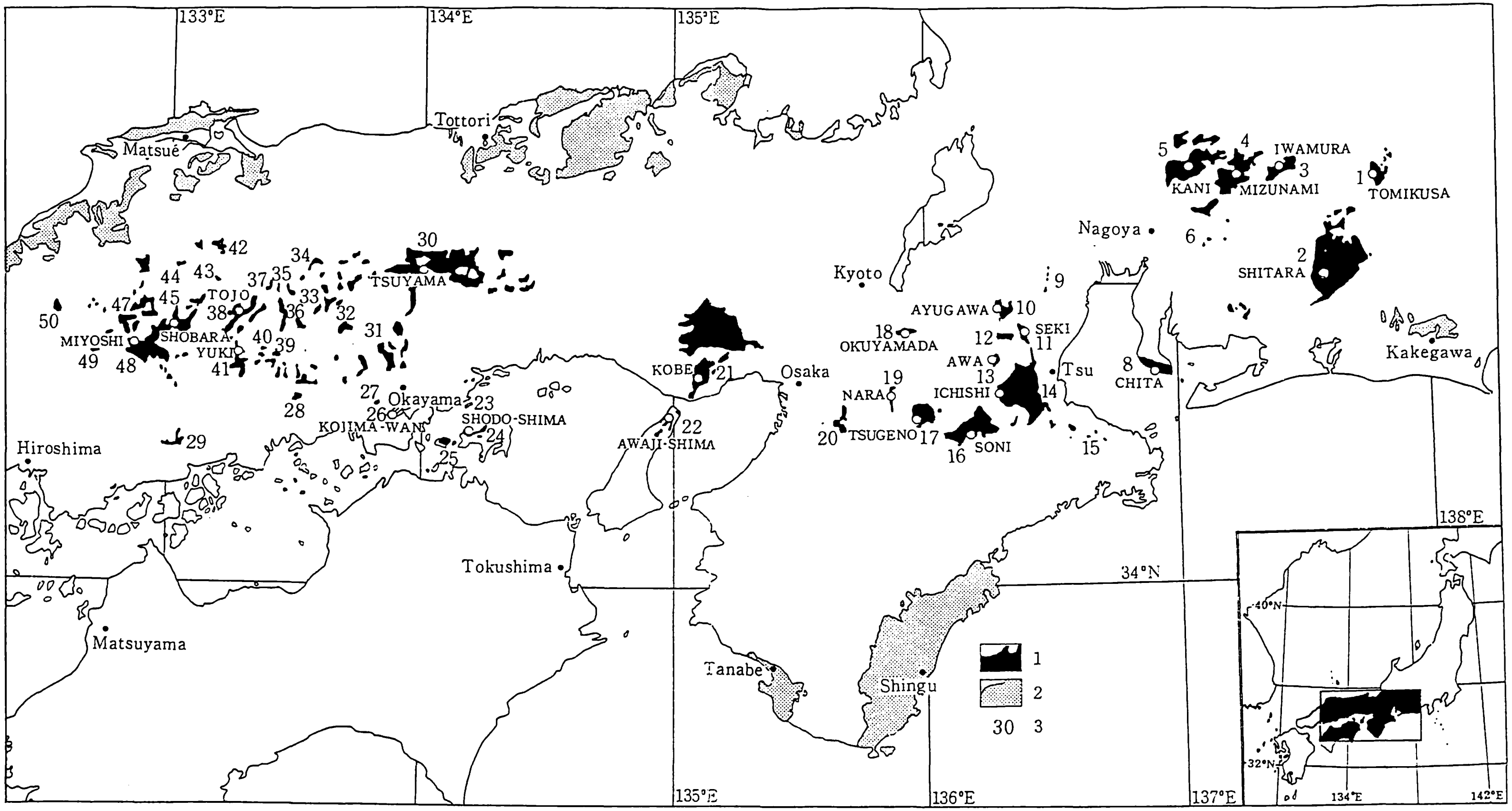
In the Mizunami basin, the area in the northern zone of the east Setouchi province, two disconformities are recognized between unit I and unit II, and unit II and unit III. This kind of disconformity does not develop in the southern zone where the Ichishi Group distributes.

These units are representation of three minor transgressive-regressive phases in a cycle of sedimentation. Presence or absence of the disconformity concerns the difference in the phase of sea invation and in the scale of the sedimentary cycles. Since difference in lithology and molluscan fossils is indistinct between units I and II, they are combined to form the lower unit and unit III constitutes the upper unit.

The geologic age of the Series is the late Early Miocene to early Middle Miocene. The estimated age of the boundary between the lower and the upper units is 15 to 16 Ma.

3. Outline of the Molluscan Fauna

Eight hundred and eighteen species of molluscs constituting of 338 Pelecypoda, 11



Text-fig. 1. Distribution of the Setouchi Miocene Series and Fossil Localities.
1. Setouchi Miocene Series, 2. Other Miocene Series, 3. Locality Number.

Scaphopoda, 447 Gastropoda, 3 Cephalopoda and 19 Polyplacophola (Table 1). These numbers are not exact and may change in the future because molluscan faunas in some areas are not examined completely and species names can be numbered a couple of times.

These molluscs involve some conspicuous species, that is *Aturia minoensis* which is a representative species of Cenozoic Cephalopoda in Japan and Polyplacophora species which are known only from this molluscan fauna in the Miocene of Japan. The fauna includes species of various types in the ecological character. Two terrestrial species of snail and 8 fresh water species of molluscs are recognized being mingled in marine species which are abundant and common in the fauna, consisting of brackish to bathyal zone inhabitants.

The number of species varies for each locality. The Mizunami Group yields 576 species. This number is the greatest in the Setouchi Miocene Series. On the contrary, the Nijo Group has no molluscs. In general, about 50–200 species occur in many localities.

Difference in constitution is recognized between the lower unit and the upper unit. This seems to be due to the difference in environmental conditions such as current system and water mass. The difference in geographical distribution of molluscan species is also noticed. With respect to the above-mentioned stratigraphic distribution of molluscan species and the absence of the lower unit in the west Setouchi province, there are differences in the constitution of molluscan species and in assemblages between the eastern and the western parts.

Representative species are illustrated in Pls. 16 and 17.

4. Molluscan Assemblages

One hundred twenty-three assemblages are described in previous works by many authors. Each formation in various localities has representative assemblages which are shown in the following lines.

1. Tomikusa Group (Nagano) – Shibata (1978): *Crassostrea* Assemblage, *Vicaryella bacula-Cyclina* A., *Barbatia* A., *Chlamys iwamurensis* A., *Turritella-Lucinoma* A., *Saccella* A., *Neilonella-Periploma* A. and *Euclio* A.

2. Shidara Group (Aichi) – Shibata (1978), Shibata & Ina (1983): *Crassostrea gigas* Assemblage, *Ostrea denselamellosa* A., *Phacosoma kawagensis* A., *Chlamys iwamurensis* A., *Arca* A., *Chama* A., *Macoma-Lucinoma* A., *Saccella* A., *Conchocele* A., *Malletia-Nuculana* A. and *Acilana* A.

3. Iwamura Group (Gifu) – Itoigawa (1955), Shibata (1978): *Cyclina-Vicarya* Assemblage, *Cyclina-Vicaryella ishiiana* A., *Barbatia* A., *Arca* A., *Phacosoma kawagensis* A., *Cyclina* A., *Nipponomarcia* A., *Protorotella depressa* A., *Batillaria mizunamiensis* A., *Felaniella* A., *Saccella* A., *Macoma-Lucinoma* A., *Malletia-Nuculana* A., *Acilana* A. and *Euclio* A.

4. Mizunami Group (Gifu) – Itoigawa et al. (1981): *Batillaria-Vicaryella* Assemblage, *Cyclina-Vicarya* A., *Nipponomarcia-Saxolucina* A., *Arca-Saccella* A., *Glycymeris-Turritella* A., *"Proclava"-Reticunassa* A., *Turritella-Euspira* A., *Homalopoma-Reticunassa* A., *Felaniella* A., *Nipponomarcia-Homalopoma* A., *Protorotella-Nipponomarcia* A., *Phacosoma-Meretrix* A., *Nipponomarcia-Phacosoma* A., *Mytilus-Arca* A., *Saccella-Lucinoma* A., *Macoma-Cultellus* A., *Saccella-Cyclocardia* A., *Macoma-Lucinoma* A., *Macoma-Ennucula* A., *Cyclina-Phacosoma* A., *Phacosoma-Turritella* A., *Macoma-Cyclocardia* A., *Zirfaea-Parapholas* A., *Turbo-Chama* A., *Cavilucina-Glycymeris* A., *Bellucina-Polinices* A., *Turbo-Glycymeris* A., *Mitrella-Vermetus* A., *Hyotissa-Aequipecten* A., *Crassostrea-Suchium* A., *Glycymeris-Chlamys* A., *Turbo-Crassostrea*

A., *Pitar-Chama* A., *Antalis-Glycymeris* A., *Chlamys-Homalopoma* A., *Chlamys-Anisocorbula* A., *Neilonella-"Dentalium"* A., *Acharax-Neilonella* A., *Acilana* A., *Vaginella* A. and *Miocenehadra* A.

5. Kani Group (Gifu) – Yoshida (1963): Fresh water molluscan assemblage ("*Lanceolaria*" sp., "*Anodonta*" sp., "*Viviparus*" sp., etc.)

6. Shinano Formation (Aichi) – Otsuka et al. (1976): *Periploma-Acila* Assemblage, *Felaniella-Glycymeris* A.

7. Okazaki Formation (Aichi) – Hayashi & Miura (1973), Shibata (1978): *Barbatia* Assemblage, *Felaniella* A. and *Macoma-Lucinoma* A.

8. Morozaki Group (Aichi) – Shibata (1977), Shikama & Kase (1976), Shibata (1978): *Macoma-Lucinoma* Assemblage, *Acilana* A., *Phanerolepida* A., *Vaginella* A. and *Neilonella-Periploma* A.

9. Chikusa Formation (Mie) – Hata (1967), Shibata (1978): *Cyclina-Vicarya* Assemblage, *Nipponomarcia* A., *Phacosoma kawagensis* A., *Patinopecten chichibuensis mitsuganoensis* A., *Saccella* A., *Neilonella-Periploma* A. and *Vaginella* A.

10. Ayukawa Group (Shiga) – Shibata (1978), Ishida et al. (1979): "*Ostrea*" Assemblage, *Cyclina-Vicarya* A., *Vicaryella bacula-Cyclina* A., *Phacosoma kawagensis* A., *Anomalocardia* A., *Nipponomarcia* A., *Turritella-Glycymeris* A., *Felaniella* A., *Saccella* A. and *Vaginella* A.

11. Suzuka Group (Mie) – Suzuki et al. (1948), Araki & Kitamura (1963), Shibata (1978): *Geloina* Assemblage, *Katelysia* A., Fresh water molluscan assemblage ("*Cristaria*" *kuboi*, "*Arconaia*" *hosonoi*)

12. Suzuka Group (Kabuto, Mie) – Suzuki et al. (1948): Fresh water molluscan assemblage ("*Viviparus*" *uryuensis*, "*Arconaia*" *hosonoi*, "*Cristaria*" *kuboi*)

13. Awa Group (Mie) – Itoigawa (1961), Shibata (1978): *Nipponomarcia* Assemblage, *Proclava* A., *Phacosoma kawagensis* A., *Chlamys iwamurensis* A., *Callista* A., *Acila* A., *Saccella* A., *Macoma-Lucinoma* A. and *Neilonella-Periploma* A.

14. Ichishi Group (Mie) – Shibata (1970, 1978): *Macoma-Lucinoma* Assemblage, *Malletia-Nuculana* A., *Conchocele* A., *Barbatia* A., *Crassostrea gigas* A., *Felaniella* A., *Cyclina* A., *Phacosoma kawagensis* A., *Nipponomarcia* A., *Patinopecten chichibuensis mitsuganoensis* A., *Saccella* A., *Neilonella-Periploma* A., *Vaginella* A. and *Acilana* A.

15. Takakura Formation (Mie) – Kimura et al. (1965), Shibata (1978): *Turritella-Glycymneris* Assemblage.

16. Yamagasu Group (Nara) – Shibata (1978): *Macom-Lucinoma* Assemblage, *Malletia-Nuculana* A., *Acilana* A. and *Euclio* A.

17. Yamabe Group (Nara) – Shiida & Shibata (1968), Shibata (1978): *Macoma-Lucinoma* Assemblage and *Cavolina* A.

18. Tsuzuki Group (Kyoto) – Itoigawa (1956), Shibata (1978): *Crassostrea gigas* Assemblage, *Proclava* A., *Nipponomarcia* A., *Protorotella yuantaiensis* A., *Ruditapes miyamurensis* A., *Anadara* A., *Phacosoma nomurai* A., *Felaniella* A. and *Saccella* A.

19. Fujiwara Group (Nara) – Sakamoto (1955), Shibata (1978): *Macoma-Lucinoma* Assemblage, *Malletia-Nuculana* A., *Saccella* A., *Protorotella* A. and *Vaginella* A.

20. Nijo Group (Nara-Osaka) – Morimoto et al. (1953): No molluscan fossils.

21. Taihata Formation (Hyogo) – Itoigawa (1983): *Cyclina-Barbatia* Assemblage.

22. Iwaya Formation (Hyogo) – Itoigawa (1983): "*Ostrea*" Assemblage, *Mactra-Acila* A. and *Cyclocardia-Nuculana* A.

23. Maeshima Formation (Okayama) – Itoigawa (1969): "*Ostrea*" Assemblage.

24. Shikai Formation (Kagawa) – Itoigawa (1983): *Glycymeris* Assemblage and "*Ostrea*" A.

25. Teshima Formation (Kagawa) – Saito et al. (1970), Itoigawa (1983): *Tapes-Glycymeris* Assemblage and *Cyclocardia* A.

26. Bihoku Group (Kojima, Okayama) – Tai (1965): *Glycymeris* Assemblage?

27. Obié Formation (Okayama) – Itoigawa (1983): *Terebralia-Batillaria* Assemblage.

28. Namigata Formation (Okayama) – Itoigawa (1983): *"Ostrea"-Cycladicama* Assemblage, *Crassostrea-Lima-Chlamys* A. and *Acila-Mactra* A.

29. Takasaka Formation (Hiroshima) – Shito (1966): *Cardita* sp.

30. Katsuta Group (Okayama) – Kawai (1957), Taguchi (1981, 1983): *Geloina* Assemblage, *Vicarya-Crassostrea* A., *Cerithidea-Vicarya* A., *Anadara-Tateiwaia* A., *Vasticardium* A. and *Propeamussium* A.

31. Nichioji Formation (Okayama) – Imamura (1966), Itoigawa (1969): "*Barbatia*"-"*Cardita*" Assemblage.

32. Bihoku Group (Shinmachi, Okayama) – Itoigawa (1971): *Acila-Macoma* Assemblage, *Joannisiella-"Cardium"* A. and *Crassostrea* A.

33. Bihoku Group (Azae, Okayama) – Itoigawa (1971): *Ringicula fragilis-Fabulina* Assemblage and *Crassostrea* A.

34. Bihoku Group (Osa, Okayama) – Itoigawa & Nishikawa (1976), Taguchi et al. (1979): *Geloina* Assemblage, *Placopecten-Tugurium* A., *Acesta-Cuspidaria* A., *Cavolinia* A., *Crassostrea-Tateiwaia* A., *Venatomya-Dosinia* A., *Cryptopecten yanagawa* A. and *Striarca-Solidicorbula* A.

35. Bihoku Group (Niimi, Okayama) – Taguchi et al. (1979): *Crassostrea-Tateiwaia* Assemblage, *Crassostrea-Cerithium-Geloina* A. and *Acila-Solidicorbula* A.

36. Bihoku Group (Hongo, Okayama) – Itoigawa (1971): "*Ostrea*" Assemblage, *Nipponomarcia* A., *Crassostrea* A., *Vasticardium* A. and *Saccella* A.

37. Bihoku Group (Yagami, Okayama) – Itoigawa (1971): *Tateiwaia-Crassostrea* Assemblage.

38. Bihoku Group (Tojo, Okayama) – Otuka (1938), Itoigawa & Nishikawa (1976), Matsuoka (1979): *Geloina* Assemblage, *Crassostrea-Tateiwaia* A. and *Batissa* A.

39. Bihoku Group (Kawakami, Okayama) – Itoigawa & Nishikawa (1976): *Turbo-Chlamys* Assemblage, *Phacosoma* A. and *Palliolum-Propeamussium-Limatula* A.

40. Bihoku Group (Yuki-Kawakami, Hiroshima-Okayama) – Itoigawa & Nishikawa (1976): *Saxolucina-Tateiwaia* Assemblage, *Crassostrea-Cyclina-Geloina* A. and *Palliolum-Propeamussium* A.

41. Bihoku Group (Yuki, Hiroshima) – Itoigawa & Nishikawa (1976), Matsuoka (1979): *Batissa* Assemblage, *Geloina* A., *Vasticardium-Phacosoma* A. and *Cyclina-Hiatula-Siratoria* A.

42. Bihoku Group (Tari, Tottori) – Igi & Sakamoto (1977), Tottori Pref. Mus. (1978): *Vasticardium* Assemblage and *Anadara-Vicaryella* A.

43. Bihoku Group (Dogoyama, Hiroshima) – Imamura (1959), Itoigawa & Nishikawa (1976): *Saxolucina-Euspira* Assemblage, *Crassostrea* A. and *Omphalius-Acesta* A.

44. Bihoku Group (Azumayama, Hiroshima) – Tai et al. (1980): *Vasticardium* Assemblage?

45. Bihoku Group (Shobara, Hiroshima) – Okamoto & Terachi (1974), Itoigawa & Nishi-

Table 1. Locality, Formation and number of molluscan species in the Setouchi Miocene Series.

No.	Locality	Formation	Number of species					
1.	Tomikusa, Nagano	Tomikusa Group	95	56	2	37	–	–
2.	Shidara, Aichi	Shidara G.	111	72	3	36	–	–
3.	Iwamura, Gifu	Iwamura G.	169	80	3	86	–	–
4.	Mizunami, Gifu	Mizunami G.	576	200	6	349	3	18
5.	Kani, Gifu	Kani G.	4	3	–	1	–	–
6.	Toyota, Aichi	Shinano Formation	28	15	–	13	–	–
7.	Okazaki, Aichi	Okazaki F.	57	43	–	14	–	–
8.	Chita, Aichi	Morozaki G.	73	39	2	30	1	1
9.	Komono, Mié	Chikusa F.	97	53	6	38	–	–
10.	Ayugawa, Shiga	Ayugawa G.	117	63	2	52	–	–
11.	Seki, Mié	Suzuka G.	29	21	–	8	–	–
12.	Kabuto, Mié	Suzuka G.	3	2	–	1	–	–
13.	Awa, Mié	Awa G.	105	71	4	30	–	–
14.	Tsu, Mié	Ichishi G.	202	95	5	101	1	–
15.	Ise, Mié	Takakura F.	6	4	–	2	–	–
16.	Soni, Nara	Yamagasu G.	47	27	2	18	–	–
17.	Tsugeno, Nara	Yamabe G.	45	26	1	18	–	–
18.	Ujidawara, Kyoto	Tsuzuki G.	70	44	1	25	–	–
19.	Nara, Nara	Fujiwara G.	38	23	1	14	–	–
20.	Mt. Nijo, Nara-Osaka	Nijo G.	–	–	–	–	–	–
21.	Kobe, Hyogo	Taihata F.	12	10	0	2	–	–
22.	Awaji-shima, Hyogo	Iwaya F.	36	24	1	11	–	–
23.	Ushimado, Okayama	Maeshima F.	2	2	–	–	–	–
24.	Shodo-shima, Kagawa	Shikai F.	11	8	–	3	–	–
25.	Te-shima, Kagawa	Teshima F.	19	9	–	10	–	–
26.	Kojima, Okayama	Bihoku G.	4	4	–	–	–	–
27.	Kurashiki, Okayama	Obié F.	6	4	–	2	–	–
28.	Namigata, Okayama	Namigata F.	34	26	–	8	–	–
29.	Mihara, Hiroshima	Takasaka F.	1	1	–	–	–	–
30.	Tsuyama, Okayama	Katsuta G.	115	73	2	40	–	–
31.	Tsudaka, Okayama	Nichioji F.	48	34	1	13	–	–
32.	Shinmachi, Kayo, Okayama	Bihoku G.	37	26	–	11	–	–
33.	Azae, Hokubo, Okayama	Bihoku G.	31	20	1	10	–	–
34.	Ôsa, Okayama	Bihoku G.	51	35	1	15	–	–
35.	Niimi, Okayama	Bihoku G.	68	40	1	27	–	–
36.	Hongo, Tetsuta, Okayama	Bihoku G.	28	21	–	7	–	–
37.	Yagami, Tetsusei, Okayama	Bihoku G.	13	10	–	3	–	–
38.	Tôjô, Hiroshima	Bihoku G.	46	31	1	14	–	–
39.	Kawakami, Okayama	Bihoku G.	45	27	2	16	–	–
40.	Yuki, Hiroshima-Kawakami, Okayama	Bihoku G.	80	42	2	36	–	–
41.	Yuki, Hiroshima	Bihoku G.	20	12	1	7	–	–
42.	Tari, Tottori	Bihoku G.	34	19	–	15	–	–
43.	Dogoyama Stn., Saijo, Hiroshima	Bihoku G.	30	17	1	12	–	–
44.	Azumayama, Hiwa, Hiroshima	Bihoku G.	8	6	–	2	–	–
45.	Shobara, Hiroshima	Bihoku G.	83	62	2	19	–	–
46.	Takano, Hiroshima	Bihoku G.	10	9	–	1	–	–
47.	Kimita, Hiroshima	Bihoku G.	12	9	–	3	–	–
48.	Miyoshi, Hiroshima	Bihoku G.	49	33	3	13	–	–
49.	Takamiya, Hiroshima	Bihoku G.	18	13	1	4	–	–
50.	Mizuho, Shimane	Bihoku G.	49	30	2	17	–	–
	Whole area		818	338	11	447	3	19
			whole species	Pelecypoda	Scaphopoda	Gastropoda	Cephalopoda	Polyplacophra

kawa (1976): *Crassostrea-Cyclina-Geloina* Assemblage, *Batillaria-Crassostrea* A., *Vasticardium-Phacosoma* A., *Crassostrea-Tateiwaia-Trapezium* A. and *Crassostrea-Saxolucina-Hiatula* A.

46. Bihoku Group (Takano, Hiroshima) – Tai (1964): *Anadara-Tateiwaia* Assemblage and *Propeamussium* A.

47. Bihoku Group (Kimita, Hiroshima) – Okamoto et al. (1978): *Crassostrea-Geloina* Assemblage.

48. Bihoku Group (Miyoshi, Hiroshima) – Imamura (1953), Itoigawa & Nishikawa (1976), Itoigawa (MS): *Crassostrea-Vicarya* Assemblage, *Vasticardium-Siratoria* A., *Fissidentalium* A. and *Palliolum-Limatula* A.

49. Bihoku Group (Takamiya, Hiroshima) – Imamura (1953), Itoigawa (MS): *Geloina* Assemblage, *Crassostrea-Tateiwaia* A. and *Yoldia* A.?

50. Bihoku Group (Mizuho, Shimane) – Sakanoue & Takayasu (1984): *Crassostrea-Tateiwaia-Anadara* Assemblage, *Vasticardium-Phacosoma* A., *Mizuhopecten kimurai-Fissidentalium* A. and *Propeamussium* A.

In these assemblages 28 basic assemblages are recognized. They are shown in Table 2 together with horizons, localities and paleoecological data. The assemblage names used in our previous works are also given in reference to the new assemblage names in this paper if they are different fossil contents.

5. Paleoecological and Paleozoogeographical Notes

Each assemblage gives data on paleoecological conditions such as mode of life, depths and bottom characters of the seas. Assemblages in land and fresh water lakes and in brackish bays and seas suggest that various kinds of molluscs were living in the Miocene Setouchi province. The seas changed from the littoral to bathyal zone with rocky-, gravelly-, sandy- and muddy-bottoms. Molluscs of various types of life mode are also recognized.

The distribution of the molluscan assemblages shows the following facts, namely:

1) The molluscan assemblages in the east Setouchi province in the lower unit belong to the same biogeographical province.
2) There is a slight difference between the molluscan assemblages in the eastern part and the western part. This fact may be due to the difference in paleocurrent which inflowed into both areas.
3) Difference in the molluscan assemblages is also found on the northern and southern sides of the western part, namely, the *Vasticardium* Assemblage and the *Mactra-Acila* Assemblage. This is also due to the difference in paleocurrent, water mass and depth.
4) The molluscan fauna of the Setouchi Miocene Series is very similar to those of the Miocene series in Japan, especially to those in southwest to central Japan except for the fauna in the Fossa Magna area in Nagano Prefecture (Itoigawa & Shibata, 1981). It belongs to the Miocene tropical to subtropical faunas in Japan.
5) Three types are especially recognized in the temporal and spatial distributions of the molluscan assemblages.

Type A. Assemblages distributed in the lower unit:

2. Fresh water molluscs, 5. *Cyclina-Vicarya,* 10. *Phacosoma,* 11. *Glycymeris-Turritella,* 14. *Protorotella-Nipponomarcia,* 16. *Arca,* 17. *Barbatia,* 20. *Felaniella,* 23. *Macoma-Lucinoma.*

Table 2. Basic molluscan assemblages from the Setouchi Miocene Series and their paleoecology.

No.	Molluscan assemblage	Horizon and locality (typical)		Paleoecology					Notes
		lower unit	upper unit	1	2	3	4	5	
1.	*Miocenehadra*	4	35	terrestrial inhabitant					
2.	Fresh water mollusca	5,11,12		fresh water inhabitant					
3.	*Batissa*		38,41	U	M, sm	L	b	T	
4.	*Geloina*	11	4,27,30,38,41,49	U	M, sm	L	b	T	
5.	*Cyclina-Vicarya*	1,3,4,7,9,10,13,14		U, R	M, sm	L	b	T-S	
6.	*Cyclina-Tateiwaia*		21,30,32,34,35,37,38,40 41,45,46,47,48,49,50	U, R	M, sm	L	b	T-S	*Cyc.-Vic.*-2 (ii, iii) *Crass.-Bat.* (i)
7.	*Crassostrea*	1,2,4,10,14,18	4,28,30,34,35,37,38,40 45,47,48,49,50	D	R, sm	L	b	(S)-W-(C)	*Crass.-Bat.* (i)
8.	*Nipponomarcia*	3,4,9,10,13,14,18	4,36,40	U	M	L-S1	b-m	(S)-(W)	
9.	*Zirfaea-Parapholas*	3,4	4	O	R	L-S1	m	S-W	
10.	*Phacosoma*	2,3,4,9,10,13,14,18		U	sm, S	L-S1	m	S-W	*Dos.-Tapes* (ii)
11.	*Glycymeris-Turritella*	3,4,6,10,13,15		U, R	S	L-S1	m	S-W	
12.	*Cavilucina-Glycymeris*		4	U, R	S	L-S1	m	(T)-S-(W)	*Cav.-Turbo* (ii)
13.	*Vasticardium*		32,33,41,42,45,48,50	U	S	L-S1	m	(T)-S-W	"*Card*"-*Dos.* (ii)
14.	*Protorotella-Nipponomarcia*	3,4,18,19		U, R	S	L-S1	m	(S)-W	*Nip.-Prot.* (iii)
15.	*Homalopoma-Chama*		4	R, D	S, R	L-S1	m	(S)-W	
16.	*Arca*	2,3,4		D	R	L-S1	m	(S)-W	
17.	*Barbatia*	1,3,7,14		D, O	R	L-S1	m	(S)-W	*Barb.-Caly.* (ii)
18.	*Barbatia-Cardita*		31	D	R	L-S1	m	(S)-W	*Barb.-Caly.* (ii), *Barb.*-2 (iii)
19.	"*Ostrea*"		22,23,24,28,36	D	R	L-S1	m	(S)-W	*Ost.* (iii), *Ost.-Balanus* (i)
20.	*Felaniella*	3,4,6,7,10,14,18		U	S	S1-S2	m	W-C-	
21.	*Mactra-Acila*		22,24,25,26,28,32,36	U	S	L-S2	m	(S)-W	*Acil.-Mact.-Gly.* (i)
22.	*Saccella*	1,2,3,4,6,9,10,13,14,18 19	22,36	U	sm	S2-S3	m	W	*Sac.-Cult.* (ii)
23.	*Macoma-Lucinoma*	1,2,3,4,7,8,13,14,16,17, 19		U	sm	S2-S4	m	W	
24.	*Fissidentalium*		4,34,39,40,45,48,50	U	M, sm	S2-S4	m	W	
25.	*Malletia-Nuculana*	1,2,3,7,14,15,16,19	22	U	M, sm	S3-B	m	(W)-C-(A)	*Nuc.-Yold.* (ii)
26.	*Acilana*	2,3,8,16	2,4,8,14	U	M	B	m	(C)-(A)	
27.	*Propeamussium-Periploma*	1,2,8,9,14	4,8,13,14,39,40,46,48,50	U	M	B-	m	(C)-A	*Neil.-Pall.* (ii)
28.	*Vaginella*	1,3,8,9,10,14,16,17,19	4,14,34	P			m	T-S	

Horizon and locality: Number: locality number in Fig. 1 and Table 1; Paleoecology: 1. mode of life:- D: adhering, P; planktonic, R: crawling epifauna, U: infauna; 2: bottom character:- M: mud, sm: sandy mud, S: sand, R: rock and gravel; 3. depth:- L: littoral or intertidal, S1: 10 m, S2: 20–30 m, S3: 50–60 m, S4: 100–200 m, B: 200 m; 4. salinity:- b: brackish, m: marine; 5. faunal region, T: tropical zone, S: subtropical z., W: warm temperate z., C: cool temperate z., A: subarctic to arctic z.; Notes: Assemblage name used in following works. i. Itoigawa (1971), ii. Itoigawa and Shibata (1973), iii. Shibata and Itoigawa (1981).

Type B. Assemblages distributed in the upper unit:

Subtype i. Assemblages distributed definitely in the eastern part: 12. *Cavilucina-Turritella*, 15. *Homalopoma-Chama*.

Subtype ii. Assemblages distributed definitely in the western part: 3. *Batissa*, 13. *Vasticardium*, 18. *Barbatia-Cardita*, 19. "*Ostrea*", 21. *Mactra-Acila*.

Subtype iii. Assemblages distributed in both areas: 24. *Fissidentalium*.

Type C. Assemblages distributed in both units:

2. *Miocenehadra*, 4. *Geloina*, 7. *Crassostrea*, 8. *Nipponomacia*, 9. *Zirfaea-Parapholas*, 22. *Saccella*, 25. *Malletia-Nuculana*, 26. *Acilana*, 27. *Propeamussium-Periploma*, 28. *Vaginella*.

Only one third of the assemblages are common in the lower and upper units. This shows that the molluscan assemblage is different between both units. Type C composed mainly of brackish bay assemblages and deeper sea inhabitants in the muddy bottom. This fact suggests that the discontinuity of environment.

Eight paleogeographic maps are drawn principally on the basis of a stratigraphic analysis and a paleoecological interpretation of the molluscan assemblages (Shibata & Itoigawa, 1980). Two or three different ages of each stage, I, II and III are selected. The distribution of the molluscan assemblages is shown in the maps together with bathymetric condition and bottom characters.

We can easily understand the presence of strong warm currents in the Setouchi Inland Sea in the Miocene time, especially in the early Middle Miocene (15 to 16 Ma). The extent of the influence of the warm currents are considered to have been different between the Japan Sea side and the Pacific Ocean side. The difference in the molluscan assemblages on the northern and southern sides of the western part in the upper unit may have resulted from this situation.

6. Summary

1) 818 species of fossil molluscs are recognized in 50 localities.

2) 123 assemblages are found and they are summarized in 28 basic molluscan assemblages.

3) There are many kinds of variety in molluscan faunas.
   a. Different number of species in each locality.
   b. Difference in the assemblage between horizons, namely the upper and lower units.
   c. Difference in the assemblage between localities, that is the eastern and western parts.
   d. Difference in the assemblage between the northern and southern sides of the west Setouchi province.

4) The fauna consists of various types of molluscs which have paleoecoogy ranging from the terrestrial and fresh water to the brackish and marine conditions. Marine conditions from littoral to bathyal zone with various bottom characters.

5) The basic molluscan assemblages are classified into three types by the difference in their temporal and spatial distributions.

6) The molluscan fauna belongs to the Miocene tropical to subtropical faunas in Japan and is very similar to the molluscan faunas of the Miocene series in southwest and central Japan except for the Fossa Magna.

7) Strong warm currents inflowed into the Setouchi Inland Sea in the Miocene time, especially in the early Middle Miocene (15 to 16 Ma). The extent of their influence might have been

greater on the Japan Sea side.

8) Paleogeography and paleoenvironments presented by us in 1980 are briefly introduced.

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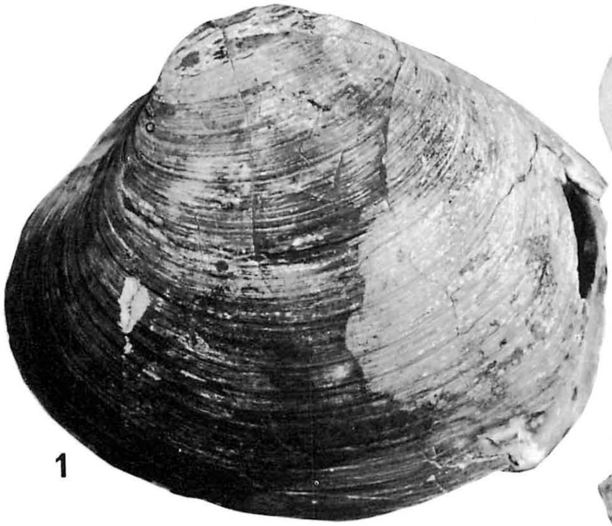
Plate 16

Explanation of Plate 16

Fig. 1. *Geloina stachi* Oyama x1, Loc. 38, Tojo
Fig. 2. *Miocenehadra mizunamiensis* Habe and Itoigawa x2, Loc. 4, Mizunami
Fig. 3. *Tateiwaia tateiwai* Makiyama x1.6, Loc. 40, Yuki
Fig. 4. *Tateiwaia yamanarii* Makiyama x1, Loc. 40, Yuki
Fig. 5. *Vicarya japonica* Yabe and Hatai x1, Loc. 40, Yuki
Fig. 6. *Cyclina lunulata* Makiyama x1, Loc. 30, Tsuyama
Fig. 7. *Cyclina japonica* Kamada x1, Loc. 4, Mizunami
Fig. 8. *Vicarya yokoyamai* Takeyama x1, Loc. 4, Mizunami
Fig. 9. *Vicaryella ishiiana* (Yokotama), x1, Loc. 4, Mizunami
Fig. 10. *Nipponomarcia nakamurai* Ikebe, x2, Loc. 10, Ayugawa
Fig. 11. *Crassostrea gravitesta* (Yokoyama) x1, Loc. 40, Kawakami
Fig. 12. *Zirfaea subconstricta* (Yokoyama) x1, Loc. 4, Mizunami
Fig. 13. *Phacosoma kawagensis* (Araki) x1, Loc. 4, Mizunami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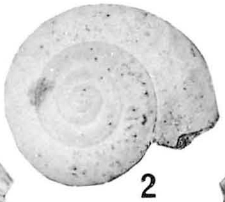
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Plate 17

Explanation of Plage 17

Fig. 1 *Glycymeris ikebei* Itoigawa and Shibata x1, Loc. 4, Mizunami
Fig. 2. *Turritella sagai* Kotaka x1, Loc. 4, Mizunami
Fig. 3. *Cavilucina kitamurai* (Hatai and Nishiyama) x1, Loc. 4, Mizunami
Fig. 4. *Glycymeris cisshuensis* Makiyama x1, Loc. 4, Mizunami
Fig. 5. *Meretrix arugai* Otuka x1, Loc. 4, Mizunami
Fig. 6. *Barbatia kubara* Itoigawa x1, Loc. 3, Iwamura
Fig. 7. *Felaniella usta* (Gould) x1, Loc. 4, Mizunami
Fig. 8. *Protorotella depressa* Makiyama x2, Loc. 4, Mizunami
Fig. 9. *Vasticardium ogurai* (Otuka) x1, Loc. 40, Kawakami
Fig. 10. *Saccella miensis* (Araki) x2, Loc. 4, Mizunami
Fig. 11. *Macoma izurensis* Yokoyama x1, Loc. 4, Mizunami
Fig. 12. *Lucinoma acutilineata* (Conrad) x1, Loc. 4, Mizunami
Fig. 13. *Periploma mitsuganoense* Araki x1, Loc. 4, Mizunami
Fig. 14. *Malletia inermis* (Yokoyama) x1, Loc. 8, Chita
Fig. 15. *Acilana tokunagai* (Yokoyama) x1, Loc. 8, Chita
Fig. 16. *Propeamussium tateiwai* Kanehara x2, Loc. 14, Tsu
Fig. 17. *Palliolum peckhami* (Gabb) x1, Loc. 8, Chita
Fig. 18. *Vaginella depressa* Daudin x3, Loc. 14, Tsu
Fig. 19 *Aturia minoensis* Kobayashi x1, Loc. 4, Mizunami


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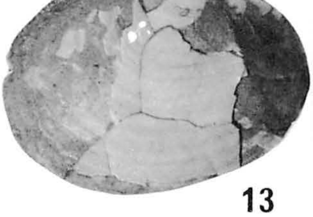
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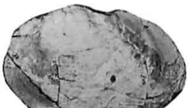
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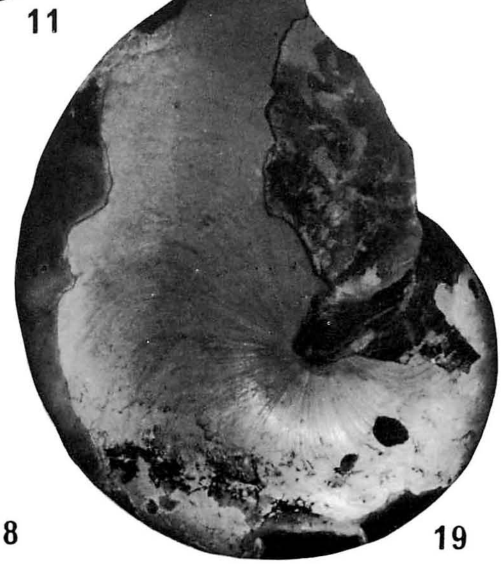
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MARINE BIOGEOGRAPHY IN NORTHERN JAPAN DURING THE EARLY MIDDLE MIOCENE AS VIEWED FROM BENTHIC MOLLUSCS

By

Kiyotaka CHINZEI

Introduction

Shallow marine molluscan faunas of the earliest Middle Miocene, between 16.5 to 15 Ma ago, in the Japanese Islands are dominantly composed of tropical and subtropical species. This indicates a remarkable climatic warming during a relatively short period. The presence of this warm water fauna has been discussed repeatedly by many investigators, since first noticed by Makiyama (1932).

A mangrove swamp association and other tropical molluscs are known from Southwest Japan, particularly in the areas of the Japan Sea coast and in the Setouchi Province (e.g., Oyama, 1950; Tsuda *et al.,* 1981). The shallow marine molluscan fauna of this period has been called the Kadonosawa fauna (Otuka, 1939; Chinzei, 1978). The characteristics of the fauna in Northeast Japan were discussed by Chinzei (1981a, b) who inferred its subtropical nature from the absence of mangrove swamp species and other tropical taxa. A contrasting cold water fauna of cold temperature or subarctic origin, the Chikubetsu fauna, is known from northern and central Hokkaido.

In this paper, I will review the distribution of principal molluscan species in northern Honshu and southern Hokkaido during the early Middle Miocene, based mainly on published information, and discuss marine biogeography around the Japanese Islands during that period.

Dating of the molluscan faunas discussed here is based on planktonic microfossils, mainly foraminifers and diatoms. According to the recent work of Tsuchi and the Japanese working group (1981), the deposits bearing the molluscan faunas are within the range of the N-8 and lower half of N-9 planktonic foraminiferal zones of Blow (1969). The age of some mollusc-bearing deposits discussed herein has not been established by direct microbiostratigraphic control. However, distinctive molluscan species in such deposits permit correlation with other mollusc-bearing deposits whose age have been determined by microfossils. All of the Kadonosawa and Chikubetsu faunas discussed here fall within an interval of around 1 to 1.5 Ma in the early Middle Miocene (refer to Chinzei, this volume, p. 17–32).

Composition of the Subtropical Kadonosawa Fauna

The Kadonosawa fauna is known throughout the Japanese Islands from southern Kyushu to southern Hokkaido. It is composed of taxa derived from tropical areas, including *Vicarya, Batillaria, Cerithidea, Anadara, Dosinia, Tapes,* etc. Some of these genera first appeared in the Japanese Islands in the late Oligocene or even earlier. However, most of the genera first came from the south in the early Middle Miocene, at which time they extended their distribution throughout the Islands and the Japan Sea coast of the Korean Peninsula (Chinzei, 1978). The Kadonosawa fauna in North Japan consists mostly of the same genera as in Southwest Japan, with the exception of some genera characteristic of mangrove swamp and associated sublittoral communities.

Environments ranging from the intertidal zone to the upper sublittoral zone are represented in the Kadonosawa fauna of North Japan. The intertidal sandy mud association and the sublittoral sandy association are ubiquitous, whereas associations from rocky, gravelly, and muddy bottoms are sporadic.

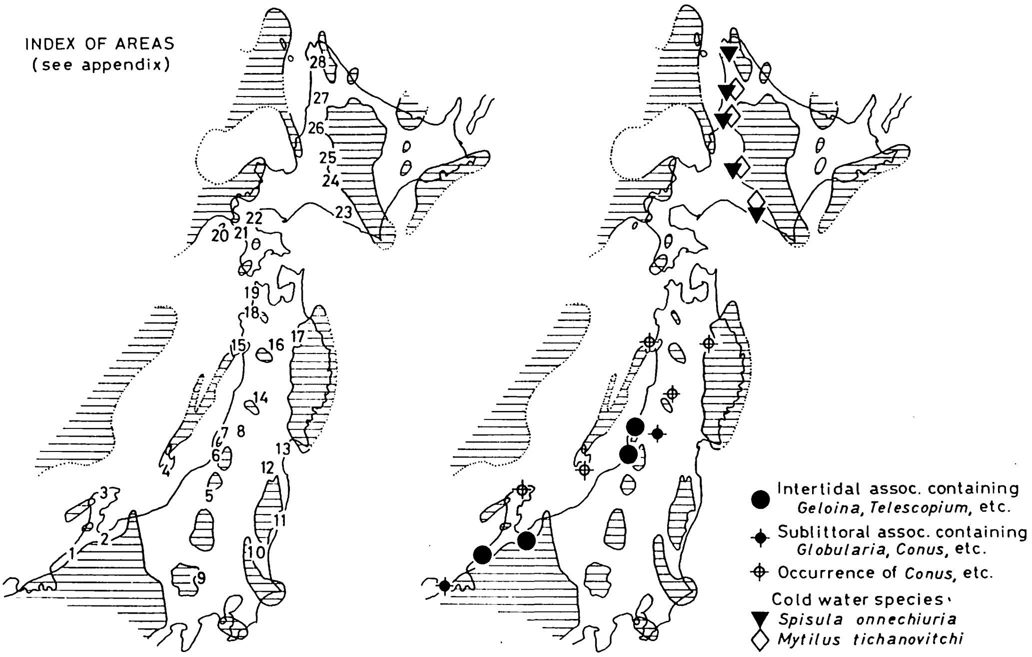
The intertidal sandy mud association is represented by epifaunal detritus feeling gastropods such as *Vicarya callosa japonica* or *V. yokoyamai, Vicaryella notoensis* or *V. ishiiana,* and *Batillaria* (*Tateiwaia*) *yamanarii,* shallow burrowing bivalves such as *Anadara daitokudoensis,* and deep burrowing bivalves such as *Saxolucina khataii, Cyclina japonica, Soletellina minoensis, Macoma incongrua,* etc. The association is found in poorly sorted muddy sand and black mud of a bayhead or marginal areas of an embayment, and occurs in the basal part of a transgressive marine sequences. In Southwest Japan, *Geloina, Telescopium* and other mangrove swamp taxa constitute a distinctive intertidal association in the same facies.

The sublittoral sandy association is composed dominantly of suspension feeding infaunal bivalves, including *Tapes* (*Siratoria*) *siratoriensis, Dosinia nomurai, Clinocardium* sp., *Meretrix arugai, Anadara ninohensis* or *A. abdita, Glycymeris cisshuensis,* and *Panopea nomurae.* Also present are the carnivorous gastropods *Euspira meisensis, Nassarius simizui,* and *Conus tokunagai.* All these species are characteristic of the early Middle Miocene sediments, and are useful as indices of the Kadonosawa fauna. The sandy association is contained in poorly sorted, muddy, medium- to coarse-grained sandstone, which accumulated on the subtidal level bottom of an embayment or sheltered coast. Small colonies of *Crassostrea gravitesta* are also common in this sandy facies. Some typical Kadonosawa genera are absent in places, and are replaced by other sandy association taxa. For example, an association dominated by *Diplodonta ferruginata* and commonly containing *Conus tokunagai* and *Tapes siratoriensis* is often recognized in a well-sorted sandstone facies. In Southwest Japan, this is the facies in which *Globularia nakamurai,* a tropical naticid gastropod, has been reported. The gastropod is associated with *Tectus, Turbo, Periglypta, Isognomon, Perna,* and other tropical sand and rocky bottom molluscs (e.g., Kobayashi and Horikoshi, 1959; Itoigawa and Tsuda, 1984).

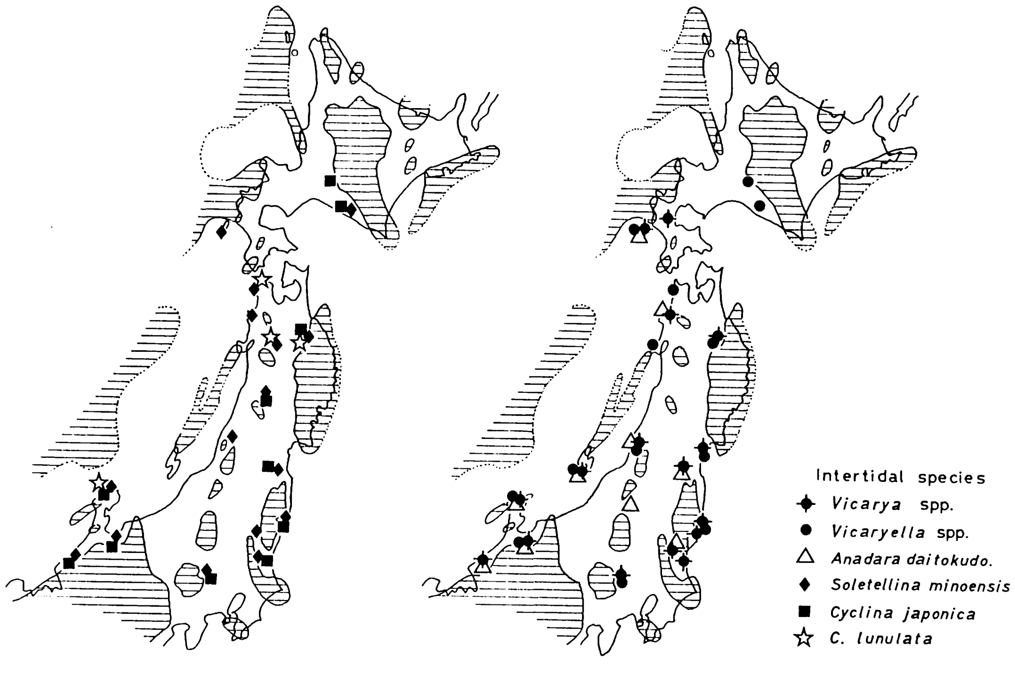
In the level bottom muddy facies, the molluscan fauna is composed mainly of *Macoma optiva, Lucinoma acutilineatum, Cultellus izumoensis, Venericardia siogamensis,* and some other bivalves. The mudstone is thought to have been accumulated in the central part of a bay or inland sea basin. A pectinid association characterized by *Nanaochlamys notoensis, Cryptopecten yanagawaensis, Chlamys arakawai, Placopecten akihoensis* and *Kotorapecten kagamianus* is known from several localities of northern Honshu (e.g., Masuda, 1962). It occurs in coarse-grained, conglomeratic sandstone that, in many areas, lies upon basement volcanic rocks and is thought to have accumulated on or around a submarine high of volcanic origin. Because these taxa of the muddy and gravelly facies are found only sporadically, geographic changes in their composition on a regional scale are not discernible.

Distribution of Representative Species of the Kadonosawa Fauna in North Japan

In North Japan, there are some 20 areas (see appendix) where the Kadonosawa associations or some of their characteristic species have been reported. In many of the areas, elements of both intertidal muddy sand and sublittoral sandy associations are known to occur. They are



Text-fig. 1. Left: Index of areas and localities of the Kadonosawa and Chikubetsu faunas (refer to (Appendix). Right: distributions of tropical species in the Kadonosawa fauna, and two representative species of the cold Chikubetsu fauna.



Text-fig. 2. Distribution of principal species of the intertidal association in the Kadonosawa fauna.

Text-fig. 3. Distribution of principal species of the sublittoral muddy sand association in the Kadonosawa fauna.

recognized as separate associations at some localities, but occur as intermingled assemblages at other localities.

Geographic distributions of the principal Kadonosawa species are shown in Figs. 1 to 3. The species are selected from among those which are found commonly in many areas, to avoid biases arising from sporadic occurrences.

Species of the Intertidal Association

Species regarded to the mangrove swamp elements, *Geloina yamanei* and *Littorinopsis miodericatura,* are reported from the Murakami area (loc. 6 in Fig. 1) in the Niigata basin (Tsuda, 1965). The mangrove dweller *Littorinopsis* is also known from the Nishitagawa Coalfield area (loc. 7), associated with *Anadara daitokudoensis, Striarca uetsukiensis, Hawaiarca uwaensis* and *Rhizophorimurex tiganouranus* (Tsuda, 1965; Kagamida, 1985 MS). This is the northernmost record of the Kadonosawa mangrove swamp molluscs. Takahashi (1984) further reported *Terebralia* sp. from the Kadono area (loc. 11) of the Pacific coast with other species of the subtropical intertidal association. No other occurrences of tropical mangrove swamp or other tidal flat species are known from North Japan (Fig. 1.).

Anadara daitokudoensis and *Vicarya callosa japonica,* representative species of the tidal flat association, are found in northern Honshu (e.g., loc. 19, Iwai, 1960; loc. 12, Ogasawara and Noda, 1978), and on Okushiri Island, southwestern Hokkaido (loc. 20, Uozumi and Fujie, 1966). They are usually associated with *Vicaryella notoensis, Batillaria yamanarii, B. tateiwai, Soletellina minoensis, Cyclina japonica* or *C. lunulata* and others. However, while *Anadara* and *Vicarya* occur only in southwestern Hokkaido and the south, *Vicaryella, Batillaria, Soletellina* and *Cyclina* range farther northward to central Hokkaido. The latter genera are known from the Takinoue (loc. 24, e.g., Kanno and Ogawa, 1964) and the Hidaka (loc. 23) areas in central Hokkaido. The northern limit of these intertidal taxa is the Takinoue area (Fig. 2).

Species of the Sublittoral Sandy Association

Strictly tropical element found in this sublittoral sandy association in northern Honshu is *Globularia* (?) sp., reported from the area northwest of Yamagata (loc. 8, Hatai, 1956). *Conus tokunagai,* known from several localities in Southwest Japan along with *Globularia* and other tropical taxa, was first reported from the Kadonosawa area in northern Honshu (loc. 17, Otuka, 1934). Ogasawara (1973) reported an occurrence of *Cypraea* and *Apollon* species from the Oga area (loc. 15). These genera are common in present-day tropical and subtropical waters.

Most of the species characteristic of this association are known as far north as in central Hokkaido (Fig. 13). This contrasts the intertidal association in which many southern elements disappear between the areas of southwestern and central Hokkaido. *Tapes siratoiensis* is particularly abundant in central Hokkaido, found forming thick, monospecific shell beds in the Uryu (loc. 26) and the Hidaka (loc. 23) areas. It is usually associated with *Dosinia nomuai, Anadara ogawai, A. ninohensis,* and *Meretrix arugai.* Among the main species in this association, only *Katelysia nakamurai* and *Conus tokunagai* are not known in central Hokkaido. Both species are common in the Setouchi Province of Southwest Japan and known from northern Honshu. The reef-builder *Crassostrea gravitesta* also occurs with these species, as small colonies in the sandy facies.

Cold Water Chikubetsu Fauna

Early Middle Miocene sediments in northern Hokkaido contain shallow-water marine molluscs quite different from the Kadonosawa fauna. The molluscan fauna is named the Chikubetsu or the Chikubetsu-Sankebetsu fauna (Uozumi, 1962), and is characterized by species of cold water inhabitants. In several areas of central Hokkaido, the fauna is found stratigraphically very close to that of the Kadonosawa fauna, proving the contemporaneity of the two. The Chikubetsu fauna is composed of sandy bottom dwellers, such as *Spisula onnechiuria, Clinocardium* spp., *Mercenaria chitaniana, Peronidia elongata, Anadara watanabei, Tectonatica ezoana,* and *Neptunea oomurai,* along with the muddy bottom species *Macoma optiva, Yoldia biremis, Y.* cf. *notabilis, Cyclocardia tokunagai,* etc. (Kanno and Matsuno, 1960; Ogasawara *et al.,* 1982). Ogasawara *et al.* (1982) found *Mytilus tichanovitchi* in the Sankebetsu Formation (loc. 27 of Fig. 1); the species regarded as a representative of the "Asahi fauna" (Uozumi, 1966) in central Hokkaido. I formerly distinguished the Asahi fauna from the Chikubetsu fauna, and placed it below the latter (Chinzei, 1978). However, here, I follow the opinion of Sato (1972) and Ogasawara *et al.* (1982) that the two faunas are stratigraphically very close, and treat them together. The Chikubetsu fauna comprises entirely northern genera, except for *Anadara* and *Sinum* found also by Ogasawara *et al.* (1982). There are no species in common with the southern Kadonosawa fauna.

Owing to sparse information on areal distribution of the whole Chikubetsu fauna, two species, *Mytilus tichanovitchi* and *Spisula onnechiuria,* are chosen to trace the distribution of this cold water fauna (Fig. 1). The two species range northward to Sakhalin and the Kuril

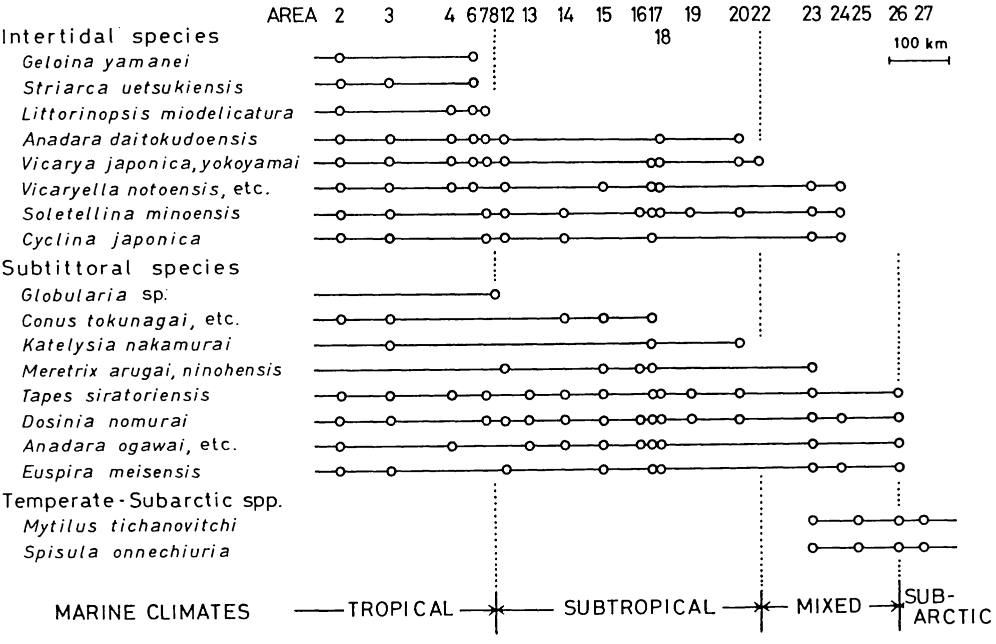
Islands, and are regarded as typical northern species. *Spisula onnechiuria* is also common in stratigraphically younger horizons in northern and eastern Hokkaido, while *M. tichanovitchi* is confined to the early Middle Miocene beds.

In the Uryu (loc. 26) and Asahi (loc. 25) areas of central Hokkaido, the two species are reported together with other cold water species at stratigraphic horizons distinct from, but very close to, those which contain warm water Kadonosawa taxa (Uozumi, 1966; Ohara and Kanno, 1969). Kikuchi (1982 MS) found *M.* cf. *tichanovitchi* in the Hidaka area (loc. 23), from the same shell beds containing *Tapes siratoriensis, Batillaria yamanarii* and other Kadonosawa species; here, *Spisula onnechiuria* occurs in shell beds that alternate stratigraphically with *Tapes* beds.

These mixed occurrences of cold water species and warm-water Kadonosawa species indicate that central Hokkaido was an intermediate zone between northern and southern faunal provinces. Sometimes the cold and warm faunas appeared alternatively, while at other times species of the two faunas lived together.

Proposed Marine Climato-Biogeographic Division during Early Middle Miocene

Fig. 4 shows the geographic distribution of representative species of the warm Kadonosawa fauna, projected on a north-northeast line passing through the Oga Peninsula in northern Honshu. All principal species of the fauna are found in the southern part of northern Honshu, and their distribution is continuous southward to Southwest Japan and farther south (Itoigawa, 1981). However, species tend to disappear, and the faunal diversity to be reduced, toward the



Text-fig. 4. Geographic distribution of principal species of the warm water Kadonosawa and the cold water Chikubetsu faunas, plotted on a line extending NNE-SSW through the Oga Peninsula (loc. 15), northern Honshu. The localities (refer to Appendix) are plotted to show their relative distances.

north. The tendency is recognized especially well in intertidal and sublittoral associations. In central Hokkaido, the diversity of both associations is low, and they frequently coexist with cold-water taxa.

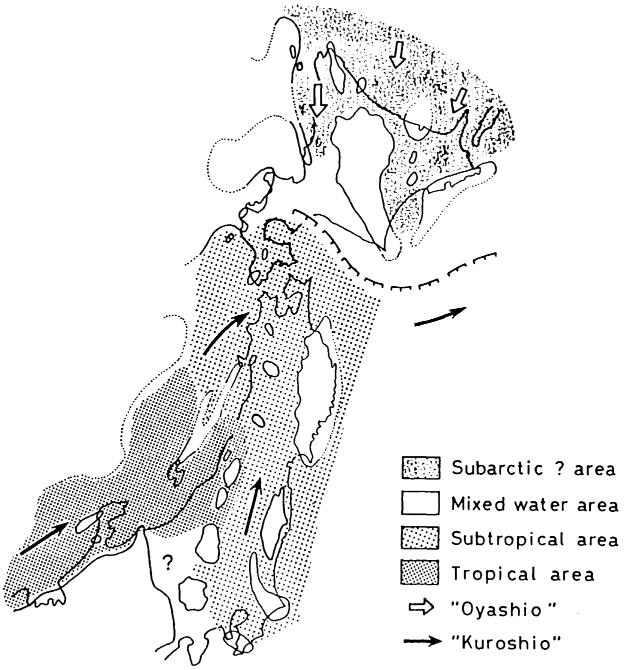
There are places where several of the principal Kadonosawa species disappear altogether. The southernmost such place is just to the north of the Nishitagawa – Murakami areas. This is the northern limit of the tropical species widely distributed along the Japan Sea coast of Southwest Japan. The generic composition of Miocene faunas in Southwest Japan is comparable to that of present-day shallow marine and mangrove swamp habitats in the Philippines (Horikoshi, 1981; Tsuda *et al.*, 1984). Although the fauna in the Nishitagawa – Murakami areas is much poorer in number of apparent tropical genera than are faunas in Southwest Japan, it is still considered to be a tropical fauna.

The associated disappearance of Kadonosawa species is also seen in the southwestern part of Hokkaido, along a line passing from the Okushiri-Kunnui areas and the Kadonosawa area of northern Honshu. Intertidal species which disappear at this line are *Vicarya callosa japonica, V. yokoyamai, Anadara daitokudoensis, Cyclina lunulata,* and some others. All thses species are representatives of the intertidal association, *Conus tokunagai, Cypraea* sp., and *Katelysia nakamurai* are not known from the north of this line. The area south of this line is best regarded as the subtropical area, because of the absence of both characteristically tropical and cold-water species. The line may be compared to the present-day subtropical front between the warm Kuroshio current and temperate waters located off the Cape of Choshi in central Honshu. There is a large marine climato-biogeographic break in the Choshi area where most Indo-Pacific molluscs such as the gastropods *Conus* and *Cypraea* disappear (Horikoshi, 1957). This faunal break is comparable to that at Cape Hatteras in the western Atlantic.

A fair number of Kadonosawa species extend their distribution beyond this line into central Hokkaido. However, none of these belongs to strictly tropical or subtropical genus. *Vicaryella* appears in central Hokkaido, but the climatological preference of this extinct genus is unknown. In central Hokkaido, warm water Kadonosawa taxa are found intermingled with, or stratigraphically very close to, cold water species. This indicates that central Hokkaido during the early Middle Miocene was zoogeographically intermediate between the realms of warm and cold water faunas. All Kadonosawa species known in central Hokkaido are thought to have lived in the sublittoral zone of embayments. The condition is similar to that north of the Cape of Choshi today, where open-coast cold water species are living in the same area with shallow warm water species.

No species of the Kadonosawa type has been reported in northern Hokkaido, the area occupied by the Chikubetsu fauna. This area may be included in the cold temperate or even subarctic zone.

The area where tropical molluscs are known is limited to the western part of northern Honshu, particularly the Japan Sea coast (Fig. 5). Tropical taxa occur continuously from there to Southwest Japan along the coast of the Japan Sea. However, no apparent tropical species are known from the Pacific coast of northern Honshu, except for a single specimen of *Terebralia* reported by Takahashi (1984). Based on this pattern of distribution of tropical molluscs, I concluded that the main stream of the warm Kuroshio current passed at that time through the Tsushima Straits, between Japan and the Korean Peninsula, then flowed into the Japan Sea (Chinzei, 1981b). Species of *Lepidocyclina* (*Nephrolepidina*), a larger foraminifera thought to be generally tropical, are known from the Pacific side of northern Honshu, while



Text-fig. 5. Proposed marine climato-geographic division of North Japan during the early Middle Miocene. SUBTROP. FR.: inferred position of the subtropical front.

Miogypsina and *Operculina* are abundant in the Japan Sea coast areas (Matsumaru, 1981). These larger foraminifera originated from the south, probably extended their distribution northward into the subtropical area of northern Honshu.

The northern limit of tropical molluscs during the early Middle Miocene is located at 38°N latitude, and that of the subtropical fauna at about 42°N. As mentioned before, the modern subtropical front is located near the Cape of Choshi in central Honshu, approximately at 35°N, although in the Japan Sea coast the warm species are living as far north as 38°N. The present-day tropical area is demarcated at around 30°N, in the northernmost part of the Ryukyu Islands where many tropical molluscan genera as well as intertidal coral reef disappear (Horikoshi, 1957, 1981). The northern limit of tropical and subtropical molluscs in the early Middle Miocene were about 6° to 8° north of their modern positions in the waters surrounding Japan.

APPENDIX: LIST OF KNOWN AREAS OF THE KADONOSAWA AND CHIKUBETSU FAUNAS IN NORTHERN JAPAN WITH OTHER LOCALITIES MENTIONED IN THE TEXT

Number corresponds to the area shown in the text anf figurtes:

1 Kaga area (Ogasawara *et al.*, 1981: Itoigawa, 1981)
2 Yatsuo area, Kurosedani Fm. (Tsuda, 1960; Tsuda *et al.*, 1981)
3 Noto area, Higashi-Innai Fm. (Masuda, 1966)
4 Sado area, Orito Fm. (Tsuda, 1965)
5 Niigata-Tsuyama Basin (Tsuda, 1965)

6 Murakami area (Tsuda, 1965)
7 Nishitagawa Coal-field (Tsuda, 1965; Kagamida, 1985 MS)
8 Mogami area (Hatai, 1956)
9 Minami-Matsuyama area (Hatai and Masuda, 1962)
10 Tanakura-Daigo area (Noda, 1973)
11 Joban Coal-field (Kamada, 1962; Takahashi, 1984)
12 South of Sendai, Tsukinoki Fm. (Ogasawara and Noda, 1978)
13 Shiogama area (Nomura, 1935)
14 Sugota area, Sugota Fm. (Saito, 1985 MS: Chinzei, unpubl. data)
15 Oga area, Nishikurosawa Fm. (Ogasawara, 1973)
16 Hanawa Basin (Mizuno, 1965)
17 Kadonosawa area (Otuka, 1934; Chinzei, 1981 and unpubl. data)
18 Nishitsugaru area (Iwai, 1960; Mizuno, 1964; Ogasawara, 1977)
19 Kitatsugaru area (Mizuno, 1964)
20 Okushiri Island (Uozumi and Fujie, 1966)
21 Kumaishi area (Hata, 1975)
22 Kunnui area (Kanno unpubl. data)
23 Hidaka area (Imai and Sumi, 1957; Yoshida *et al.*, 1959; Kikuchi, 1982 MS)
24 Takinoue area (Kanno and Ogawa, 1964)
25 Asahi area, Horomui Fm. (Uozumi, 1962; Kanno *et al.*, 1968)
26 Northern Uryu Coal-field (Ohara and Kanno, 1969, 1973)
27 Chikubetsu area, Sankebetsu and Chikubetsu Fms. (Ogasawara *et al.*, 1982)
28 Wakkanai area (Otuka, 1940)

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DIVERSIFICATION IN THE MOLLUSCAN FAUNA OF THE MIOCENE IZUMO GROUP, SAN-IN DISTRICT, SOUTHWEST JAPAN

By

Katsumi TAKAYASU

Introduction

The molluscan fossils from the Miocene deposits of Izumo district, Southwest Japan, have been studied by Yokoyama (1913, 1923), Nomura and Hatai (1939), Okamoto (1959), Suehiro (1979), Ogasawara and Nomura (1980), Takayasu (1980, 1982, 1985), Takayasu and Nakamura (1984) and others. Those of the Fujina Formation are especially well preserved, composed of diverse species, and are considered to represent a Shiobara-type fauna (Iwasaki, 1970; Chinzei, 1978; etc.).

The Shiobara-type fauna is reported from the Middle to Upper Miocene deposits of Northeast Honshu and the Japan Sea coast, and its distribution is thought to correspond with the area under the influence of cold water currents at that time. The Izumo district is the southwesternmost occurrence of the fauna. The molluscan fauna of the Fujina Formation essentially originated in boreal waters. It is also true, however, that several important species in the Fujina Formation are evidently descendants of the Japanese early Middle Miocene subtropical Kadonosawa-type fauna (Suehiro, 1979; Ogasawara and Nomura, 1980; Takayasu and Nakamura, 1984; Takayasu, 1986). Although the presence of subtropical species is recognized in other assemblages correlated with the Shiobara-type fauna (Chinzei, 1978), it seems to be more prevalent in the present district because of local paleogeography. From this viewpoint, the formation and diversification of the Shiobara-type fauna in the district will be discussed in this paper.

Before attending to this subject, the author would like to express his appreciation to Professor Tamio Kotaka of Tohoku University, leader of the researhch project "Origin and Migration of Japanese Cenozoic Molluscs", for valuable discussion and for giving an opportunity to publish the paper. He also expresses his deep gratitude to the members of the research project for many helpful suggestions, and to Professor Junji Itoigawa of Nagoya University for critical reading of the manuscript.

Outline of Geology

The stratigraphy of the Miocene deposits in the Izumo district was first studied in detail by Tomita and Sakai (1937), and subsequently by Okamoto (1959), Doi *et al.* (the report on the regional geology "Kita-shimane", 1968), Miyajima *et al.* (1972), Ogasawara and Nomura (1980), Takayasu and Nakamura (1984), and so on. According to them, the Miocene deposits are divided into the Lower to Middle Miocene Iwami Group and the Middle to Upper Miocene Izumo Group.

The Iwami Group is mainly composed of dacitic and andesitic pyroclastics, so-called "Green Tuff". In the upper part of the group, sandstones and shales named the Kawai and the

Kuri Formations, respectively, are included, and these yield a Kadonosawa-type fauna.

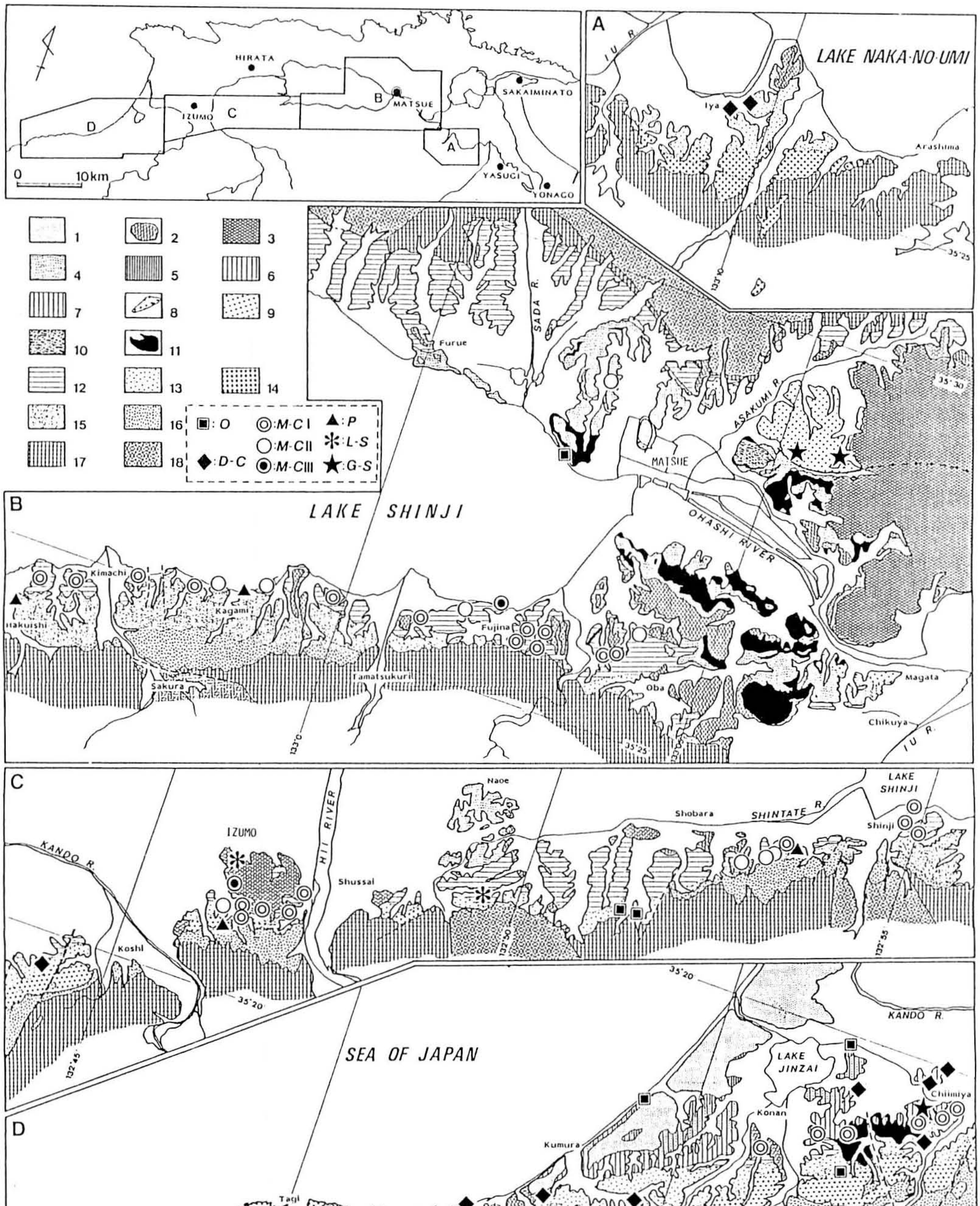
The Izumo Group is subdivided lithologically into the Kimachi, the Fujina and the Matsue Formations in ascending order (Text-fig. 1). The Matsue Formation is correlated with the Hikawa and the Jinzai Formations as noted below.

The Kimachi Formation is mainly composed of tuffaceous sandstones, conglomerates and andesitic pyroclasitics. The lithology of this formation is similar to the andesitic pyroclastics of the Omori Formation, which is the uppermost formation of the Iwami Group. For this reason, the stratigraphic relationship between these formations has been somewhat confused. Ogasawara and Nomura (1980) suggested that the Kimachi and Omori Formations are close in the stratigraphical position, and thought that the Kimachi Formation is covered unconformably by the Fujina Formation. But the present author has observed no outcrops showing clearly unconformable relationships between these formations. On the other hand, a remarkable conglomerate bed which has been considered to be situated at the upper horizon of the Omori Formation unconformably covers andesite lavas and pyroclastics at many localities. Hence the author and his colleague proposed that the base of the Kimachi Formation coincides with the base of that conglomerate (Takayasu and Nakamura, 1984). Mollusks occer at only a few localities in the Kimachi Formation, and the marine vertebrates as *Paleoparadoxia tabatai* and *Carcharodon megalodon* were reported from coarse-grained massive sandstones (Okubo *et al.*, 1980; Hirota, 1979). The total thickness of the formation is about 300 meters.

The Fujina Formation rests conformably upon the Kimachi Formation and consists of massive gray mudstones or fine-grained sandstones exposed along the southern coast of Lake Shinji. Toward the east and the southwest, however, the formation becomes coarser-grained facies. About one hundred molluscan fossil localities are known in the Fujina Formation. The occurrence of molar teeth of *Desmostylus japonicus* was reported by Yoshiwara and Iwasaki (1902) and by the Ichinotani Research Group (1982) and of a metatarsus of *Desmostylus* sp. by Inuzuka *et al.* (1985). Recently, Nomura and Maiya (1984) estimated the geological age of the Formation based on the planktonic foraminifers to be from N.9 to N.11 of Blow's zones. The Formation attains a maximum thickness of more than 400 meters. In the area along the northern coast of Lake Shinji, massive gray siltstones named the Furue Formation crop out, and they are correlated with the Fujina Formation.

Text-fig. 1. Geologic map of the study area and the distribution of molluscan assemblages. Map compiled from Miyajima *et al.* (1972), Ogasawara and Nomura (1980), Takayasu and Nakamura (1984), etc.

1–2; Pleistocene-Holocene, 1. Dune sand, 2. terrace deposits, 3; Upper Miocene-Pliocene, the Wakurayama Andesite, 4–16; Middle Miocene, the Izumo Group, 4. sandstone (the Matsue and Hikawa Formation), 5. sandy mudstone (the Jinzai Formation), 6. alternating beds of sandstone and mudstone (the Jinzai Formation), 7. mudstone (the Jinzai Formation), 8. acidic tuff (the Matsue Formation), 9. basaltic tuff (the Kawatsu Tuff Bed of the Matsue Formation), 10. basaltic conglomerate (the Matsue Formation), 11. basalt lava and dikes (the Matsue and Jinzei Formations), 13. sandstone with gravel (the Fujina Formation), 14. conglomerate (the Fujina Formation), 15. coarse-grained massive sandstone (the Kimachi Formation), 16. tuffaceous sandstone, andesitic pyroclastics and conglomerate (the Kimachi Formation), 17–18; Early-Middle Miocene, the Iwami Group, 17. andesite lava and pyroclastics (the Omori Formation), 18. shale and arkosic sandstone (the Kuri and Kawai Formations). O; the *Ostrea* assemblage, D-C; the *Dosinia-Cardium* assemblage, M–CI; the I-type of the *Macoma-Cultellus* assemblage, M-CII; the II-type of the *Macoma-Cultellus* assemblage, M-CIII; the III-type of the *Macoma-Cultellus* assemblage, P; the *Pecten* assemblage, L-C; the *Lucinoma-Saccella* assemblage, G-S; the *Glycymeris-Saxidomus* assemblage.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✻: L-S
★: G-S
LAKE NAKA-NO-UMI
Iya
Arashima
I U R.
35°25'
133°10'
SADA R.
Furue
ASAKUMI R.
35°30'
MATSUE
OHASHI RIVER
LAKE SHINJI
Kimachi
Hakuishi
Kagami
Sakura
Tamatsukuri
Fujina
Oba
Magata
Chikuya
I U R.
133°0'
35°25'
Naoe
LAKE SHINJI
Shobara
SHINTATE R.
Shinji
IZUMO
HII RIVER
KANDO R.
Shussai
Koshi
35°20'
132°45'
132°50'
132°55'
35°20'
KANDO R.
SEA OF JAPAN
LAKE JINZAI
Chiimiya
Konan
Kumura
Oda
Tagi
Asayama
Hane
132°35'
35°15'
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0 1 2 3 4 5km

The Matsue Formation, which is distributed in the hills around Matsue City, consists of sandstones, alkali basaltic lavas and pyroclastics. It rests unconformably upon the Fujina and Furue Formations. Several of molluscan fossil localities are known in the Matsue Formation. In particular, the Kawatsu Tuff Bed, which is situated stratigraphically near the middle of the formation (Miyajima *et al.,* 1972), yields abundant fossils (Otuka, 1938; Takayasu, 1980). Total thickness of the formation is about 400 meters.

The Hikawa Formation (Ogasawara and Nomura, 1980) which is correlated stratigraphically with the Matsue Formation, is exposed in a limited area around Shussai and Naoe, Hikawa Town. The lithology of the formation is arkosic sandstone and conglomerate. The relationship between the Hikawa and the Fujina Formations is inferred to be unconforamble (Takayasu and Nakamura, 1984). Except for leaves, fossils have not been found. The thickness of the formation exceeds 150 meters.

The Jinzai Formation (Takayasu and Nakamura, op. cit.) is distributed in the hills around Lake Jinzai, southwest of Izumo City. The basal rocks, as in the Matsue Formation, are alkali basaltic lavas and pyroclastics, overlain by fine-grained sandstones, alternating beds of mudstone and sandstone, and sandy mudstones with gravels, in ascending order. The Jinzai and the Fujina Formations are considered to be essentially conformable, though the basalts apparently have an unconformable relationship with the underlying beds. Molluscan fossils are known from many localities. The maximum thickness is more than 400 meters.

These formations mentioned above are covered in places with Quaternary terrace gravels or dune sands.

Description of Molluscan Assemblages

1) The Kimachi Formation

Although molluscan fossils previously have been scarcely reported from the coarse-grained massive sandstone of the typical lithofacies of the Kimachi Formation, several fossil localities are now assigned to this formation, based on the author's stratigraphic ideas. That is, all of the localities assigned to the Omori Formation by Ogasawara and Nomura (1980) are regarded herein as belonging to the Kimachi Formation.

Aside from this, the author recently collected molluscan fossils from a new outcrop at Sai, Shinji Town (Takayasu, 1985). This outcrop is composed of andesitic lapilli tuffs interbedded with muddy tuffs, and contains following molluscs: *Acila submirabilis, Saccella confusa toyomaensis, Kotorapecten kagamianus moniwaensis, Glycymeris* sp., *Modiolus difficilis, Crassostrea gigas, Mercenaria yokoyamai, Cyclocardia* cf. *fujinaensis, Teredo* sp., *Fissidentalium yokoyamai* and *Neverita kiritaniana.* The assemblage shows a mixed composition of muddy and sandy bottom dwellers of the upper sublittoral zone.

Several other localities of molluscan fossils are known sporadically in the uppermost horizon of the Kimachi Formation distributed in the area from Tamatsukuri, Tamayu Town, to Kimachi, Shinji Town. They are composed of medium-grained sandstones, and yield *Kotorapecten kagamianus* (s.s.) and *"Nautilus" izumoensis.* The latter species is now assigned to the genus *Argonauta* (Okubo, 1975a)*. These molluscs indicate a so-called "clean washed" sandy bottom under the influence of oceanic water.

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*Recently, Noda *et al.* (1986) established a new genus *Mizuhobaris* and a new subfamily Mizuhobariidae of Argonautidae for the species.

2) The Fujina Formation

Takayasu and Nakamura (1984) divided the molluscan fauna of the Fujina Formation into the *Ostrea,* the *Dosinia-Cardium,* the *Macoma-Cultellus* and the *Pecten* assemblages. Subsequent investigations made the present author recognize further one assemblage, the *Lucinoma-Saccella* assemblage, and subdivide the *Macoma-Cultellus* assemblage into three types (Text-figs. 2, 3).

Ostrea assemblage: This assemblage is found in muddy sandstone lenses interbedded in the conglomeratic facies of the southwestern area. It is generally regarded as a biostrome of *Crassostrea gigas.* Other species are very scarce. Based on the ecology of living *Crassostrea gigas,* this assemblage may have been distributed in intertidal or slightly greater depths in an outlet or bay head. This assemblage is similar to the *Ostrea* assemblage of the Shiobara-type fauna (Iwasaki, 1970, 1982).

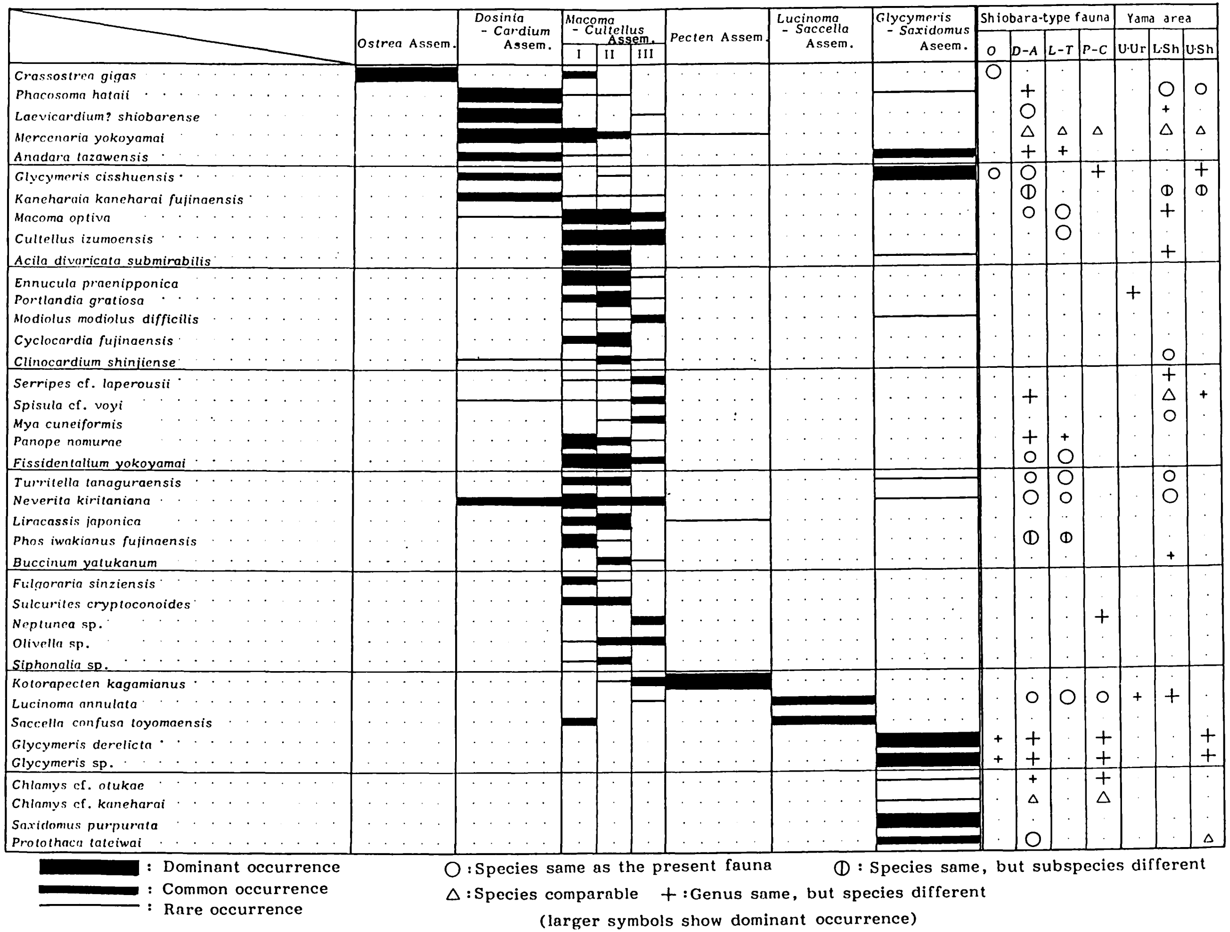
Dosinia-Cardium assemblage: This assemblage is confined to the medium-grained sandy facies occurring in the southwestern area and the vicinity of Iya, Higashi-izumo Town. In this assemblage, *Phacosoma hataii* and *Laevicardium? shiobarense* are representative species, and *Glycymeris cisshuensis, Mercenaria yokoyamai, Anadara tazawensis* and *Kaneharaia kaneharai fujinaensis* are commonly found. These bivalves occur as well preserved but usually disarticulated valves. Most of them are semi-infaunal or shallow infaunal suspension feeders in a subtidal sandy bottom. The *Dosinia-Cardium* assemblage is comparable to the *Dosinia-Anadara* assemblage of the Shiobara-type fauna. In the *Dosinia-Anadara* assemblage, however, *Spisula kurikoma, Panope japonica* and *Phos iwakianus* are also representative species. In the present area, these species occur abundantly in the *Macoma-Cultellus* assemblage rather than in the *Dosinia-Cardium* assemblage.

Macoma-Cultellus assemblage: This assemblage is widely distributed in fine-grained sandstone facies along the southern coast of Lake Shinji. It is composed of various kind of molluscs, and the respresentative species among them are *Macoma optiva* and *Cultellus izumoensis.* It is regarded that the co-occurrence of them is slightly dissimilar at different localities. By reference to the Jaccard coefficient calculated for the similarity of the interspecies association (R-mode), the assemblage is subdivided into the following three types (Text-fig. 3).

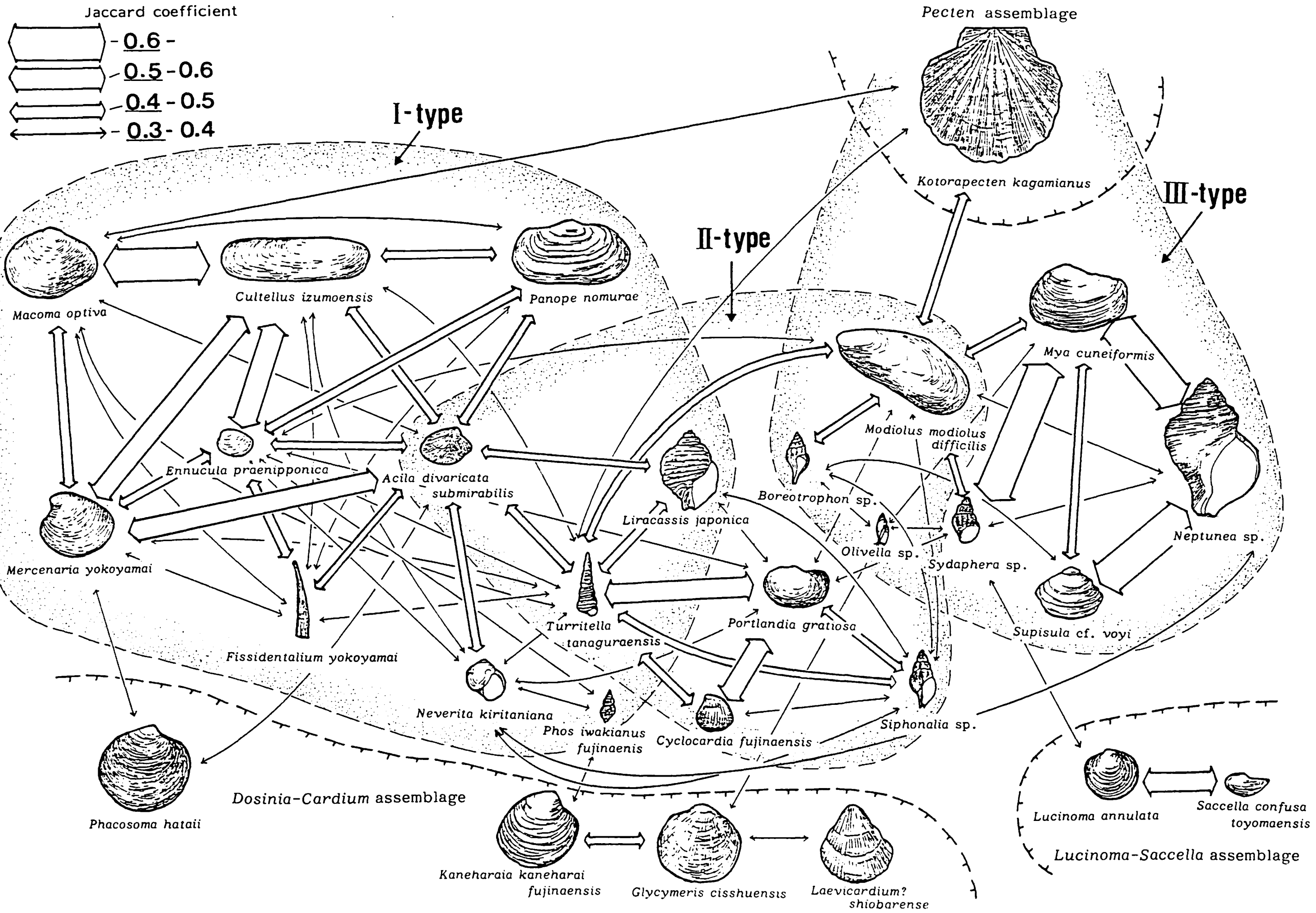
The first type (I-type in abbreviation) is mainly composed of *Panope nomurae* as well as *Macoma optiva* and *Cultellus izumoensis,* which are all deep infaunal bivalves of muddy bottoms. They are associated with semi-infaunal or shallow infaunal species such as *Ennucula praenipponica, Acila divaricata submirabilis, Mercenaria yokoyamai, Fissidentalium yokoyamai, Neverita kiritaniana* and *Phos iwakianus fujinaensis.* They are well preserved in most cases. *Macoma, Cultellus* and *Pannope* in particular are often found almost *in situ.* The I-type is, so to speak, the typical *Macoma-Cultellus* assemblage, and about three quarters of the localities of this assemblage are included in this type.

The second type (II-type) is allied to the I-type, but rather frequently yields *Portlandia gratiosa, Cyclocardia fujinaensis, Clinocardium shinjiense, Liracassis japonica* and *Buccinum yatukanum.* In this type, deep infaunal species are somewhat reduced in proportion and shallowly buried or vagile forms are dominant.

The third type (III-type) is characterized by common occurrence of *Kotorapecten kagamianus* (s.s.), *Modiolus modiolus difficilis, Serripes* cf. *laperousii, Spisula* cf. *voyi, Mya cuneiformis* and *Neptunea* sp. Most of them are less dominant or unimportant species in the former two types. On the other hand, *Mercenaria yokoyamai, Portlandia gratiosa, Cyclocardia fujinaense, Panope nomurae, Turritella tanaguraensis, Liracassis japonica, Sulcurites cryptoco-*



Text-fig. 2. Characteristic species of molluscan assemblages of the Izumo Group. The right columns showing the comparison between the present assemblages and the Shiobara-type fauna (Iwasaki, 1970, 1971) and the fauna of Yama area, Fukushima Prefecture (Ogasawara, *et al.*, 1983).
O; the *Ostrea* assemblage, D-A; the *Dosinia-Anadara* assemblage, L-T; the *Lucinoma-Turritella* assemblage, P-C; the *Pecten-Chlamys* assemblage U•Ur, the upper Urushikubo Formation, L•Sh;the lower Shiotsubo Formation, U.Sh; the upper Shiotsubo Formation.



Text-fig. 3. Diagram showing the similarity of species composition in the *Macoma-Cultellus* assemblage and in the subdivisions of the assmblages.

noides, etc. are scarcely found in this type. Epifaunal and semi-infaunal taxa such as *Kotorapecten* and *Modiolus* seem to be the most dominant in this third type.

In general, it can be said that the species of the *Macoma-Cultellus* assemblage are mostly inhabitants of muddy sand bottoms of the sublittoral zone. The I- and II-types, however, include species such as *Ennucula praenipponica, Portlandia gratiosa* and *Fulgoraria sinziense,* whose modern analogs are living in the outer sublittoral to bathyal zone. Ogasawara and Nomura (1980) already pointed out this fact and mentioned that the molluscan fauna of the Fujina Formation contains elements not only of the Shiobara-type fauna but also of the Yama fauna. The Yama fauna is typically found in the upper Urushikubo Formation, Fukushima Prefecture, and is composed of deep water muddy bottom dwellers (Chinzei and Iwasaki, 1967; Chinzei, 1978; Ogasawara *et al.,* 1983). In the III-type, these Yama-type components are rare. Therefore, with respect to depth, the III-type may represent shallower conditions than the I- and II-types. Other factors, such as the slight differences in substrate, may also have influenced community structure. Additional data, however, are needed to settle this problem.

The *Macoma-Cultellus* assemblage is correlative on the whole with the *Lucinoma-Turritella* assemblage of the Shiobara-type fauna, although *Lucinoma* is not dominant in the former.

Pecten assemblage: This assemblage is characterized by *Kotorapecten kagamianus* (s.s.) and also includes *Liracassis japonica* and *Mercenaria yokayamai* as noteworthy species. *Kotorapecten kagamianus* usually occurs as detached valves, and other species are distinctly worn or broken. The assemblage is sporadically found in the coarse-grained sandstone facies of the lowest horizon of the Fujina Formation. The bottom environment suggested by the paleontological and sedimentological evidence is assumed to be the more turbulent waters of the inner sublittoral zone. This assemblage is ecologically comparable to the *Pecten-Chlamys* assemblage of the Shiobara-type fauna, although there are no common species between them and the species composition of the former is far smaller than that of the latter.

Lucinoma-Saccella assemblage: This assemblage is generally characterized by a small number of *Lucinoma annulata* and *Saccella confusa toyomaensis.* It occurs sporadically in the mudstone facies of the Fujina Formation, and also is found in the same facies of the Furue Formation. Both of these species are deposit feeders that live in muddy bottoms of the outer sublittoral zone. There is no comparable assemblage known from the Shiobara-type fauna, but the assemblage of the upper Urushikubo Formation, composed of *Yoldia, Portlandia, Lucinoma, Limatula,* etc. (Ogasawara, *et al.*, 1983) is considered to be rather similar to the *Lucinoma-Saccella* assemblage of the Fujina Formation.

3) The Matsue and the Jinzai Formations

The classification of the assemblages mentioned above is generally applicable to the Matsue and the Jinzai Formations. The fauna from the Kawatsu Tuff Bed of the Matsue Formation, however, differs from others, and the *Pecten* and the *Lucinoma-Saccella* assemblages are not found in both formations.

Ostrea assemblage: This assemblage is confined to sandy mud facies of the uppermost member of the Jinzai Formation and to mudstone lenses interbedded in medium-grained sandstones of the Matsue Formation.

Dosinia-Cardium assemblage: This assemblage is found in alternating beds of sandstone and mudstone in the middle member of the Jinzai Formation. In general, *Anadara* occurs more commonly there than in the Fujina Formation. Therefore, it can be said that the present assemblage is more similar to the *Dosinia-Anadara* assemblage of the Shiobara-type fauna.

Macoma-Cultellus assemblage: This assemblage is recognized in the fine-grained sandstone facies of the Matsue Formation and in the lower member of the Jinzai Formation. Among the species making up this assemblage in the Fujina Formation, *Cyclocardia fujinaensis, Kotorapecten kagamianus* (s.s.), *Liracassis japonica, Buccinum yatukanum, Fulgoraria sinziense, Sulcurites cryptoconoides,* etc. are not found in the Matsue and the Jinzai Formations. The Matsue Formation also has not yielded *Macoma optiva,* and its assemblage is typified by *Cultellus izumoensis* and *Modiolus modiolus difficilis* and probably correlates with the II- or III-type subassemblage. In the case of the Jinzai Formation, the characteristic species are *Macoma optiva, Cultellus izumoensis, Ennucula praenipponica, Anadara tazawensis* and *Spisula* cf. *voyi.* These species are well preserved and individuals of the first three species are usually found *in situ.* The assemblage of the Jinzai Formation may be essentially correlated with the I-type, though several shallow-water elements of the *Dosinia-Cardium* assemblage are present in it.

Glycymeris-Saxidomus assemblage: This assemblage is confined in the basalt tuff of the Kawatsu Tuff Bed of the Matsue Formation, and an allied assemblage is found in the basaltic pyroclastics at the base of the Jinzai Formation. *Glycymeris cisshuensis, Glycymeris* sp., and *Saxidomus purpurata* are predominant, and *Protothaca tateiwai, Chlamys* cf. *otukae, Chlamys* cf. *kaneharai, Anadara tazawensis, Modiolus modiolus difficilis,* etc. are also present. In this assemblages, deep infaunal species are entirely absent, and most species are inhabitants of coarse-grained sandy bottoms of the subtidal zone. Furthermore, the assemblage includes warm water taxa such as *Trochus* sp., *Geleoastraea* sp., *Ocenebra*? sp., and so on (Takayasu, 1980; Okamoto, 1981a, b). No comparable assemblage is found in the Shiobara-type fauna, but molluscs from the upper Middle Miocene Ginzan Formation, Yamagata Prefecture, including abundant pectinids and warm water gastropods (Nomura and Zinbo, 1937; Saito, 1960), have a close resemblance to the present assemblage.

Discussion of the Transition of Paleoenvironments and Molluscan Faunas

Upon examination of the lithology and molluscan assemblages, the transition of the paleoenvironments and the diversification of molluscan faunas in the Izumo Group are recognized as follows.

At the time of deposition of the Kimachi Formation, andesitic volcanism became less active in comparison with that of the preceding period. The bottoms of upper sublittoral zones may have been composed of tuffaceous sands and muds. Some of the bottom sediments may have been cleanly washed by turbulent currents. The occurrence of *Paleoparadoxia tabatai, Carcharodon megalodon* and *"Nautilus" izumoensis* is consistent with these environments.

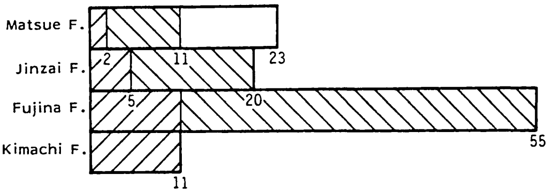
The molluscan species and genera known from the Kimachi Formation, as already pointed out by Ogasawara and Nomura (1980), are generally comparable to those of the Kadonosawa-type fauna, though many important species of the latter indicating tropical or subtropical environments are absent in the former. On the other hand, it is also true that several species not known in the Kadonosawa-type fauna, such as *Saccella confusa toyomaensis, Modiolus modiolus difficilis, Mercenaria yokoyamai* and *Cyclocardia fujinaensis* occur in the Kimachi Formation. Species allied to them are still living in Japanese waters. Therefore, it is not necessary to think that the Kimachi Formation contains a fauna as warm as that of the early Middle

Miocene. There may have been conciderable influence from cold water that reached southward to the southern Japan Sea coast.

Molluscs of the Kimachi Formation are also found in the Fujina Formation, either as identical species or as closely allied species.

At the beginning of deposition of the Fujina Formation, the bottom environments seemed to remain almost unchanged from those of the former period, except that volcanism ceased. The *Pecten* assemblage must have lived in a coarse-grained sandy bottom of the upper sublittoral zone, facing an open sea.

Thereafter, the bottom material of the main part of the area was rapidly replaced by fine-grained sands and muds. Besides, gravelly bottoms of intertidal or slightly deeper deltaic facies appeared to the east and southwest. The transitional zone from the gravelly to the fine-grained sandy bottoms was composed of medium-grained sands. This diversity of bottom environments must have allowed various species of benthic molluscs to immigrate to this area. At present, genera of molluscs known from the Fujina Formation number 55, and this is the overwhelmingly majority known from the Izumo Group (Text-fig. 4).



Text-fig. 4. Diagram showing the successive change in the number of genera.

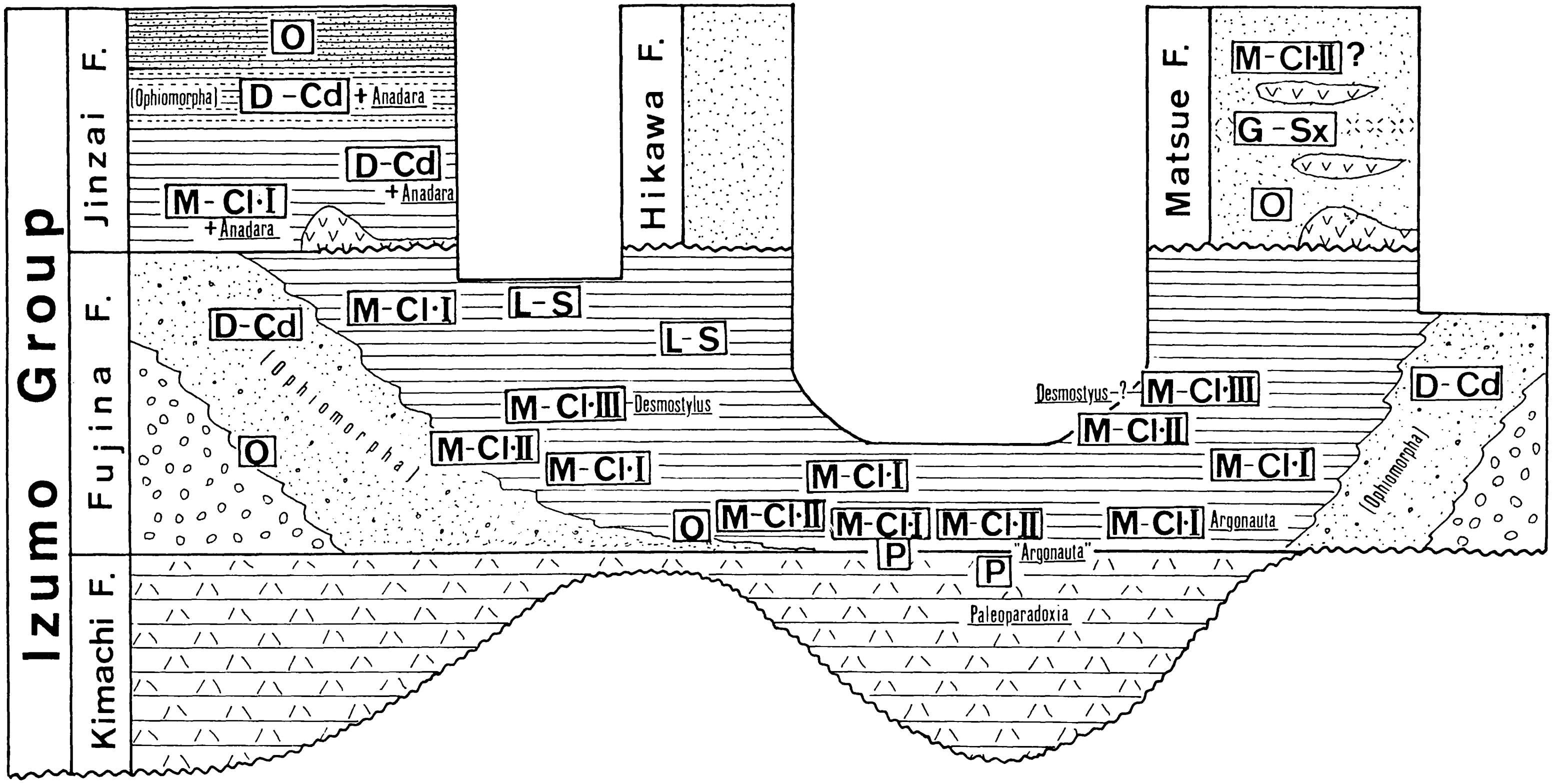
The distribution of molluscan assemblage is clearly shown as being in accordance with the differences of the bottom condition (Text-fig. 5).

In the muddy sand bottom that locally occurred within the deltaic outlet, the *Ostrea* assemblage was distributed sporadically. Adjoining it, the *Dosinia-Cardium* assemblage evidently flourished in the medium-grained sandy bottom of the subtidal zone. The characteristic components of this assemblage, such as *"Dosinia"*, *Anadara* and other genera, are regarded as the descendants of invaders from the Indo-Pacific region in the early Middle Miocene (Chinzei, 1978), and apparent cold water taxa, except for *Spisula,* are scarcely included in it.

The deeper and fine-grained facies of the Fujina Formation is mostly occupied by the *Macoma-Cultellus* assemblage. The stratigraphical distribution of the three type subassemblages is poorly known because of the homogeneous lithology. General indications are that the I- and II-types are distributed in the lower horizon of the formation and III-type is in the middle horizon of it.

Though the representative species of the assemblage, such as *Macoma optiva, Cultellus izumoensis* and others, are considered to be remains of a warmer stage in the early Middle Miocene, apparent cold water elements, such as *Serripes, Spisula, Mya, Buccimum,* and *Neptunea,* also are present. Especially in the III-type, the cold water elements are included characteristically. With reference to this, it is interesting that the locality of *Desmostylus* are correlated with the III-type subassemblage, for this extinct marine vertebrate is thought to have immigrated to Japanese seas during a cooler interval (Itoigawa, 1984).

On the other hand, the I- and II-types of the lower horizon tend to contain warm water taxa rather frequently, including *Liracassis japonica, Sulcurites cryptoconoides,* etc. Furthermore, planktonic or necroplanktonic warm water cephalopods, *Argonauta tokunagai* and *"Nautilus" izumoensis,* and known from the I- and II-types of the lower horizon, respectively.



L-S; the *Lucinoma-Saccella* assemblage

D-Cd; the *Dosinia-Cardium* assemblage

O; the *Ostrea* assemblage

P; the *Pecten* assemblage

G-Sx; the *Glycymeris-Saxidomus* assemblage

M-Cl; the *Macoma-Cultellus* assemblage
- I-type
- II-type
- III-type

Text-fig. 5. Schematic diagram showing the stratigraphic distribution of molluscan assemblages in relation to lithological change.

Therefore, it can be said that the warm current had streamed upon occasion into the present area until the early stage of deposition of the formation, and the cold current with boreal marine fauna advanced apparently at the middle stage of it.

As for the upper horizon of the formation, the information concerning paleoenvironments is insufficient. However, from the sporadical distribution of the *Lucinoma-Saccella* assemblage, muddy bottoms of the deeper sea may have been widespread, presumably opening toward the sedimentary basin of the Furue Formation.

After that, the area was probably changed into an enbayment by uplift of the Shimane Peninsula. The local unconformity between the Fujina Formation and the overlaying beds is considered to have resulted from this movement. The opening of the bay is assumed to face westward, based on the lithology and fossil assemblages of the Matsue and the Jinzai Formations.

In the Jinzai Formation, more than half of the genera of the Fujina assemblages are absent and no new genera took their place. As already mentioned, several important components of the *Macoma-Cultellus* assemblage in the previous stage are not found in the same assemblage of the lower part of the Formation. The middle part of the Formation is represented by the shallow facies of the simplified *Dosinia-Cardium* assemblage and the sea was terminated in the brackish facies of the *Ostrea* assemblage.

On the other hand, in the Matsue Formation, only one fifth of the genera of the Fujina Formation remains and 12 genera are newly added. The newcomers, including warm water elements, are all found in the *Glycymeris-Saxidomus* assemblage of the Kawatsu Tuff Bed. Several components of the assemblage, such as *Anadara, Saxidomus, Protothaca,* etc., are regarded as the dwellers of larger embayments (Oyama, 1967). Furthermore, fossil fish and prawns which are thought to have lived in warm water brackish embayments (Sato, 1974; Okubo, 1975b) are known to occur from the tuffaceous mudstone correlated with the Kawatsu Tuff Bed. Judging from these facts, it is hard to avoid the inference that the warm current inflow became strong once more during deposition of the Kawatsu Tuff Bed (Okamoto, 1981a, b). Such a phase is known neither in the Jinzai Formation nor in comparable formations in the southwestern part of the Japan Sea coast. The geohistorical meanings of this phase is not yet known.

The *Macoma-Cultellus* assemblage and the *Ostrea* assemblage found from sandstone beds of the Matsue Formation are thought to represent environments that temporarily and/or locally appeared in the embayment.

Summary

Although some details are left pending, the discussion is summarized as follows:

(1) The molluscan fauna of the Izumo Group is divided into the following six assemblages; the *Ostrea,* the *Dosinia-Cardium,* the *Macoma-Cultellus,* the *Pecten,* the *Lucinoma-Saccella* and the *Glycymeris-Saxidomus* assemblages. The *Macoma-Cultellus* assemblage is subdivided into three subassemblages.

(2) The time and space distribution of the assemblages relates to the transition and diversity of bottom environments.

(3) In the assemblage from the Kimachi Formation, taxa of temperate or cold waters rather predominate, but warmer water taxa that dominated during the early Middle Miocene

are also present.

(4) The bottom environment was rapidly diversified at the beginning of the deposition of the Fujina Formation. Consequently the assemblage was diversified and enriched by various benthic molluscs.

(5) The *Macoma-Cultellus* assemblage especially flourished in the fine-grained sandy bottom of the sublittoral zone during Fujina Formation deposition. The immigration of typical cold-water elements is seen in this aseemblage within the middle horizon of the formation.

(6) The Matsue and Jinzai Formations are assumed to have been deposited in a large bay during the succeeding regressive stage. Except for the deeper and offshore assemblages, most assemblages remained the same, though there was some loss of species. However, the *Glycymeris-Saxidomus* assemblage with warm water elements appeared during deposition of the Matsue Formation.

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AGE AND CHARACTERISTICS OF THE SO-CALLED "ATSUNAI-TOGESHITA FAUNA" IN HOKKAIDO

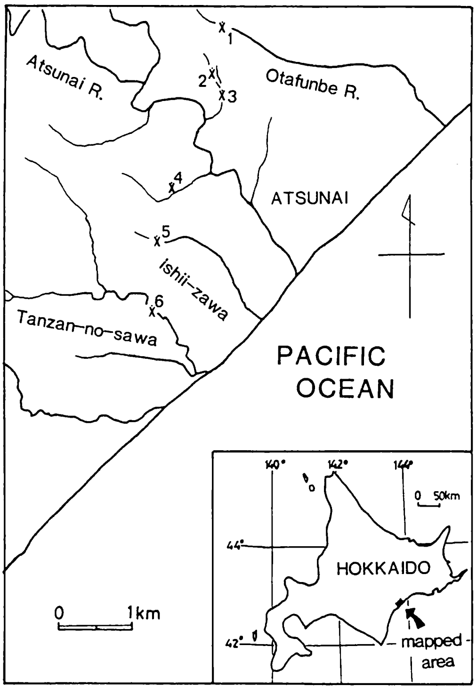
By

Kazutaka AMANO

Introduction

The "Atsunai-Togeshita fauna" is well known as a representative fauna of the Late Miocene Wakkanai stage in Hokkaido (Uozumi, 1962). Recently, it became clear that the "Togeshita fauna" in the Rumoi district should be subdivided into two different faunas based on the specific composition and fossil horizons. The molluscan fauna from the upper part of the Togeshita Formation includes many more cold water and modern species than does the lower fauna. These molluscan faunas have been named the Upper and Lower Togeshita faunas (Amano, 1983). Therefore, it is necessary to reexamine the age and characteristics of these two faunas. Moreover, it remains to be decided whether the "Atsunai fauna" in the Kushiro district of Hokkaido should be correlated with the Upper or the Lower Togeshita.

Before going on to a discussion of the "Atsunai-Togeshita fauna", the usage of the term "fauna" must be clear. The term of "fossil fauna" was first used in Japan by Otuka (1939). He used the term "fauna" with the following meanings. Namely, a fossil fauna includes all species which live in any confined area as well as any age interval. Various interpretations of this "confined area" have caused differences in the use of the term "fauna" by many authors. In this paper, the author uses the term "fauna" to include all species in one biogeographic unit developed in a broad area.



Text-fig. 1. Fossil localities of the Ishiizawa Formation in Kushiro district, Hokkaido.

On the "Atsunai fauna"

The "Atsunai fauna" occurs in the Ishiizawa Formation (Akiba *et al.,* 1982) in the Atsunai area of the Kushiro district. Thirty three species of mollusks were identified from six localities in the Ishiizawa Formation (Text-fig. 1). These molluscan fossils comprise twenty five species of bivalves, seven species of gastropods and one species of scaphopod (Table 1). Among these species, the following are common in the Lower Togeshita fauna, but are rarely present in the Upper Togeshita: *Glycymeris idensis, Dosinia* cf. *kaneharai rumoiensis, Mercenaria protostimpsoni* and

Table 1 Molluscan fossils from the Ishiizawa Formation. Number in the list shows individuals.

Species \ Localities	1	2	3	4	5	6
Anadara (*Andara*) *hokkaidoensis* Noda					29	
A. (*A.*) sp. indet.						1
Glycymeris (*Glycymeris*) *idensis* Kanno	17	28		249	198	25
Modiolus cf. *lagunanus* Loel and Corey						1
Mizuhopecten ? sp. indet.					1	
Limatula (*Limatula*) cf. *vladivostokensis* (Scarlato)					1	
Lucinoma cf. *annulata* (Reeve)					1	
Clinocardium sp. indet.		1		1		1
Dosinia (*Phacosoma*) *ettyuensis* Hatai and Nishiyama					4	
D. (*P.*) cf. *owadaensis* Amano	2			8		
D. (*Kaneharaia*) cf. *kaneharai rumoiensis* Amano					4	
D. (*K.*) sp. indet.						2
Mercenaria yiizukai (Kanehara)					15	2
M. protostimpsoni Amano		5				3
M. sp.				14		
Spisula (*Pseudocardium*) *haboroensis* (Yokoyama)	8		3		2	19
S. sp.			1	4		
Peronidia protovenulosa (Nomura)					2	
Macoma (*Macoma*) cf. *incongrua* (v. Martens)						1
M. ? sp. indet.					1	
Solen cf. *krusensterni* Schrenck					1	
S. sp. indet.				4		
Cryptomya? sp. indet.					1	
Panope japonica (Adams)				1	3	
Pandora sp. indet.					1	
Minolia? sp. indet.			1	1		
Crepidula jimboana Yokoyama					1	
C. cf. *grandis* Middendorff	1					
C. sp. indet.				1		
Cryptonatica sp. indet.				2	1	1
Naticidae gen. et sp. indet.	1					1
Nucella cf. *tokudai* (Yokoyama)						1
Nassariidae gen. et sp. indet.					1	
Inquisitor? sp.					2	
Antalis sp.					4	

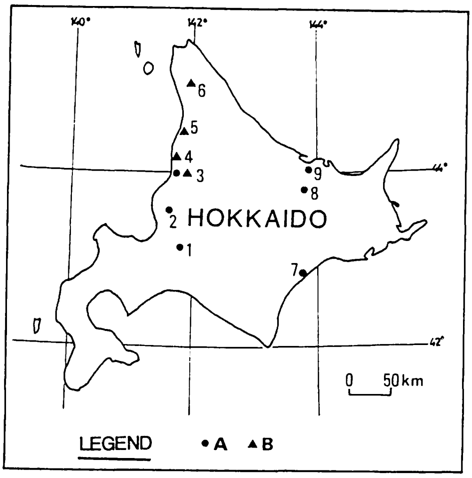
Crepidula jimboana. Moreover, the following species are common to both the Lower and Upper Togeshita faunas: *Anadara hokkaidoensis, Mercenaria yiizukai, Peronidia protovenulosa, Solen* cf. *krusenterni* and *Panope japonica.*

Stratigraphically, the Ishiizawa Formation unconformably overlies the Tokomuro Formation that yields two characteristic species of the early Middle Miocene Sankebetsu-Chikubetsu fauna (Kanno and Matsuno, 1960), *Turritella shataii* and *Venericardia abeshinaiensis.* This stratigraphic position of the Ishiizawa Formation is similar to that of the lower part of the Togeshita.

Therefore, the Atsunai fauna is correlated with the Lower Togeshita on the basis of its faunal composition and stratigraphic position.

Age of the Lower Togeshita-Atsunai fauna

The Lower Togeshita-Atsunai fauna is defined as follows. This fauna is represented by mollusks from the lower part of the Togeshita Formation in the Rumoi district, the Hattari in the Kabato Massif, the Kuriyama Conglomerate of Maoi Hill, the Ishiizawa Formation in the Kushiro district, and the Ainonai and Chirai formations in the Abashiri district (Fig. 2). These formations yield the following characteristic species: *Ennucula haboroensis, Anadara hokkaidoensis, Glycymeris idensis, Lithophaga chikubetsuensis, Chlamys kaneharai, Clinocardium decoratum, Serripes japonica, "Dinocardium" shiobarense, Trapezium cheonbugensis, "Pitar" hokkaidoensis, Dosinia kaneharai rumoiensis, Protothaca nodai, Mercenaria yiizukai, Spisula haboroensis, S. ezodensata, S. voyi onnechiuria, Macoma incongrua, Panomya simotomensis, Mya cuneiformis, Periploma pulchella, Turritella fortilirata, Crepidula jimboana, Nassarius kannoi, Olivella koishii* and *Neptunea modesta.*



Text-fig. 2. Map showing the distribution of the Lower Togeshita-Atsunai and the Upper Togeshita faunas in Hokkaido. A. Lower Togeshita-Atunai fauna, B. Upper Togeshita fauna., 1. Kuriyama Conglomerate, 2. Hattari Formation, 3. Togeshita Formation, 4. Onishika Formation, 5. Chepotsunai Formation, 6. Wakkanai Formation, 7. Ishiizawa Formation, 8. Ainonai Formation, 9. Chirai Formation.

The above listed species includes two groups; (1) characteristic species of the Middle to Late Miocene Shiobara type fauna (Chinzei, 1963; Iwasaki, 1970, 1981), and/or related species, (2) relict species of the early Middle Miocene Sankebetsu-Chikubetsu fauna (Kanno and Matsuno, 1960). The first specific group consists of *Chlamys kaneharai, "Dinocardium" shiobarense, Dosinia kaneharai rumoiensis* and *Protothaca nodai.* The second specific group is composed of *Ennucula haboroensis, Lithophaga chikubetsuensis, Serripes japonica, Spisula haboroensis, S. ezodensata, S. voyi onnechiuria* and *Periploma pulchella.* It is noteworthy that many Middle Miocene species are included in this fauna.

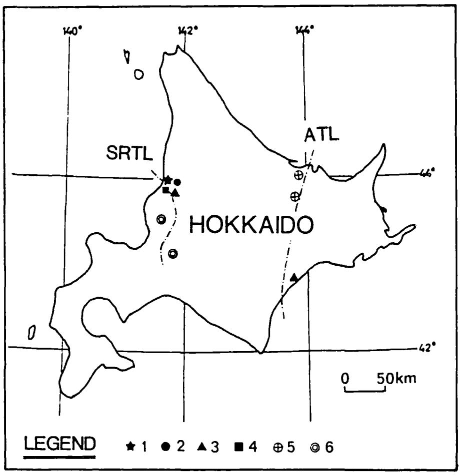
In the Otodo district, just north of Rumoi, the Onishika Formation conformably overlying the Kotanbetsu Formation yields the Upper Togeshita fauna (Amano, 1983). The Onishika Formation consists of conglomerate and fine- to medium-grained sandstone (110m) and tuff breccia (25m), whereas the upper part of the Togeshita Formation is composed of massive fine-grained sandstone (150m). Therefore, the Onishika Formation is correlated with the upper part of the Togeshita, based on its fauna, lithofacies and thickness. As mentioned above, the lower part of the Togeshita is correlated with the Kotanbetsu Formation that was deposited during the Middle Miocene Kawabata stage.

From the above data, the Lower Togeshita-Atsunai fauna is assigned not to the Late Miocene Wakkanai stage, but to the Middle Miocene Kawabata stage.

Characteristics of the Lower Togeshita-Atsunai fauna

The Lower Togeshita-Atsunai fauna has a characteristic distribution and faunal composition.

The distribution of this fauna is confined to the Shintotsugawa-Rumoi tectonic line (Agatsuma, 1962) and to the Abashiri tectonic line (Kimura, 1981), as shown in Fig. 3.



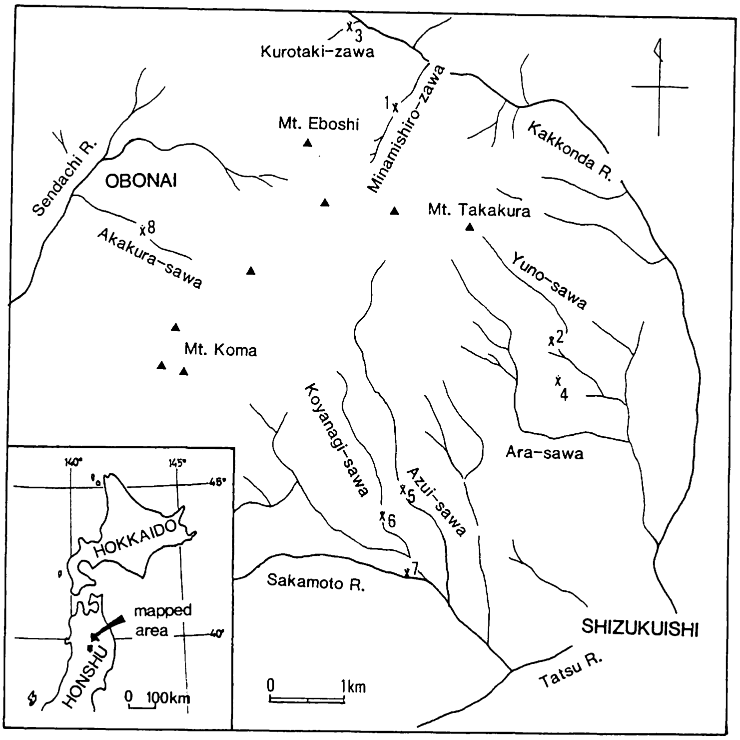
Text-fig. 3. Distribution of the assemblages of the Lower Togeshita-Atsunai fauna. ATL = Abashiri Tectonic Line, SRTL = Shintotsugawa-Rumoi Tectonic Line. 1. *Corbicula-Crassostrea* assemblage, 2. *"Pitar"-Anadara* Assemblage, 3. *Mercenaria-Clinocardium* and *Glycymeris-Mercenaria* assemblages, 4. *Mya-Turritella* assemblage, 5. *Patinopecten-Chlamys* assemblage, 6. Mixed assemblage.

This fauna is composed of the *Corbicula-Crassostrea, "Pitar"-Anadara, Mercenaria-Clinocardium, Glycymeris-Mercenaria, Mya-Turritella, Patinopecten-Chlamys* assemblages and a mixed assemblage (Fig. 3). In the Rumoi district, the *Corbicula-Crassostrea, "Pitar"-Anadara, Mercenaria-Clinocardium* and *Mya-Turritella* assemblages are recognized in and around Paleo-Togeshita Bay (Amano, 1983). From the Hattari Formation and the Kuriyama Conglomerate, some shallow marine species occur with rather deep water species (Kakimi and Uemura, 1958; Sasa *et al.*, 1964). In the Kushiro district, the *Glycymeris-Mercenaria* assemblage is recognized in the Ishiizawa Formation. As shown in Table 1, this assemblage is chiefly composed of *Glycymeris idensis, Mercenaria yiizukai, M. protostimpsoni* and *Spisula haboroensis. Clinocardium* sp., *Peronidia protovenulosa, Solen* cf. *krusensterni*, and *Panope japonica* are sometimes associated with the above dominant species. This composition of the *Glycymeris-Mercenaria* assemblage resembles that of the *Mercenaria-Clinocardium* assemblage in the Rumoi district. In the Abashiri district, the Chirai and Ainonai formations yield the following species: namely, *Chlamys kaneharai, C. cosibensis hanzawae, Miyagipecten saromensis, Swiftopecten swiftii, Mizuhopecten matsumoriensis* and *M. kitamiensis* (Hashimoto and Kanno, 1958; Uozumi *et al.*, 1966). This specific composition corresponds to that of the *Patinopecten-Chlamys* assemblage of Chinzei and Iwasaki (1967).

The Lower Togeshita-Atsunai fauna mainly consists of cold water species, but it includes some warm water dwellers. For example, in the Rumoi district, *Crassostrea gigas, Lithophaga chikubetsuensis* and *Trapezium cheonbugensis* are recognized. The latter two species in particular are relict forms of early Middle Miocene faunas.

Lastly, it is necessary to examine the relationship between the Lower Togeshita-Atsunai and the Shiobara type faunas, because Iwasaki (1981) stated that the Shiobara type fauna gradually changes northward into the "Atsunai-Togeshita fauna".

Molluscan fossils from the Yamatsuda Formation in the Shizukuishi district are the northernmost occurrence of the Shiobara type fauna. From this formation, twenty four species of mollusks were obtained (Fig. 4, Table 2), and four assemblages are recognized: the *Crass-*



Text-fig. 4. Fossil localities of the Yamatsuda Formation in Shizukuishi district, Iwate Prefecture.

ostrea, *Anadara-Pseudamiantis*, *Anadara-Dosinia* and *Anadara-Macoma* assemblages. The composition of the first two assemblages resembles that of the *Corbicula-Crassostrea* and *"Pitar"-Anadara* assemblages in the Rumoi district. The generic composition of mollusks from the Yamatsuda Formation is very similar to that of the Lower Togeshita-Atsunai fauna. Some species common or related to the Lower Togeshita-Atsunai fauna also occur in the Yamatsuda Formation. But, the mollusks from the Yamatsuda Formation include many more individuals of *"Dinocardium" shiobarense* and *Dosinia kaneharai kaneharai* than does the Lower Togeshita-Atsunai fauna. Moreover, it slightly differs from the latter by including some warm water gastropods such as *Neverita kiritaniana* and *Phos* cf. *iwakianus*. For the above mentioned reasons, the author agrees with the opinion of Iwasaki (1981) that there is a gradual northward change from the Shiobara type fauna to the Lower Togeshita-Atsunai fauna. The Lower Togeshita-Atsunai fauna gradually changes southward into the Shiobara type fauna by increasing the number of some temperate and warm water species.

Age of the Upper Togeshita fauna

The Upper Togeshita fauna is defined as follows. This fauna is represented by mollusks from the upper part of the Togeshita Formation in the Rumoi district, the Onishika Formation in the Otodo district, the Chepotsunai in Tomamae and the lower part of the Wakkanai Formation in the Teshio district (Fig. 2). This fauna is characterized by the following species: *Anadara hokkaidoensis*, *Mizuhopecten togeshitensis*, *Chlamys* cf. *setsukoae*, *Clinocardium decoratum*,

Table 2 Molluscan fossils from the Yamatsuda Formation in Shizukuishi district, Iwate Prefecture. Number in the list shows individuals.

Species / Assemblages	C	AP	AD					AM
Localities	1	2	3	4	5	6	7	8
Crassostrea gigas (Thunberg)	4	1						
Anadara (*Anadara*) *arasawaensis* Noda		35	2		4	2		
Pseudamiantis aff. *tauyensis* (Yokoyama)		14	1	1				
Mya? sp. indet.		1		1				
Cancellaria hukusimana Nomura and Hatai		2						
Olivella sp. indet.		1						
Anadara (*Anadara*) cf. *ogawai* Makiyama			1					
A. (*A.*) sp. indet.				5		6	1	4
Crassostrea sp. indet.				1				1
Lucinoma annulata Reeve)				2				
"Dinocardium" shiobarense (Yokoyama)			2	15	2	1	3	1
Clinocardium (*Clinocardium*) *decoratum* (Grewingk)				1				
Dosinia (*Phacosoma*) *ettyuensis* Hatai and Nishiyama					3		1	
D. (*P.*) sp. indet.			1	1				
D. (*Kaneharaia*) *kaneharai kaneharai* Yokoyama				12	4			
Macoma (*Macoma*) sp. indet.				5				
Mya (*Mya*) *cuneiformis* (Böhm)				2				
Panope japonica (Adams)				7				
Neverita (*Glossaurax*) *kiritaniana* (Yokoyama)				3				
Cancellaria cf. *rara* Aoki				1				
Clinocardium (*Ciliatocardium*) cf. *ciliatum* (Fabricius)								1
Serripes groenlandicus (Bruguiere)			1					1
Macoma (*Macoma*) *tokyoensis* Makiyama			1					4
Phos cf. *iwakianus* (Yokoyama)								1

Abbreviations of the assemblage name; C = *Crassostrea*, AP = *Anadara-Pseudamiantis*, AD = *Anadara-Dosinia*, AM = *Anadara-Macoma*.

Serripes groenlandicus, Dosinia owadaensis, Mercenaria yiizukai, Peronidia protovenulosa, Nuttallia commoda, Mya cuneiformis, Turritella fortilirata, Crepidula grandis, Boreotrophon solitarius, Mitrella bicincta, Neptunea cf. *otukai, Admete couthouyi, Cancellaria* cf. *hukusimana, Rectiplanes sanctiioannis, Suavodrillia oyamai, Propebela candida* and *Oenopota kagana* (Amano, 1983). Among these species, many dominant forms are confined to Miocene strata and/or range from Miocene to Pliocene: *Anadara hokkaidoensis, Clinocardium decoratum, Mercenaria yiizukai, Peronidia protovenulosa, Mya cuneiformis* and *Cancellaria* cf. *hukusimana*. On the other hand, some Plio-Pleistocene forms are included in this fauna: *Chlamys* cf. *setsukoae, Boreotrophon solitarius, Neptunea* cf. *otukai, Suavodrillia oyamai* and *Oenopota kagana*. In addition, some other species range from Pliocene to Recent: *Admete couthouyi, Rectiplanes sanctiioannis* and *Propebela candida*.

The Upper Togeshita fauna includes many more recent species than the Lower Togeshita-Atsunai fauna and does not contain any species characteristic of the Shiobara type fauna. Moreover, in the Rumoi district, the upper part of the Togeshita Formation is partly overlain by the Mashike Formation with conformity and partly interfingers with the latter. The Mashike yields a few Miocene species such as *Yoldia sagittaria, Portlandia ovata* and *Neptunea modesta* (Amano, 1983).

Therefore, the Upper Togeshita fauna is assigned to the Late Miocene Wakkanai stage.

Characteristics of the Upper Togeshita fauna

The Upper Togeshita fauna occurs in Northwestern Hokkaido. As stated before, this fauna is recognized from the upper part of the Togeshita Formation, the Onishika and Chepotsunai formations and the lower part of the Wakkanai Formation.

The Upper Togeshita fauna is mostly composed of cold water species. Many cold water genera newly appeared in the Upper Togeshita, compared with the Lower Togeshita-Atsunai fauna: *Buccinum, Admete, Rectiplanes, Suavodrillia, Propebela,* and *Oenopota.* On the other hand, some warm water forms such as *Lithophaga, Crassostrea* and *Trapezium* do not appear in the Upper Togeshita fauna.

The faunal composition of the Upper Togeshita resembles the molluscan faunas from the Etolon Formation in Kamchatka and the lowest part of the Maruyama Formation in Sakhalin (Amano, 1983). The Upper Togeshita fauna includes some mollusks in common with, or closely related to, species of the Pliocene Sannohe Group (Chinzei, 1959, 1961; Masuda, 1962) in Iwate Prefecture: *Chlamys* cf. *setsukoae, Lucinoma acutilineata, Peronidia protovenulosa, Turritella fortilirata, Neptunea* cf. *otukai, Suavodrillia oyamai* and *Propebela candida.* It also contains some species in common with the Plio-Pleistocene Omma-Manganzian fauna of the Japan Sea Borderland (Otuka, 1939; Kaseno and Matsuura, 1965; Ogasawara, 1977; Masuda and Ogasawara, 1981): *Spisula grayana, Solen krusensterni, Mya cuneiformis, Rectiplanes sanctiioannis, Propebela candida* and *Oenopota kagana.* However, the Upper Togeshita fauna differs from the Sannohe and Omma-Manganzian faunas as follows. The dominant genera of the latter two faunas are descended from ancestral genera of the Upper Togeshita fauna, such as *Anadara, Mizuhopecten, Dosinia* and *Mercenaria.* Moreover, the Upper Togeshita does not include some characteristic genera of Pliocene and Pleistocene faunas, such as *Fortipecten, Pseudamiantis* and *Callithaca.*

From the above characteristics, the Upper Togeshita fauna is considered as an ancestral type of the Pliocene Sannohe and Omma-Manganzian faunas.

Redescription on two species in the Lower Togeshita-Atsunai fauna

Genus *Glycymeris* Da Costa, 1778
Subgenus *Glycymeris* s.s.
Glycymeris (*Glycymeris*) *idensis* Kanno, 1956
Pl. 1, figs. 1a–b, 2a–b, 4

Glycymeris idensis Kanno, 1956, p. 267–268, pl. 38, figs. 1–5; Masuda and Takegawa, 1965, pl. 1, figs. 2–3; Mizuno, Sumi and Yamaguchi, 1969, pl. 28, fig. 10.
Glycymeris (*Glycymeris*) *idensis* Kanno, Amano, 1983, p. 41, pl. 2, fig. 7.

Description:

Seventy specimens from the Ishiizawa Formation were examined. Shell small in size, equilateral, equivalve, moderately inflated. Test rather thick. Beak situated at central part of shell length. Surface ornamented with about thirty shallow radial grooves, obsolete at both ends of shell, crossed by fine growth lines. Chevron wide and with six or seven inverted V-shaped grooves. Anterior adductor scar circular; posterior one subtriangular. Inner margin deeply crenulated. Number of crenulations between anterior and posterior adductor scars 20–25 (most commonly 22). Morphological variation distinct, but roughly subdivided into the following two types.

Type 1 (pl. 1, figs. 1a–b, 4): Shell rather inflated, subcircular in shape. Both anterior and posterior dorsal margins nearly straight; ventral margin well rounded. Anterior end subangular while posterior one rounded. Beak not so produced and pointed.

Type 2 (Pl. 1, figs. 2a–b): Shell moderately inflated, longitudinally ovate. Both anterior and posterior dorsal margins broadly arcuated; ventral margin well rounded. Anterior end well rounded and posterior one also rounded. Beak not so produced and pointed.

Of these two types, the shell shape of type 1 is common and that of type 2 is rare.

Remarks:

The Ishiizawa specimens are identified with *Glycymeris idensis* Kanno because of their shell shape, thick test, equal number of radial grooves and nearly equal number of crenulations between the adductor scars.

The present species is closely allied to *Glycymeris yessoensis* (Sowerby), living in boreal waters around Japan and Sakhalin, in its shell shape and nearly equal number of crenulations between the adductor scars. However, the former differs from the latter by having a smaller and heavier test, no feeble striation between radial grooves on the exterior surface, and by having some elongate specimens belonging to type 2, described above.

Measurements (*in mm*):

Specimens	Length	Height	Thickness	Nc*
JUE no. 15028-3	–	–	–	21
" 15028-4	28.6	26.7	–	22
JUE no. 15028-5	–	–	–	25
" 15028-6	–	–	–	20
" 15028-7	29.3	28.2	–	23
" 15028-9	–	–	–	22
" 15028-10	–	–	–	22
" 15028-11	–	–	–	21
" 15028-13	–	–	–	23
" 15028-14	29.4	25.4	–	22
" 15028-15	–	–	–	21
" 15028-16	–	–	–	23
" 15028-18	–	–	–	22
" 15028-19	33.8	32.0	–	–
" 15028-20	30.5	28.2	–	–
" 15028-21	36.8	35.8	–	–
" 15028-22	32.6	31.0	14.8	–
" 15028-23	31.8	29.8	–	–
" 15028-24	28.3	25.3	–	–
" 15028-25	33.8	31.0	16.0	–
" 15028-26	36.4	36.5	20.8	–
" 15028-27	35.2	37.3	21.4	–
" 15028-28	33.4	34.4	–	–
" 15028-29	33.3	32.5	18.0	–
" 15028-30	30.0	29.3	19.1	–
" 15028-31	34.4	32.4	22.0	–
" 15028-32	29.4	29.0	17.3	–
" 15028-33	38.0	38.1	21.5	–
" 15028-34	27.4	25.1	13.5	–

* Nc = number of marginal crenulations between adductor scars

Specimens	Length	Height	Thickness	Nc
JUE no. 15028-35	26.1	27.4	–	–
” 14028-36	31.0	30.0	–	–
” 15028-37	29.4	26.8	–	–
” 15028-38	28.8	28.1	–	–
” 15028-39	28.1	30.5	–	–
” 15028-40	29.5	28.3	–	–
” 15028-41	36.4	34.4	–	–
” 15028-42	34.7	33.0	–	–
” 15028-43	25.0	22.2	–	–
” 15028-44	34.0	36.0	21.5	–
” 15028-45	29.4	30.0	–	–
” 14028-46	28.9	30.0	–	–
” 15028-47	31.3	29.0	–	–
” 15028-48	32.5	30.0	–	–
” 15028-49	30.3	28.3	–	–
” 15028-50	26.0	28.6	–	–
” 15028-51	30.0	28.7	–	–
” 15029-2	–	–	–	20
” 15029-4	35.7	33.6	–	21
” 15029-7	–	–	–	23
” 15029-8	35.0	34.9	–	23
” 15029-11	34.3	34.4	–	22
” 15029-12	31.0	30.6	–	23
” 15029-13	–	–	–	22
” 15029-14	–	–	–	23
” 15029-15	33.5	32.8	–	22
” 15029-27	–	–	–	22
” 15029-29	–	–	–	24
” 15029-30	–	–	–	22
” 15029-31	32.7	33.0	18.2	–
” 15029-32	33.1	33.2	17.7	–
” 15029-33	32.0	30.7	–	–
” 15029-34	35.8	35.9	–	–
” 15029-35	34.0	33.6	–	–
” 15029-36	32.0	30.9	–	–
” 15029-37	27.5	27.4	–	–
” 15029-38	29.8	27.8	–	–
” 15029-39	30.4	32.4	–	–

Distribution: Miocene Yoshigasawa, Kanagase, Ishiizawa and Togeshita formations

Genus *Spisula* Gray, 1927
Subgenus *Pseudocardium* Gabb, 1866
Spisula (*Pseudocardium*) *haboroensis* (Yokoyama, 1927)

Pl. 1, figs. 9, 10

Mactra haboroensis Yokoyama, 1927, p. 108–109, pl. 52, figs. 3–4.

Mactra kurikoma Nomura, 1935, p. 92–93, pl. 3, figs. 2–4.

Mactra (*Mactra*) *sachalinensis* Schrenck subsp. *haboroensis* Yokoyama, Kubota and Uozumi, 1950, p. 11–12, figs. 42–44.

Spisula (*Pseudocardium*) *kurikoma* (Nomura), Chinzei, 1962, p. 119–120, pl. 4, fig. 2–3, 5–6,

8, 10, 14.
Spisula (*Pseudocardium*) cf. *undilifera* (Weaver), Kanno and Ogawa, 1964, pl. 3, figs. 12–17.
Spisula kurikoma (Nomura), Mizuno, Sumi and Yamaguchi, 1969, pl. 28, fig. 4.

Description:

Sixteen specimens from the Ishiizawa Formation were examined. Shell small, ovate, thick, inequilateral, equivalve, moderately inflated. Anterior dorsal margin short and nearly straight; posterior one long and slightly arcuated. Anterior margin truncated and posterior one well rounded. Ventral margin broadly arcuated. Beak situated at anterior one-third of shell length and not so swollen. Surface smooth, except for fine growth lines. Both anterior and posterior lateral teeth thick and long. Resilium wide. Anterior cardinal tooth small; posterior one plate-like and vertical. Anterior adductor scar large and subquadrate; posterior one also subquadrate. Pallial sinus shallow and rounded at end.

Remarks:

The Ishiizawa specimens are identified as *Spisula haboroensis* (Yokoyama) based on shell shape, size and hinge features.

The present species is closely allied to *Spisula sachalinensis* (Schrenck), which lives in boreal waters. However, it is distinguishable from the latter by having a smaller shell size, vertically truncated anterior margin and no radial striation from beak to postero-ventral corner.

Spisula kurikoma was first described by Nomura (1935) from the Miocene Orose Formation as *Mactra*. Nomura (1935) pointed out that his species can be distinguished from *Spisula sachalinensis* by its smaller shell, more inflated beaks and more trigonal outline. However, his species is based on some ill-preserved specimens whose shell material is mostly eroded away. Some molds of *Spisula haboroensis* at hand also show produced beaks and trigonal outline. Moreover, a specimen illustrated by Nomura (1935, pl. 2, fig. 3) has a distinctly truncated anterior margin. Therefore, it is not certain that *Spisula kurikoma* can be distinguished from the present species.

Measurement (*in mm*):

Specimen	Length	Height	Thickness
JUE no. 15030-1	61.6	54.0	40.7+

Distribution: Miocene Chikubetsu, Yudoro, Takinoue, Ishiizawa, Orose and Shiotsubo formations; Pliocene Togawa Formation

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Plate 18

Explanation of Plate 18

Molluscan fossils from the Ishiizawa Formation
(All figures in natural size, unless otherwise stated)

Figs. 1a–b, 2a–b, 4. *Glycymeris* (*Glycymeris*) *idensis* Kanno
figs. 1a–b, JUE no. 15028–25, Loc. no. 5; figs. 2a–b, JUE no. 15028–52, Loc. no. 5; fig. 4, JUE no. 15029–15, Loc. no. 4.

Fig. 3. *Anadara* (*Anadara*) *hokkaidoensis* Noda
JUE no. 15031–1, Loc. no. 5.

Fig. 5. *Mercenaria protostimpsoni* Amano
x 0.8, JUE no. 15032–1, Loc. no. 6.

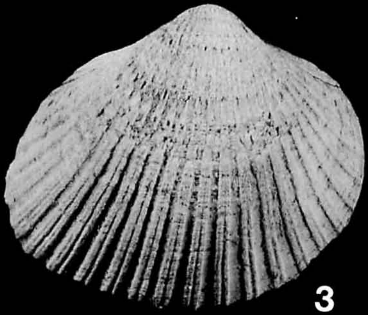
Fig. 6. *Crepidula jimboana* Yokoyama
JUE no. 15033, Loc. no. 5.

Fig. 7. *Mercenaria yiizukai* (Kanehara)
JUE no. 15034–1, Loc. no. 5.

Fig. 8. *Dosinia* (*Kaneharaia*) cf. *kaneharai rumoiensis* Amano
JUE no. 15035–1, Loc. no. 5.

Figs. 9, 10. *Spisula* (*Pseudocardium*) *haboroensis* (Yokoyama)
fig. 9, x 0.8, JUE no. 15030–1, Loc. no. 6; fig. 10, JUE no. 15030–2, Loc. no. 6.


1a


3

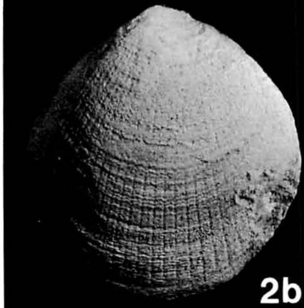

4


2a


1b


5

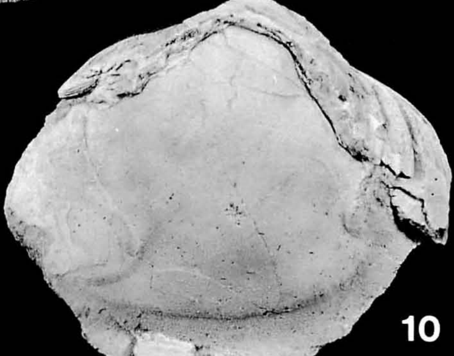

6


2b


7


8


9


10

ORIGIN AND DEVELOPMENT OF THE KAKEGAWA FAUNA

By

Tsugio SHUTO

What is the Kakegawa fauna?

The molluscs of the Kakegawa Group in Central Japan were first described by Yokoyama (1923, 1926). Makiyama was the first who dealt with the Kakegawa molluscs in a zoogeographical sense. He defined the Dainichian (Dainitian) fauna on the basis of his comprehensive work on molluscs of the lower Kakegawa Group (1927). On that occasion he distinguished four elements in the Dainichian fauna, namely living East Asian warm water elements, japonic ones, tropical ones and extinct species. In 1931 he noted a faunal difference between the Dainichian (s.s.) of the lower Kakegawa Group and the succeeding Kechienjian (Ketienjian) fauna of the upper Kakegawa Group. Otuka considered the molluscs of the lower through upper Kakegawa Group as a single faunal unit representative of the Pliocene warm waters of Japan and named it the Kakegawa fauna (1939). He also regarded it as contemporaneous with the Manganji fauna of cooler waters. Following Otuka's concept of the Kakegawa fauna, Tsuchi (1961) clarified the succession within this fauna from the Totomian through the Suchian to the Kechienjian Stage based on his restudy of the litho- and biostratigraphy of the Kakegawa Group. He recognized the coexistence of relics of the Upper Miocene Yuian molluscs with a few Kakegawa members in the Totomian Stage, the Acme of the fauna in the Suchian and decline and some modification of the fauna in the Kechienjian. If importance is attached to the above noted faunal succession, species ranging from the Totomian to the Kechienjian and those ranging from the Totomian to the Suchian must be evaluated as the most typical elements of the Kakegawa fauna. They are *Scapharca* (*Hataiarca*) *castellata* (Yokoyama), *Amussiopecten praesignis* (Yokoyama), *Crassatella foveolata* Sowerby, *Venericardia* (*Megacardita*) *panda* (Yokoyama), *Ventricolaria foveolata* (Sowerby) (= *V. cassinaeformis* (Yokoyama)), *Mercenaria yokoyamai* (Makiyama), *Suchium suchiense* (Yokoyama), *Turritella perterebra* (Yokoyama), *Babylonia elata* (Yokoyama), *Sydaphera pristina* (Yokoyama) and *Bathytoma luedorfi* (Lischke). Species whose occurrence is restricted to the Suchian are also significant to characterize the fauna. They are *Chlamys* (*Mimachlamys*) *satowi* (Yokoyama), *Siphonalia declivis* Yokoyama, *Nassarius* (*Zeuxis*) *caelatus dainitiensis* Makiyama, *Ancilla* (*Baryspira*) *albocallosa okawai* Yokoyama, and *Lyria* (*Paralyria*) *mizuhonica* Makiyama. Furthermore, species ranging from the Suchian to the Kechienjian include such important indices as *Siphonalia totomiensis* Makiyama, *Nassaria yokoyamai* Tsuchi, *Scalptia kurodai* (Makiyama) and *Makiyamaia subdeclis* (Yokoyama).

Faunules showing concurrent occurrences of all or most of the above mentioned species are known from several formations on the Pacific coast of Southwest Japan, such as the Tonohama Group in Shikoku, the Miyazaki Group in Kyushu and the Shimajiri Group in Okinawa.

Stratigraphic occurrences of the characteristic species of the Kakegawa fauna do not necessarily coincide between the Kakegawa Group and other contemporaneous faunas. For example, *Amussiopecten praesignis, Suchium suchiense subsuchiense* Makiyama, *Turritella* *perterebra, Siphonalia declivis, Nassaria yokoyamai, Sydaphera pristina,* and *Makiyamaia subdeclivis* show a concordant range in the Kakegawa and the Miyazaki Group, whereas *Scapharca* (*Hataiarca*) *castellata, Chlamys* (*Mimachlamys*) *satowi, Cryptopecten vesiculosus* (Dunker), *Venericardia* (*Megacardita*) *panda, Orectospira excelsa* (Yokoyama), *Babylonia elata, Lyria* (*Paralyria*) *mizuhonica,* and *Ancilla* (*Baryspira*) *albocallosa okawai* are remarkably different in their ranges within the two groups. Differences in range are rather slight for *Scalptia kurodai* and *Bathytoma luedorfi.* Besides, there is no evident tendency for the first occurrence of a species to be earlier in the south area than in the north, or vise versa. Under these circumstance, it is thought that the occurrences of species must be strongly controlled by local ecological factors, and the stratigraphic ranges of species must be longer than recognized in a single area. Therefore all the typical species known from the Totomian, Suchian and Kechienjian Stages of the Kakegawa group are regarded here as characteristic elements of the Kakegawa fauna, irrespective of their stratigraphic ranges in the type section. Thus, faunules of other stratigraphic sections that contain those species may be easily included in the Kakegawa fauna.

Geographic extension of the Kakegawa fauna

The Kakegawa fauna passes northward into a fauna of the Oyashio type, which shows a close affinity to the Omma-Manganji fauna. A molluscan faunule showing the Kakegawa affinity has been known from the lower Nakatsugawa Formation, which is distributed one hundred kilometers northeast of Kakegawa (Kojima, 1955; Uyeno and Matsushima, 1975). It, on one hand, includes in considerable number such Kakegawa elements as *Scapharca* (*Hataiarca*) *castellata, Glycymeris nakamurai* Makiyama, *Mercenaria yokoyamai, Suchium suchiense, S. obsoletum* Yokoyama and rarely *Venericardia* (*Megacardita*) *panda.* On the other hand, important Kakegawa elements, *Amussiopecten praesignis, Turritella perterebra, Siphonalia declivis, Scalptia kurodai, Makiyamaia subdeclivis,* etc. have no representative in the Nakatsugawa Formation and another important species, *Chlamys* (*Mimachlamys*) *satowi* is replaced by *C. miurensis* Yokoyama in that formation. Furthermore cool water elements *Spisula* (*Pseudocardium*) *sachalinensis* (Schrenck) and *Clinocardium* (*Fusocardium*) *braunsi* (Tokunaga) are mixed in the lower Nakatsugawa faunule. This faunule is considered a northern marginal facies of the Kakegawa fauna. Contemporaneous formations distributed a few tens to one hundred kilometers farther northeast are featured by faunules of cool water and quite different from the Kakegawa fauna. In short, the boundary zone of the Kakegawa and cool water faunas recognized in the Kwanto region is rather narrow. On the contrary, the Kakegawa fauna very gradually changes its specific compositon southward as one species substitutes for another. Therefore it is not easy to recognize the southern boundary of the Kakegawa fauna. Geographic ranges of the characteristic species of the Kakegawa and related faunas are shown in Table 1, which is based on several faunal studies of the Kakegawa Group (Yokoyama, 1923, 1926; Makiyama, 1927, 1931; Tsuchi, 1955, 1961; and Yoshida, 1981), the Miyazaki Group (Yokoyama, 1928; Shuto, 1961 and MS; and Yoshida, MS), the Shimajiri Group (Nomura and Zimbo, 1935; MacNeil, 1960; Noda, 1980; Sato, Shuto and Masuda, MS; and Sato, Masuda and Shuto, 1980) and the Cabatuan Formation in northern Luzon (Shuto, MS). Molluscan data from Taiwan, particularly of the Miaoli Group are indispensable for the present study, but I am unfortunately not familiar with the Plio-Pleistocene molouscs of Taiwan and I must exclude the information given by Yokoyama (1928), Nomura (1933, 1936) and Kotaka (1978)

Table 1. Geographic range of characteristic species of the Kakegawa and related faunas.
Sz: Shizuoka, Mz: Miyazaki, Ok: Okinawa Island, Mk: Miyako Island and Lz: Northern Luzon.

species	Sz	Mz	Ok	Mk	Lz
Nucula (Lamellinucula) tokyoensis Yokoyama		x			
N. (L.) njalindungensis Martin					x
Acila (Acila) divaricata (Hinds)	x	x	x	x	
A. (Truncacila) minuta Makiyama	x	x			
Nuculana (Costanuculana) omuensis Noda			x		x
N. (Thestileda) soyomaruae Habe		x			x
Saturnia (Saturnia) gushikamiensis (Noda)			x		x
Saccella confusa (Hanley)	x	x			
Scapharca (Hataiarca) castellata (Yokoyama)	x	x			
S. (H.) shizuokaensis Noda	x				
S. (Scapharca) tricenicosta (Nyst)		x		x	
S. (S.) suzukii Yokoyama	x				
Hawaiarca uwaensis (Yokoyama)	x	x	x	x	
Bathyarca kiurokujimana (Nomura et Hatai)	x	x			
B. gerthi (Koperberb)			x		x
Cucullaea granulosa (Jonas)		x	x	x	
Glycymeris (Glycymeris) nakamurai Makiyama	x	x			
G. (G.) totomiensis Makiyama	x	x			
G. (G.) imperialis Kuroda			x		
G. (G.) rotunda (Dunker)	x	x		x	
G. (G.) okinawaensis Noda		x	x		
G. (Tucetilla) laticardo Altena et Beets					x
Limopsis tajimae Sowerby	x	x			
L. tokaiensis (Yokoyama)	x	x	x		
Oblimopa japonica (A. Adams)	x	x	x	x	
Crenulilimopsis oblonga (A. Adams)		x	x		
Chlamys (Mimachlamys) satowi (Yokoyama)	x	x		x	
C. (M.) javanus (Martin) var. of Martin					x
Mizuhopecten tokyoensis hokurikuensis (Akiyama)	x	x			
Amussiopecten praesignis (Yokoyama)	x	x	x	x	
Gloripallium pallium (Linnaeus)				x	
Cryptopecten vesiculosus (Dunker)	x	x			
Polynemamussium intuscostatum (Yokoyama)		x			x
Placuna (Placuna) placenta (Linnaeus)				x	
Neopycnodonte musashiana (Yokoyama)	x	x			
Plicatula (Plicatula) rostrata Martin			x		x
Crassatina (Crassatina) uchidana (Yokoyama)	x	x			
C. (Chattonia) amputata (Martin)			x		x
Crassatella (Crassatella) takanabensis Shuto		x			
C. (C.) tosaensis Nomura		x			
Cycladicama luciniformis Valencienne		x			x
Bellucina civica (Yokoyama)		x	x		x
Goniomyrtea (Goniomyrtea) fabula (Reeve)			x		x
Lucinoma annulata (Reeve)		x	x		
Megacardita panda (Yokoyama)		x	x		

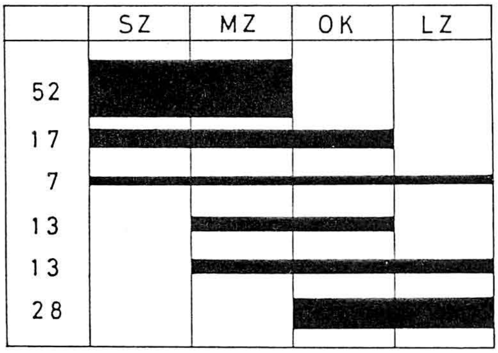
	Sz	Mz	Ok	Mk	Lz
M. granulicostata (Nomura)		x	x		
M. crenulicostata (Nomura)				x	
Grans javanus (Martin)					x
Keenaea samarangae Makiyama	x	x			
Fulvia mutica (Reeve)	x	x			
Azorinus minutus (Dunker)		x	x	x	x
Veremolpa mindanaoensis (Smith)		x	x		x
V. gonzalesi Shuto			x		x
Placamen tiara (Dillwyn)	x	x			
Ventricolaria foveolata (Sowerby)	x	x	x	x	
Clementia (Clementia) papyracea Gray	x	x		x	
Lioconcha (Sulcilioconcha) philippinarum (Hanley)				x	x
Paphia (Paphia) amabilis (Philippi)	x	x			
P. (P.) euglypta (Philippi)	x				
P. (P.) lirata (Philippi)				x	
P. (P.) takanabensis Shuto		x			
Panope japonica A. Adams	x	x			
Solidicorbula erythrodon (Lamarck)	x	x		x	
Anisocorbula scaphoides (Hinds)	x		x		x
Lischkeia alwinae (Lischke)	x	x			
Suchium suchiense (Yokoyama)	x	x			
S. suchiense subsuchiense (Makiyama)	x	x			
S. mysticum (Yokoyama)	x				
S. obsoletum obsoletum Makiyama	x				
S. obsoletum arenarium Makiyama	x	x			
Umbonium vestiarium (Linnaeus)				x	x
Turbo petholatus Linnaeus				x	
Astraea (Guildfordia) triumphator (Martin)			x		x
Orectospira excelsa (Yokoyama)	x	x			
Bittium (Bittium) kurodai Makiyama	x				
B. (B.) spinigerum (Martin)			x		x
B. (B.) premelvilli MacNeil			x		x
Turritella (Turritella) perterebra Yokoyama	x	x			
T. (T.) terebra (Linnaeus)				x	x
T. (Kurosioia) fascialis Menke		x	x		x
Onustus exutus (Reeve)	x	x			
Tibia fusus (Linnaeus)				x	x
Strombus (Euprotomus) vomer (Roeding)				x	x
Erosaria erosa (Linnaeus)				x	
Mauritia mauritiana (Linnaeus)				x	
Cryptonatica janthostomoides (Kuroda et Habe)	x	x			
Neverita reiniana (Dunker)	x	x			
N. hyugaensis Shuto	x	x		x	
N. hagenoshitaensis Shuto	x	x			
Polinices flemingianus (Recluz)				x	x

	Sz	Mz	Ok	Mk	Lz
Lunatia pallida (Broderip et Sowerby)	x	x		x	
Eunaticina papilla (Gmelin)	x	x		x	
Calyptraea yokoyamai Kuroda	x	x			
Lachryma callosa (Adams et Reeve)	x	x			
Trivirostra pellucidula (Gaskoin)					x
Semicassis pila (Reeve)					x
S. pila japonica (Reeve)	x	x			x
Cassidaria echinophorella Hirase		x			x
Distorsio (Distorsio) reticulatus decipiens (Reeve)				x	x
Tonna costata Menke		x			x
Murex (Murex) rectirostris Sowerby	x	x		x	x
M. (M.) bantamensis coulsoni Ladd				x	x
M. (Siratus) pliciferoides Kuroda		x			x
Tolema serratiformis (Noda)			x		x
Mitrella (Mitrella) bicincta (Gould)	x	x			
M. (Indomitrella) lischkei (Smith)	x	x			
Siphonalia declivis Yokoyama	x	x			
S. tonohamaensis totomiensis Makiyama	x				
S. tonohamaensis delicatula Shuto		x			
S. tosaensis Nomura		x			
Babylonia elata (Yokoyama)	x	x			
B. areolata (Link)		x		x	
Nassaria yokoyamai Tsuchi	x	x			
N. solida sanzaiana		x	x		
N. varicifera (Sowerby)					x
Siphonofusus japonicus Shuto		x		x	
Galeodea noharai Noda			x		x
Nassarius (Zeuxis) caelatus verbeeki (Martin)				x	x
N. (Z.) caelatus dainitiensis Makiyama	x	x			
N. (Z.) kurodai Makiyama	x				
Granulifusus dualis (Yokoyama)	x	x			
G. koyuanus Shuto		x			
G. matsumotoi Shuto		x	x	x	
G. rufinodes timorensis (Koperberg)					x
Latirus (Laticopsis) mamillifer Oostingh				x	
L. (Pseudolatirus) esi (Koperberg)					x
Oliva rufula Duclos				x	x
O. ispidula (Linnaeus)				x	x
Ancilla (Baryspira) albocallosa okawai (Yokoyama)	x	x			
Fulgoraria (Psephaea) concinna (Broderip)				x	
F. (P.) concinna corrugata Shikama	x				
F. (P.) hyugaensis Shuto		x			
Lyria (Paralyria) mizuhonica Makiyama	x	x			
L. (P.) koyuana (Yokoyama)		x			
Nebularia hanleyana (Dunker)		x			

	Sz	Mz	Ok	Mk	Lz
Vexillum (Costellaria) obeliscus (Reeve)		x	x	x	x
V. (C.) rubricatum (Reeve)				x	x
Uromitra nakamurai ugariensis Makiyama	x	x			
Tiara flammea (Quoy et Gaimard)		x		x	x
T. isabella (Swainson)				x	x
Cancellaria (Merica) asperella Lamarck			x	x	x
C. (M.) reevei laticostata (Loebecke)		x	x		
Sydaphera spengleriana (Deshayes)	x	x			
S. pristina (Yokoyama)	x	x			
Scalptia kurodai (Makiyama)	x	x		x	
Gibberula (Kogomea) novemprovincialis (Yokoyama)	x	x			
Marginella (Stazzania) flaccida (Yokoyama)	x	x			
Thatcheria gradata (Yokoyama)		x	x		
Comitas (Fusiturricula) habei Shuto	x	x			
Nihonia soyomaruae takanabensis (Otuka)		x		x	
N. pervirgo (Yokoyama)		x			
N. santosi Shuto					x
Makiyamaia coreanica (Adams et Reeve)	x	x	x		
M. subdeclivis (Yokoyama)	x	x	x	x	
Paradrillia dainichiensis (Yokoyama)	x	x			
P. astuta (Yokoyama)	x	x			
P. serana (Fischer)					x
Gemmula (Gemmula) speciosa (Reeve)				x	x
G. (G.) kieneri woodwardiana (Martin)		x	x	x	x
G. (G.) pulchella Shuto		x	x		
G. (Unedogemmula) gendinganensis (Martin)					x
G. (Kuroshioturris) kurodai (Makiyama)	x	x			
Parabathytoma striatotuberculata (Yokoyama)	x	x			
Inquisitor batavianus (Martin)			x	x	x
I. pseudoprincipalis (Yokoyama)	x	x			
Splendrillia praegracilis (Makiyama)	x	x			
Conus (Lithoconus) ngawianus Martin				x	
C. (L.) decoratus Martin				x	
Asprella orbignyi (Audouin)	x	x		x	
Terebra (Myurella) torquata (Adams et Reeve)			x	x	x
T. (Strioterebrum) woodwardi Martin	x	x		x	x
Acteon (Punctacteon) fabraeus Crosse	x	x			x
Ringicula (Ringiculina) arctata Gould	x	x			x
Cylichna (Eocylichna) musashiensis (Yokoyama)	x	x			x

from the present work.

Species ranging over two or more areas of Kakegawa, Miyazaki, Okinawa and Luzon are counted among the characteristic elements of those faunules (Table 1). Species ranging from Kakegawa to Miyazaki are extremely abundant (52 spp., 30%). Next most abundant are the species ranging from Okinawa to Luzon (28 spp., 16%). While molluscs from the Shimajiri Group include both those of shallower and deeper facies and the faunule of the shallower facies contains several species of cypraeids, mitrids, conids and bursids, the molluscs of the Cabatuan Formation are chiefly of deeper facies and nearly lack cypraeids, conids, etc. This fact is clearly reflected in the number of common species occurring in both areas on my list. Species ranging from Okinawa to Luzon would be much more abundant, if the faunules of shallower facies were contained in the Cabatuan Formation. The above mentioned faunal continuity may suggest a faunal gap between Miyazaki and Okinawa, so that the Kakegawa fauna would only be distributed from Kakegawa to Miyazaki. If this were the case, the faunule of Okinawa would be regarded as a part of the typical tropical fauna. However, a detailed examination shows that the faunal change from Miyazaki to Okinawa is actually gradual with many species (50 spp.) occurring in both areas. This species count of 50 is comparable with the number of species ranging from Kakegawa to Miyazaki (52 spp.). Closer comparison of the faunules reveals some evidence to support the last mentioned linkage between Miyazaki and Okinawa.



Text-fig. 1. Number of species ranging through two or more neighbouring regions. Data from Table 1.
SZ: Shizuoka, MZ: Miyazaki, OK: Okinawa including Okinawa Island and Miyako Island and LZ: Northern Luzon.

The following species among the characteristic elements of the Kakegawa Group range from Kakegawa to Miyazaki. They are *Scapharca (Hataiarca) castellata, Glycymeris nakamurai, G. totomiensis* Makiyama, *Neopycnodonte musashiana* (Yokoyama), *Crassatella (Crassatina) oblonga uchidana* Yokoyama, *Venericardia (Megacardita) panda, Suchium suchiense subsuchiense, S. obsoletum arenarium* Makiyama, *Orectospira excelsa, Turritella perterebra, Siphonalia declivis, Babylonia elata, Nassaria yokoyamai, Nassarius (Zeuxis) caelatus dainitiensis, Granulifusus dualis* (Yokoyama), *Ancilla (Baryspira) albocallosa okawai, Lyria (Paralyria) mizuhonica, Uromitra nakamurai ugariensis* Makiyama, *Sydaphere pristina, Gibberula (Kogomea) novemprovincialis* (Yokoyama), *Turricula sobrina* (Yokoyama), *Kuroshioturris kurodai* (Makiyama), *Paradrillia dainichiensis* (Yokoyama), *P. astuta* (Yokoyama) and *Parabathytoma striatotuberculata* (Yokoyama).

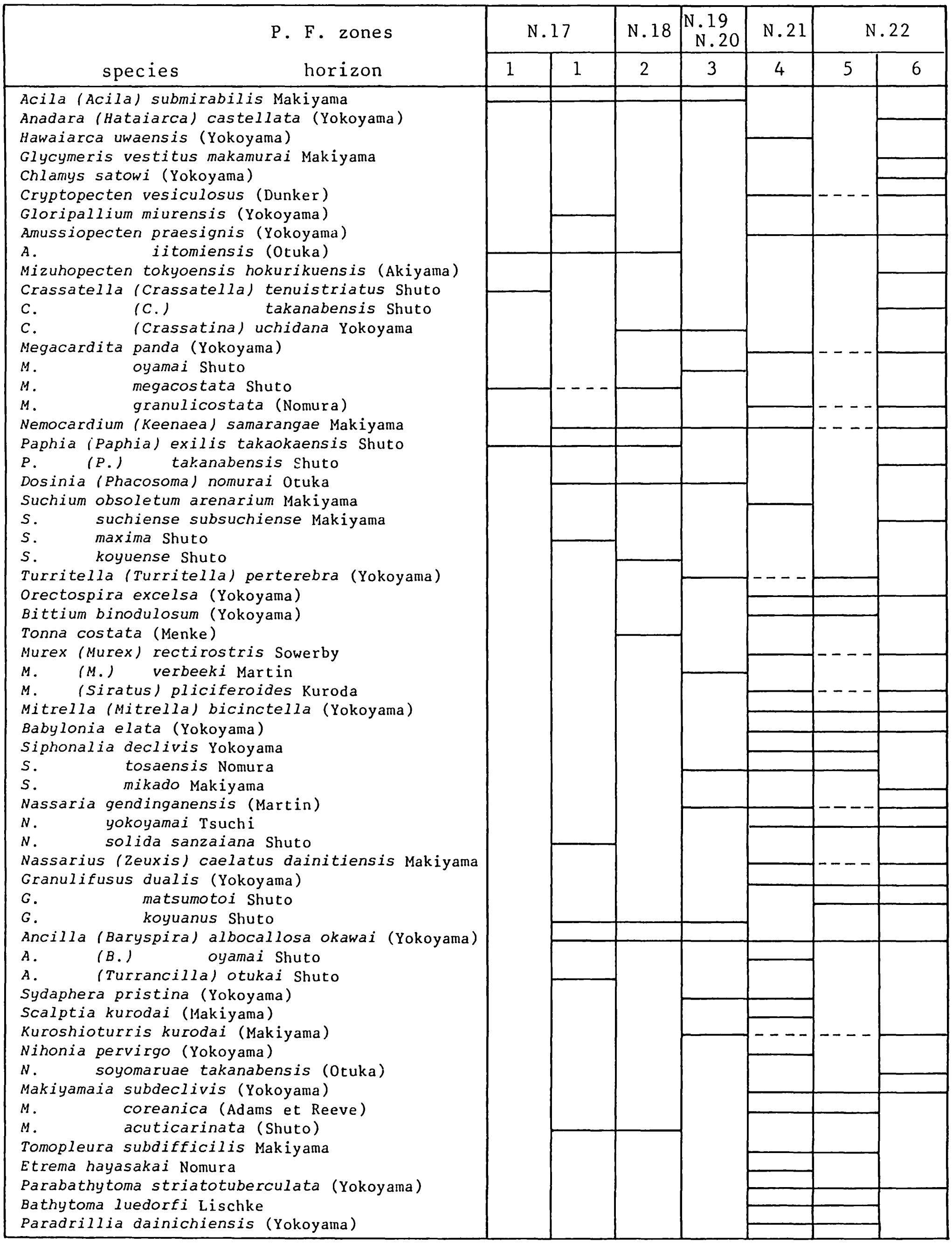
Species distributed rather commonly from Kakegawa to Okinawa are *Hawaiarca uwaensis, Chlamys (Mimachlamys) satowi, Amussiopecten praesignis, Ventricolaria foveolata, Scalptia kurodai, Makiyamaia subdeclivis, M. coreanica* (Adams and Reeve), *Neverita hyugaensis* Shuto and *Limopsis tokaiensis* (Yokoyama). The majority of these species have been regarded as characteristic of the type Kakegawa fauna.

The following species range from Miyazaki to Okinawa or farther south: *Scapharca tricenicosta* (Nyst), *Cucullaea granosa* (Jonas), *Venericardia* (*Megacardita*) *granulicostata* Nomura, *Azorinus abbreviatus* (Dunker), *Veremolpa mindanensis* (Smith), *Nassaria solida sanzaiana* Shuto, *Siphonofusus japonicus* Shuto, *Granulifusus matsumotoi* Shuto, *Nebularia hanleyana* (Dunker), *Vexillum* (*Costellaria*) *obeliscus* (Reeve), *Tiara flammea* (Quay and Gaimard), *Cancellaria* (*Merica*) *reevei laticosta* (Loebbecke), *Thatcheria gradata* (Yokoyama), *Nihonia soyomaruae takanabensis* (Otuka), *Gemmula* (*Gemmula*) *kieneri woodwardiana* (Martin) and *Kuroshioturris pulchella* Shuto. It must be noted that these species are not the typical tropical species in spite of their southward distribution.

Considering all the above facts, the Kakegawa fauna is defined by the co-occurrence of *Amussiopecten praesignis, Chlamys* (*Mimachlamys*) *satowi, Hawaiarca uwaensis, Ventricolaria foveolata, Scalptia kurodai, Makiyamaia subdeclivis* and *Limopsis.* The faunules of Okinawa are, of course, included in it. Thus, characteristic taxa of the Kakegawa fauna range from Kakegawa, Central Japan, to Okinawa, although local faunules contain many species of limited geographic range. For example, *Mathilda totomiensis* Makiyama, *Bittium kurodai* Makiyama, *Reishia nakamurai* Makiyama, *Cantharus totomiensis* Makiyama, *Maoritomella yokoyamai* (Makiyama), *Scapharca* (*Hataiarca*) *shizuokaensis* Noda, etc. characterize the faunule of the Kakegawa Group. The faunule of the Miyazaki Group is characterized by *Crassatella takanabensis* Shuto, *Paphia takanabensis* Shuto, *Siphonalia hyugaensis* Shuto, *Lyria* (*Paralyria*) *mizuhonica koyuana* (Yokoyama), *Fulgoraria* (*Psephaea*) *hyugaensis* Shuto, *Comitas habei* (Shuto), *C. makiyamai* (Shuto), *Kuroshioturris hyugaensis* Shuto, *Ptychosyrinx nipponicus* Shuto, *Borsonia miyazakiensis* Shuto, etc. Tropical species typify the faunule of the Shimajiri Group, as mentioned before.

The lower boundary of the Kakegawa fauna

The Miyazaki Group is probably more suitable than the Kakegawa Group for examining the stratigraphic ranges of Kakegawa molluscs, because fossils of several biofacies exist throughout the stratigraphic section of the former. Seven molluscan horizons (1α, 1β, 2–6) are recognized in the Miyazaki Group on the basis of the stratigraphic occurrences of molluscan fossils (Shuto, 1961). Fossil assemblages from the fourth horizon through the sixth, an interval included in planktonic foraminiferal zone N 21–22 (Natori et al., 1972), contain abundant typical Kakegawa molluscs (Text-fig. 2). The fossil assemblage from the third horizon, which is situated at about the transition between N 19 and N 20, consists of 67 species, of which 53 are known species. Twelve species out of 53 in this horizon are characteristic elements of the Kakegawa fauna: *Glycymeris totomiensis, Crassatella* (*Crassatella*) *tosana* Nomura, *Calliostoma* (*Otukaia*) *kounjianum* (Yokoyama), *Turritella perterebra, Siphonalia declivis tosaensis* Makiyama, *S. dainitiensis* Makiyama, *Nassaria yokoyamai, Ancilla* (*Baryspira*) *albocallosa okawai, Sydaphera pristina, Turricula sobrina* Yokoyama, *Nihonia pervirgo* (Yokoyama), *Kuroshioturris kurodai.* Another 15 species, rather ubiquitous, also occur at higher horizons. *Vepricardium kyushuense* Shuto, *Paphia tsumaensis* Shuto, *Dosinia* (*Phacosoma*) *nomurai* Otuka, *Granulifusus koyuanus* Shuto and four other species also occur in lower horizons. In short, the assemblage of the third horizon is closely related to the Kakegawa fauna, although it lacks the most important species of the latter such as *Amussiopecten praesignis, Chlamya* (*Mimachlamys*) *satowi, Scapharca* (*Hataiarca*) *castellate* and *Venericardia* (*Megacardita*) *panda.*



Text-fig. 2. Stratigraphic occurrence of selected molluscan species in the Miyazaki Group.

It is regarded as a transition facies between the ancestral and the true Kakegawa fauna, as is demonstrated by the mixted occurrence of Kakegawa taxa with such immediate forerunners as *Venericardia* (*Megacardita*) *oyamai* Shuto, *Granulifusus koyuanus*. The latter two species are respectively immediate forerunner of *V.* (*M.*) *panda* and *G. matsumotoi.*

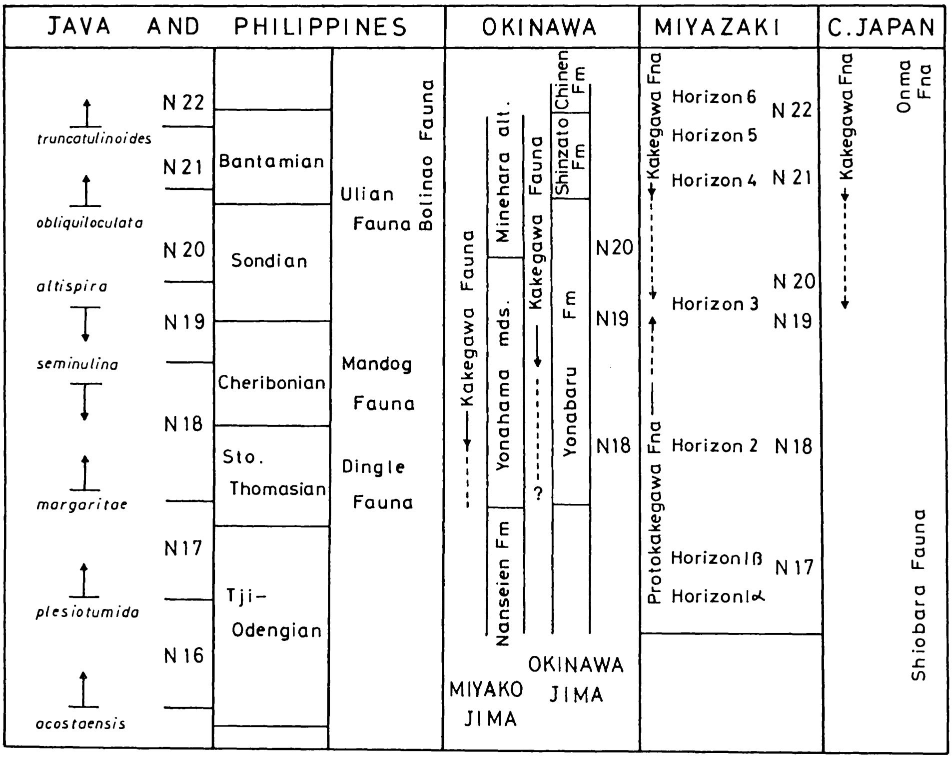
Of the 66 species from the second horizon eight are typical Kakegawa taxa, 17 species also occur at higher horizons, and 25 species range into lower horizons. *Amussiopecten iitomiensis* (Otuka), *Venericardia* (*Megacardita*) *megacostata* Shuto, *Paphia exilis takaokaensis* Shuto, *Suchium koyuense* Shuto, and *Makiyamaia subdeclivis acuticarinata* Shuto from this horizon are regarded as the ancestral form of *A. praesignis, V.* (*M.*) *oyamai, P. takanabensis, S. suchiense* and *M. subdeclivis,* respectively. As a whole the assemblage of the second horizon is obviously allied to the Kakegawa fauna, but its relationship is more tenuous than between the assemblage of the third horizon and the Kakegawa fauna. In conclusion the lower boundary of the Kakegawa fauna in the Miyazaki Group is better placed between the third and fourth horizons, which allows the occurrence of *Amussiopecten praesignis, Chlamys* (*Mimachlamys*) *satowi, Scapharca* (*Hataiarca*) *castellata* and *Venericardia* (*Megacardita*) *panda* to harmonize with the geographic definition of that fauna noted in the preceding section. The boundary is probably situated in N 20 or between N 20 and N 21.

While the molluscan assemblages from the Shimajiri Group on Okinawa Island mostly consist of species of deeper facies, the Shimajiri Group on Miyako Island, 300 km southwest of Okinawa Island, contains molluscan assemblages of shallower facies. Shallow offshore assemblages from two horizons of th Yonahama Formation of that group on Miyako Island contain a tropical association of *Umbonium* (s.s.), *Tibia, Dientomochilus,* cypraeids, *Cyllene* (s.s.), *Oliva, Harpa, Vexillum* and conids. They contain many species in common with the Sondian and Bantamian of Indonesia, but still contain such characteristic species of the type Kakegawa fauna as *Hawaiarca uwaensis, Chlamys* (*Mimachlamys*) *satowi, Amussiopecten praesignis, Scalptia kurodai* and *Makiyamaia subdeclivis,* together with such Kakegawa elements of the Miyazaki Group as *Neverita* (*Glossaulax*) *hyugaensis, Siphonofusus japonicus, Granulifusus matsumoti* and *Nihonia soyomaruae takanabensis* (Otuka). Accordingly, the molluscan assemblages of the Yonahama Formation, which is referred to N 18–N 19 (Ujiie et al., 1974), is regarded as part of the Kakegawa fauna. The Kakegawa fauna undoubtedly merges southward into the equatorial Sondian-Bantamian fauna, although the transition between Okinawa and Luzon is not clear because of lack of adequate information from Taiwan.

species	Miyako	Miyazaki
Hawaiarca uwaensis (Yokoyama)	N.21	N.21
Amussiopecten praesignis (Yokoyama)	N.19	N.21
Chlamys satowi (Yokoyama)	N.19	N.22
Bellucina civica (Yokoyama)	N.22	N.22
Ventricolaria foveolata (Sowerby)	N.19	N.17
Polinices (Glossaulax) hyugaensis Shuto	N.19	N.21
Siphonofusus japonicus Shuto	N.19	N.22
Nassarius (Zeuxis) verbeeki (Martin)	N.19	N.19/20
Granulifusus matsumotoi Shuto	N.19	N.21
Oliva (Carmione) mustellina Lamarck	N.19	N.21
Mitra (Nebularia) hanlayana (Dunker)	N.19	N.21
Vexillum (Costellaria) obeliscus (Reeve)	N.19	N.19/20
Trigonostoma (Scalptia) kurodai Makiyama	N.19	N.21
Makiyamaia subdeclivis (Yokoyama)	N.19	N.21
Nihonia soyomaruae takanabensis (Otuka)	N.19	N.22
Architectonica perspectiva (Linnaeus)	N.19	N.19/20

Table 2. First occurrence of selected species in the Shimajiri Group on Miyako Island and the Miyazaki Group in Kyushu.

In conclusion, the first appearance of the Kakegawa fauna is in N 18 in Okinawa and N 20 or between N 20 and N 21 in Miyazaki. That is to say, it is time-transgressive northward, although it is almost contemporaneous in Miyazaki and Shizuoka (Text-fig. 3). It seems also important that several elements of the Kakegawa fauna were preceded by closely related forerunners.



Text-fig. 3. Distribution of the Kakegawa fauna in time and space.

Origin of the Kakegawa fauna

As mentioned above, the Kakegawa fauna grades southward into a typical tropical fauna. This fact indicates that the development of the Kakegawa fauna must be intimately related to a true tropical fauna. Therefore, the rise and fall of tropical faunas during the Cenozoic in Japan was investigated to search for clues to the origin of the Kakegawa fauna. In this study, marine climate was inferred from the percentage of tropical gastropod genera in each faunule (Table 3). The result is shown in Text-fig. 4. The percentage may be different between the inshore and offshore assemblages of the same age and area, because temperature is generally lower on a deeper bottom than on a shallower one, although temperature decline is not proportional to depth. Accordingly, the comparison of assemblages must be done among those of similar facies. If bathyal and intertidal assemblages are excluded, a figure of twenty percent is regarded as a tentative criterion to distinguish the tropical assemblage from the subtropical and cooler one. As indicated in Text-fig. 4, typical tropical faunas invaded South-

Table 3. Gastropod genera adopted as indicators of tropical marine climate.

Marmorostoma
Vicaryella
Rimella
Tibia
"Cypraea"
Magilus
Melongena
Mitra
Oliva
Volutospina
Marginella
Telescopium
Tateiwaia
Rostellaria
Cromium
Cassis
Coralliophila
Clavilithes
Harpa
Voluta
Pseudoliva
"Conus"
Vicarya
Terebralia
Dientomochilus
Pachycromium
Phalium
Cyllene
Metula
Lyria
Athleta
Pseudoperissolax

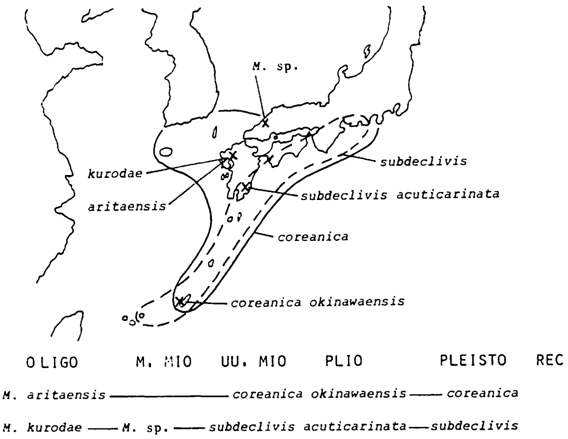
	IN	INDN	PH	TAI	JAPAN							N. AM	
					I	II	III	IV	V	VI	VII	W	SE
Quat		22		26	32 23	24		1 6					
Plio		28	19 19 (7)		(13) 43 (9)	19 27 24 22 30		6 18	5 4 10	0 0		8 0 11 2	
Mio	36	24 23 40	37		(16)	40 13	22 (7) 23	12 13 12 17	0 0 4 0	33	0	24 4 36 12 24 5	20
Oligo		(9)				7 0 50 50			17 21 21			17 19 11 17	56 44
Eo	50	17				57						24 17 34 43 29 26	42 36 25 28

Text-fig. 4. Rise and fall of tropical faunas in Japan through the Cenozoic Era, in terms of percentage of tropical genera in gastropod faunules (cf. Table 3).

Twenty percent is a tentative criterion to distinguish a tropical faunule from a cooler one. Numbers in parentheses represent deeper offshore faunules. IN: India, INDN: Indonesia, PH: Philippines, TAI: Taiwan, I: Okinawa, II: Kyushu, III: Chugoku and Shikoku, IV: Kinki and Chubu, V: Kwanto, VI: Tohoku, VII: Hokkaido and N. AM: North America (W=western, SE=southeastern).

west Japan three times during the Cenozoic Era, if small oscillations are disregarded. The first invasion was in the Eocene to Early Oligocene, the second in the Medial Miocene and the third in the Mio-Pliocene to earliest Pleistocene. Is any faunal continuity expected between successive tropical phases separated by a cooler phase? Comparison of the Kakegawa fauna with the Middle Miocene fauna shows that it is difficult to find direct lineal relations between many of the Kakegawa elements and Middle Miocene species, except for a few cases such as *Makiyamaia subdeclivis* from the Middle Miocene *M.* sp. via *M. subdeclivis acuticrinata* (Text-fig. 5), *Chlamys* (*Mimachlamys*) *satowi* from the Middle Miocene *C.* (*M.*) *kaneharai* (Yokoyama) and *Orectospira excelsa* from the Lower Miocene *O. nenokamiensis* Kanno. The lineage of *Suchium koyuense* to *S. suchiense subsuchiense* exemplifies a more drastic change from the Japanese Middle Miocene ancestor, *Protorotella* to *Suchium*. The evolution of the above mentioned lineages seems to have occurred in Japanese waters, because representative of these lineages has not been found outside Japan, although it is not clear how they behaved in the cooling phase of the Late Miocene. The Late Miocene was not only a period of climatic deterioration in Japan, but also a regressive phase in Southwest Japan and consequently the marine evidence of this phase is not preserved in the geological record. Naturally I cannot offer any concrete evaluation of an evolutionary role of the "Late Miocene fauna" in connection with the birth of the Kakegawa fauna.

Considering the general tendency for speciation to be greatly stimulated under the environ-



Text-fig. 5. Lineage and geographic distribution of *Makiyamaia* (Gastropoda).

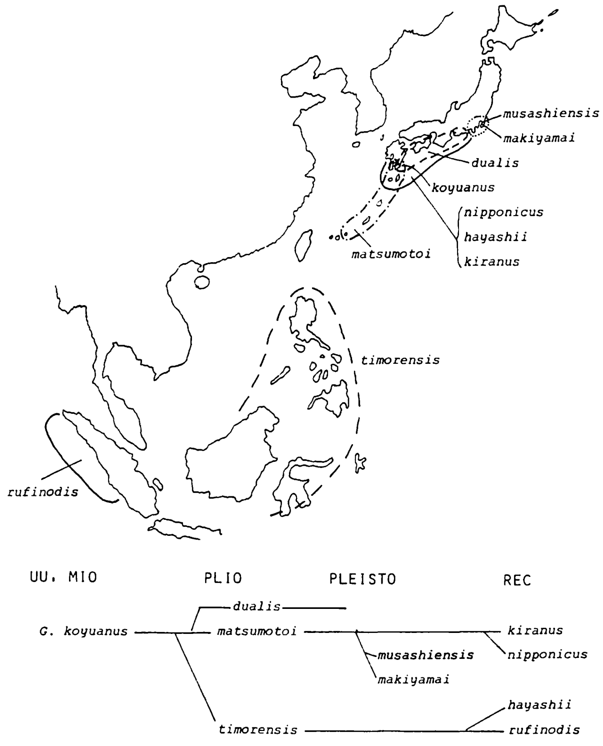
mental stresses along marginal areas of a species' geographic range, most of the forerunners of the characteristic elements of the Kakegawa fauna should evolved from a tropical species either when the tropical climate deteriorated in Japan in the Late Miocene or when marine tropical conditions returned to Japan in the Latest Micoene. As is demonstrated by many glycymeririds (Matsukuma, 1985), speciation of the former case seems more likely than speciation of the latter case, becasue environmental stresses for tropical taxa must be severer in the former case than in the latter. The above noted speciation of *M. subdeclivis, C. satowi, O. excelsa* and *S. suchiense subsuchiense* are, of course, included in the former. Examples of the inferred speciation of this kind are, however, much less than expected and many Kakegawa elements seem to exemplify the latter case (Table 4).

Forerunners of those lineages of *Amussiopecten praesignis, Paphia takanabensis, Turritella perterebra, Siphonofusus japonicus, Lyria* (*Paralyria*) *mizuhonica,* etc. were differentiated in south Japanese waters in the Latest Micoene from ancestral species, which florished in low latitude regions.

Granulifusus, a subtropical to tropical genus, illustrates another case. A direct ancestral form of *Granulifusus* has not been found in Middle Miocene and older faunas of Japan or regions to the south. *Granulifusus koyuanus,* the oldest species of the genus, abruptly appeared in Kyushu in the Latest Micoene and then it was differentiated into Japanese and southern forms, of which the latter was far less prosperious. The lineage of a warm water taxon, *Veneri-*

Table 4. Inferred lineages of characteristic Kakegawa species with their ancestors in regions of low latitude.

Amussiopecten kankoensis Tan (Low. Mio., Taiwan)	*A. iitomiensis* (Otuka) (up. Up. Mio., SW Japan)	*A. praesignis* (Yokoyama) (Plio.- Pleist., SW Japan)
Paphia lirata (Philippi) (Low. Mio.- Rec., S & SE Asia)	*P. exilis takaokaensis* Shuto (up. Up. Mio.- Low. Plio., SW Japan)	*P. takanabensis* Shuto (Low. Pleist., SW Japan)
Turritella terebra talahabensis Martin (Low. Mio., Java)	*T. terebra* (Linne) (Up. Mio.- Rec., S & SE Asia)	*T. perterebra* Yokoyama (Plio., SW Japan)
Siphonofusus wanneri (Beets) (low. Mid. Mio., Java)	*S. macneili* Shuto (Up. Mio., Okinawa)	*S. japonicus* Shuto (Plio., SW Japan)
Lyria (Paralyria) edwardsi (D'Archiac) *L. (P.) jugosa* (Sowerby) (Mid. Mio.- Rec., S & SE Asia)	*L. (P.) mizuhonica koyuana* (Yokoyama) (Plio., SW Japan)	*L. (P.) m. mizuhonica* Makiyama (Plio.- Low. Pleist., SW Japan)



Text-fig. 6. Lineage and geographic distribution of *Granulifusus* (Gastropoda).

cardia (*Megacardita*) *panda* illustrates a similar evolutionary feature to the above. It shows a clear phyletic evolution after Latest Micoene through Pliocene from *V.* (*M.*) *megacostata* to *panda* via *oyamai.* Its ancestral form, however, has not been found nowhere. These two lineages are also considered to have diferentiated in the recurring phase of the tropical condition to Japan.

In conclusion, the majority of the characteristic species, particularly the Japonic elements, of the Kakegawa fauna must evolved from ancestral tropical species in the marginal zone of their geographic ranges when the tropical marine climate moved northward in the Latest Miocene and some others are considered to have differentiated from the Middle Miocene ancestors of Japanese waters when the tropical condition was retreating southward in the Late Micoene.

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TAKIKAWA-HONBETSU AND TATSUNOKUCHI FAUNAS

(*Fortipecten takahashii*-bearing Pliocene faunas)

By

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1. Introduction

It is well known that there are three zoogeographically distinct Pliocene molluscan faunas in Japan. The three faunas are the Kakegawa fauna (Makiyama, 1927; Otuka, 1939), the Onma-Manganji fauna (Otsuka, 1936, 1939), and the Takikawa-Honbetsu fauna (Fujie and Uozumi, 1957; Uozumi, 1962) (the latter fauna of Hokkaido is equivalent to the Tatsunokuchi fauna of northern Honshu) (Nomura, 1938; Otuka, 1941). The first of these is characterized by warm-tropical species, such as *Umbonium, Siphonalia, Amussiopecten* and *Venericardia panda,* etc., and flourished on the Pacific coast of southwestern Japan. The second is characterized by the cool water elements, such as *Turritella saishuensis, Anadara amicula* and *Mercenaria stimpsoni,* etc., and is distributed mainly along the Japan Sea coast of northern Honshu. The last type includes the unique hunchback-like pectinids, *Fortipecten* species, and *Anadara tatünokutiensis,* etc., and is found widely in central and eastern Hokkaido, and along the Pacific coast of northern Honshu; its southern limit of distribution is near 38°N latitude in central Honshu. Here it should be mentioned that the *Fortipecten*-bearing fauna is not limited in its geographical distribution to the Japanese archipelago, but is wide-spread northeastward from Hokkaido-Sakhalin along the Kamchatkan and Alaskan coasts in deposits considered to be of Pliocene age. On the other hand, it is also remarkable that such fauna is never found in deposits on the Japan Sea side which are considered to be contemporaneous with the *Fortipecten*-bearing formations. From such distributions, it may said that the *Fortipecten*-bearing faunas belong to the diagnostic Pliocene molluscan types found only on the northern Pacific side of Japan.

It has been shown that the "Setana*" fauna (Uozumi, 1962) is closely related bio-chronologically to the Takikawa-Honbetsu fauna and flourished from the late Neogene to early Quaternary in Hokkaido. The assemblage of this fauna seems to resemble that of the Onma-Manganji fauna rather than the Takikawa-Honbetsu fauna. Some Japanese geologists have suggested that this fauna is coeval and heterogenous in faunal assemblage with the Takikawa-Honbetsu and Tatsunokuchi faunas. Others, including the authors, have felt that the "Setana" fauna is not coeval with the other above-mentioned Pliocene faunas. The "Setana" fauna may be younger in geologic age than the Takikawa-Honbetsu and Tatsunokuchi faunas, and may straddle the Pliocene/Pleistocene boundary. However, there is as yet very little published information on late Neogene to early Quaternary faunal changes in Hokkaido, so it is not entirely clear how the "Setana" fauna is biostratigraphically related to the Takikawa-Honbetsu fauna.

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*From the results of a recent study, the so-called Setana fauna possibly can be divided into two faunas, each from a different stratigraphic horizons.

The strata containing the Takikawa-Honbetsu fauna are not extensively exposed in a single area, but are found discontinuously in central and eastern Hokkaido. They are quite variable in thickness, between about 2,000 meters and 50 meters, according at a given lcoality, but show rather similar lithic facies. These strata consist mainly of tuffaceous coarse sandy beds with marine molluscan fossils in their lower half, and conglomerates with lignite beds in the upper half. Beds in the upper half do not contain marine molluscan remains and change gradually upwards from marine facies into terrestial facies.

The representative species of the Takikawa-Honbetsu fauna, such as *Fortipecten takahashii* and *Anadara tatunokutiensis*, etc., are not found continuously throughtout the whole formation, but their occurrences are rather confined to lower parts of the formation. Therefore, it is doubtful whether or not this fauna indicates the age of the "formation" units, or only the age of some of the stratigraphically limited horizons within the formation. That is, it is uncertain whether or not the differences in thickness of these fossil-bearing strata are due to different rates of sediment accumulation or to different lengths of sediment accumulative time at a given locality.

In order to re-examine some of these problems, the following points were investigated:

1) The biostratigraphical relationships between the Takikawa-Honbetsu and the "Setana" faunas within the nearly continuous stratigraphic sequence of late Neogene to early Quaternary age in eastern Hokkaido, which contain the above-mentioned two faunas in one sedimentary basin, were studied. Simultaneously, the first and last known occurrences of numerous representative species of the Takikawa-Honbetsu fauna were re-examined.

2) The provincial bio-stratigraphic standard sequence for late Neogene to early Quaternary faunas in Hokkaido was correlated with the geologic timescale using magnetostratigraphy and radiometric dating within the same stratigraphic sequence.

3) The biostratigraphies of sedimentary basins in other areas were correlated, as well as possible, with the provincial standards using radiometric dating and other data.

4) The geological and geographical ranges of the Takikawa-Honbetsu fauna were confirmed.

Based on these studies, the authors speculated on the origin and migration of the Takikawa-Honbetsu fauna, taking into account allied faunas in the north Pacific region.

II. The provincial biostratigraphic and geochronologic standard sequence of late Neogene to early Quaternary age in Hokkaido

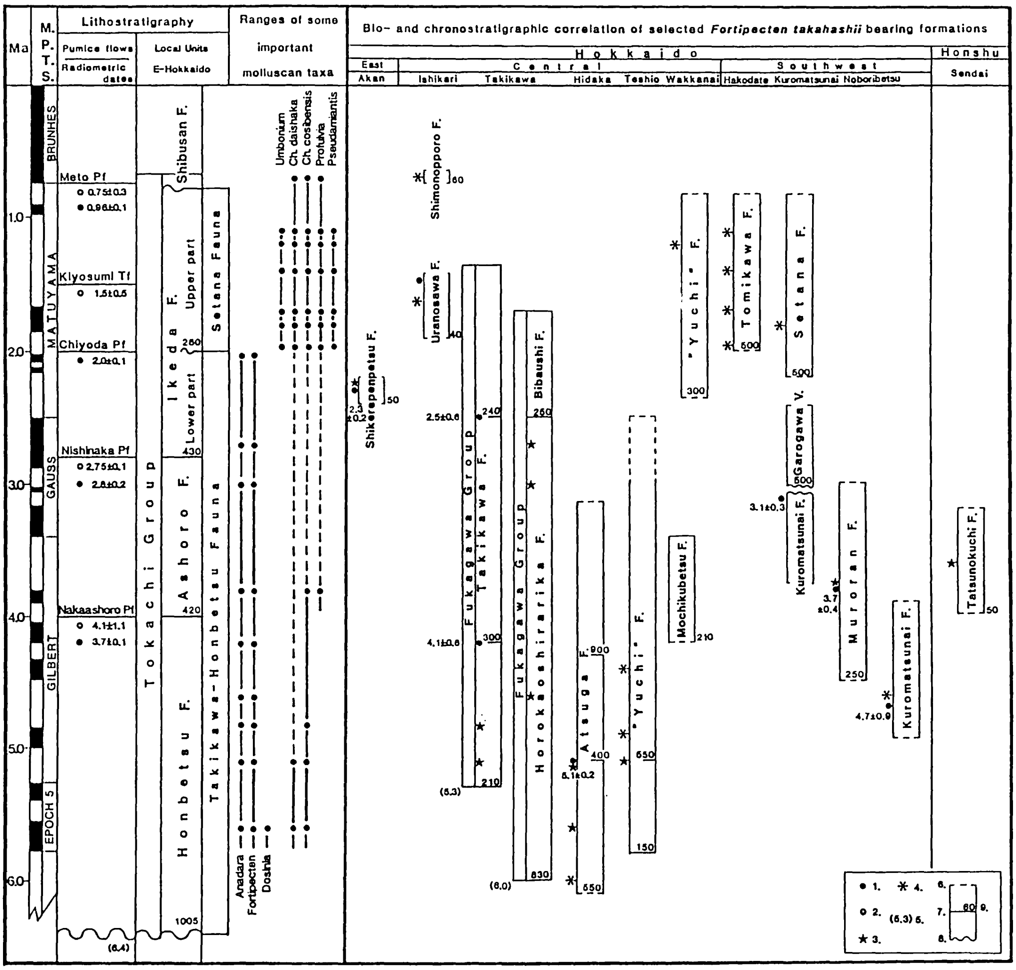
(1) The provincial late Neogene to early Quaternary standard sequence

The Tokachi area in southeastern Hokkaido is located eastward of the Hidaka Mountains, the backboen of Hokkaido that was formed by geo-tectonic upheaval. This lowland is named the plain of Tokachi. In this area, late Neogene to early Quaternary strata are thickly and nearly continuously developed to more than 2,000 meters in thickness, and are mainly composed of marine deposits that are occasionally interbedded by pyroclastic materials. These strata yeild many marine molluscs: some of the fossil assemblages are thought to belong to the Takikawa-Honbetsu fauna and others to the "Setana" fauna. For these reasons, the strata have been investigated by many various workers, including biostratigraphically, paleontologically, magnetostratigraphically and radiochronologically. These studies have provided many basic data for definition of the Pliocene/Pleistocene or the Neogene/Quaternary boundary within provincial sequences and for correlation of provincial faunas with the worldwide geologic timescale.

Summarizing the results of these stratigraphic and chronologic studies, the late Neogene to early Quaternary strata in this area represent nearly continuous deposition without a large hiatus, and they are named the Tokachi Group as an undivided whole. This group is lithologically divided into the following four formations in ascending order: the Honbetsu, Ashoro, Ikeda (upper and lower) and Shibusan Formations. The Honbetsu Formation is unconformably underlain by Miocene deposits and is mainly composed of coarse grained materials that are occasionally intercalated with pyroclastic deposits. The basal parts of the Honbetsu Formation are composed of volcanic rocks, the middle parts of coarse grained marine sediments, and the upper parts mainly of pyroclastic materials. Also three parts yield many marine molluscan species that are characteristic of the Takikawa-Honbetsu fauna. The Ashoro Formation disconformably overlies the Honbetsu Formation and consists of dacitic pumice flow deposits. The overlying Ikeda Formation is subdivided into two members, upper and lower. The Lower Member is characterized by a rhythmic alternation of conglomerate, sandstone and mudstone, occasionally intercalated by thin layers of tuff and lignite. This member yeilds many marine mulluscan fossils, including *Fortipecten takahashii*, etc. The upper Member above the Chiyoda pumice flow deposits (Fig. 1) consists mainly of conglomerate, intercalated thin beds of tuff and lignite. The upper half of this member yields many marine molluscs including the characteristic species of the "Setana" fauna. The uppermost formation, the Shibusan Formation, disconformably overlies the Ikeda Formation and is composed mainly of pumice flows and lacustrine deposits with thin lignite beds and contains molluscan remains at some localities.

Shibata et al. (1975, 1979) Koshimizu (1981, 1982) and Ganzawa (1983, MS) have conducted radiometric surveys of the pyroclastic deposits interbedded within the Tokachi Group and other strata. They have double-checked all of the radiometric ages of stratigraphically important pumice flows and tuff layers by means of fission-track and K-Ar age determinations, and demonstrated that they agree with one another, as shown in Fig. 1. In addition, the age of the basal beds of the Tokachi Group, lacking any radiometric dates, has been estimated from the rate of sediment accumulation within its sedimentary basin. From the ages demonstrated by radiometry and other methods, the Tokachi Group have probably deposited within an age range of about 6.0~0.7 million years: in more detail, the Honbetsu Formation is overlain by the Naka-Ashoro Pumice Flow, dated at about 4.1 million years, and from the rate of sediment accumulation, the age of the basal beds of the Tokachi Group has been estimated to be about 6.4 million years. The Ashoro Formation has an age range of about 4.1~2.7 million years, and the Ikeda Formation is estimated to have an age range of about 2.7~0.7 million years. The Chiyoda Pumice Flow situated in the boundary between the Upper and Lower Members of the Ikeda Formation is about 2.0 ± 0.1 million years: the age of this boundary corresponds approximately to the age of the Pliocene/Pleistocene or Neogene/Quaternary boundary. Also, the age of the basal beds (Meto Pumice Flow) of the Shibusan Formation, disconformably overlaying the Ikeda Formation, is about 0.7 million years.

In addition to these radiochronologic studies, Fujiwara and Yoshida of our university have been engaged in conducting paleomagnetic surveys for several years in this area (Yosida, 1982 MS; Yoshida et al., 1982). They have recognized four polarity zones within the Tokachi Group and have undertaken the correlation of the sequence with the worldwide geologic timescale using magnetostratigraphy, as shown in Fig. 1. In descending order, the first normal



Text-fig. 1. Biostratigraphic and geochronologic correlation of selected Plio-Pleistocene sequences in Hokkaido.

Legend: 1: Fission-track dates; 2: K-Ar dates; 3: *Fortipecten takahashii* occurrence; 4: Abundant molluscan fossils; 6: Presumed biostratigraphic position of upper or lower limit of the strata; 7: Conformity; 8: Unconformity; 9: Thickness in meters of the strata; Anadara: *Anadara* (*A*) *tatunokutiensis*; Fortipecten: *F. takahashii*; Dosinia: *D.* (*Kaneharaia*) *rumoiensis*; Ch. daishaka: *Chlamys daishakaensis*; Ch. cosibensis: *Chlamys cosibensis*; Profulvia: *Profulvia kurodai*; Pseudaminatis: *Pseudamiantis tauyensis.*

polarity episode is recognized in the lowest part of the Shibusan Formation and in the uppermost part of the Ikeda Formation. The second normal event with a short reversed polarity episode extends from the Lower Member of the Ikeda Formation to the upper parts of the Ashoro Formation. Each normal polarity zone may be respectively correlated to the Brunhes and Gauss Normal Epochs. The remaining polarity zone between the normal ones is characterized as a reversed or intermediate polarity zone with several short normal polarity episodes, and is correlated with the Matuyama Reversed Epoch. The second reversed polarity zone is recognized from the lower parts of the Ashoro Formation to the Honbetsu Formation, and probably correlates with an age range from the Gilbert Reversed Epoch to Epoch 5.

The above data indicate that the Tokachi Group represents nearly continuous deposition from Epoch 5 (5.7 million years ago) to the early Brunhes Normal Epoch (0.73 million years ago). In conjunction with the Neogene/Quaternary boundary, the normal polarity found at about 10 meters above the Chiyoda Pumice Flow may be correlated to the Olduvai Event (1.67~1.87 million years), and the normal magnetized Kiyoshumi Tuff may be correlated to the Jaramillo Event (0.9~0.97 million years) in the Matuyama Reversed Epoch. Consequently, taking the age of the Olduvai Event and the age of the Chiyoda Pumice Flow, 2.0 million years into consideration, the writers are strongly inclined to regard the boundary between the Upper and the Lower Members of the Ikeda Formation as being nearly coincident with the Pliocene/Pleistocene or Neogene/Quaternary boundary in Italy as reported by Nakagawa *et al.* (1976).

(2) The geological range of the Takikawa-Honbetsu and Tatsunokuchi faunas

The Takikawa-Honbetsu fauna, including the Tatsunokuchi fauna, seems to have flourished within homogeneous paleoenvironments in northern Japan, and to have the following common characteristics without regard to location, as already pointed out by Uozumi (1962).

1) Large number of individuals but rather scant number of species, a maximum of about 60 species in the Atsuga Formation, Hidaka area, central Hokkaido.

2) The number of species of Pectinidae and Mactridae greatly exceed those of the other families.

3) Abundant numbers of single valves of Pectinidae occasionally making a particular shell bed or shell biostrome.

4) Many pelecypods have large and/or heavy shells and are of shallow water aspect, as seen in the representative species, *Fortipecten takahashii* and *Anadara tatunokutiensis.*

5) Few taxa range down to the Miocene, a considerable number of species appeared and became extinct during this period, and some species occur in Recent boreal sea.

Representative species of this fauna which are widespread geographically and have large and/or heavy shells are the following: some *Anadara* species (*A. tatunokutiensis, A. amicula elongata* and *A. uozumii,* etc.), *Fortipecten* species (*F. takahashii, F. kenyoshiensis* and *F. halle*), *Dosinia tatunokutiensis* and others. However, it is not clear whether or not the first and last known occurrences of these species in the different parts of one area or in different areas are coincident in geological time. Examinated biostratigraphically within the provincial standard sequence mentioned above, *Fortipecten takahashii,* associated occasionally with *Anadara* species is observed in abundance from four horizons: the uppermost part of the Honbetsu Formation (a little below the Nakaashoro pumice flow deposits, about 3.7 million years ago); the middle parts of the Ashoro Formation; the basal parts of the Lower Ikeda Member (above the Nishinaka pumice flow deposits, 2.8 million years ago) and the uppermost part of the Lower Ikeda Member (at or very near the Chiyoda pumice flow deposits, about 2.0 million years ago). The last known occurrences of these species within the provincial standard sequence were found a little below the Chiyoda pumice flow deposits, although the upper half of the Upper Ikeda Member is composed mainly of marine deposits with many molluscan remains. Consequently, these seems to be little doubt that *Fortipecten* and *Anadara* species mentioned above ranged stratigraphically from the uppermost part of the Honbetsu Formation to the uppermost part of the Lower Ikeda Member, and have spanned during an age range of about 4.0 to 2.0 million years (radiometrically determined). Additionally, it should be kept in mind that multiple disappearances of some species, ranging upwards from

Table 1. Takikawa-Honbetsu fauna from the Atsuga Formation, central Hokkaido.

Acila(Truncacila) nakazimai Otuka
A.(T.) gottschei (Böhm)
A.(T.) sp. nov.
Yoldia(Yoldia) sp.
Megayoldia thraciaeformis (Storer)
Portlandia(Portlandia) japonica (A.Adams and Reeve)

Anadara tatunokutiensis Nomura
Glycymeris yessoensis (Sowerby)

Modiolus(Modiolus) modiolus (Linné)
Musculus(Musculus) cf. niger (Gray)
Chlamys(Azumapecten) cf. daishakaensis Masuda and Sawada
C.(Chlamys) cosibensis (Yokoyama)
Patinopecten(Mizuhopecten) sp.
Fortipecten takahashii (Yokoyama)
Monia macrochisma (Deshayes)
M. sp.

Conchocele bisecta (Conrad)
Lucinoma actilineata (Conrad)
Cyclocardia crassidens (Broderip and Sowerby)
C. crebricostata (Krause)
C. isaotakii (Tiba)
Tridonta(Tridonta) alaskensis (Dall)
T.(T.) borealis Schumacher
T.(T.) sp. nov.

Ciliatocardium cf. ciliatum (Fabricius)
Keenocardium cf. californiense (Deshayes)
Clinocardium(Clinocardium) sp.
Serripes groenlandicus (Bruguière)
Spisula(Mactromeris) polynympha Stimpson
Macoma(Macoma) calcarea (Gmerin)
M.(M.) incongrua (Martens)

Mercenaria chitaniana (Yokoyama)
Callithaca adamsi (Reeve)
Dosinia(Phacosoma) sp.
D.(Kaneharaia) rumoiensis Amano
Pseudamiantis sp.

Mya(Mya) truncata Linne
M.(Arenomya) sp.
Panomya ampla Dall
Panope japonica A.Adams

Turriyella(Neohaustator) fortilirata Sowerby
T.(N.) f. habei Kotaka

Boreoscala greenlandica (Perry)
Cryptonatica janthostomoides (Kuroda and Habe)
Crepidula cf. grandis Middendorff

Voltharpa ampullacea perryi (Jay)
Fusitriton oregonensis (Reinfield)
Helicofusus minor (Dall)
Buccinum cf. planeticum Dall
B. cf. stratissinum Sowerby
Neptunea intersculapta constricta (Dall)
N. cf. modesta (Kuroda)
Aulacofusus esychus (Dall)
A. cf. periscelidus (Dall)
Beringion sp.
Japerion sp.
Fulgoraria sp.
Turbonilla(Paramomula) sp.

Miocene, have been recognized until the uppermost part of the Lower Ikeda Member. The lower parts of the Upper Ikeda Member, about 200 meters in thickness, between the Chiyoda Pumice Flow and the Kiyosumi Tuff, are mainly composed of coarse grain materials intercalated by lignite beds and do not yield marine molluscan fossils. Meanwhile, the uppermost parts of the Upper Ikeda Member, 80 meters in thickness, are composed of marine sedimentary materials, and yield rather abundantly marine molluscs, especially *Pseudaminatis tauyensis, Nipponopagia ommaensis, Umbonium akitanum* and others. The first appearances of these species within the Tokachi Group are not only of local significance, but they seem to reflect a faunal change that is traceable over a wide area. The general aspect of the Upper Ikeda fauna can be outlined as follows. This fauna consists of intermingled cool and warm water taxa, and of those that are still living cool water taxa predominate in numbers of individual and species. Also, extinct taxa are vey small in number. Moreover, representative species of the Takikawa-Honbetsu fauna are not entirely intermingled within this fauna.

From the foregoing information, it may be said with certainty that the characteristics of the Upper Ikeda fauna correspond almost exactly to those of the "Setana" fauna from the Setana Formation. The Setana Formation was deposited under the influence of both cool and warm currents in southwestern Hokkaido. If this speculation is valid, the writers are strongly inclined to believe that the differences recognized between the Setana fauna (s.l.) and the Takikawa-Honbetsu fauna are most likely related to difference in the stratigraphic position rather than to differences of paleo-environmental conditions. More exactly, the boundary between the final disappearance of the Takikawa-Honbetsu fauna and the first appearance of the "Setana" fauna, may be situated at or very near the Chiyoda Pumice Flow, dated at about 2.0 million years ago. Strictly speaking, the "Setana" fauna (s.l.) existed within an age range of about 1.5 to 0.7 million years ago within the provincial chronostratigraphic standard sequence. However, as stated above, it is not yet clear what kind of molluscan fauna flourished during an age range of 2.0 to 1.5 million years in the lower half of the Upper Ikeda Member. If the "Setana" fauna (s.l.) ranged down into this interval, its maximum age range would be about 2.0 to 0.7 million years ago.

The correlation of selected provincial Plio-Pleistocene biostratigraphies with the chronostratigraphic standard mentioned above is shown in Fig. 1. In the eastern margin of the Tokachi area, the other *Fortipectin*-bearing formation, the Shikerepenbetsu Formation is composed of very thin marine deposits, less than 50 meters in thickness, intercalated occasionally by fossiliferous beds and tuff layers. The tuff near the fossiliferous beds, yielding *Fortipecten takahashii,* has a fission-track age of 2.4 ± 0.3 million years. This age suggests without any contradiction that this formation corresponds to the uppermost parts of the provincial standard sequence mentioned above. In central Hokkaido, westward of the Hidaka Mountain Range, the *Fortipecten*-bearing formations occur extensively in a narrow outcrop belt with a North-South trend along the western slope of this range. Such formations may extend southward far beyond the present shoreline of Hokkaido, to at least the Sanriku coast in northern Honshu (Uozumi, 1967). The Takikawa and Fukagawa Groups are known very well as the formations yielding abundant and well-preserved fossils of *Fortipecten takahashii,* and they are 780 and 1,080 meters in thickness respectively. The faunas associated with *Fortipecten* are mainly found in the lower parts of these formations, about 210 meters below the tuff dated at 4.1 ± 0.6 million years ago by fission-track determinations. The age of the basal beds of the Takikawa Group is estimated, though with some uncertainty, to be about 5.3 million years ago, and that of the Fukagawa Group is about 6.0 million years ago, judging from the rate of sediment accumulation in this region. The Atsuga Formation developed in the Hidaka region in the southern part of central Hokkaido is about 1,850 meters in thickness, and molluscan fossils associated with *Fortipecten* are found from about 250 meters below the tuff bed, dated at 5.1 ± 0.2 million years ago by the fission-track method. The upper half of this formation consists of very coarse grained materials and does not yield any marine molluscan remains. In the northern parts of central Hokkaido, the Yuchi Formation has been generally considered to be equivalent to the Takikawa-Honbetsu fauna-bearing formation. However, from the recent information, the Yuchi Formation developing near Wakkanai City, the northern boundary of Hokkaido, yields a fauna allied to the "Setana" fauna. This fauna is characterized by *Umbonium akitanum* and *Mizuhopecten poculum,* etc. (Noda *et al.,* 1982). However, a formation of the same name, occurring near Teshio-Machi, a little southward from the above-mentioned region, contains a fauna bearing *Fortipecten takahashii.* Consequently, these two formations, may not be equivalent to each other in geological age, but seem to belong to different stratigraphic horizons, as shown in Fig. 1. This misunderstanding may be related to their very similar lithofacies. The Setana Formation in southwestern Hokkaido (Oshima Peninsula) is thought to belong to the so-called "Green Tuff Region" (Minato et al., 1965) based on lithostratigraphic characteristics of the Neogene deposits. And the characters of Neogene to early Quarternary deposits and faunas are rather similar to those distributed along the Japan Sea coast in northern Honshu, but not to those of the main area of Hokkaido. Until quite recently, *Fortipecten*-bearing assemblages had not been found in this region, although such assemblages are found rather widely and abundantly in central and eastern Hokkaido, as stated above. In 1979 *Fortipecten takahashii* and *Anadara tatunokutiensis* etc. were found in the Muroran Formation distributed near Muroran City in the Green Tuff Region (Akamatsu et al., 1979). This formation is composed of marine deposits intercalated by green-coloured tuff breccia and tuff. Because of its lithofacies, this formation was long considered by Hokkaido's geologists to be equivalent to the Kuromatsunai Formation, the uppermost Miocene formation within the provincial Neogene sequence of the Green Tuff Region of Hokkaido. However, the beds of volcanic ash above the fossiliferous beds within this formation have been dated at 3.7 ± 0.4 million years by a fission-track determinations (Ganzawa, 1983 MS). Additionally, the Kuromatsunai Formation at its type locality is interbedded in its upper part with tuff having a fission-track age of 3.1 ± 0.3 million years. Strata referred to to the same formation, cropping out northward of the area of broadest distribution of the Setana Formation in the Kita-hiyama region, is interbedded near its base by tuff having a fission-track age of 4.7 ± 0.9 million years (Ganzawa, 1983 MS). Generally speaking, the Setana Formation (s.l.) and its equivalent are unconformably underlain at various localities by one of the above-mentioned formations or other older formations. From these stratigraphical and chronological relationships, there seems to be no doubt that the formations bearing the "Setana" fauna have an age no older than 3.7 million years, the age of the *Fortipecten*-bearing Muroran Formation. The "Setana" fauna, in the broad sense, may include the Tomikawa fauna, characterized by *Umbonium akitanum* and *Pseudaminates tauyensis,* etc., reported by Sakagami *et al.* (1966) and Takagi (1982 MS) from near Hakodate City, at the southern end of the Oshima Peninsula.

Based on the above-mentioned information concerning the ages of the *Fortipecten*-bearing formations in Hokkaido, the writers feel assured that the following conclusions concerning the geological range of the Takikawa-Honbetsu and the Setana faunas are correct: the Takikawa-Honbetsu fauna existed from 5.0 (6.0 maximum) to 2.0 million years ago, and the "Setana" fauna from 1.5 (2.0 maximum) to 0.7 million years ago.

The geological range of the Tatsunokuchi fauna found in the vicinity of Sendai City, northeastern Honshu may be assigned to the magnetostratigraphical interval from the early Gauss Normal Epoch down to the late Gilbert Reversed Epoch, based on paleomagnetic data of Manabe (1979, 1980). Such an age is roughly contemporaneous with that of the Ashoro Formation, about 4.1~2.7 million years ago, in the Tokachi Group, as shown in Fig. 1.

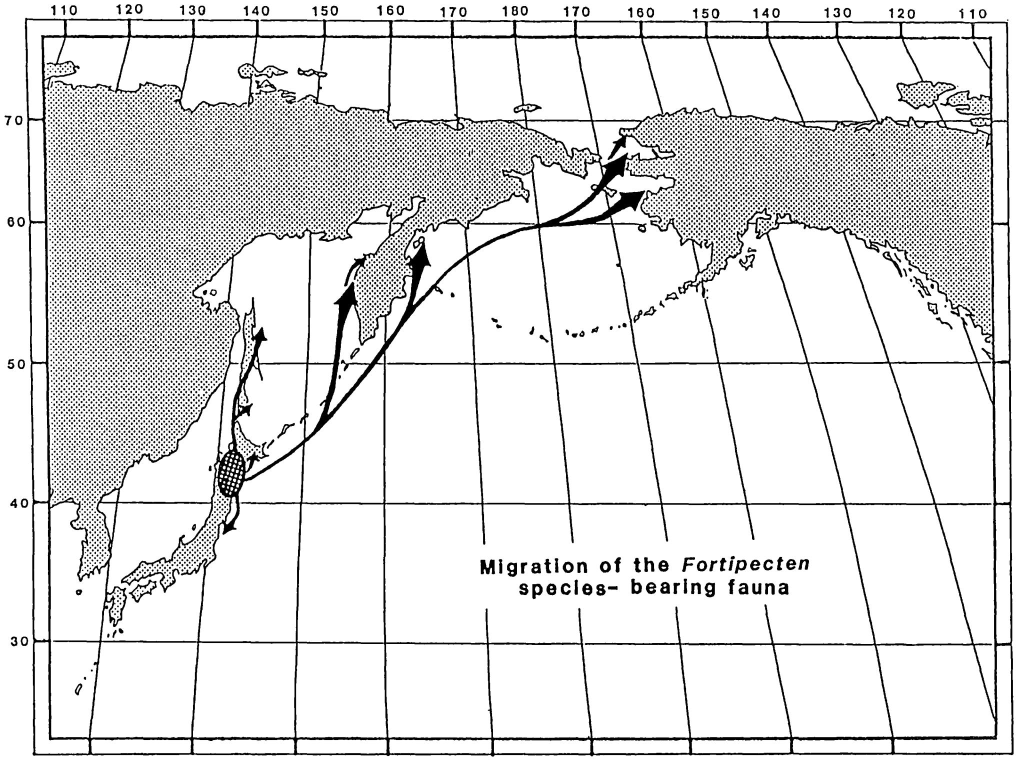
III. Origin and migration of the Takikawa-Honbetsu and the Tatsunokuchi faunas

Fortipecten takahashii, the unique hunchback-like scallop that has a very wide geographical range in Hokkaido is a most important species in the Pliocene Takikawa-Honbetsu fauna.

The genus *Fortipecten* was established on the basis of *Pecten takahashii* Yokoyama from Sakhalin by Yabe and Hatai (1940) as a new subgenus of *Patinopecten,* and raised to the rank of genus by Hatai and Nishiyama (1952). Subsequently, this genus was thought to occur only from the Pliocene deposits. In 1967 Kotaka and Noda described *F. kuroishiensis* from the middle Miocene Ogawara Formation, Aomori Prefecture, northern Honshu, which was found together with *Anadara ogawai* (Makiyama), *Chlamys cosibensis hanzawae* Masuda, *Mizuhopecten matumoriensis* (Nakamura), *Musashia desicrotata* Shikama, *Turritella fortilirata chikubetsuensis* Kotaka and *Neverita coticazae* (Makiyama) etc. Judging from this associated faunal assemblage, they stressed that the first known appearance of *Fortipecten* was undoubtedly during the middle Miocene in Japan. On the other hand, MacNeil (1967) described *Fortipecten mollerensis* from the late Miocene deposits near the Herendeen Bay, Alaska, and stated as follows: "If the known Japanese *Fortipecten* are confined to the lower half of the Pliocene, the genus may be migrant to Japan from elsewhere in the northern Pacific." However, Masuda (1978) re-examined the holotype and topotype of this species and referred it to *Mizuhopecten.* The other Alaskan species, *F. hallae* has been found in late Pliocene or earliest Pleistocene deposits on Alaskan shores both north and south of Bering Strait (MacNeil *et al.,* 1943). Furthermore, *F. takahashii, F. plutuneisis, F. kenyoshiensis* and *F. sachalinensis* have been reported from the Pliocene deposits of Sakhalin and Kamchatka by Russian geologists (Khomenko, 1931; Slodkewitsch, 1938; Ilyina, 1963; Krishtofovich, 1964; Zhidkova *et al.,* 1968).

As part of the present study, a large number of Pliocene *Fortipecten* individuals from Hokkaido, were examined and found to vary considerably in form. *Fortipecten* flourished especially well around Hokkaido at that time. However, it remains a mystery why the ancestral form of *F. takahashii, F. kuroishiensis* or its allied species, is not found in the subjacent Miocene deposits of Hokkaido, which are several thousand meters thick and yield rather abundant pectinid remains.

Fortipecten, seems to have originated in the middle Miocene and developed remarkably during the early Pliocene along the Pacific side of northern Japan. The best-known species, *F. takahashii,* seems to have migrated northward from Hokkaido through the seaway of central Hokkaido to northern Sakhalin, as shown in Fig. 3. It also probably migrated eastward along the Kurile Islands from the Hokkaido coast via Kamchatka to the Alaskan coast, and as a result of this migration, some morphological differences developed. *Fortipecten takahashii* itself has not found in Alaska, although other species occur there. The eastward invasion of this genus was restricted to be the Alaskan coast, north and south of the Bering Strait, and did



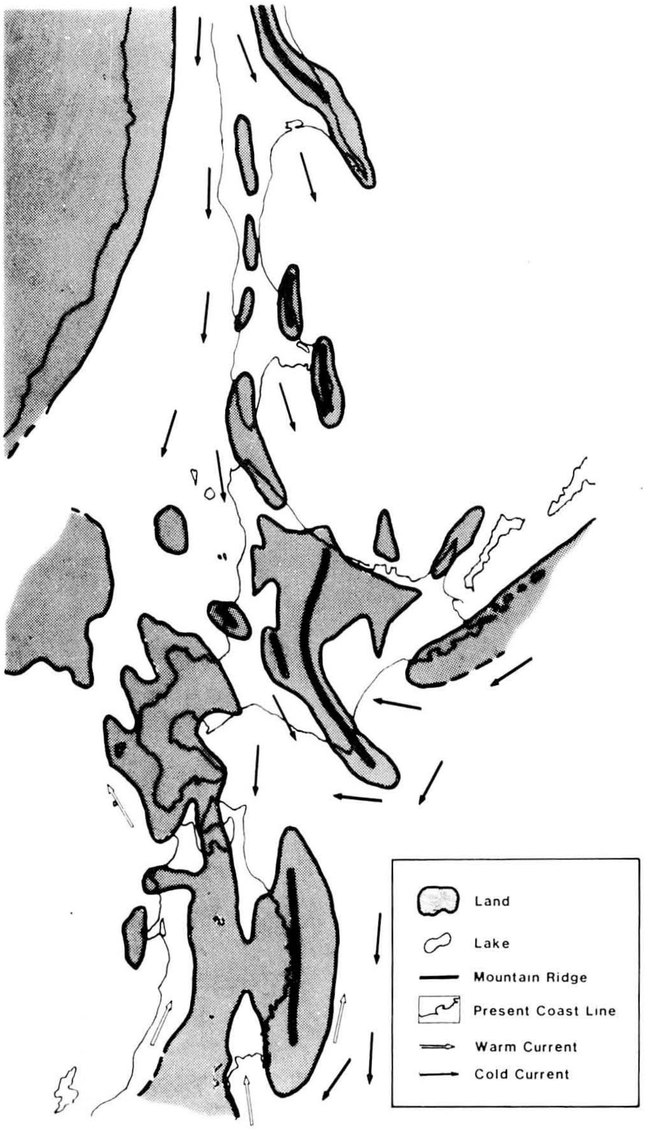
Text-fig. 2. Map showing the migration of the *Fortipecten* species-bearing fauna.

not reach very far south and north. *Fortipecten takahashii* probably was accompanied by species of *Mizuhopecten, Swiftopecten, Chlamys* and *Anadara* (*Anadara*) on this journey: these latter scallops extended as far south as northern California, while ark-shells did not reach the Alaskan coast but were confined to Kamchatka. Of course, it is likely that the Bering Strait was closed by a land bridge during the early Pliocene and late Miocene (Masuda, 1978), so that, a considerable number of species from East Asia could have migrated along that land bridge to the eastern coast of Pacific durig the Miocene to Pliocene interval.

Other species that shed light on the above interpretation of migration are the Pliocene *Anadara* species. Although it is not clear how the Kamchatkan taxon, is identified as the American species *Anadara trilineata,* is related conchologically to the Japanese species, *A. tatunokutiensis* and *A. uozumii,* the writers are inclined to believe that they are closely related to each other. This problem will be discussed when the associated fossils are reexamined in detail on a future occasion.

Taken as a whole, the Takikawa-Honbetsu fauna, with an age range of about 6.0 to 2.0 million years, does not contain typical north Pacific elements, but some survivors of the Miocene, such as *Anadara* (*Anadara*) and *Dosinia* (*Kaneharaia*) species, and some endemic genera, such as *Fortipecten* and *Pseudaminatis.* It is thought that this fauna lived within cool water currents similar to those of the present day running along the Pacific coast of eastern Hokkaido. It seems that, although water temperatures around Hokkaido indicated by this fauna differed little from present day temperatures, the cool water currents extended farther southward in the western Pacific at that time. This cool water extended from North Sakhalin via central Hokkaido to the vicinity of Sendai City, northeastern Honshu, and converged with the warm current near 38°N latitude. It is thought that the cool water conditions, which gradually develop from Miocene warm water conditions, would have persisted with little change during the lengthy interval from 6.0 to 2.0 million years, and that such conditions were favorable to the appearances of the characteristic Pliocene genera and species of Hokkaido.

The succeeding "Setana" fauna that lived during the interval of about 2.0 to 0.7 million years is largely composed of species still living in the Japan Sea, southwestern Hokkaido, and



Text-fig. 3. Paleogeography and current systems during the Takikawa-Honbetsu-Tatsunokuchi faunal Epoch (Pliocene).

contains a few extinct species, including *Chlamys diashakaensis, C. cosibensis, Pseudaminatis tauyensis* and *Umbonium akitanum.* The writers assume that this fauna lived in water that was cool, but still a slightly warm than that of the Takikawa-Honbetsu fauna. This fauna contains intermingled cool and warm elements. In other words, the waters adjacent to Hokkaido at that time were mixed alternately with the cool and warm currents from the side of the Japan Sea or the Pacific Ocean, and two currents intermingled in this area. Some limited marine transgressions might have connected with the Japan Sea and the Pacific Ocean through Hokkaido, as shown in Fig. 4. Cool water currents ran down further southward along the Japan Sea side and facilitated the migration of cool water elements, such as *Astarte, Tridonta*

Text-fig. 4. Paleogeography and current systems during the "Setana" faunal Epoch (Early Pleistocene).

and *Mercenaria,* etc., that are found in the Uonuma Group, Niigata Prefecture, northern Honshu (Kobayashi, 1983). At the same time, the warm water currents ran up eastward farther along the Pacific side, and facilitated the migration of warm water elements, including *Anadara, Pseudaminatis* and *Umbonium* etc., which are found in the upper parts of the Ikeda Formation, Tokachi area, eastern Hokkaido (Akamatsu, 1986 MS). Also, from the prevailing southward cool currents, it appears that the ancestral Bering Strait marine passageway first opened up narrowly at that time, but the passageway had little direct effect upon the adjacent faunas around Hokkaido. In general, the present geomorphological reliefs and geography were produced, on the whole, by the variations in the degree of uplift of the Pliocene broad and flattish epicontinental sea floor: the uplift tends to be greater on the present land and subdued in the submerged area. Marine incursions which subsequently flooded the rising epicontinental sea floor were the result of the global sea level rises which more than compensated for upwarping. With some reservation, the writers suggest that the present straits and some parts of the adjacent lowlands around the Japan Islands, Soya, Tsugaru and Korea Straits, were, like the Bering Strait, flooded by under the sea at nearly the same time (Uozumi, 1967). The opening of these straits altered the pattern of cool and warm currents and had a considerable effect upon the adjacent faunas of Hokkaido and north Honshu. Some Mio-Pliocene eastward migrants from north Japan probably retreated westward, with the lowering of water temperatures, from the Alaskan and/or Kamchatkan coast before the end of the Pliocene, and thereupon were replaced by the species that still live in nearby waters. The retreated taxa returned and survived again in the adjacent waters of northern Japan or became extinct by the end of Pliocene. Some suggestions of such eastward invasion followed by a westward retreat to north Japan are furnished by species of *Anadara* (*Anadara*), *Swiftopecten* and *Chlamys,* etc., the Plio-Pleistocene species of *Anadara* (*Anadara*) in Hokkaido are the representative survivors, similar to the *Swiftopecten* species and *Chlamys consibensis,* etc., which accommodated themselves to the lowered water temperatures in northern Japan during Miocene to early Pliocene time. Such taxa spread themselves widely eastward along the coast of North Pacific during the Pliocene, and returned again to reside, with a little morphological variations, in the adjacent waters of Hokkaido until the early Quaternary period.

The faunas in the Shibusan Formation and its equivalents, having a radiometric age of 0.7 million years, consist largely of species that continue to inhabit the cold waters of the northern hemisphere, north of Hokkaido. Such faunas contain species represented by very large numbers of individuals such as *Chlamys islandica, Tridonta borealis* and *T. alaskensis,* etc., but contain almost no extinct species. They may be coeval with the molluscan fauna from the *Mammuthus*-bearing Shimonopporo Formation in central Hokkaido (Akamatsu *et al.,* 1981), although the Quaternary faunas, estimated to have existed since about 0.7 million years, will be discussed in detail in future reports. Concerning this Shimonopporo faunal assemblage, the present writers assumed that the spectacular southward migrants of the North Pacific-related molluscs, at about 0.7 million years ago, into northern Japan must have resulted from the prevailing southward cold currents coming through re-opened seaway across Beringia. After this, the adjacent molluscan faunas around northern Japan were largely affected by the intermittent opening and closing of Bering Strait resulting from the climatic fluctuations that repeatedly produced extensive glaciations.

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Plate 19

Explanation of Plate 19

(All figures in natural size, unless otherwise stated)

Fig. 1. *Chlamys (Chlamys) consibensis* (Yokoyama)
Left valve, Loc. Tomikawa, southwestern Hokkaido, Tomikawa Formation.

Fig. 2. *Fortipecten takahashii* (Yokoyama)
Right valve, Loc. Numata, central Hokkaido, Horokaoshirarika Formation. x0.7.

Fig. 3. *Dosinia (Phacosoma) tomikawensis* Takagi
Right valve, Loc. Tomikawa, southwestern Hokkaido, Tomikawa Formation.

Fig. 4. *Tridonta (Tridonta) alaskensis* (Dall)
Right valve, Loc. Higashi-Setana, southwestern Hokkaido, Setana Formation.

Figs. 5–6. *Umbonium (Suchium) akitanum* Suzuki
Fig. 5, Loc. Moacha, eastern Hokkaido, Upper Part of Ikeda Formation, x2; Fig. 6, Loc. Tomikawa, southwestern Hokkaido, Tomikawa Formation. x2.

Fig. 7. *Tridonta (T.) borealis* Schumacher
Loc. Tomikawa, southwestern Hokkaido, Tomikawa Formation.

Fig. 8. *Anadara (Anadara) uozumii* Noda
Left valve, Loc. Utanobori, nothern Hokkaido, Shibiutan Formation.


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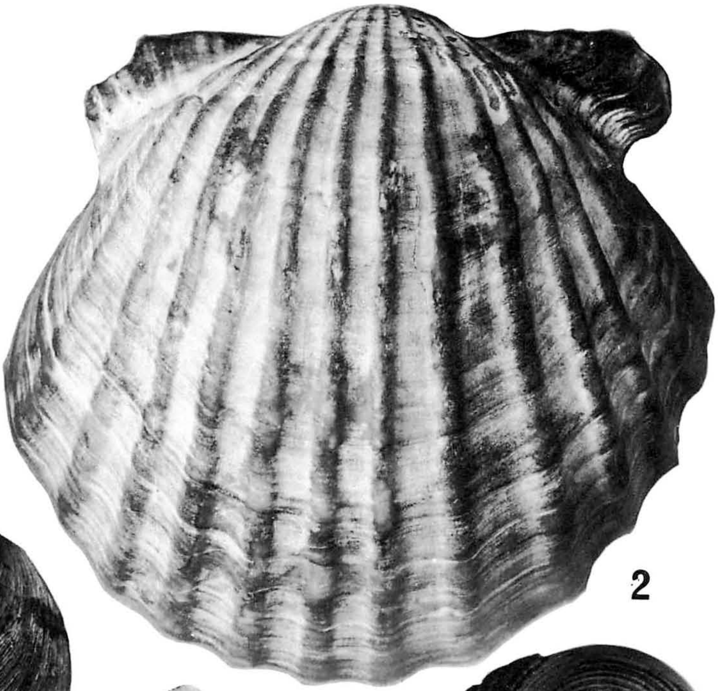
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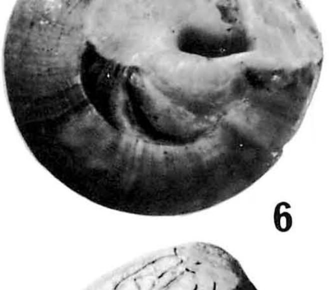
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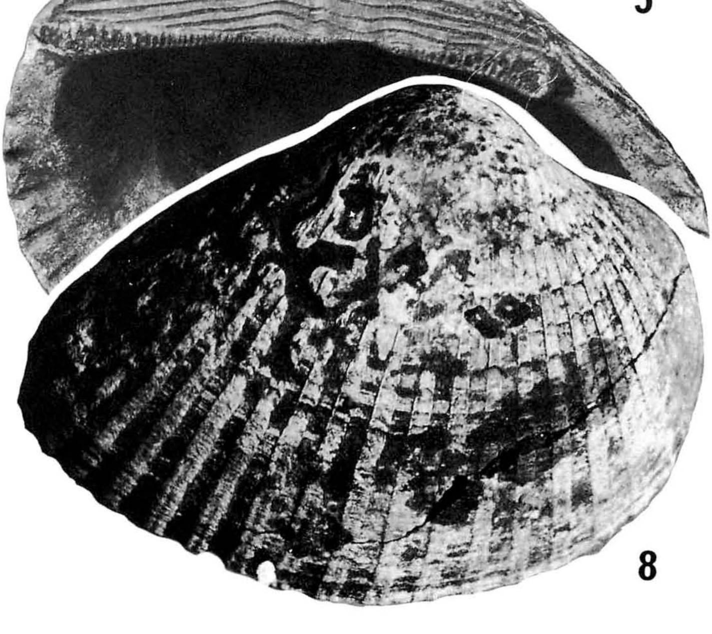
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Plate 20

Explanation of Plate 20

(All figures in natural size, unless otherwise stated)

Fig. 1. *Profulvia kurodai* (Sawada)
Left valve, Loc. Kuromatsunai, southwestern Hokkaido, Setana Formation.
Fig. 2. *Acila (Truncacila) gottschei* (Böhm)
Right valve, Loc. Atsuga, central Hokkaido, Atsuga Formation.
Fig. 3. *A. (T.) nakazimai* Otuka
Right valve, Loc. Tomikawa, southwestern Hokkaido, Tomikawa Formation.
Fig. 4. *Rectiplanes sanctioannis* (Smith)
Loc. Tomikawa, southwestern Hokkaido, Tomikawa Formation. x1.5.
Fig. 5. *Aforia diomedea* Bartsch
Loc. Tomikawa, southwestern Hokkaido, Tomikawa Formation. x1.5.
Fig. 6. *Anadara (Anadara) tatunokutiensis* Nomura
Right valve, Loc. Atsuga, central Hokkaido, Atsuga Formation.
Fig. 7. *Rectiplanes contraria* (Yokoyama)
Loc. Tomikawa, southwestern Hokkaido, Tomikawa Formation. x1.2.
Fig. 8. *Pseudaminatis tauyensis* (Yokoyama)
Right valve, Loc. Moacha, eastern Hokkaido, Upper part of the Ikeda Formation.
Fig. 9. *Panomya ampla* Dall
Right valve, Loc. Atsuga, central Hokkaido, Atsuga Formation.
Fig. 10. *Chlamys (Chlamys) daishakaensis* Masuda & Sawada
Left valve, Loc. Kuromatsunai, southwestern Hokkaido, Setana Formation.


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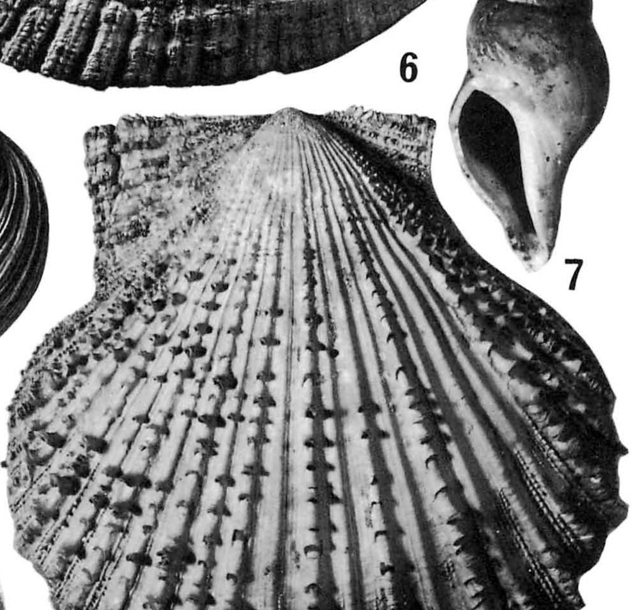
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NOTES ON ORIGIN AND MIGRATION OF THE OMMA-MANGANZIAN FAUNA, JAPAN

By

Kenshiro OGASAWARA

Introduction

A specific set of steps should be followed to understand the origin and migration of a fossil fauna. A "fauna" is used here as an assemblage of species interconnected in a consistent ecological relationship. By analogy with the modern fauna, such an assemblage can be recognized as a biological unit (community) that occupied a particular environment. It is reasonable to consider that a fossil fauna had a developmental history from first appearance through developing, optimum and declining stages, to extinction. Such changes seem likely to correspond to changes in environmental conditions. In other words, the faunal assemblage serves as a key for the interpretation of paleoenvironments and, in addition, it is a more reliable unit than are single species for paleoenvironmental interpretation. Of course, when considering the origin of a fauna, phylogenetic studies of the individual taxa are a desirable basis, but unfortunately, the phylogeny of most molluscan groups is poorly known. In these circumstances, paleoenvironmental and paleozoogeographical studies are almost the only sources of information on the origin of a fauna.

The name Omma-Manganzian fauna (Onma-Manganjian fauna) was originally proposed by Otuka (1936, 1939a, b), for a "Molluscan fauna that invaded the Sea of Japan from the North, comparable with the Recent Oyashio current, and corresponding to a so-called Pliocene transgression". This concept has been accepted by many geologists and paleontologists and has frequently been discussed from such points of view as paleogeography, paleoclimatology, paleoecology, and systematic paleontology. Thus, the literature concerning the Omma-Manganzian fauna consists of more than 300 papers published during the last fifty years.

Recent progress in the study of Japanese Cenozoic bio- and chrono-stratigraphy (Ikebe *et al.,* 1972; Tsuchi edit., 1979, 1981a, b, etc.) provides many new data and interpretations for consideration of the paleozoogeography of this fauna and of its distribution in time and space.

The Omma-Manganzian fauna occurs from the Cheju Islands of southern Korea through the borderland of the Japan Sea to Hokkaido. Also, some Omma-Manganzian faunal elements have been recorded not only from the area of the Japan Sea borderland but also from the Pacific Sea coast of northern Japan, in the Kanto region, the Sannohe area, and the Hamada area of Aomori Prefecture and also, tentatively, from the Kuril Islands, USSR. However, as the Omma-Manganzian fauna is defined somewhat differently by different investigators, the fundamental elements of the fauna will be summarized in the present article.

The framework of Japanese Neogene molluscan biostratigraphy and paleozoogeography was outlined by Masuda (1963, 1973b), and recently Chinzei (1978) synthesized its chronology and paleoecology, based mainly on the new data of Ikebe and Tsuchi mentioned above. According to this new interpretation, the formation containing the Omma-Manganzian faunal elements can be assigned to the Pliocene to Early Pleistocene, although there is still some confusion on the correlation of some geological sections in northern Japan that might have been influenced by cool or cold water masses. In the present article, the writer wishes to discuss the origin and migration of the Omma-Manganzian fauna in the strict sense, which is correlatable with the Tatsunokuchi and Kakegawa faunas, as pointed out by Masuda and Ogasawara (1981).

Characteristics of the Omma-Manganzian fauna

The faunal characteristics of the Omma-Manganzian fauna are reconsidered to give a useful definition of the fauna, by a comparison with the cold-water Tatsunokuchi and warm-water Kakegawa faunas.

Otuka (1939b) originally stated that the Omma-Manganzian fauna is composed of 201 species, of which 101 species are extinct. This was calculated from faunal lists reported from various localities along the Japan Sea by Yokoyama (1923a, 1926, 1927), Onoyama (1933), Otuka (1936, 1939a) and Nomura (1937). However, more recent work shows that the number of molluscan species in the fauna is more than 250 and less than 300 species, although not all small shells are fully identified.

The ratio of extinct species, shown in Table 1, is about 20 per cent. Among them, some species are recorded only from a portion of the faunal province, which extends for about 1500 km along the Japan Sea. Such local phenomena will be discussed later from a paleozoogeographical point of view. Among the extinct species, *Turritella saishuensis* is the most significant fossil for recognizing not only the zoogeographical character, but also the stratigraphic horizons of the Omma-Manganzian fauna. This species was originally described by Yokoyama (1923) from the Seikiho Formation of Saishu Island (in the Cheju Islands off southern Korea), and later has been recorded from Otuka's Omma-Manganzian province by many molluscan paleontologists. Kotaka first established the phylogenetic systematics of the *Turritella saishuensis* Bioseries, which began with the ancestral *T. saishuensis motidukii,* and continued through *T. saishuensis saishuensis, T. saishuensis etigoensis, T. otukai,* and *T. andenensis*

Table 1. Extinct species of the Omma-Manganzian fauna.

Bivalvia	Gastropoda
Acila nakazimai Otuka	*Umbonium akitanum* Suzuki
Portlandia hirosakiensis Iwai	*Turritella saishuensis motidukii* Otuka
Limopsis tokaiensis Yokoyama	*T. s. saishuensis* Yokoyama
Anadara amicula elongata Noda	*T. s. etigoensis* Ida*
A. a. rotunda Noda	*Trophonopsis kagaensis* Hatai et Nisiyama
A. ommaensis Otuka	*Searlesia japonica* Yokoyama
A. pseudosubcrenata Ogasawara*	*Fulgoraria masudae* Hayasaka
Chlamys cosibensis (Yokoyama)	*Ophiodermella ogurana* (Yokoyama)
C. daishakaensis Masuda et Sawada	*O. maekawaensis* Hatai, Masuda et
C. foeda (Yokoyama)	*Mesalia ommaensis* Ogasawara Suzuki
Pecten naganumanus Yokoyama	*Tachyrhyncus venustellus* (Yokoyama)
Mizuhopecten yessoensis yokoyamae (Masuda)	*T. turberculosus* (Yokoyama)
M. tokyoensis hokurikuensis (Akiyama)*	*Bittium horinjiense* Oinomikado et Ikebe
M. poculum (Yokoyama)	*Epitonium yabei echigonum* Kanehara
Yabepecten tokunagai (Yokoyama)	*Babylonia elata* (Yokoyama)
Cyclocardia ferruginea complexa (Ogasawara)	*Cancellaria kobayashii* (Yokoyama)
C. f. orbicularis (Yokoyama)	*Menestho incisa* (Yokoyama)
C. myodadaniensis (Itoigawa)	*Turbonilla inscitula* Yokoyama
Megacardita ommaensis (Ogasawara)	*Crassispira pseudoprincipalis* (Yokoyama)
Clinocardium chikagawaense Kotaka	*Bittium yokoyamai* Otuka
C. fastosum Yokoyama	*Natica tugaruana* Nomura et Hatai
Nipponopagia ommaensis Ogasawara	*Alvania akibai* Yokoyama
Pseudamiantis tauyensis (Yokoyama)	*Indomitrella tokyoensis* (Yokoyama)

* : younger Ommaian elements

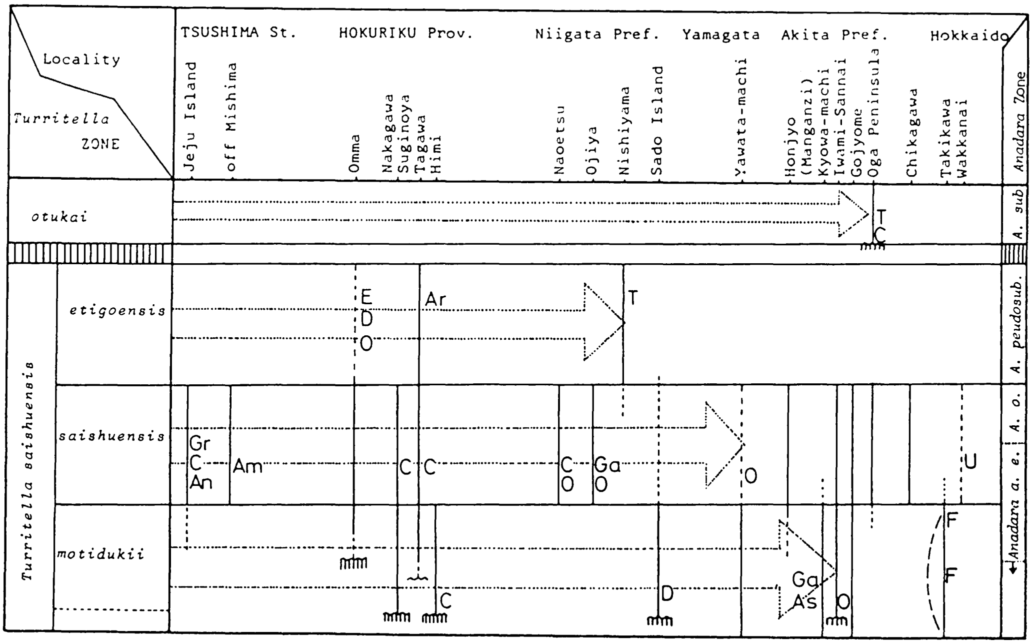
(Kotaka, 1959, 1960, 1973, 1978, 1981, etc.). The first three subspecies of *Turritella saishuensis* are indexes for the biozone and have been recorded from sandy sediments of the Japan Sea borderland (Kotaka and Ogasawara, 1977; Ogasawara, 1981, 1983).

Based mainly on the *Turritella saishuensis* biozones, the Omma-Manganzian fauna can be divided into three zones. The uppermost of these zones (characterized by *T. saishuensis etigoensis*) is the horizon of the younger Ommaian fauna (Ogasawara, 1981), and the lower two comprise the Omma-Manganzian fauna in the strict sense (Fig. 1).

The younger Ommaian fauna contains only a few extinct forms, as shown in Table 1, while the Omma-Manganzian fauna proper contains at least 45 extinct species or subspecies.

For the Omma-Manganzian fauna, two important observations have been made by the writer (Ogasawara, 1977, 1981, 1983) and Masuda and Ogasawara (1981). The first one is the occurrence of warm water species in the Omma-Manganzian fauna, and the second is the presence of faunas with mixed elements of the Omma-Manganzian fauna and the Kakegawa and Tatsunokuchi faunas. Some interpretations of these phenomena are given by the writer (Ogasawara, 1981, 1983), but a more detailed discussion follows.

Based on numerous publications on molluscs, some genera and species such as *Anadara, Glycymeris*, some pectinids, *Cyclocardia, Astarte, Turritella*, etc. have been selected from the



ꟷ : Unconformity
Gr : *Glycymeris rotunda*
C : *Cryptopecten vesiculosus*
An : *Ancilla okawai*
Am : *Amussiopecten praesignis*
E : *Endemoconus sieboldii*
D : *Doxander japonicus*
O : *Oliva mustelina*
Ar : *Architectonica* sp.
T : *Tucetilla pilsbryi*
Ga : *Glycymeris albolineata*
As : *Anadara (Scapharca) satowi*
U : *Umbonium akitanum*
F : *Fortipecten takahashii*
Anadara a. e. : *Anadara amicula elongata*
A. o. : *Anadara ommaensis*
A. peudosub. : *Anadara pseudosubcrenata*
A. sub. : *Anadara subcrenata*

Text-fig. 1. The relationship between *Turritella* zones and warm-water molluscan elements along the Japan Sea borderland during the Pliocene and Early Pleistocene; arrows indicate warm-water intermingling.

Table 2. Comparison of the Omma-Manganzian molluscan elements along the Japan Sea borderland.

Area	Tsushima St.		Hokuriku			Niigata			Yamagata		Akita					Aomori				Hokkaido			USSR	
Locality / Species	Cheju Islands	off Mishima	Omma Formation	Jyunicho Formation	Nakagawa Formation	Byobedani Formation	Nishiyama Formation	Sawane Formation	Kannonji Formation	Sakekawa Formation	Manganji	Kyowa-machi	Sasaoka(Tofuiwa)	Gojyome	Futatsui	Hirosaki	Hamada Formation	Sannohe	Togawa Formation	Setana Formation	Takikawa Formation	Tenpoku area	Sachalin	Kuril Islands
Anadara																								
amicula elongata			●	○		○						○									●			
amicula rotunda												○	●	●										
amicula (s. l.)		●		●		●						●	●		●	●								
ommaensis			●								●	○	●											
tatunokutiensis																		●						
sp.		●	●				●		●			●		●	●								●	
Glycymeris																								
yessoensis	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●			●	
nipponica									○			●	●	●		●	●		●					
echigoensis												●												
rotunda	●		●										●											○
vestita				○							●			●										
sp.			●					●		●		●		●										●
Chlamys																								
cosibensis	●		●	●	●	●	●	●		●	●	●				●	●			●				●
daishakaensis				●				●		○		●				●	●	●		●				
nipponensis		●	●	●	●	●					●									●			●	●
foeda								●																
imanishii																	●			●				
sp.																	●	●		●				●
Swiftopecten swiftii				●		●	●	●							●	●	●			●			●	●
Cryptopecten vesiculosus	●			●	●	●		●																
Pecten																								
albicans	●		●						●															
naganumanus	●		○																					
Mizuhopecten																								
yessoensis yessoensis			●							○				●		●				●			●	
yessoensis yokoyamae		○	●	●	●	●		●	●			●					●		●					●
tokyoensis hokurikuensis	●	●	●	●	●	●	●						●				●			●				
poculum							●	●			●	●	●	●	●	●					●	●		
sannohensis																		●						
Yabepecten tokunagai				●				●	●	●			●			●	●		●	●				●
Amussiopecten praesignis		●																						
Fortipecten takahashii																		●	●		●	●	●	
F. kenyoshiensis																		●						
Megacardita																								
ommaensis			●	●								○												
corrensis	●																							
ferruginosa				●		●														●				
sp.	●																●							
Cyclocardia																								
ferruginea ferruginea		○					●				●				●	●	●		●		●		●	●
ferruginea orbicularis			●						●															
ferruginea complexa			●																					
ferruginea ochiaiensis																		●						
myogadaniensis			●				●										●							
aomoriensis													●					●			○			
crebricostata																●	●	○		●		●	●	●
crassidens																	○							●
Astarte																								
alaskensis				●			●	●						●		●				●			●	
borealis			●	●	●			●	●		●			●	●	●		●		●		○		●
hakodatensis				●			●				●													
aomoriensis																●								
Umbonium akitanum			●								●	●	●	●	●									
Turritella																								
saishuensis saishuensis	●	○	●	●	●	●	●	●			●	●		●		●	●		○					
saishuensis motidukii			●	●				○	●					●	●	●					●			
nipponica														●	●		●			●				
fortilirata habei																●	●			●				
fortilirata (s. l.)										●						●		●			●	●	●	
Faunal division	Southern		Central											Northern (Mixed)									Kuril	

○ : cf. species

Omma-Manganzian horizon proper and its equivalent horizons, and defined as the *Turritella saishuensis motidukii* and *T. saishuensis saishuensis* biozones (Table 2). Fossil localities are arranged from the Cheju Islands in the south to the Kuril Islands in the north, and among them are some localities such as Sannohe, Togawa and Takikawa that yield Tatsunokuchi faunal elements. Occurrences of species at each locality have been recorded, to show the geographical distribution of the species, including specimens from various lithofacies and adjacent horizons. Therefore, in the strict sense these sets of species are different from the faunal assemblages or communities reported by Chinzei (1973), Ogasawara (1977), Honda (1978), and Shimamoto (1984).

Typical sets of Omma-Manganzian species are recognized in Hokuriku area and Akita Prefecture, which include the type localities of the Omma fauna and the Manganzi fauna of Otuka (1939b), respectively. The typical assemblage includes *Anadara amicula elongata, A. ommaensis, Glycymeris yessoensis, Chlamys cosibensis, C. daishakaensis, Mizuhopecten yessoensis yokoyamae, M. tokyoensis hokurikuensis, M. poculum, Yabepecten tokunagai, Astarte borealis, Umbonium akitanum* and *Turritella saishuensis.*

Within the faunal province, except for a few localities yielding *Fortipecten* species, there is some variety in groups of species and subspecies, particularly in *Glycymeris,* some pectinids, *Cyclocardia,* and *Turritella.* For example at the Cheju Islands and off Mishima, *Cryptopecten vesiculosus, Amussiopecten praesignis* and *Megacardita coreensis* are noteworthy species, because these species have previously been considered to be characteristic elements of the warm-water Kakegawa fauna. Moreover, some warm-water species as *Ancilla okawai* and *Megacardita* n. sp. are reported from the Cheju Islands (Yoon, 1981). Among these just cited, *Cryptopecten vesiculosus* can be traced northwards to the Sado Islands, as shown in Fig. 1.

In northern Akita and Aomori prefectures, the *Turritella saishuensis* group occurs with *Anadara amicula* (s. l.), *Glycymeris nipponica, Chlamys imanishii, Cyclocardia crebricostata, Turritella nipponica,* and *T. fortilirata habei.* These combination of species are slightly different from those of the Hokuriku and southern Akita areas.

In more northern areas, *Turritella saishuensis* (s. l.), is not known except at Takikawa and a few other localities, where *Turritella saishuensis motidukii* occurs with *Fortipecten takahashii.*

In general, *Turritella* species are very significant for zoogeographical considerations, especially along the northern border of the Omma-Manganzian faunal province. *Turritella saishuensis* of the southern areas is replaced by *T. fortilirata* in northern districts and is associated with *T. nipponica* around northern Akita and Aomori prefectures.

In northern areas, *Fortipecten takahashii,* which is the most characteristic element of the Tatsunokuchi fauna (and the Takikawa-Honbetsu fauna), occurs in association with *Mizuhopecten poculum, Chlamys daishakaensis, Yabepecten tokunagai, Mizuhopecten yessoensis yokoyamae,* and others in Aomori Prefecture and on Hokkaido. Among these, all species except for *Fortipecten takahashii* have been assigned as index species of the Omma-Manganzian fauna, and Masuda and Ogasawara (1981) pointed out that the molluscs cited above can be considered as a mixed fauna of the Omma-Manganzian and Tatsunokuchi faunas.

It is important to define reliably the characteristic elements of the Omma-Manganzian fauna. The writer considers that the geographic extent of Otuka's Omma-Manganzian fauna is very similar to the distribution of *Turritella saishuensis saishuensis,* and that of *Yabepecten* *tokunagai, Mizuhopecten yessoensis yokoyamae, M. tokyoensis hokurikuensis,* and *Anadara* species also are important elements of the fauna. These pectinids and *Anadara* species are useful as indexes of the Omma-Manganzian fauna because they have the same geographical distribution pattern as that of *Turritella saishuensis,* although they have not actually been recorded at the same sites as *Turritella saishuensis*; i.e., they occupied different ecological niches than *T. saishuensis,* but lived throughout the same geographic area.

Consequently, an assemblage of species occurring in the Kuril Islands (Zhidkova *et al.,* 1982), and including *Yabepecten tokunagai,* can be tentatively regarded as belonging to the Omma-Manganzian fauna.

As stated above, there is some variety in assemblages within the Omma-Manganzian fauna. This appears to result from interaction with a warm-water fauna at the southern margin and a cool or cold water fauna at the northern margin of the province.

In general aspect, the Omma-Manganzian faunal province can be divided into three or four subprovinces. One is the southern subprovince, which is represented at two localities, in the Cheju Islands and off Mishima Island (Text-fig. 4, loc. no. 15). This subprovince is characterized by some warm-water molluscan elements such as *Amussiopecten praesignis, Pecten naganumanus, Ancilla okawai,* etc. The second subprovince is the central one, which can be traced from Omma (Text-fig. 4, loc. no. 16) to Sasaoka (Text-fig. 4, loc. no. 29), and is characterized only by the occurrence of *Turritella saishuensis* (s.l.) (i.e., without any other turritellid species). The third subprovince is the northern one, represented by localities at Gojome, Futatsui, Hirosaki, Hamada, and Setana (Text-fig. 4, loc. nos. 31–36 and 44–46). The northern subprovince is characterized by *Turritella nipponica* or *T. fortilirata habei, Chlamys* species such as *Chlamys imanishii* and the *C. islandica* group, and by *Cyclocardia crebricostata* and *C. paucicostata.*

The fourth is the Kuril subprovince, which is included only tentatively, because the composition and distribution of this fauna are not well known.

Comparison with faunas along the Pacific coast

According to many publications, the number of species in the warm-water Kakegawa and cold-water Tatsunokuchi faunas can be estimated at about 250 and 50, respectively. From these, characteristic genera and species have been selected for comparison in the same manner as for the Omma-Manganzian fauna (Table 3).

Localities are arranged from south to north along the Pacific coast of the Japanese Islands. Selected species on the left side are subtropical or warm-water indicators which have been considered typical species of the Kakegawa fauna (Otuka, 1939b; Makiyama, 1927, 1931; Yokoyama, 1923b). The species on the right side are cool or cold indicators. From this it is easy to determine typical sets of species.

For example, at the type locality of the Kakegawa fauna (in Shizuoka; the so-called Dainichi fauna), *Anadara castellata, A. suzukii, Glycymeris totomiensis, G. rotunda, Chlamys satoi, Mizuhopecten tokyoensis hokurikuensis, Cryptopecten vesiculosus, Amussiopecten praesignis,* and *Turritella perterebra* are the characteristic species. Also in Sendai, the typical Tatsunokuchi fauna consists of *Anadara tatunokutiensis, Glycymeris gorokuensis, Chlamys sendaiensis, Fortipecten takahashii, Dosinia tatunokutiensis,* and so on.

As noted above, the Kakegawa and Tatsunokuchi faunas are each characterized by some species that do not occur in the other fauna, although it is difficult to know how to interpret

Table 3. Comparison of molluscan elements between the Omma-Manganzian and Kakegawa, Tatsunokuchi faunas along the Pacific Ocean.

Region	SW Japan					Kanto				Tohoku							Hokkaido			Region
Location / Characteristic species (warm water elements)	Okinawa	Tanegashima	Miyazaki	Kochi	Shizuoka	Yamanashi	Kanagawa	Boso(Chiba)	Choshi	Ibaragi	Hirono	Namie	Sendai	Koromogawa	Gobanshoyama	Sannohe	Mutsu	Takikawa	Honbetsu	Akan	Location / Characteristic species (cool water elements)
Anadara																					*Anadara*
castellata			O		O																
suzukii		X		O	O																
						●				●	●						X	●			*amicula elongata*
													●		●	●		●			*tatunokutiensis*
Glycymeris																					*Glycymeris*
nakamurai			O	O	O																
totomiensis			O		O																
yamaguchii												O									
rotunda	O		O		O																
													●		●			●			*gorokuensis*
																●	●				*yessoensis*
Chlamys																					*Chlamys*
miurensis							O	O	O		O										
satoi	O		O	O	O																
							●		●		●				●		●				*cosibensis*
											●						●				*daishakaensis*
													●	●							*sendaiensis*
									●												*foeda*
Mizuhopecten																					*Mizuhopecten*
planicostulatus							O														
tokyoensis hokurikuensis		O	O					O			O										
										X				X	X		●		X	X	*yessoensis yokoyamae*
														●			●				*poculum*
Cryptopecten vesiculosus	X	O	O		O		O	O			O										
															●		●			●	*Swiftopecten swiftii*
Amusium pleronectes	O		O																		
											●					●	●				*Yabepecten tokunagai*
Amussiopecten praesignis	O	O	O	O	O	O	O	O													
											X	●	●	●	●	●		●	●	●	*Fortipecten takahashii*
		X	X						X			●			X	X					*Dosinia japonica*
													●			●					*D. tatunokutiensis*
Turritella																					*Turritella*
perterebra				O	O																
totomiensis					O																
														●			●				*saishuensis*
											●					●	●				*fortilirata habei*
							●									●	●				*nipponica*

▭ : Type locality (location) X : cf. species

the occurrence of these species in the transitional area. The transitional-zone species are *Mizuhopecten yessoensis yokoyamae, Chlamys cosibensis, C. foeda,* and *Anadara amicula elongata* in the Kanto region. To these occurrences, Masuda (1963, 1973b) gave the name Kanto-Hokuriku faunal province, as similar specific compositions are observed in the Naarai Formation of the Choshi area and in the Omma Formation of Hokuriku area. Also, Noda and Amano (1977) proposed the name "Transitional Zone" for them, meaning a transitional biofacies between the Kakegawa and Tatsunokuchi faunal provinces, based mainly on occurrence of *Anadara amicula elongata* at some localities in the Kanto region.

In general, a faunal province can be recognized only by the continuous geographical distribution of some genera and species, or by breaks in the fauna's distribution in time and space. Therefore, it is rather difficult to apply the same name for isolated areas or horizons without detailed reasons. However, the writer proposes to name the transitional fauna as the Kanto-type subprovince of the Omma-Manganzian faunal province, because its characteristic elements can be correlated with those of the northern Omma-Manganzian subprovince recognized around Aomori Prefecture.

Paleozoogeography and paleocurrent reconstruction

For a benthic species, understanding migration routes and environmental conditions are fundamental to explain its distribution pattern. Based on the molluscan faunas listed above, the writer proposes an approximate pattern of current directions which might have permitted larvel dispersal of the Omma-Manganzian province.

Concerning the northern molluscan elements, several papers have described the paleontological and geological significance of fossil species. Among them, Chinzei's synthesis (1978) and Masuda's papers on such pectinids as *Chlamys cosibensis, Fortipecten* species, and so on (1962a, b, 1973a, 1978, 1983, etc.) provide important clues to understanding the migration process and paleoenvironments in the Northern Pacific region.

Chinzei (1978) pointed out that the differences between the Tatsunokuchi and Omma-Manganzian faunas can be explained by the embayment environment of the former and the off-shore environment of the latter. Also, the writer considers that these two faunas can be assigned to the cool or cold water type, in the broad sense. However, as noted before, the Omma-Manganzian fauna consists of assemblages of southern, central and northern types. Thus, to arrive at another reasonable explanation for these differences between the Tatsunokuchi and Omma-Manganzian faunas it is necessary to understand their paleozoogeography and paleoenvironments.

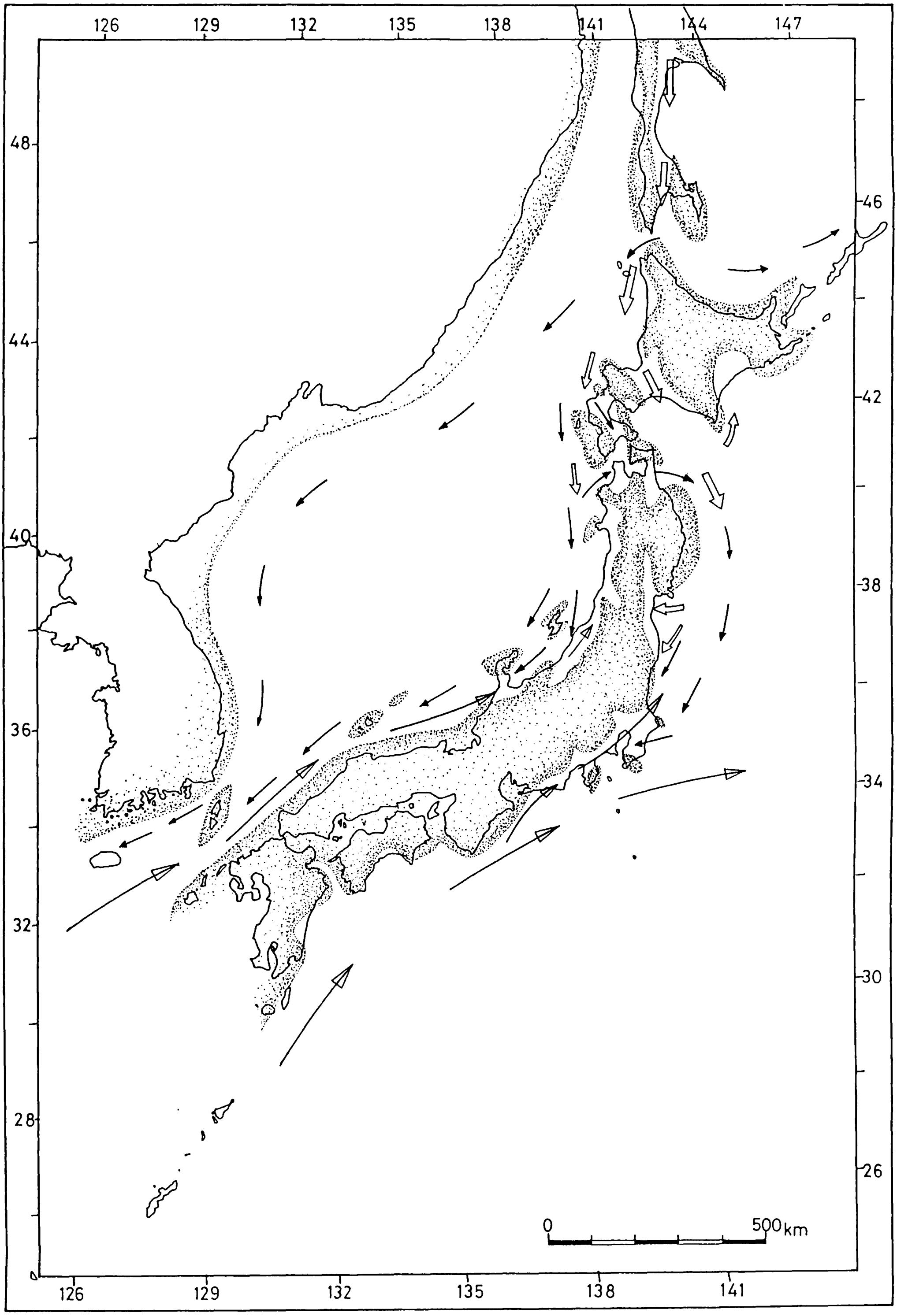
Masuda (1962a, b, 1973a, 1983) pointed out that *Chlamys cosibensis* may have had the widest dispersal of any mollusca during the Omma-Manganzian period in the Northern Pacific region, and that *Fortipecten* species can be traced from northern Japan and Hokkaido through Sakhalin to Kamchatka and Alaska in restricted horizons (Masuda, 1978, 1983, etc.). It is interesting to note that before the Omma-Manganzian period, there were no pectinids distributed as widely as these two species. Such a wide migration presumably results from the appearance of a peculiar environment.

In contrast, there is some confusion about the paleoenvironmental interpretation of the pectinid *Mizuhopecten tokyoensis hokurikuensis.* This subspecies has been considered to be an index species of the Omma-Manganzian fauna. However, it been recorded from Tanegashima Islands, Miyazaki and Shizuoka in association with Kakegawa faunal elements consisting of typical subtropical or warm-water species. Of course, the species associated with *M. tokyoensis hokurikuensis* within the Omma-Manganzian province are different from those associated with it along the Pacific coast of southwestern Japan. This subspecies can be regarded as a warm to temperate one but at least not a cold one.

According to Kaseno and Matsuura (1965), the analogue of the paleo-latitude of the Omma fauna shows a small shift to the north from the present latitude of Kanazawa. These data indicate that the Omma fauna does not imply temperatures as cold as those of the present Oyashio Current.

As the writer pointed out (Text-fig. 1), the Omma-Manganzian fauna is not extremely cold and not extremely warm. In other words, the faunal composition indicates that it is transitional between the Kakegawa and Tatsunokuchi faunas, as is the Kanto-type Omma-Manganzian fauna.

The paleocurrent system around the Japanese Islands during the Omma-Manganzian period (Pliocene and early Pleistocene) (Text-fig. 2) was closely similar to that of the present. However, as noted above, it appears that the southern warm-water current into the Sea of Japan may



Text-fig. 2. Paleogeography and current system during the Omma-Manganzian, Tatsunokuchi and Kakegawa faunal period.

have been rather weak, because the first appearance of a molluscan assemblage comparable to that of the present Tsushima Current is first recognized in the younger Ommaian fauna on the Japan Sea side. Specifically, this warm-water current permitted the immigration of such species as *Cryptopecten vesiculosus, Oliva mustelina, Mizuhopecten tokyoensis,* and so on. It is interesting that such warm-water to temperate elements can be traced northwards to around Akita Prefecture, as shown in Figure 1. Similarly, in the southern subprovince, a few Kakegawa elements can be recognized, as cited above, and in the northern area, a northern-type assemblage which is characterized by *Turritella nipponica, Chlamys imanishii, C. islandica* (s. l.) and *Cyclocardia crebricostata* is readily recognised. These faunal characteristics agree well with those of the Kanto-type Omma-Manganzian fauna, although the Kanto-type subprovince is much narrower than the Omma-Manganzian province along the Sea of Japan.

It is possible that there was some connection between the Sea of Japan and the Pacific Ocean in northeast Japan through Aomori Prefecture. The molluscan fauna there represents the northern-type Omma-Manganzian fauna, and is similar to that of the Kanto-type Omma-Manganzian fauna. Such would explain the mixed Omma-Manganzian and Tatsunokuchi faunas recognized along the northern part of the Pacific coast of the Japanese Islands.

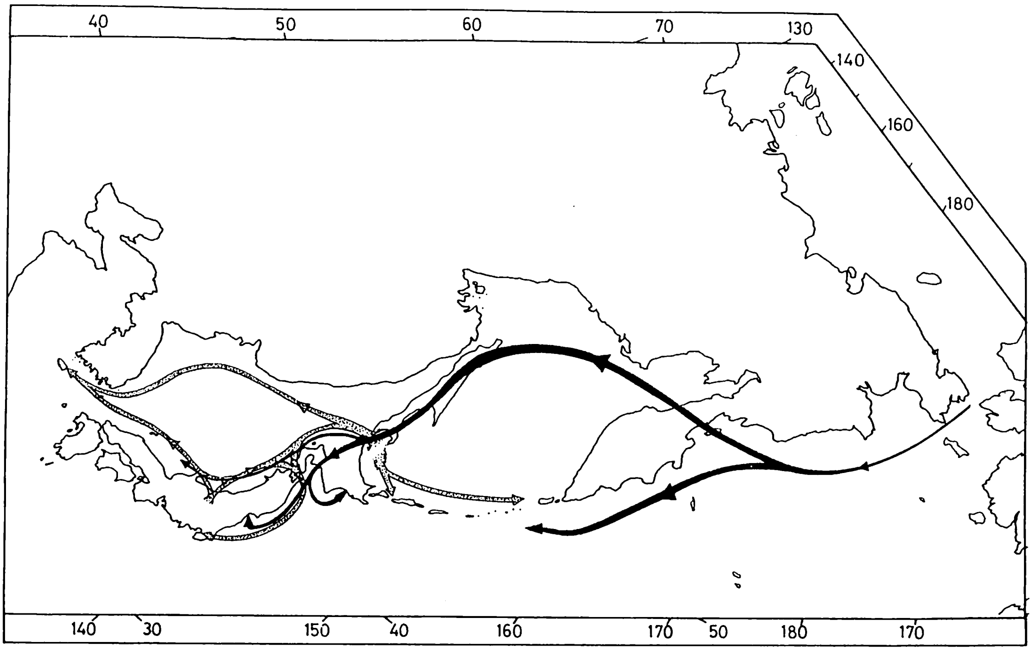
The existence of a current along the continent from the north is suggested by the occurrence of some species in the Cheju Islands as *Chlamys erythrocomatus, Thracia itoi* and *Panomya* sp. (Yoon, 1981) which have not been recorded in the Omma-Manganzian fauna distributed along the Sea of Japan. This current is named here the paleo-Liman Current.

From this account, it can be seen that, during the Omma-Manganzian period, there was a distinct convergence of currents around the Kanto region, and a rather gradual change of assemblages along the Sea of Japan.

Origin of the Omma-Manganzian fauna

Based on paleoecological studies, Chinzei and Iwasaki (1967) and Chinzei (1978) pointed out that the generic composition of Japanese Neogene molluscan remains similar through the Miocene and Pliocene and into the Recent. They also noted that generic composition is very similar over much of Japan despite different paleoenvironmental conditions, such as subtropical (in the area of the Kuroshio Current) and cold (in the area of the Oyashio Current), although there are strong differences at the specific level. These data show that genera are of little use in paleoenvironmental interpretation of Japanese Neogene faunas, and only species can be used for this analysis. However, it is interesting how replacement at the specific level within the same genus or allied genera took place. Chinzei (1978) has pointed out some evolutionary and adaptational processes for *Anadara* and *Dosinia,* which originally migrated from the south (an Indo-West Pecific origin), but in the writer's opinion it is still unclear whether such species are exotic or are a result of evolutionary change of one stock (a Japanese endemic one).

To solve this problem, it is considered that the study of systematic phylogeny combined with paleo-climatology is important. As pointed out above, the mixture of faunal elements from three faunas recognized by previous workers can be explained by interpreting the Omma-Manganzian fauna as characterized by moderately cool and moderately warm elements, compared with those of the warmer Kakegawa and colder Tatsunokuchi faunas, respectively. The distribution patterns of the three faunas suggest that the Omma-Manganzian faunal province is restricted to the Japanese Islands along the Sea of Japan, in the Kanto area, and tentatively



Text-fig. 3. Idealised migration routes of the Omma-Manganzian (dotted arrow) and Tasunokuchi (black arrow) faunas.

in the Kuril Islands. The southern, central, northern and Kanto subprovinces are interpreted as corresponding to warm-temperate, temperate, cool-temperate, and again cool-temperate zones, respectively, based on analogy with Nishimura's proposal of marine zoogeographical areas around the Japanese Islands (Nishimura, 1981, p. 246, fig. 116).

However, the Tatsunokuchi faunal element, which is represented by *Fortipecten,* can be traced from northern Japan through Sakhalin to Kamchatka and Alaska (Text-fig. 3). This faunal province can be assigned to the sub-boreal water mass of Nishimura (1981) because of its wide distribution to the north, its abundant individuals of the same species, its limited composition (about 50 species), the large and thick shells of pectinids and venerids, and its fossil evidence of cold-water taxa. The characters of the Tatsunokuchi and Takikawa-Honbetsu faunas have been pointed out by several authors (Nomura, 1938; Yabe and Hatai, 1940; Uozumi, 1962; Masuda and Ogasawara, 1981; and so on).

The Kakegawa fauna corresponds well with the subtropical to warm-temperate zones of Nishimura (1981), though there is some variation in the molluscan assemblage within the wide faunal province in the south of Japan.

From the systematic view point, some ancestral forms of the Omma-Manganzian elements have been recorded from the Shigarami Formation, Nagano Prefecture, Central Japan. These are *Anadara amicula* and *Turritella saishuensis motidukii,* which are considered to be ancestral forms of *Anadara amicula elongata* and *Turritella saishuensis saishuensis,* respectively (Kotaka, 1959; Noda, 1966). The Shigarami fauna (Yokoyama, 1925; Tomizawa, 1959) may represent a somewhat earlier fauna than the Omma-Manganzian fauna, because the Shigarami fauna contains not only the two species cited above but also other forms of molluscs quite different from those of the Omma-Manganzian fauna, such as *Glycymeris yamasakii, Chlamys tanakai,* *Mizuhopecten naganoensis, M. tryblium* and *Mercenaria sigaramiensis,* etc. So it may be that at least some elements of the Omma-Manganzian fauna were derived from the fauna of the Shigarami Formation and/or adjacent horizons in central Japan (Fig. 3).

In addition to the example of the Shigarami fauna, it is evident that many species in the Omma-Manganzian fauna might have been derived from the endemic fauna of the Japanese Islands in Late Miocene or Earlist Pliocene, because many species allied to those in the Omma-Manganzian fauna have been recorded from the so-called Shiobara-Yama fauna by many molluscan paleontologists (Iwasaki, 1970; Chinzei and Iwasaki, 1967; Chinzei, 1978; Masuda, 1962a, b; Kotaka, 1959; Noda, 1966; Amano, 1983; and so on).

To date, it appears that the Shiobara-Yama fauna is the fauna most likely to have been ancestral to the Omma-Manganzian fauna, although it is still difficult to show how one fauna changed to the other. Moreover, it can be estimated from general paleoenvironmental analogy that the Omma-Manganzian fauna was first established through upheaval of the Japanese Islands, when a distinct barrier between the Sea of Japan and the Pacific Ocean was first established. Such a major environmental event could have permitted the evolution of new forms from ancestral endemic species of the Shiobara-Yama fauna just before the Omma-Manganzian period.

Although the paleoenvironmental conditions of the Shiobara-Yama fauna have been interpreted as cold by some investigators, the writer considers that the Shiobara-Yama fauna represents a transitional biofacies that lived in a cool-temperate or cool marine climate, because: (1) the fauna contains many endemic species and/or genera derived from the subtropical or warm-water Kadonosawa fauna; (2) it includes some elements that are imcompatible with deposition in northern areas such as Sakhalin and Kamchatka, and (3) geographic reconstruction of the Shiobara-Yama faunal epoch by Chinzei (1978) shows nearly the same paleogeography as that of the Omma-Manganzian period.

Shiobara-Yama genera or species that are compatible with cold northern conditions are: *Mercenaria, Peronidia, Thracia, Felaniella, Serripes,* some *Macoma* and *Clinocardium* species, the *Mizuhopecten yessoensis* group, *Spisula,* some Buccinidae, *Ophiodermella, Propebela,* and others.

On the other hand, a major immigration into the Sea of Japan from the north is supported by the first appearance in the Omma-Manganzian fauan of *Macoma* spp., *Chlamys* spp., *Liocyma, Astarte, Cyclocardia,* and some gastropods. It is necessary to study the fauna in more detail to be sure of such considerations, however, as the diversity of the fauna may indicate the existence of accretional taxa or exotic taxa. *Astarte* is considered to be the most significant taxon needing more careful study to provide data on migration to Japan from the north.

Several *Astarte* species have been recorded from Pliocene and Pleistocene formations of the Japanese Islands (Table 4). As far as is known, *Astarte* first appeared in Japan in the so-called Pliocene formations bearing the Omma-Manganzian and Tatsunokuchi faunas in northern Japan (Text-fig. 4). Its earliest records are from the middle horizon of the Jyunicho Formation in the Hokuriku area, and it is associated with *Fortipecten* in formations in Hokkaido and Northern Honshu.

Menner *et al.* (1977) and Gladenkov (1977, 1984) treated the first appearance of *Astarte* as an index of the Upper Pliocene Ustlimimtevayamian Stage (Beringian) in the North Pacific region of the USSR. Nelson *et al.* (1974) estimated that large *Astarte* species migrated into the North Pacific region from the Arctic Ocean through paleo-Bering Strait during the Miocene

Table 4. Fossil records of *Astarte* species of Japan.

Astarte (Tridonta) alaskensis Dall, 1903
Hokkaido: Chinkope, Tomikawa, Yuchi
Aomori Pref.: Hamada (Chikagawa), Higashimeya
Akita Pref.: Sasaoka
Niigata Pref.: Nishiyama
Toyama Pref.: Shimazaki (Jyunicho)

Astarte (Tridonta) alaskensis shinadae Kanno, 1962
Hokkaido: Pirika (Setana)

Astarte (Tridonta) aomoriensis Nomura et Hatai, 1935
Aomori Pref.: Daishaka, Soma, Higashimeya

Astarte (Tridonta) borealis (Schumacher, 1817)
Hokkaido: Nakanogawa, Soibetsugawa, Tomikawa
Aomori Pref.: Hamada (Chikagawa), Daishaka, Higashimeya, Soma, Shohoji (Togawa)
Akita Pref.: Futatsui (Sasaoka), Sasaoka, Shibikawa
Yamagata Pref.: Kannonji
Niigata Pref.: Sawane
Ishikawa Pref.: Suginoya, Omma

Astarte (Tridonta) sulcata (Dacosta), Yokoyama, 1926
Niigata Pref.: Sawane

Astarte (Tridonta) teshioensis Yokoyama, 1926
Hokkaido: Yuchi, Enbetsu
Nagano Pref.: Ogikubo (Shigarami) ?

Astarte (Nicania ?) bennetti Dall, 1903
Niigata Pref.: Nishiyama
Ishikawa Pref.: Omma, Uji shell bed

Astarte (Astarte) hakodatensis Yokoyama, 1920
Ishikawa Pref.: Shimazaki (Jyunicho), Omma
Toyama Pref.: Asahiyama shell bed
Chiba Pref.: Katori
Kanagawa Pref.: Koshiba

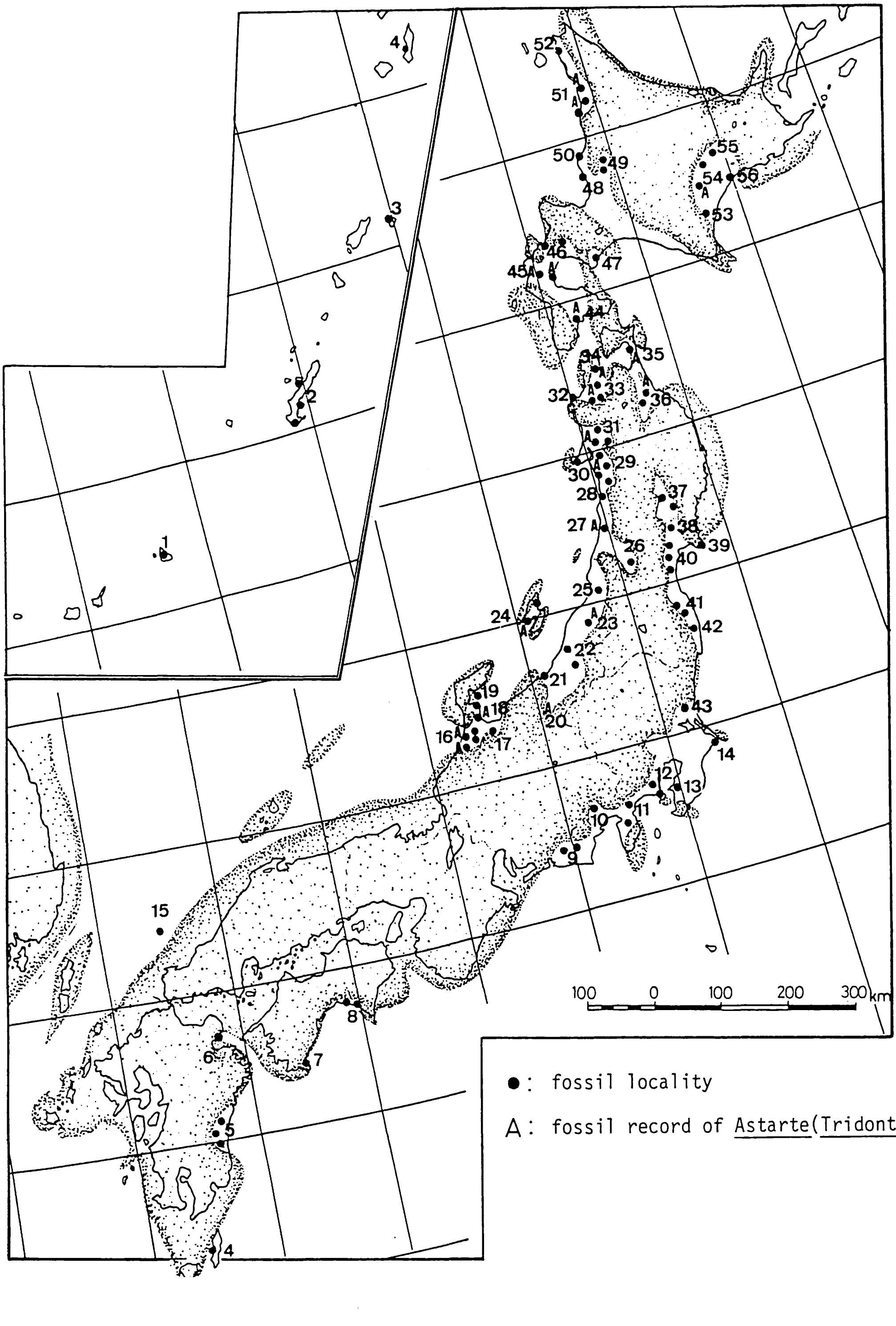
(about 10 M.A.). However, recent fossil data do not support their estimation. According to Hopkins and Marincovich (1983) and Marincovich (1984), the Beringian Transgression (Hopkins, 1967) took place in the Pliocene (3.5 to 3.0 M.A.).

Data on fossils from Japan, including Sakhalin and the Kuril Islands, suggest that the first appearance of the genus *Astarte* (*Tridonta*) in the Pacific Ocean may have been caused by the Beringian Transgression.

Many species of molluscs migrated to the Atlantic Ocean from the Pacific through the northern path (the Bering Strait), but only relatively few species might have reached the Pacific from the Atlantic Ocean (Durham and MacNeil, 1967). MacNeil (1973) suggested that the Arctic region might have been much warmer during the Pliocene than it was during the glacial periods.

Although the environmental effects of the break-up of the Bering Land Bridge are still unclear, it seems likely that *Astarte* migrated into the Tatsunokuchi and Omma-Manganzian faunal provinces from the north during the Beringian Transgression.

Thus, it is reasonable to consider that most of the Omma-Manganzian faunal elements may have been established previously to the north of Japan. It seems probable that the fauna originated in the paleo-Sea of Okhotsk, because some Omma-Manganzian elements are known from the Kuril Islands and northern Hokkaido. The area of the Sea of Okhotsk may represent the northern marginal area of the Shiobara-Yama fauna during the Miocene, as shown by the presence of the Tachikara-Ushinai molluscan assemblage in northern Hokkaido (Ogasawara, 1981, 1983).



●: fossil locality

A: fossil record of Astarte (Tridonta)

Discussion

The writer has described the approximate paleoenvironmental conditions and migration of the Omma-Manganzian fauna. However, there are many problems still to be solved before we fully understand its origin and migration. One is the degree of precision in biostratigraphy and geochronology, and another is the accuracy of reconstruction of paleotemperature or paleoclimatology for a fossil fauna. Roughly speaking, the Omma-Manganzian and Tatsunokuchi faunas prospered at about 2 M.A. and were introduced by the direct or indirect effect of the Beringian Transgression from the North; detailed data on biostratigraphy and chronology are needed for a more extensive discussion.

Recent progress in marine zoogeography provides many important and significant data that are useful for interpreting paleozoogeography and environmental conditions. Among recent studies, those of Nishimura (1981) and Scarlato (1981) are helpful for understanding the so-called cold-water province of the North Pacific region. For example, Nishimura (1981) proposed 4 faunal provinces around the Japanese Islands and Scarlato (1981) divided these into 7 subprovinces based mainly on Bivalvia. However, it sppears that these subdivisions are insufficient, when considering paleozoogeography, to discern a distinct convergence between the Kuroshio Current (subtropical water) and the Oyashio Current (sub-boreal water), which many molluscan paleontologists have considered occurred.

The concept and definition of paleoclimatological subdivisions as warm, temperate, cool, and cold are sometimes quite different between different workers. Therefore, there is a need for paleoenvironmental discussion based not only on marine organisms, but also on terrestrial fossils.

Recent marine zoogeographical studies of the present fauna provide some rules about migration: larval dispersal principally depends on the current direction; sometimes a topographic barrier or water-mass does not permit larval dispersal and so has a role in causing zoogeographic subdivisions; and for northern (cold) species, the maximum summer water temperature strongly affects migration to the south, into warmer water.

Text-fig. 4. Paleogeography and fossil localities of the Omma-Manganzian, Tatsunokuchi and Kakegawa faunas; A indicates *Astarte* (*Tridonta*) localities.

1. the Shimajiri Group of Miyako-jima, 2. the Shimajiri Group of Okinawa-jima, 3. the Shimajiri Group of Kikaijima, 4. the Tajima Formation of Tanega-shima, 5. the Miyazaki Group of Miyazaki Basin, 6. Ooita, 7. Ashizuri, 8. Nobori and Tonohama, Kochi Prefecture, 9. the Kakegawa Goup (Dainichi), 10. the Akebono Formation of Yamanashi Prefecture, 11. Izu and Hakone, 12. Koshiba of Kanagawa Prefecture, 13. Kurotaki, 14. Choshi, 15. off Mishima, 16. the Himi Group (the Omma, Nakagawa, Jyunicho formations), 17. Akae-gawa near Yatsuo, 18. Sakiyama Peninsula, 19. Noto-jima, 20. "Shigarami" near Nagano City, 21. Jyoetsu, 22. Nishiyama and Ojiya, 23. Kamo City, 24. the Sawane Formation of Sadoga-shima, 25. Nakajyo, 26. Shinjo Basin, 27. Yawatamachi (Akumi oil-field), 28. Manganzi, 29. the Sasaoka Formation in Akita oil-field, 30. Wakimoto of the Oga Peninsula, 31. Futatsui and Noshiro, 32. Narusawa, 33. the Hirosaki Basin (the Higashimeya, Daishaka formations), 34. Kanita of the Tsugaru Peninsula, 35. Hamada near Mutsu City (Chikagawa), 36. Sannohe (Shohoji and Kenyoshi), 37. Koromogawa (the Yamada and Ohdaira formations), 38. Furukawa and Sanbongi, 39. the Gobanshoyama Formation in the Ojika Peninsula, 40. the Tasunokuchi Formation in and around Sendai, 41. the Ishiguma Formation near Namie, 42. Hirono, 43. the Kume Formation near Hitachi-Oota, 44. Tomikawa near Hakodate, 45. the Setana Formation, 46. Kuromatsunai, 47. Horobetsu near Muroran, 48. Morai, Atsuta-mura, 49. Takikawa, 50. Rumoi, 51. the Yuchi Formation, 53. Bakkai near Wakkanai, 53. Kankan-yama near Urahoro, 54. Honbetsu, 55. Akan, 56. Shiranuka near Kushiro.

In the case of the Omma-Manganzian and Tatsunokuchi faunas, it is evident that the effect of the last two rules, above, possibly caused a distinct separation between the faunal provinces around the Japanese Islands.

However, there are still many problems for future study. Important aspects in need of further work are a comparative study between the invasion history of marine animals into the Sea of Japan through the paleo-Tsushima Strait and the migration history of land mammals to the southwestern islands of Japan across the East China Sea; the zoogeographical and paleoenvironmental effects of a current flowing into the North Pacific from the Arctic Ocean; and faunal changes corresponding to word-wide cooling that was probably taking palce gradually through the Late Miocene, and so on. These are future topics of interest for paleontologists.

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CHARACTER AND DEVELOPMENT OF THE OMMA-MANGANJI FAUNA IN THE NIIGATA OIL-FIELD, CENTRAL JAPAN

By

Iwao KOBAYASHI

Introduction

Strata of Pliocene – Early Pleistocene age are widely distributed in the Niigata oil-field and on Sado Island, Central Japan, and contain abundant, well preserved marine molluscs. For the most part, the molluscan fossils belong to the Omma-Manganji fauna (Otuka, 1939) that dwelled in the Japan Sea borderland province (Masuda, 1980). In the Niigata oil-field these fossil-bearing strata consist of the Uonuma Group (or Formation), and the Haizume and Nishiyama formations, in descending order, although there are some problems in deciphering the stratigraphic sequence. The equivalent strata on Sado Island are the Sawane and Kawauchi formations.

Molluscan fossils from the Haizume and Sawane formations were first described by Yokoyama (1925, 1926, 1928). He noted that the molluscs of the Higashiyama oil-field, the eastern part of the Niigata oil-field, were similar to those of the Omma Formation in the Kanazawa district (Sugai, 1935) and to the fauna of the Sawane Formation (Kanehara, 1938). Otuka (1939) defined the Omma-Manganji fauna stratigraphically and chronologically, and demonstrated that the Haizume and Sawane molluscs, including many characteristically cold water taxa, belong to this fauna. After that, many biostratigraphic, paleogeographic and paleoecologic investigations of molluscan fossils from the Haizume, Nishiyama and Sawane formations, and two molluscan reports on the Uonuma Group, were published (Ikebe, 1940, 1941, 1942; Itoigawa, 1958; Noda, 1961, 1962; Oyama & Ishiyama, 1974; Masuda & Ogasawara, 1981; Ogasawara, 1981, 1983).

The following characters have been noted in the Pliocene – Early Pleistocene molluscan faunas of the Sawane, Nishiyama and Haizume formations: 1) These molluscs were defined as part of the Omma-Manganji fauna (Otuka, 1939), 2) Cold water and shallow water elements prevail (Otuka, 1939), but the Nishiyama Formation yields both shallow water and deep offshore elements, 3) Warm water elements are present at several horizons (Oyama & Ishiyama, 1974; Ogasawara, 1981; Kobayashi, 1983), 4) Brackish embayment molluscs occur in the Uonuma Group (Ikebe, 1942; Molluscan Group of the Uonuma Hills Collabrative Research Group, 1983), 5) Some Pacific species such as *Pecten albicans* and *Glycymeris nakamurai* are present (Noda, 1961; Chinzei, 1978).

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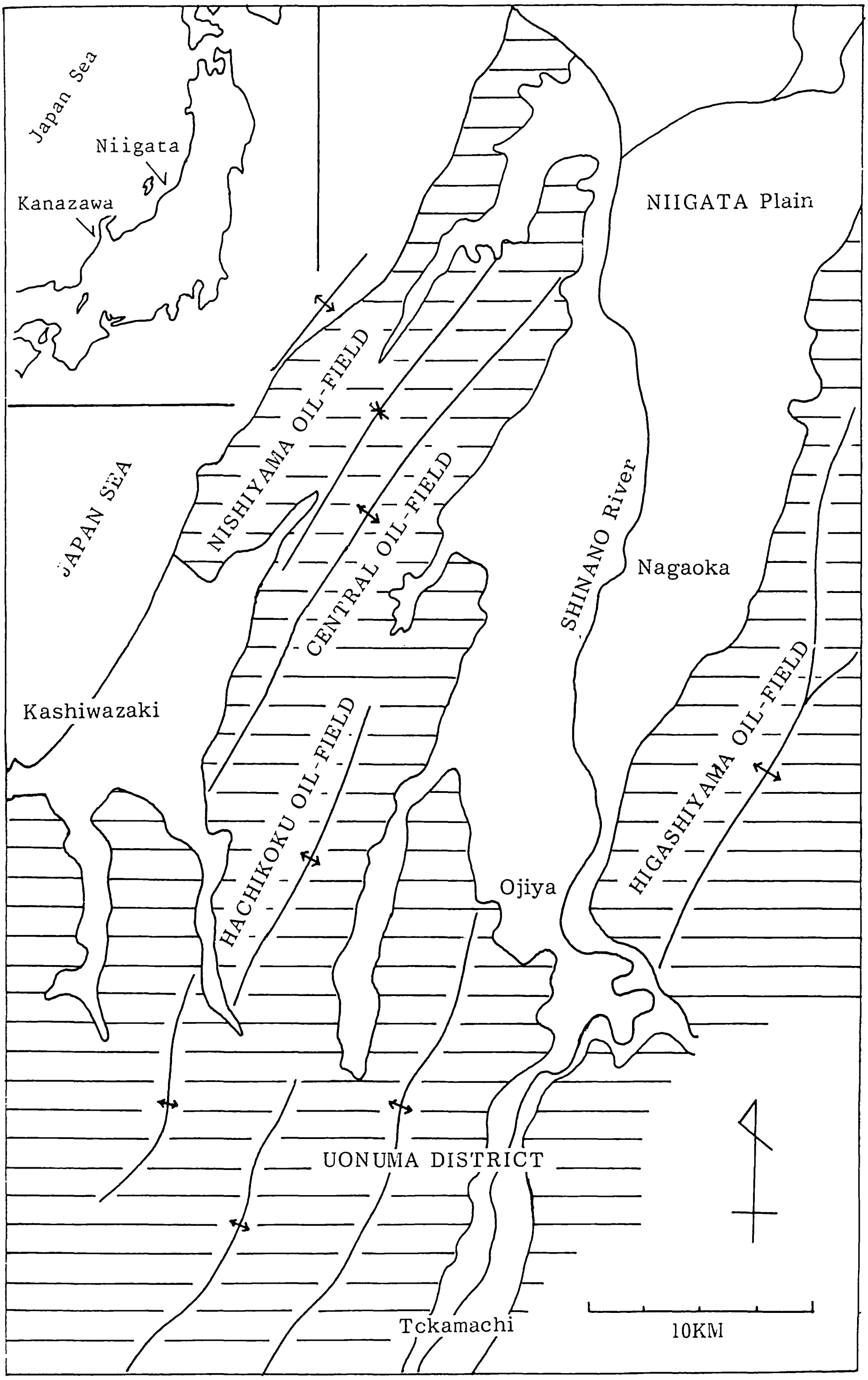
Stratigraphy and geologic age

The general stratigraphic succession on the Niigata oil-field is as follows, in descending



Text-fig. 1. Index map showing the Niigata oil-field.

order.

Uonuma Group (or Formation)
  Upper formation
  Middle formation
  Lower formation
  Lowermost formation
Haizume Formation
Nishiyama Formation

However, our study of the stratigraphy in this area has shown that the Haizume Formation in the Nishiyama oil-field is nearly coeval with the Middle formation of the Uonuma Group (Uonuma Hills Collaborative Research Group, 1983), and also that the upper part of the Nishiyama Formation in the Central oil-field is coeval with the Lowermost and Lower formations of the Uonuma Group (Kobayashi, 1983; Yasui *et al.*, 1983; Kikuchi *et al.*, 1984). Moreover, the horizon containing the type locality of the Haizume Formation in the Nishiyama oil-field has been accurately correlated with the boundary between the Upper and Middle formation of the Uonuma Group, based on tephrostratigraphy. Accordingly, it is accepted here that instead of the Haizume Formation, the Hachioji Formation [which was defined by Yasui *et al.* (1983) in the Hachikoku oil-field and correlated with the middle horizon of the Nishiyama Formation in the Nishiyama oil-field] is exposed in the Uonuma district. The new stratigraphic scheme and lithologies of these formations are shown in Table 1.

The geologic age of these strata was inferred by several means, namely fission-track dating, paleomagnetic and biostratigraphy (planktonic Foraminifera and nannoplankton).

According to fission-track dating of volcanic ash bed SK 130 (Muramatsu, 1983), the base of the Uonuma Group is about 2.9 m. y. old. And also, based on dating of volcanic ash bed SK 110 and 100, the horizon at the boundary between the Lower and Middle formations

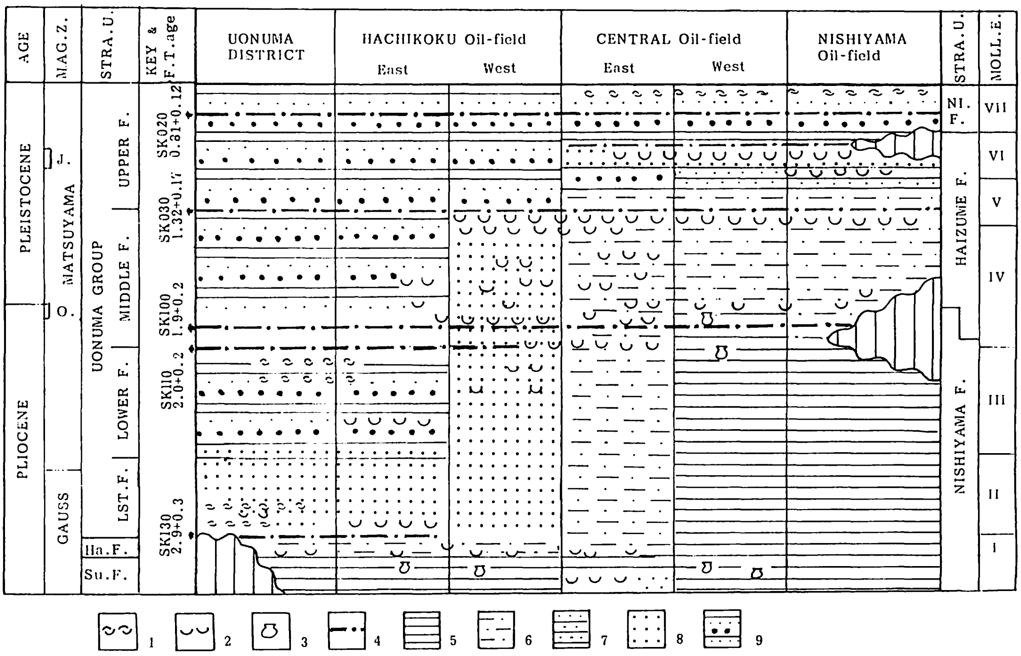
Table 1. Stratigraphic succession of the Niigata oil-field.

Age	UONUMA DISTRICT			CENTRAL and NISHIYAMA OIL-FIELD	
	Stratigraphic unit		Lithology	Stratigraphic unit	Lithology
EARLY PLEISTOCENE	UONUMA Group	UPPER Formation	conglomerate, fine-coarse sand, mud	NISHIGOSHI Formation	fine-coarse sand, mud, rarely conglomerate
		MIDDLE Formation	fine-coarse sand, mud, conglomerate	HAIZUME Formation	fine-coarse sand, calcareous sand, bluish grey sandy siltstone
PLIOCENE		LOWER Formation	fine-coarse sand, mud, conglomerate	NISHIYAMA Formation	bluish green massive mudstone
		LOWERMOST Formation	fine-coarse sand, conglomerate		
	HACHIOJI Formation		bluish grey sandy siltstone		
	SUGANUMA Formation		bluish green massive mudstone		

of the Uonuma Group is about 2.0 m. y. old. According to paleomagnetostratigraphic studies (Yoshikoshi, 1983), the Olduvai event is in the lower part of the Middle formation of the Uonuma Group, so the Pliocene – Pleistocene boundary is located in the middle horizon of the Middle formation. One key bed, SK 030, consists of volcanic sediments that include cordierite and is dated by fission-track means at about 1.3 m. y. The Jaramillo event is present in the middle part of the Upper formation of the Uonuma Group, and the boundary between Brunhes and Matsuyama epochs occurs in the upper part of this formation.

Micropaleontological data from the Central oil-field indicate that the Pliocene-Pleistocene boundary may be in the uppermost part of the Nishiyama Formation, based on the first occurrence of *Gephyrocapsa* (Takayama, 1983). The *Globorotalia inflata* zone I (Watanabe, 1983) may be present in the uppermost horizon of the Haizume Formation (Kudo & Sakaki, 1983). Planktonic foraminiferal marker event A, which is where *Globigerina pachyderma* changes from left- to right-coiling, is present in the lower part of the Haizume Formation. Moreover, the *Globorotalia inflata* bed II, including *Globoquadrina himiensis, G. kagaensis, Globorotalia inflata* and *G. inflata preinflata,* is present in the uppermost part of the Nishiyama Formation (Watanabe & Kobayashi, MS).

Lateral and vertical changes of rock facies, representing paleoenvironments from terrestrial to marine, are present in Pliocene – Lower Pleistocene deposits of the Niigata oil-field (Fig. 2). Terrestrial conditions appeared in the southern part of this area during the Late Pliocene. However, in the northern part of this area the timing of the change to the terrestrial condition was later, and the shallow marine conditions prevailed until the Middle Pleistocene.



Text-fig. 2. Chronological and geographical distribution of molluscan assemblage and lithology.
NI.F.: the Nishigoshi Formatiohn, 1: the embayment group, 2: the shallow water group, 3: the deep water group, 4: Key bed (volcanic ash), 5: mud facies, 6: sandy silt facies, 7: alternation facies of mud and sand, 8: sand facies, 9: alternation facies of mud, sand and conglomerate.

Main characters of the molluscan fossils

The Nishiyama and Haizume formations and the Uonuma Group contain abundant molluscan fossils representing three different ecological groups, namely the embayment group, the shallow water group and the deep water group.

1. The embayment group

They occur in the Lowermost, Lower and Middle formations (refer to Text-fig. 2) of the Uonuma Group, as well as in the Nishigoshi Formation. A mud layer containing molluscan fossils occurs as an interbed at several horizons. In these deposits, *Barnea* and *Crassostrea* surely are autochthonous and other taxa may be semi-autochthonous. The molluscs lived in the littoral to sublittoral zone of an embayment with a sandy mud or mud bottom. Main fossil assemblages are as follows.

Muddy facies	*Crassostrea* Fossil Assemblage
	Corbicula-Potamocorbula Fossil Assemblage
	Anadara-Raetellopsis-Theora Fossil Assemblage
	Barnea-Macoma-Raetellopsis Fossil Assemblage

2. The shallow water group

These mainly occur in the Haizume and Hachioji formations and the Lowermost formation of the Uonuma Group. There are not only a lot of fossil localities, but also abundant fossils that are well preserved. Most of the species of this group are common to the Omma-Manganji fauna, and almost are allochthonous, rarely autochthonous. Molluscs of the littoral and sublittoral zones were mixed into one fossil assemblage. They lived in the shallow water of open sea. The bottom sediments were of sandy silt, fine- and medium-grained sand, calcareous sand, conglomerate and rocky bottom. Many fossil assemblages of this group are as follows.

Sandy facies	*Glycymeris-Umbonium* Fossil Assemblage
	Anodontia-Lucinoma Fossil Assemblage
	Glycymeris-Mizuhopecten Fossil Assemblage
	Turritella-Lucinoma Fossil Assemblage
	Lucinoma-Astarte-Macoma Fossil Assemblage
Conglomerate facies	*Monia-Chlamys* Fossil Assemblage
Sandy silt facies	*Acila-Siphonodentalium* Fossil Assemblage
	Limopsis-Glycymeris Fossil Assemblage

3. The deep water group

The Nishiyama Formation in the Central and Hachikoku oil-fields consists of diatomaceous mud bed containing *Palliolum peckhami* at a few horizons. This may indicate a deep water fauna.

4. Warm water fauna

Not only cold water species characterize the Omma-Manganji fauna, but also warm water species (Recent Kuroshio fauna). Such warm water taxa are found from several horizons of the Haizume Formation and the Uonuma Group. These strata yield a mixed assemblage of cold and warm water species. For example, warm water species are *Pecten albicans, Megacardita ferruginosa, Anodontia stearnsiana, Paphia amabilis, Oliva musterina, Papyridea kurodai* and

Table 2. List of Pliocene – Early Pleistocene molluscs in the Niigata oil-field.
List of mollusca from the Higashigawa and Nitta Formations (after Noda, 1962)

SPECIFIC NAME	NISHIGOSHI F.	u. HAIZUME F.	m. HAIZUME F.	l. HAIZUME F.	L. UONUMA G.	1ST. UONUMA G.	HACHIOJI F.	HIGASHIGAWA F.	NITTA F.	SHIODANI F.	SAWANE F.
Acila insignis (GOULD)		*	*	*			*	*	*		
A. nakazimai KURODA			*				*				
Trisidos kiyonoi (KURODA)	*										
Anadara amicula (YOKOYAMA)							*	*			
Scapharca subcrenata (LISCHKE)	*				*						
Glycymeris cf.albolineata (LISCHKE)										*	
G. echigoensis KANEHARA									*	*	
G. minochiensis (YOKOYAMA)							*				
G. nipponica (YOKOYAMA)				*							*
G. yessoensis (SOWERBY)		*	*		*	*	*	*	*		*
Tucetilla pilsbryi (YOKOYAMA)		*	*								*
Limopsis tokaiensis YOKOYAMA		*		*			*				
Empleconia cumingii (A.ADAMS)			*								
Crenulilimopsis oblonga (A.ADAMS)			*	*	*						
Chlamys cosibensis YOKOYAMA		*	*	*			*	*			*
Ch. foeda (YOKOYAMA)		*									*
Ch. swiftii (BERNARDI)		*	*					*			*
Cryptopecten vesiculosus (DUNKER)											*
Pecten albicans (SCHRÖTER)	*	*	*								
Mizuhopecten yessoensis yessoensis (JAY)		*									
M. yessoensis yokoyamai (MASUDA)		*	*	*			*		*		*
M. tokyoensis hokurikuensis (AKIYAMA)		*	*								
Yabepecten tokunagai (YOKOYAMA)			*	*							*
Monia macroschisma (DESHAYES)				*							*
Crassostrea gigas (THUNBERG)					*	*		*			
Wallucina lamyi (CHAVAN)		*	*								
Lucinoma annulata (REEVE)		*	*				*			*	*
L. acutilineata (CONRAD)		*	*			*			*		
Anodontia stearnsiana OYAMA					*	*					
Conchocele bisecta (CONRAD)			*	*							
Felaniella usta (GOULD)		*	*		*			*	*	*	*
Megacardita ferruginosa (A.ADAMS and REEVE)		*	*								*
Cyclocardia ferruginea ferruginea (CLESSIN)		*	*	*			*				*
C. ferruginea complexa (OGASAWARA)		*	*								
C. ferruginea orbicularia (YOKOYAMA)			*								
Miodontiscus prolongatus nakamurai (YOKOYAMA)		*	*	*							
Astarte hakodatensis YOKOYAMA		*	*								*
Tridonta borealis SCHUMACHER		*	*	*							*
T. alaskensis (DALL)			*	*							
Keenaea samarangae (MAKIYAMA)		*	*	*							

Fulvia mutica (REEVE)	*		*								
Papyridea kurodai HATAI and NISHIYAMA				*							
Nitidotellina nitidula (DUNKER)		*					*				*
Macoma incongrua (MARTENS)	*		*				*				*
M. nipponica (TOKUNAGA)			*								*
M. tokyoensis MAKIYAMA	*				*			*	*		*
Phacosoma japonicum (REEVE)			*								*
Spisula voyi GABB											*
S. sachalinensis (SCHRENCK)								*	*		
Mercenaria stimpsoni (GOULD)		*				*		*			
M. yokoyamai MAKIYAMA											*
Mya japonica JAY						*	*				
Anisocorbula venusta (GOULD)		*	*	*			*				
Panopea japonica A.ADAMS								*			
Barnea dilatata (SOULEYET)	*										
Pandora pulchella YOKOYAMA		*		*							
Myadora fluctuosa GOULD		*	*	*							
Laternula navicula (REEVE)				*							
Acmaea pallida (GOULD)		*	*	*			*				*
Punctrella nobilis A.ADAMS		*	*	*							*
Umbonium akitanum SUZUKI		*				*		*	*		
Liotinaria semiclathratula (SCHRENCK)		*	*								
Homalopoma amussitatum (GOULD)		*	*	*							*
Turritella saishuensis etigoensis IDA		*	*								
T. saishuensis saishuensis YOKOYAMA			*				*				
T. saishuensis motidukii OTUKA							*	*	*		
Bittium a-satoi OINOMIKADO and IKEBE		*	*	*							
B. etigoense OINOMIKADO and IKEBE		*									
Antisabia foliacea (QUDY and GAIMARD)		*									
Proterato callosa (ADAMS and REEVE)		*	*								
Tectonatica janthostomoides (KURODA and HABE)		*	*	*			*	*	*		*
Cryptonatica russa (GOULD)		*	*	*							
Mitrella bicincta (GOULD)		*	*	*							*
Oliva musterina LAMARCK		*									
Olivella japonica PILSBRY		*									
Tritia japonica (A.ADAMS)		*	*								
Antiplanes contraria (YOKOYAMA)		*	*	*			*				
Ringicula doliaris GOULD		*									
Ophiodermella ogurana (YOKOYAMA)		*	*								

Proterato callosa. The middle horizon of the Nishigoshi Formation characteristically yields warm, shallow water molluscs such as *Trisidos, Barnea* and *Fulvia.* Most of the embaymet fauna consists of warm-temperate species. This occurrence in the upper horizon of the Haizume Formation has already been noted by Oyama and Ishiyama (1974). Moreover, warm water species are found from a bed at Gozu, west of the Niigata oil-field, and this bed may be correlated with the Haizume Formation (Ogasawara, 1981), and also from the Sawane Formation on Sado Island that includes *Cryptopecten* (Kobayashi *et al.,* 1976).

Development of the molluscan fauna

The chronologic and geographic changes of molluscan fauna from the Late Pliocene to Early Pleistocene in the Niigata oil-field are recognized and tentatively divided into seven epochs.

Epoch I (The age of the Hachioji Formation and the lower part of the Nishiyama Formation, ca. 3.1 Ma)

In the Uonuma district, shallow water molluscs were widely distributed, although deep water existed where *Palliolum* lived in the Central and Nishiyama oil-fields. Representative shallow water species are *Acila insignis, A. nakazimai, Anadara amicula, Glycymeris yessoensis, Chlamys cosibensis, Mizuhopecten yessoensis yokoyamai, Felaniella usta, Lucinoma annulatum, Anisocorbula venusta, Umbonium akitanum* and *Turritella saishuensis motidukii.*

Epoch II (The age of the Lowermost formation of the Uonuma Group and the middle part of the Nishiyama Formation, ca. 2.9 Ma)

In the Uonuma district, shallow water molluscs are distributed throughout the section, and show that the sea became shallower through time. The number of shallow water coastal species or of species living in the coarser sediments increased more than the number in Epoch I. Epoch II probably was a regressive stage. *Glycymeris yessoensis, Umbonium akitanum, Mercenaria stimpsoni, Lucinoma acutilineatum* and *Felaniella usta* are abundant instead of *Acila* and *Nuculana* in sandy siltstone. In the southern area of the Uonuma district, embayment taxa such as the genera *Crassostrea* and *Macoma* appeared along with warm water taxa such as *Anodontia* and *Placamen.* In the Central oil-field, deep sea taxa such as *Palliolum* continued to prevail.

Epoch III (The age of the Lower formation of the Uonuma Group and the upper part of the Nishiyama Formation, ca. 2.0–2.4 Ma

Embayment species are widely distributed at several horizons in the Uonuma district. They are *Crassostrea gigas, Potamocorbula amuruensis, Corbicula japonica, Musculista senhousia, Macoma tokyoensis, Scapharca subcrenata, Raetellops pulchella, Theora fragilis, Solen* sp. and *Phacosoma* sp.

Northwards, the shallow water species such as *Glycymeris yessoensis, Mizuhopecten* sp., *Felaniella usta* and *Crenulilimopsis oblonga* occur in the Hachikoku and southern Central oil-fields, whereas deep sea species were still present in the Nishiyama and northern Central oil-fields.

Epoch IV (The age of the lower part of the Middle formation of the Uonuma Group and the lower part of the Haizume Formation, ca. 1.7 Ma)

Embayment species are rare in the Uonuma district, and shallow water species are widely present in the Nishiyama and southern Central oil-fields. The representative shallow water species are *Acila insignis, Crenulilimopsis oblonga, Limopsis tokaiensis, Chlamys cosibensis, Mizuhopecten yessoensis yokoyamai, Monia macroschisma, Cyclocardia ferruginea, Keenaea samarangae, Tridonta borealis, Acmaea pallida, Puncturella nobilis, Turritella saishuensis* and *Antiplanes contraria.* The characteristic pectinid of the Omma-Manganji fauna, *Yebepecten tokunagai* (Masuda, 1980), is also present at this horizon as is *Globorotalia inflata* II and the dextral form of *Globigerina pachyderma.*

Epoch V (The age of the middle part of the Haizume Formation, ca. 1.4 Ma)

Terrestrial conditions largely prevailed throughout the Uonuma district. However, a shallow open sea was still present in the northern part of this area and the Central and Nishiyama oil-fields. The main species that lived there were *Acila insignis, A. nakazimai, Crenulilimopsis oblonga, Chlamys swiftii, Astarte hakodatensis, Tridonta borealis, Glycymeris yessoensis, Mizuhopecten yessoensis yokoyamai* and *Turritella saishuensis.* The sinistral form of *Globigerina pachyderma* is also present in this horizon. The latest part of this epoch might have been regressive.

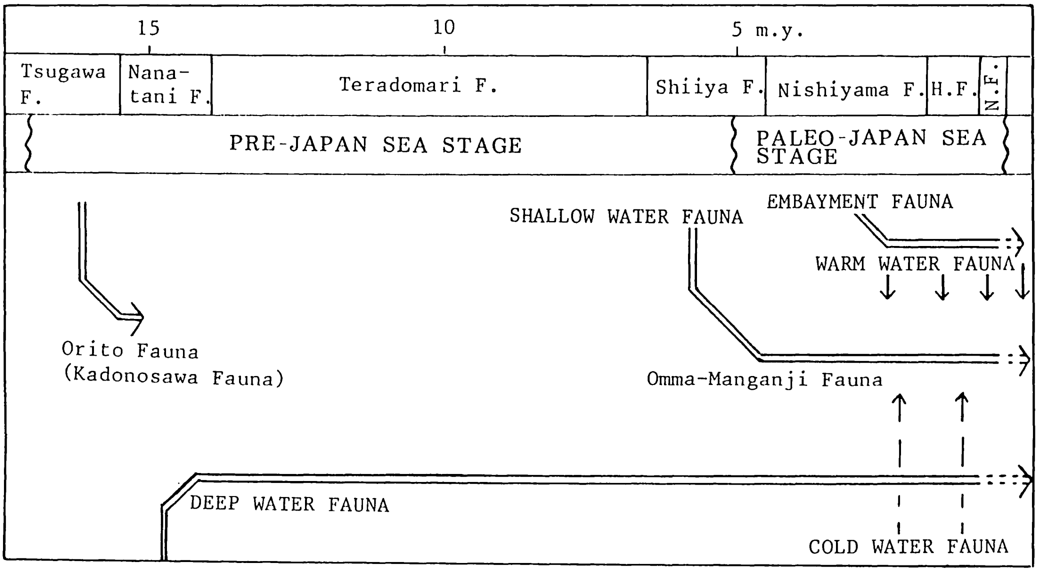
Epoch VI (The age of the upper part of the Haizume Formation, ca. 1.0 Ma)

Terrestrial condition widely prevailed in the Uonuma district, although a shallow sea was present in the Central and Nishiyama oil-fields. A minor transgression probably took place at this time. The main species are *Acila insignis, Tucetilla pilsbryi, Mizuhopecten tokyoensis hokurikuensis, Lucinoma annulatum, Mercenaria stimpsoni* and *Turritella saishuensis etigoensis.* Warm water taxa such as *Oliva* are also found from this horizon. At the top of the Haizume Formation a serious regression in the Nishiyama and Central oil-fields, although shallow marine conditions prevailed on the Niigata Plain.

Epoch VII (The age of the middle part of the Nishigoshi Formation, ca. 0.7 Ma)

An embayment was again extensively present, extending to the northern part of the Uonuma district. The main taxa are *Barnea dilatata, Anadara* sp., *Fluvia mutica, Pecten albicans, Macoma* sp. and *Trisidos kiyonoi.,* which are warm-temperate elements.

The Omma-Manganji fauna in the Niigata oil-field was present from Pliocene to Early Pleistocene (Text-fig. 3), but the species composition of this fauna changed during this interval. The characteristic species in the Early Pleistocene were *Anadara amicula, Glycymeris nakamurai* (cf. *alborineata*), *G. echigoensis, G. minochiensis, G. yessoensis, Mercenaria yokoyamai* and others. Most of Pliocene species were derived from a Miocene fauna such as the Shiobara-type fauna (Iwasaki, 1970). During regressive Latest Miocene and transgressive Early Pleistocene, shallow water species probably migrated into the new habitats of the Niigata sedimentary basin. Such species are also presented in other faunas. For example, *Anadara amicula, Limopsis*



Text-fig. 3. Development of Neogene molluscan faunas in the Niigata sedimentary basin.

tokaiensis, Chlamys cosibensis, Swiftpecten swiftii, Lucinoma acutilineatum and *Panopea japonica* are in common with the Shigarami fauna, whereas *Glycymeris nipponica, Cryptopecten vesiculosus, Keenaea samarangae* and *Mercenaria yokoyamai* are in common with the Kakegawa fauna.

Some Early Pleocene species disappeared or decreased in the Niigata sedimentary basin during Epoch II–III interval. On the other hand, several new taxa such as *Anadara subcrenata* group appeared, and new species of *Turritella* gradually made an appearance. Moreover, cold and warm water species migrated in the shallow water of the Niigata sedimentary basin due to major plaeogeographic changes during the Late Pliocene. After that, the mixed fauna of dominant cold water and some warm water species thrived in this basin. This is the so-called Omma-Manganji fauna.

In addition, another fauna first appeared during these epoch as terrestrial conditions developed. This was an embayment fauna of the continental margin (Itoigawa, 1970), and may have been related to the Miocene embayment fauna (Chinzei, 1978).

During Epoch IV the proportion of Recent species and the pace of morphological change increased. The repetition of regression and transgression became more and more conspicuous. Cold water species in Epoch V increased in number and the regression continued to occur. Epoch VI was a transgressive interval that the migration of warm water species was allowed. This age is perhaps correlated to the Upper Omma Stage (Ogasawara, 1981) that has dominant *Mizuhopecten tokyoensis hokurikuensis, Oliva* and *Turritella saishuensis etigoensis.* After serious regression occurred, the warm-temperate species again migrated into a relatively wide transgressive embayment.

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Plate 21

Explanation of Plate 21

Fig. 1. *Acila insignis* (Gould)
Loc. Inagawa, Izumozaki-machi, the upper part of the Haizume Formation, x 1.
Fig. 2. *Limopsis tokaiensis* Yokoyama
Loc. Kuta, Izumozaki-machi, the lower part of the Haizume Formation, x 1.
Fig. 3. *Glycymeris yessoensis* (Sowerby)
Loc. Aburaden, Kariwa-mura, the upper part of the Haizume Formation, x 0.6.
Fig. 4. *Tucetilla pilsbryi* (Yokoyama)
Loc. Ogi, Izumozaki-machi, the upper part of the Haizume Formation, x 1.
Fig. 5. *Glycymeris nipponica* (Yokoyama)
Loc. Kuta, Izumozaki-machi, the lower part of the Haizume Formation, x 1.
Fig. 6. *Anadara amicula* (Yokoyama)
Loc. Ishiguro, Takayanagi-machi, the Hachioji Formation, x 1.
Figs. 7, 8. *Mizuhopecten yessoensis* (Jay)
Loc. Inagawa, Izumozaki-machi, the upper part of the Haizume Formation, x 0.7.
Fig. 9. *Chlamys cosibensis* Yokoyama
Loc. Ichinotsubo, Izumozaki-machi, the upper part of the Haizume Formation, x 0.6.
Fig. 10. *Monia macroschisma* (Deshayes)
Loc. Haizume, the middle part of the Haizume Formation, x 0.6.
Fig. 11. *Chlamys foeda* (Yokoyama)
Loc. Inagawa, Izumozaki-machi, the upper part of the Haizume Formation, x 1.
Fig. 12. *Pecten albicans* (Schröter)
Loc. Aida, Izumozaki-machi, the upper Haizume Formation, x 0.6.
Fig. 13. *Mizuhopecten tokyoensis hokurikuensis* (Akiyama)
Loc. Kogayama, Izumozaki-machi, the upper part of the Haizume Formation, x 0.5.
Fig. 14. *Lucinoma annulatum* (Reeve)
Loc. Ogi, Izumozaki-machi, the upper part of the Haizume Formation, x 1.
Fig. 15. *Cyclocardia ferruginea complexa* (Ogasawara)
Loc. Shimokotake, Izumozaki-machi, the middle part of the Haizume Formation, x 1.
Fig. 16. *Megacardita ferruginosa* (A. Adams & Reeve)
Loc. Ogi, Izumozaki-machi, the upper part of the Haizume Formation, x 0.6.
Fig. 17. *Mercenaria stimpsoni* (Gould)
Loc. Aburaden, Kariwa-mura, the upper part of the Haizume Formation, x 0.6.
Fig. 18. *Pandora pulchella* Yokoyama
Loc. Ogi. Izumozaki-machi, the upper part of the Haizume Formation, x 1.
Fig. 19. *Umbonium akitanum* Suzuki
Loc. Kotaka, Kawaguchi-machi, the Lowermost formation of the Uonuma Group (the Wanazu Formation), x 1.
Fig. 20. *Oliva musterina* Lamarck
Loc. Aburaden, Kariwa-mura, the upper part of the Haizume Formation, x 1.
Fig. 21. *Antiplanes contraria* (Yokoyama)
Loc. Kuta, Izumozaki-machi, the lower part of the Haizume Formation, x 1.
Fig. 22. *Turritella saishuensis motidukii* Otuka
Loc. Mukaiyama, Kawaguchi-machi, the Shiraiwa Formation (the Hachioji Formation), x 0.8.
Fig. 23. *Turritella saishuensis etigoensis* Ida
Loc. Funahashi, Izumozaki-machi, the upper part of the Haizume Formation, x 0.8.


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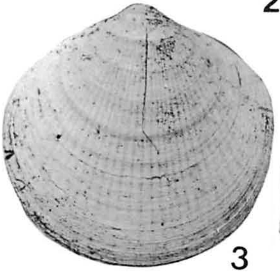
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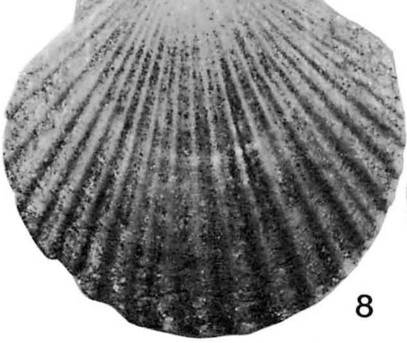
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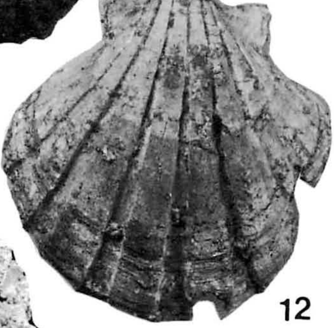
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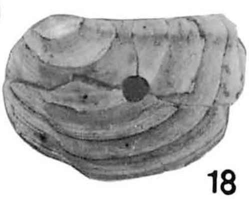
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