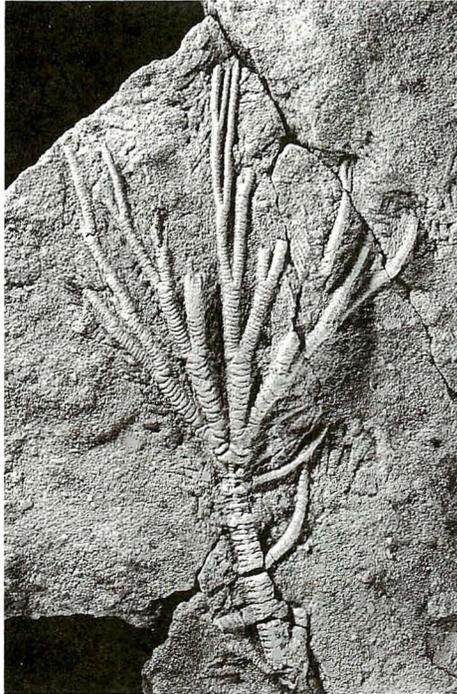


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The fossil on the cover is *Isocrinus (Chladocrinus) hanaii* Oji, an Early Cretaceous (Aptian) crinoid, which was described from the Hiraiga Formation exposed at Haipe, Tanohata-mura, Shimo-Hei County, Iwate Prefecture, Northeast Japan. (University Museum of the University of Tokyo coll. cat. no. ME6950, paratype specimen, length about 11 cm)

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PALAEONTOLOGICAL SOCIETY OF JAPAN

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977. *KOIZUMIA* YANAGISAWA GEN. NOV., A NEW MARINE FOSSIL ARAPHID DIATOM GENUS*

YUKIO YANAGISAWA

Geology Department, Geological Survey of Japan,
1-1-3 Higashi, Tsukuba, Ibaraki, 305

Abstract. A new marine fossil araphid diatom genus *Koizumia* is established to receive three species, *Koizumia tatsunokuchiensis* (Koizumi) Yanagisawa comb. nov. (originally described as *Rhaphoneis tatsunokuchiensis* by Koizumi, 1972), *K. adaroi* (Azpeitia) Yanagisawa comb. nov. (originally described as *Cymatosira adaroi* by Azpeitia, 1911), and *K. akibae* Yanagisawa sp. nov. Detailed morphologies of the genus are presented with its precise stratigraphic and geographic distributions. The genus is characterized by cribrum-like siliceous layers across the pores of marginal ridge, the suture line on the marginal ridge and the presence of transapical and longitudinal rows of areolae on the valve face. The three features are unique to the genus and have never been observed in its related genera *Rossiella* Desikachary et Maheshwari and *Bogorovia* Jousé. *Koizumia* is typically neritic in distribution mainly in near-shore or upwelling regions of the middle latitudes, and is significantly different from *Rossiella* and *Bogorovia*, both of which have essentially an oceanic and tropical to subtropical distribution. Both the morphological uniqueness and the differing geographic distribution pattern are considered to be distinctive enough to form the basis of a new generic erection of *Koizumia*. The genus has a rimoportula in the pattern of "one per cell" with an apical pore field at each apex, and forms a long colony chain connected by marginal ridges. These features suggest that the genus can be placed in the family Cymatosiraceae Hasle, von Stosch et Syvertsen.

Key words. Diatom, fossil, marine, morphology, stratigraphy, *Koizumia*

Introduction

During the past three decades, taxonomy of marine fossil diatoms has greatly improved through steady accumulation of knowledge on morphology revealed by scanning electron microscopy along with advanced diatom biostratigraphy using well preserved and well-dated materials provided by deep sea coring projects. However, many fossil diatoms have not been examined in detail from taxonomic view point, and therefore the taxonomy of fossil diatoms still remains largely incomplete.

The current study was prompted by the need to reveal the morphology and precise stratigraphic ranges of the two araphid diatom genera *Rossiella* Desikachary et Maheshwari 1958 and *Bogorovia* Jousé 1973 in order to build a firm basis for the taxonomy of the two genera. The two diatom genera share many common features and constitute an important fossil diatom group. Although the two genera were both monotypic when erected, subsequent studies have added many new members by descriptions of new species and generic transfers, some of which are of great importance in Paleogene and Neogene diatom marine biostratigraphies (e.g. Fenner, 1985; Barron, 1985). Recently, Gersonde and Schrader (1984) and Desikachary *et al.*

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(1984) clarified the taxonomy of the two genera. More recently, Fourtanier (1987) made a detailed taxonomic revision on almost all species known then, demonstrating their stratigraphic and paleoceanographic value. She also first examined some species by scanning electron microscopy to reveal the unique structure of the genera, and proposed an evolutionary lineage for some members. However, the whole evolutionary lineage of this diatom group has been still unknown.

As a result of my investigations of the two genera, I came to the conclusion that the diatom group can be clearly subdivided into three distinct units which are significantly different from each other in both morphology and geographic distribution, and that these units should be treated as three separate genera, i.e. *Rossiella* Desikachary et Maheshwari, *Bogorovia* Jousé and *Koizumia* Yanagisawa gen. nov.

In this paper, the new genus *Koizumia* is defined to receive three species, *Koizumia tatsunokuchiensis* (Koizumi) Yanagisawa comb. nov. (originally described as *Rhaphoneis tatsunokuchiensis* by Koizumi, 1972), *K. adaroi* (Azpeitia) Yanagisawa comb. nov. (originally described as *Cymatosira adaroi* by Azpeitia, 1911) and *K. akibae* Yanagisawa sp. nov. The morphology of each species is described on the basis of detailed light and scanning electron microscopic observations. The stratigraphic ranges of the

three species based on the analysis of DSDP Hole 438A off Japan and their geographic distributions surveyed in literature are presented.

Redefined descriptions of the genera *Rossiella* and *Bogorovia* will be provided in separate papers (Yanagisawa, in prep. a, b), and phylogenetic and evolutionary relationships between the three genera will be discussed in a later paper (Yanagisawa, in prep. c).

Material and methods

For biostratigraphic study, samples from the Lower Miocene through Quaternary section of DSDP Hole 438A were analyzed (Table 1). Hole 438A is located in the northwestern Pacific, off northeast Honshu, Japan, and contains an almost complete reference section for Lower Miocene through Quaternary North Pacific diatom biostratigraphy (Barron, 1980; Akiba *et al.*, 1982; Maruyama, 1984; Koizumi, 1985; Oda, 1986; Akiba, 1986). In this study, the slides analyzed by Akiba *et al.* (1982), Maruyama (1984) and Akiba (1986), together with the slides deposited in DSDP Reference Center in National Science Museum (Tokyo) were re-examined with special attention to the genus *Koizumia*. For taxonomic study and detailed scanning electron microscopy (SEM), several selected samples were also used (Table 1).

Table 1. Cores and samples used in this study.

No.	Cores & samples	Area	Location	Formation	References and remarks
1	DSDP Hole 438A	Northwest Pacific	40°37.79' N, 143°14.15' E	DSDP core	Scientific Party (1980)
2	A-1	Tomioka, Fukushima, Japan	37°20.26' N, 140°59.31' E	Drill core	Yanagisawa et al. (1989)
3	D-1	Sunda Forearc, Java	9°45.57' S, 111°36.68' E	Dredge sample	Yanagisawa (1987)
4	JDS 8842	San Felipe, Baja California	31° 8.89' N, 115° 1.48' W	Upper Miocene	coll. by Mr. N. Ogura
5	M 32	Ajigaura, Ibaraki, Japan	36°22.82' N, 140°37.42' E	Isozaki F.	Maruyama (1984)
6	Ya 185	Matsushima, Miyagi, Japan	38°28.78' N, 141°11.45' E	Tatsunokuchi F.	Akiba et al. (1982)
7	Mzn 09	Mizunami, Gifu, Japan	35°23.71' N, 137°14.66' E	Oidawara F.	Yanagisawa (1993)
8	Nmy 13A	Sumon, Niigata, Japan	37°22.11' N, 139°02.04' E	Nishimyo F.	Yanagisawa et al. (1986)
9	Ha 67 (Se 40)	Iwanuma, Miyagi, Japan	38°06.59' N, 140°50.56' E	Tatsunokuchi F.	Yanagisawa (1990a)
10	Km 09	Kamogawa, Chiba, Japan	35°03.56' N, 140°05.04' E	Nabuto F.	coll. by Y. Yanagisawa

The samples were prepared following the method of Koizumi and Tanimura (1985) or Maruyama (1984). A strewn slide for light microscopy (LM) was prepared for each sample on an 18×18 mm cover glass and mounted in Pleurax on a glass slide.

One hundred diatom valves were counted for each sample at ×1,000 magnification, following the counting criteria of Schrader and Gersonde (1978). After the counting, the entire slide was examined to record the presence of species missed in the counting. Estimate of the quality of diatom preservation was generally subjective. An Olympus BH-2 light microscope was used in this study.

For SEM observation, samples were prepared following Akiba and Yanagisawa (1986). The samples used for SEM were processed by nearly the same method of LM examination, but clay minerals were removed completely by the decantation with 0.01 N sodium pyrophosphate ($\text{Na}_2\text{P}_2\text{O}_7$) (at least 10 times). Using a micropipette, 0.5 ml of the suspended sample was placed on a slide glass, and dried on a hot plate at 60°C. Using a tiny paint brush, diatom valves of good preservation were picked up from the slide glass under the light microscope at ×100 magnification and mounted in a small tip of cover glass. The tip was then put on a sample stage. SEM observation was carried out using HITACHI S-405 scanning electron microscopes at Osaka University and the Geological Survey of Japan.

Some dimensions such as length, width, the number of transapical costae and number of areolae per 10 μm were measured from LM photomicrographs in order to reveal metric relationship between these parameters.

Results

Morphologic terminology for description

For description of the genera *Koizumia*, *Bogorovia* and *Rossiella*, morphologic terminology common to the three genera is introduced in this section. General mor-

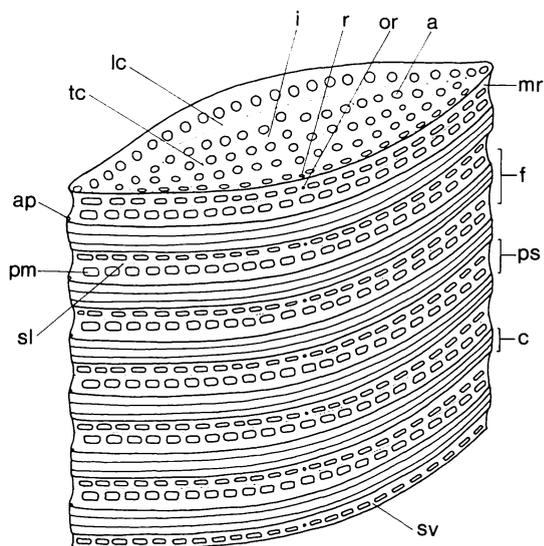


Figure 1. Colony chain of *Koizumia akibae* Yanagisawa sp. nov. Note the fusion of sibling valves. **a**: areola, **or**: external pore of rimoportula, **r**: inner aperture opening of rimoportula, **i**: inner surface of valve face, **lc**: longitudinal costa, **tc**: transapical costa, **ap**: apical pore field, **pm**: pore of marginal ridge, **sl**: suture line formed by fusion of sibling valves, **sv**: separation valve, **c**: cingulum, **ps**: pair of sibling valves, **f**: frustule, **mr**: marginal ridge.

phologic terms follow Anonymous (1975), Ross *et al.* (1979), Simonsen (1979) and Round *et al.* (1990).

Figure 1 illustrates the part of a colony chain of *Koizumia akibae*, showing the basic structure of the genus. The valve outline of the three genera is basically linear-lanceolate with more or less rostrate apices. At each apex there is an apical pore field (ap) consisting of fine puncta.

Marginal ridge (mr) is a continuous ridge between the valve face and the valve mantle, and is the most important structure that characterizes the three genera. All members of the genera *Koizumia*, *Rossiella* and *Bogorovia* have marginal ridges on both margins without exception. Four types of marginal ridges are recognized (Figure 2). Type 1 is a separate-type marginal ridge with a single longitudinal row of pores. This type has

been observed in *Rossiella elongata* (Barron) Desikachary (Figure 3-1) and *R. paleacea* (Grunow) Desikachary et Maheshwari. The remaining three are of fused types where the marginal ridges of two sibling valves are completely fused so that a pair of fused sibling valves (ps) seems as if it were a single frustule. Type 2 marginal ridge has two longitudinal rows of pores. This type has been reported in *Bogorovia praepaleacea* (Schrader) Jousé (Fourtanier, 1987). Type 3 is a fused-type marginal ridge with three lon-

gitudinal rows of pores. *Bogorovia veniamini* Jousé is characterized by this type of marginal ridge (Figures 3-2, 3-3). Type 4 marginal ridge with two rows of pores is apparently similar to type 2, but clearly distinguished by having a cribrum-like siliceous layer across the pore (Figure 14-8) and a faint suture line between the rows of pores (denoted as "sl" in Figure 1; Figure 14-9). The cribrum-like layer is perforated by regularly arranged minute pores, showing virtual resemblance to the cribrum. The layer is thin and delicate so that it might be easily dissolved or detached in poorly preserved specimens, leaving only several short connecting bars around the inner margin of the pore (Figures 12-7, 14-5). This cribrum-like layer is unique to the type 4 marginal ridge, and has never been observed in the other types of marginal ridges. The type 4 appears, therefore, to be distinct from the other three types of marginal ridges.

The spacing of pores of marginal ridge almost equals that of transapical costae in the fused-type marginal ridges (types 2, 3 and 4). In the separated-type marginal ridge (type 1), the spacing of the pores is nearly equal to the spacing of marginal areolae on the valve face.

Species with the fused-type marginal ridges may form a long chain colony by the fusion

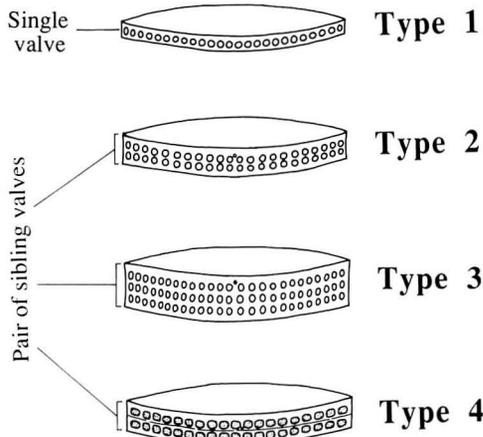


Figure 2. Types of marginal ridge in the genera *Koizumia*, *Bogorovia* and *Rossiella*.

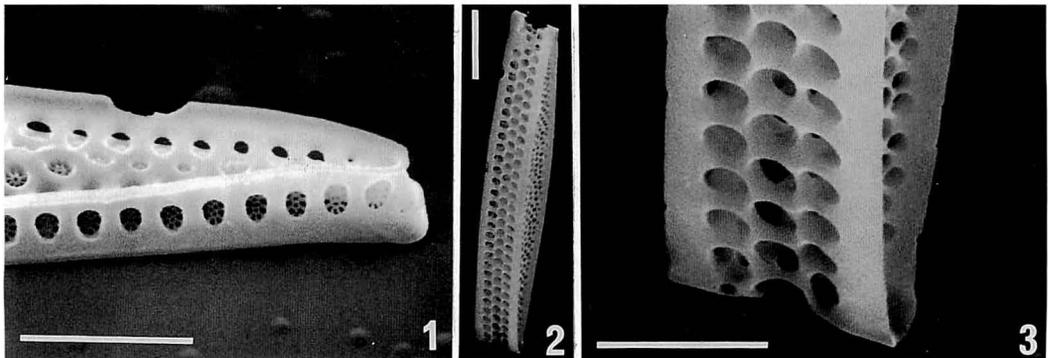


Figure 3. SEM photomicrographs of marginal ridges of *Rossiella* and *Bogorovia*. Scale bars equal 10 μm for Figs. 3-1, 3-3, and 5 μm for Fig. 3-2, respectively. 1. Type 1 marginal ridge of *Rossiella elongata* (Barron) Desikachary; Sample M32, Izozaki Formation, Ajigaura, Ibaraki, Japan. 2, 3. Type 3 marginal ridge of *Bogorovia veniamini* Jousé; Sample RC 12-65, 1,065 cm.

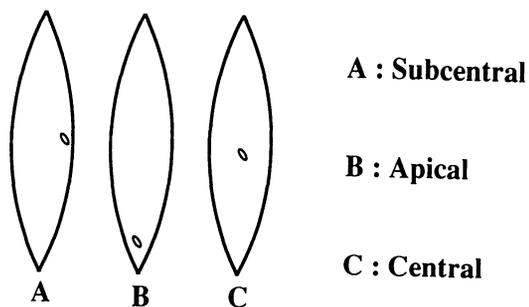


Figure 4. Location of rimoportula in the genera *Koizumia*, *Bogorovia* and *Rossiella*.

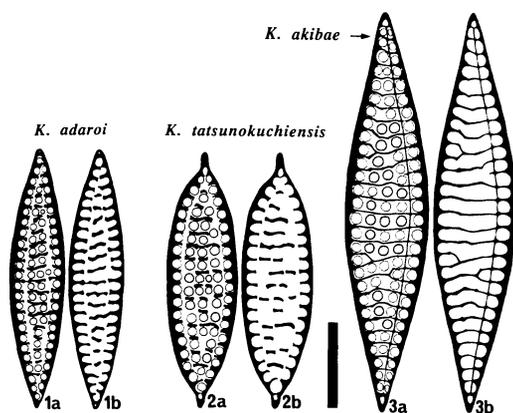


Figure 5. Morphology of the three species in the genus *Koizumia*. Figs. 1a, 2a and 3a show the LM images of *K. adaroi* (Azpeitia) Yanagisawa comb. nov., *K. tatsunokuchiensis* (Koizumi) Yanagisawa comb. nov. and *K. akibae* Yanagisawa sp. nov., respectively. Figs. 1b, 2b and 3b are the schematic drawings demonstrating transapical and longitudinal costae.

of their marginal ridges (Figure 1). Fourtanier (1987) reported a relatively long chain of *Koizumia adaroi* composed of seven frustules (Fourtanier, 1987, pl. 16, fig. 5). I have also observed short chains consisting of two or three sets of fused sibling valves (Figures 12-5, 14-3). On the contrary, the species with the separate-type marginal ridge may be solitary.

Transapical costae (tc) which extend from both valve margins are present in some members of the three genera (Figure 1). For

description, the spacing of the transapical costae is classified into two categories; narrowly spaced type (9-14 costae in 10 μm) and broadly spaced type (6-8.5 costae in 10 μm). An additional longitudinal costa (lc) parallel to the side is present only in *K. akibae* (Figure 1).

A rimoportula(r) is present generally in "one per cell pattern"; a frustule consists of a process valve and a non-process valve, and thus the frustule is heterovalvate. Three patterns of location of the rimoportula are recognized; subcentral, apical and central positions (Figure 4). The species which make a colony chain by their fusion of marginal ridges (types 2, 3 and 4) have a subcentral rimoportula without exception. The subcentral rimoportula has an external pore (or) on the marginal ridge (Figure 1; Figures 12-3, 14-6). This is probably because the process may function to communicate some substance between the cell interior and the external environment. If the rimoportula of a valve with the fused-type marginal ridge would open on the valve face, it could not function as the pathway of chemical matter, because its outer opening does not lead to the external space. The apical and central positions of rimoportula are observed only in some species of *Rossiella* which have the separated-type marginal ridges (type 1).

The areolae of the genera *Koizumia*, *Bogorovia* and *Rossiella* show a wide range of variation in size. The size of areolae is classified into five ranks for description: coarse (ca. 1.2-1.5 μm in diameter), medium (ca. 0.8 μm in diameter), fine (ca. 0.4-0.5 μm in diameter), very fine areolae (less than 0.1 μm in diameter) and the absence of areolae (hyaline). The coarse areolae are polygonal in shape and compactly packed. The medium to very fine areolae are circular in shape and distributed sparsely and randomly in some species, but in *Koizumia*, they are arranged in transapical and longitudinal rows (Figure 5).

The cingulum (c) may be composed of

some bands, but its detailed structure and composition are not known at present.

At the end of a colony chain, there is a separation valve (sv), a special valve that shows a different morphology from other

vegetative valves and functions to separate a long chain into short chains of suitable length (Figure 1).

Table 2. Occurrence of *Koizumia* species in DSDP Hole 438A. Diatom zones after Akiba (1986).

Diatom zones		NPD	Core Section Interval (cm)	Preservation Abundance	<i>Koizumia. akibae</i> <i>K. adaroi</i> <i>K. tatsunobuchiensis</i> <i>Bogorovia. puncticulata*</i> <i>Rossiella paleacea</i>
<i>Neodenticula kamschatica</i>	7B	6 - 1 , 18 - 22	G A	- - R - -	
		11 - 6 , 20 - 24	G A	- - F - -	
		13 - 3 , 19 - 23	G A	- - R - -	
		21 - 3 , 20 - 24	G A	- - R - -	
		23 - 1 , 10 - 14	G A	- - F - -	
		24 - 3 , 10 - 12	G A	- - R - -	
		26 - 4 , 10 - 14	G A	- - F - -	
		26 - 6 , 15 - 19	G A	- - R - -	
		27 - 4 , 20 - 24	G A	- - R - -	
		28 - 2 , 20 - 24	M A	- - R - -	
		29 - 2 , 20 - 24	M A	- - C - -	
		31 - 1 , 20 - 24	G A	- - R - -	
		33 - 1 , 120 - 124	G A	- - R - -	
		34 - 1 , 22 - 24	M C	- - C - -	
		35 - 3 , 24 - 28	M A	- - R - -	
		36 - 1 , 32 - 36	M C	- - R - -	
37 - 3 , 10 - 14	G C	- - F - -			
40 - 2 , 20 - 24	M A	- - R - -			
41 - 1 , 45 - 49	M A	- - R - -			
41 - 3 , 30 - 34	G A	- - F - -			
41 CC , -	G A	- - R - -			
<i>Rouxia californica</i>	7A	42 - 4 , 73 - 74	G A	- - R - -	
		42 - 5 , 100 - 101	P R	- - R - -	
		42 - 6 , 16 - 20	M C	R - R - -	
<i>Thalassionema schraderi</i>	6B	43 - 1 , 59 - 63	P R	R - - - -	
		43 - 6 , 82 - 86	M R	R - - - -	
		44 - 1 , 60 - 64	M R	R - - - -	
		44 - 3 , 10 - 14	M R	R - - - -	
		47 - 1 , 10 - 14	M F	- - F - -	
		48 - 1 , 14 - 18	M R	- - R - -	
		48 - 3 , 46 - 50	M A	R - R - -	
		49 - 3 , 10 - 14	P R	- - R - -	
		49 - 6 , 10 - 14	P R	R - - - R	
		<i>Thalassionema schraderi</i>	6B	49 - 7 , 10 - 11	P R
50 - 1 , 20 - 24	P R			- - R - -	
50 - 3 , 20 - 24	P C			- - R - -	
50 - 6 , 20 - 24	P C			R - R - -	
50 - 7 , 10 - 11	P C			F - - - R	
51 - 1 , 16 - 20	P A			- - F - -	
51 - 4 , 16 - 20	P F			- - F - -	
51 - 6 , 16 - 20	P A			- - R - -	
52 - 3 , 36 - 38	G A			F - - - -	
52 - 4 , 36 - 38	G A			R - - - R	
<i>Denticulopsis katayamae</i>	6A	53 - 1 , 77 - 81	G A	R - - - R	
		54 - 1 , 110 - 114	G A	R R R - R	
		55 - 1 , 70 - 74	P R	- R - - R	
		55 - 3 , 70 - 74	P R	- R - - -	
		56 - 3 , 60 - 62	G A	- R - - -	
		57 - 1 , 115 - 117	P C	- R - - -	
<i>Denticulopsis dimorpha</i>	5D	57 - 2 , 31 - 35	G A	- R - - -	
		57 - 3 , 31 - 35	M R	- R - - -	
		57 - 4 , 59 - 61	G A	- R - - -	
		58 - 1 , 16 - 20	P R	- R - - -	
		59 - 4 , 17 - 21	P R	- R - - -	
		59 - 5 , 17 - 21	G C	- R - - -	
<i>T. yabei</i>	5C	62 - 1 , 20 - 24	G A	- R - - -	
		63 - 1 , 110 - 112	P F	- R - R -	
		64 - 1 , 10 - 14	G A	- - - R -	
<i>Denticulopsis praedimorpha</i>	5B	64 - 3 , 10 - 14	G A	- - - R -	
		64 - 5 , 30 - 32	G A	- R - - -	
		65 - 1 , 54 - 56	M R	- R - - -	
		65 - 7 , 17 - 18	P R	- - - - -	
<i>C. nicobarica</i>	5A	66 - 2 , 82 - 84	G A	- - - - -	
<i>Denticulopsis hyalina</i>	4B	67 - 1 , 27 - 32	G A	- R - - -	
		67 - 1 , 112 - 113	G A	- R - - -	
		68 - 1 , 101 - 103	P A	- R - - -	
69 CC , -	G A	- - - - -			

Preservation : G=good, M=moderate, P=poor. Abundance : A=abundant, C=common, F=few, R=rare. Abundance of each species : A=abundant (>8%), C=common (5-7%), F=few (2-4%), R=rare (<1%). **Bogorovia puncticulata* Yanagisawa MS will be described in Yanagisawa (in prep. b).

Morphology of the genus *Koizumia*

The valve outline of this genus is linear-lanceolate with slightly rostrate apices (Figure 5). Each apex carries an apical pore field consisting of fine puncta (Figure 12-5). The transapical costae which extend from both valve margins are nearly continuous in *K. akibae*, but they are discontinuous, interrupted broken lines in *K. adaroi* and *K. tatsunokuchiensis*. *Koizumia akibae* has an additional longitudinal costa running along one side of the margin. The valve face is more or less convex, and perforated with areolae. The areolae are arranged in transapical rows between each two transapical costae and also form longitudinal rows. Each areola might be occluded with a mesh-like cribrum, but the cribrum is completely dissolved in specimens observed. The marginal ridge is of type 4 with two longitudinal rows of pores occluded by the cribrum-like siliceous layers. The cingulum is composed of a few bands with a row of small puncta (Figure 12-6, 14-4), but its detailed composition is not known at present.

Stratigraphic distribution

The stratigraphic occurrence of *Koizumia* species is presented in Table 2 and Figure 6 for DSDP Hole 438A. The biostratigraphic zonation is based on Akiba (1986).

The stratigraphic ranges of *Koizumia* species are shown in Figure 7, which is mainly based on Figure 6, as well as on some other important biostratigraphic studies such as Schrader (1973, 1974a, 1974b, 1976), Barron (1980, 1981a, 1981b, 1985, 1992), Fenner (1984a, 1984b, 1985), Koizumi (1985, 1992), Koizumi and Tanimura (1985), Akiba (1986), Fourtanier (1987), Yanagisawa (1987) and Bodén (1992). Correlation to the time scale of Berggren *et al.* (1985) is adjusted through Barron *et al.* (1985) and Oda (1986).

Geographic distribution

The geographic distribution of each *Koizumia* species was surveyed from the litera-

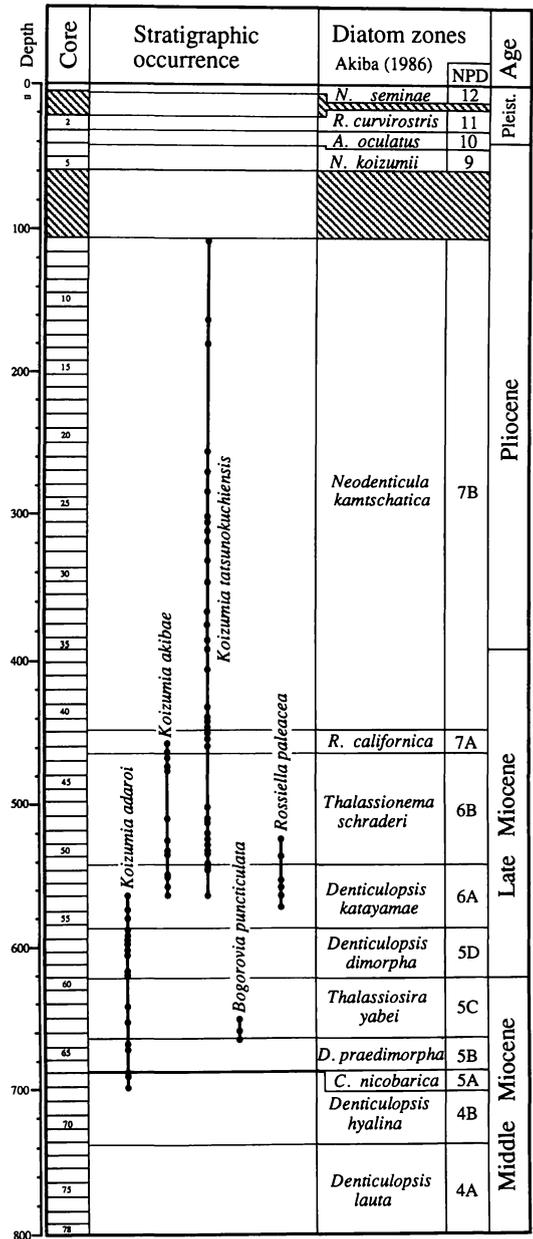


Figure 6. Stratigraphic distribution of *Koizumia* species in DSDP Hole 438A. Each dot indicates the presence of each species. Original data are presented in Table 2. Stratigraphic range of *Rossella paleacea* (Grunow) Desikachary et Maheshwari and *Bogorovia puncticulata* Yanagisawa MS are presented as well. The latter species will be described in a separate paper (Yanagisawa, in prep. b).

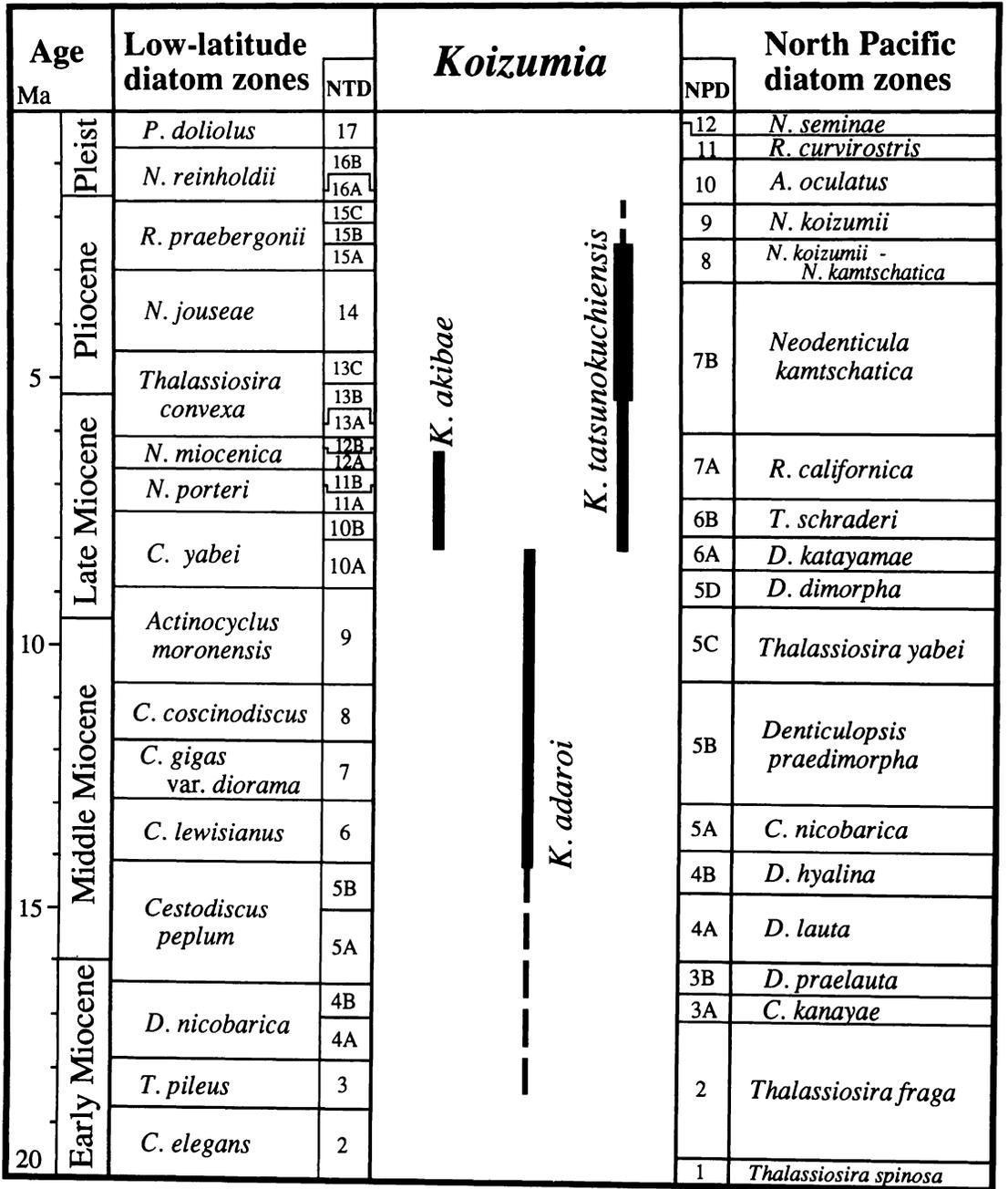


Figure 7. Stratigraphic distribution of *Koizumia* species. Low-latitude diatom zones after Barron (1985) and Fenner (1985), and North Pacific diatom zones after Akiba (1986). Correlation to the time scale of Berggren *et al.* (1985) is adjusted through Barron *et al.* (1985) and Oda (1986).

ture (Figures 11, 13, and 16). All species have been reported from near-shore or on-shore sequences mainly in the middle latitudes and rarely in low and high latitudes, and have never been recorded in purely oceanic regions such as the central equatorial Pacific.

Systematic descriptions

In this paper, the classification system of Round *et al.* (1990) is adopted for the description of the genus *Koizumia* because the system appear to be the most natural diatom system at present.

Class Coscinodiscophyceae Round
et Crawford, 1990

Subclass Cymatosiropycidae Round
et Crawford, 1990

Order Cymatosirales Round
et Crawford, 1990

Family Cymatosiraceae Hasle,
von Stosch et Syvertsen, 1983

Subfamily Cymatosiroidae Hasle,
von Stosch et Syvertsen, 1983

Genus *Koizumia* Yanagisawa gen. nov.

Generic type.—*Koizumia tatsunokuchiensis* (Koizumi) Yanagisawa comb. nov.

Description.—Cell heterovalvate, rectangular in girdle view, forming inseparable chain colonies. Separation valve or end valve that separates chain colonies. Cingula with several bands with fine puncta. Valve slightly convex, linear-lanceolate in outline. Apices with small apical pore field, slightly or strongly rostrate. Marginal ridge of sibling valves completely fused so that a set of fused sibling valves seems as if it were a frustule. Marginal ridge with two longitudinal rows of pores occluded with cribrum-like siliceous layers perforated with regularly arranged minute pores. A suture line present between two longitudinal rows of pores on marginal ridge. Rimoportula one per cell; a frustule

consisting of a process valve and a non-process valve. Rimoportula located at sub-central position near the margin, oblique to apical direction. Transapical costae extending from both margins, continuous or broken. Areolae circular, arranged in transapical rows between each two transapical costae, and also in longitudinal rows.

Comparison.—The genus is morphologically similar and probably related to the genera *Rossiella* and *Bogorovia* in a number of common features such as the linear-lanceolate valve outline, the presence of marginal ridges, the presence of the completely fused sibling valves, the apical pore field, the one-per-cell pattern of rimoportula and so on. However, *Koizumia* differs significantly from the latter two genera by the cribrum-like siliceous layers across the pores of the marginal ridge, the suture line on the marginal ridge, and the presence of transapical and longitudinal rows of areolae on the valve face, all of which are never observed in *Rossiella* nor *Bogorovia*. Of the three features, the cribrum-like siliceous layers are the most distinct character unique to the genus *Koizumia*.

The genus *Koizumia* has a close resemblance to some genera under the family Cymatosiraceae such as *Cymatosira* Grunow and *Campylosira* Grunow in Van Heurck in that they commonly possess a generally dipolar outline, chain colonies connected by marginal ridge or linking spines, rimoportula in the pattern of one per cell, the presence of ocellus or apical pore field at each apex. The genus *Koizumia* is within the morphological criteria of Cymatosiraceae defined by Hasle *et al.* (1983), and therefore it should be placed in the family Cymatosiraceae. However, *Koizumia*, as well as the related genera *Rossiella* and *Bogorovia*, differs from the other members of this family in that it has completely fused marginal ridges. As it appears that the actual fusion between siliceous components of different cells has not been known in diatoms except for one example in the Chaetoceracea (Round *et al.*, 1990,

p. 25), the completely fused marginal ridge is a nearly unique character to the three genera.

Stratigraphic occurrence.—The genus *Koizumia* appeared in the late Early Miocene and disappeared near the end of the Pliocene (Figure 7).

Habitat.—The members of *Koizumia* appear to have flourished as planktons forming long colony chains.

Geographic distribution.—The three species which constitute the genus *Koizumia* have been reported from near-shore or onshore sequences mainly in the middle latitudes and rarely in the low and high latitudes, and have never been recorded in purely oceanic regions such as the central equatorial Pacific where both *Rossiella* and *Bogorovia* are distributed abundantly (Figures 11, 13 and 16). This pattern of distribution implies that the *Koizumia* species appear to have flourished in shallow-shelf marine environments. As they are abundant especially off the western part of continents such as Peru, Baja California and Angola, characterized by strong structural upwelling and resultant high productivity, the three species may be called upwelling species. From this point of view, the three species seem to constitute a distinct group different from the *Rossiella* and *Bogorovia* species, all of which are distributed mainly in purely oceanic tropical regions.

Etymology.—As the generic names of *Rossiella* and *Bogorovia* were both derived from person names, the name of this new genus *Koizumia* is also taken from the name of a person, Professor Itaru Koizumi of Hokkaido University (Japan), who described the type

species of this genus as *Rhaphoneis tatsunokuchiensis* from the Pliocene deposits in Japan.

Discussion.—The genus is characterized by cribrum-like siliceous layers across the pores of marginal ridge and the presence of trans-apical and longitudinal rows of areolae on the valve face. The three features are unique to the genus and have never been observed in its related genera *Rossiella* and *Bogorovia*. *Koizumia* is typically neritic in distribution mainly in near-shore or upwelling regions of the middle latitudes, and significantly different from *Rossiella* and *Bogorovia*, both of which have essentially an oceanic and tropical to subtropical distribution. Both the morphological uniqueness and the differing geographic distribution pattern are considered to be distinctive enough to form the basis of the erection of the new genus *Koizumia*.

Key to species.—Key to species of the genus based on light microscopy is presented in Table 3.

***Koizumia adaroi* (Azpeitia)
Yanagisawa comb. nov.**

Figures 8-1-7, 12, 13; 9-1-3.

Basionym.—*Cymatosira adaroi* Azpeitia, 1911, p. 201, pl. 9, fig. 5; Pastor, 1991, fourth figure in p. 81.

Synonyms.—*Rhaphoneis modiopunctata* Hajós, 1968, p. 143, pl. 41, figs. 16-27; Hajós, 1977, pl. 9, fig. 3; *Rhaphoneis mediopunctata* var. *matraensis* Hajós, 1968, p. 144, pl. 42, figs. 1-5; *Cussia mediopunctata* (Hajós) Schrader, 1974a, p. 542; *Cussia mediopunctata* var. *matraensis* (Hajós)

Table 3. Key to species of the genus *Koizumia* based on light microscopy.

- | | |
|--|-----------------------------|
| 1a. Transapical costae broken and longitudinal costae absent..... | 2 |
| 1b. Transapical costae continuous and longitudinal costae present..... | <i>K. akibae</i> |
| 2a. Valve with slightly rostrate apices..... | <i>K. adaroi</i> |
| 2b. Valve with strongly rostrate apices..... | <i>K. tatsunokuchiensis</i> |

Schrader, 1974a, p. 542; *Cussia moholensis* Schrader, 1974a, p. 542-543, fig. 1.1-4; *Coscinodiscus praepaleaceus* Schrader, Barron, 1975, p. 136, pl. 7, fig. 11; *Bogorovia moholensis* (Schrader) Jousé, 1976, p. 1233; *Cussia praepaleacea* (Schrader) Schrader, Abbott and Andrews, 1979, p. 241, pl. 3, fig. 15; *Cussia* aff. *paleacea* (Grunow) Schrader, Andrews, 1980, p. 28, pl. 2, fig. 2, pl. 4, fig. 6; *Cussia praepaleacea* Schrader, Abbott, 1980, p. 62, pl. 3, fig. 2; Abbott and Ernissee, 1983, p. 299, pl. 12, fig. 3; *Bogorovia tatsunokuchiensis* (Koizumi) Jousé, Barron, 1981a, pl. 4, fig. 17; *Rossiella mediopunctata* (Hajós) Gersonde et Schrader., 1984, p. 106; Yanagisawa, 1990b, pl. 1, fig. 6; *Rossiella mediopunctata* var. *matraensis* (Hajós) Gersonde et Schrader, 1984, p. 106; *Rossiella moholensis* (Schrader) Gersonde et Schrader, 1984, p. 106; *Rossiella praepaleacea* (Schrader) Gersonde et Schrader, 1984, p. 104-105, pl. 1, figs. 11, 12; Powers, 1988, pl. 9, figs. 10-12; *Rossiella moholensis* (Schrader) Desikachary, Desikachary et al., 1984, p. 338; *Rossiella paleacea* (Grunow) Desikachary et Maheshwari, Hajós, 1986, pl. 50, figs. 18-20; *Rossiella praepaleacea* (Schrader) Gersonde (sensu Abbott and Andrews, 1979), Fourtanier and Macharé, 1988, pl. 3, fig. 39.

Original description.—Valva lanceolada de 29 μ de longitud y 7 de anchura, con perlas relativamente gruesas, no bien definidas y dispuestas en filas transversales. Cada una de las filas centrales contiene cinco perlas, y este número disminuye hacia los dos extremos hasta llegar á las punctas, en las que hay una sola, que parece más saliente que las otras. En el ejemplar fotografiado se cuentan 20 ó 22 filas en toda la longitud de la valva (Azpeitia, 1911, p. 201, as *Cymatosira adaroi* Azpeitia).

Translation.—Valve lanceolate, 29 μ m in length, 7 μ m in width, with pearls (puncta) relatively large, not well defined and disposed in transverse rows. Each one of the central rows contains five pearls (puncta), and this number decreases toward both ends until reaching the points, where there is only one (puncta), which appears more salient than the others. In the specimen photographed, 20 or 22 rows are counted in the whole length of the valve.

Observation.—Valve linear-lanceolate with

slightly rostrate apices, 20-55 μ m long, 6-8.5 μ m wide (Figure 10). Valve face convex, with transapical costae 8-9 in 10 μ m, often branching and interrupted to broken lines. Areolae medium to fine, arranged in transapical rows between each two transapical costae and also in three to seven longitudinal rows. Marginal ridge of fused type with two longitudinal rows of pores occluded by cribrum-like layers (type 4). A subcentral rimoportula, one per cell, located near the valve edge as the simple rimoportula with its lip-shaped internal inner aperture opening diagonally to the apical axis and its external pore being flush with the marginal ridge surface.

A long colony chain composed of seven frustules has been observed with all sibling valves connected to each other by the fused marginal ridge (Fourtanier, 1987, pl. 16, fig. 5).

The species shows gradual variation in valve shape. The specimens from the early Middle Miocene *Denticulopsis lauta* Zone (Figure 8-1) have a broadly lanceolate form, whereas those from the upper *Denticulopsis hyalina* Zone (Figures 8-3, 8-4) are more slender. The valves from the late Middle Miocene *Denticulopsis praedimorpha* Zone (Figures 8-5, 8-7) are larger, showing more similarity to *R. akibae*. Among them, specimens from the *D. hyalina* Zone are the most similar to the holotype specimen discovered in Spain.

Holotype.—Azpeitia, 1911, pl. 9, fig. 5 or Pastor, 1991, 4th figure in p. 81 (Azpeitia-871016-19, deposited in Instituto Tecnológico GeoMinero de España).

Type locality.—Sample from gypsiferous deposits of the "serrata" (small ridge of mountains), Lorca, Spain.

Type level.—Late Miocene in age, Messinian (Sancetta et al., 1985).

Comparison.—*Koizumia adaroi* very closely resembles *K. akibae*, but is distinguished from the latter by its broken lines of transapical costae and the lack of longitudinal

costa (Figure 5). The species resembles *K. tatsunokuchiensis*, but differs by non-rostrate apices. This species has been often misidentified as *Bogorovia praepaleacea* (Schrader) Jousé (e.g. Barron, 1975; Abbott and Andrews, 1979; Gersonde and Schrader, 1984; Powers, 1988), but is clearly distinguished from the latter by the presence of areolae on the valve face.

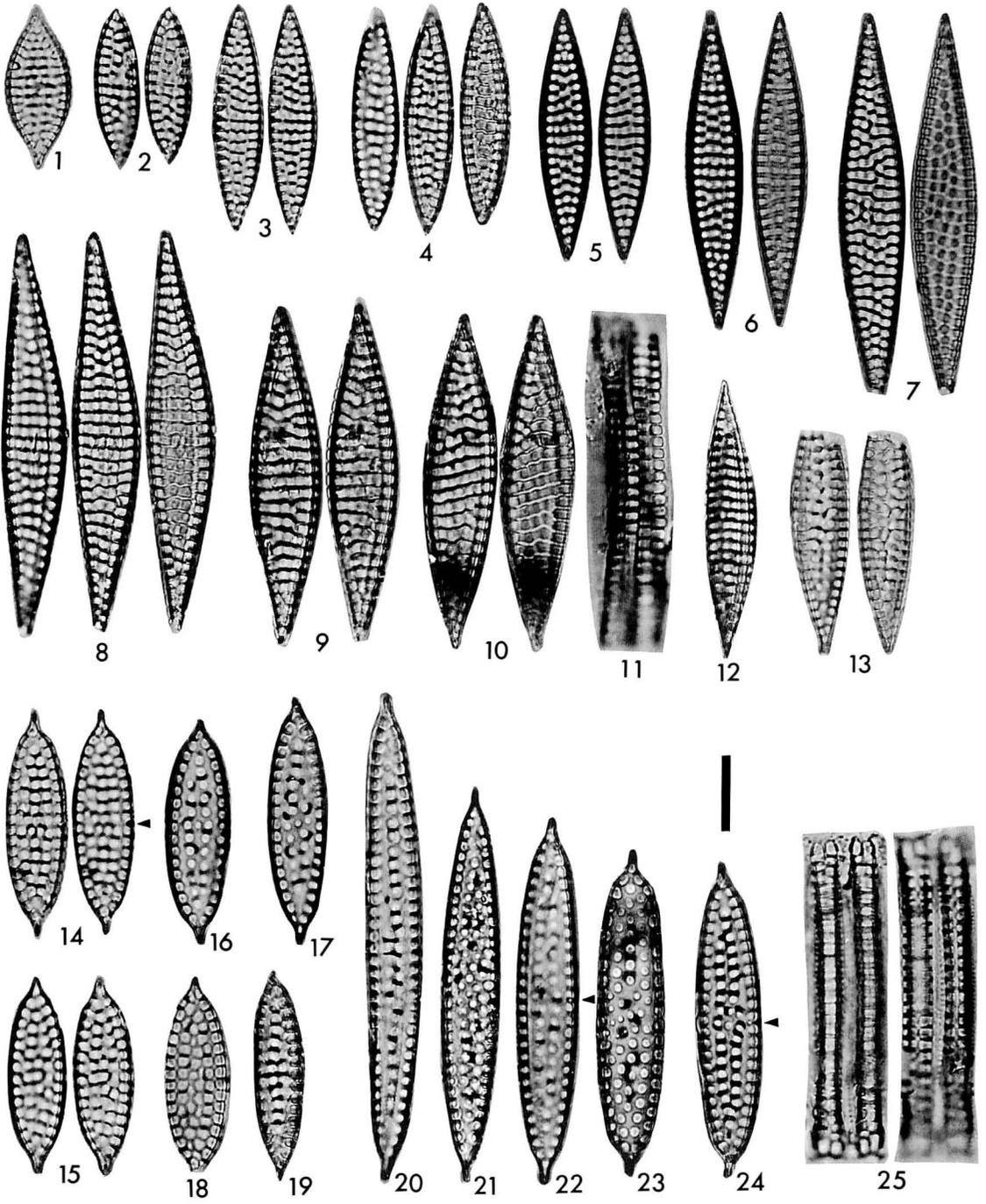
Stratigraphic range.—In DSDP Hole 438A, this species occurs from the upper part of the *Denticulopsis hyalina* Zone (NPD 4B) to the middle part of the *Denticulopsis katayamae* Zone (NPD 6A) (Figure 6). However, its first occurrence may range down to the late Early Miocene (Figure 7); the species is found from the early Middle Miocene Oidawara Formation in Mizunami area in central Japan, which can be correlated with the lower part of the *Denticulopsis lauta* Zone (NPD 4A) (Figure 8–1). Moreover, the species occurs in the upper part of the late Early Miocene *Thalassiosira fraga* Zone (NPD 2) in the Nabuto Formation, Chiba, Boso Peninsula, Japan (Figure 8–13).

Fourtanier (1987) reported the stratigraphic range of *Rossiella mediopunctata* (Hajós) Gersonde et Schrader in the South Atlantic off Angola and Namibia. Although *Rossiella mediopunctata* is a synonym of *Koizumia adaroi* as will be discussed later, Fourtanier's (1987) species concept of *R. mediopunctata* is apparently broader than that of *K. adaroi* in this paper, including

both *K. adaroi* and *K. akibae*. Therefore *R. mediopunctata* in Fourtanier (1987) has a longer stratigraphic range than *K. adaroi* in this paper. The last occurrence of *R. mediopunctata* falls below the top of the *Nitzschia miocenica* Zone (NTD 12) in the South Atlantic off Angola and Namibia (Fourtanier, 1987), which is apparently younger than that in the North Pacific (Figure 7). The last occurrence of *R. mediopunctata* in Fourtanier (1987) is coincident with that of *K. akibae* in the North Pacific (Figure 7).

Geographic distribution.—This species has been mainly found in the middle-latitude areas (Figure 11). In the Northern Hemisphere, the species has been reported from Spain (Azpeitia, 1911; Gersonde and Schrader, 1984; Monjanel, 1987), Hungary (Hajós, 1968, 1977, 1986), the Atlantic coast of U.S.A. (Abbott and Andrews, 1979; Abbott, 1980; Andrews, 1980; Abbott and Ernissee, 1983; Powers, 1988), California and its environs (Barron, 1975, 1981a; Schrader, 1974a; Fourtanier, 1987) and Japan (Fourtanier, 1987; Yanagisawa, 1990b; this study). In the Southern Hemisphere, the species occurs in the South Atlantic near Angola (Fourtanier, 1987) and Peru (Fourtanier, 1987; Fourtanier and Macharé, 1988). It has never been identified in the low latitudes, e.g. the DSDP Hole 77B drilled in the tropical eastern Pacific. As this species has been reported mainly from on-land or near-

→ **Figure 8.** LM photomicrographs of *Koizumia* species. Scale bar equals 10 μ m. Arrow heads indicate the location of rimoportula. **1–7.** *Koizumia adaroi* (Azpeitia) Yanagisawa comb. nov. (1) Sample Mzn 09, Oidawara Formation, Mizunami area, Gifu Prefecture, Japan (the *Denticulopsis lauta* Zone). (2, 3) Sample Nmy 13A, Nishimyo Formation, Niigata area, Japan (the *Denticulopsis hyalina* Zone). (4) DSDP Hole 438A, 67–1, 27–32 cm. (5–7) Sample M32, Izozaki Formation, Ajigaura area, Japan (the *Denticulopsis praedimorpha* Zone). **8–11.** *Koizumia akibae* Yanagisawa sp. nov. (8) DSDP Hole 438A, 52–3, 36–38 cm. (9) Holotype, DSDP Hole 438A, 50–6, 20–24 cm. (10) DSDP Hole 438A, 50–7, 10–11 cm. (11) DSDP Hole 438A, 52–4, 36–38 cm. **12, 13.** *Koizumia adaroi* (Azpeitia) Yanagisawa comb. nov. (12) DSDP Hole 438A, 59–4, 17–21 cm. (13) Km 09, Nabuto Formation, Kamogawa, Chiba Prefecture, Boso Peninsula, Japan (the upper part of the *Thalassiosira fraga* Zone). **14–25.** *Koizumia tatsunokuchiensis* (Koizumi) Yanagisawa comb. nov. (14, 15) A-1, 11.00–11.23 m, Tomioka, Fukushima, Japan. (16–18, 20, 22, 24, 25) JDS 8842, San Felipe, Mexico. (19) Sample Ha 67 (Se 40), Tatsunokuchi Formation, Iwanuma, Miyagi, Japan. (21) D-1, Sunda Forearc, off Java Island. (23) DSDP Hole 438A, 51–1, 16–20 cm.



shore sequences, it seems to have flourished in shallow-shelf marine environments and may be adapted to the coastal upwelling zones.

Discussion.—The species was originally described as *Cymatosira adaroi* from the Upper Miocene gypsiferous deposits of Lorca, Spain (Azpeitia, 1911). However, no one referred to it before Pastor (1991) recently presented an excellent photomicrograph of the type specimen. Gersonde and Schrader (1984) reported this species as *Rossiella praepaleacea* (Schrader) Gersonde et Schrader from the Lorca Basin. Gersonde and Schrader's (1984) specimens might have been obtained from the same stratigraphic unit of Azpeitia (1911) although the exact location is not clear.

Rhaphoneis mediopunctata Hajós, a species described from the Miocene deposits in Hungary (Hajós, 1968), is considered to be a synonym of *K. adaroi* because of the same morphologic features. Hajós (1968) also described *R. mediopunctata* var. *matraensis*, a variety that is distinguished from the nominated variety *mediopunctata* by the number of middle longitudinal rows of areolae; the variety *mediopunctata* has two rows while the variety *matraensis* has only one row. However, this difference is thought to be a continuous intraspecific variation, as more clearly seen in *K. tatsunokuchiensis* (see Figures 8-20, 8-14, 8-17), and therefore the variety *matraensis* is also a synonym of *K. adaroi*.

Cussia moholensis Schrader, which was described by Schrader (1974a) from the experimental Mohole site off California, has morphologic characteristics well fitting those of *K. adaroi* except for a very long valve. The holotype and paratype specimens of *C. moholensis* may be identified as extremely long specimens of *K. adaroi*, because they almost fall within the variation of *K. adaroi* in biometric plots (Figure 10). *Cussia moholensis* is therefore considered to be a synonym of *K. adaroi*. The specimens of *C. moholensis* are similar to *K. akibae*, but are

clearly distinguished from the latter by the broken transapical costae. Fourtanier (1987) has already pointed out that *C. moholensis* is probably a synonym of *Rossiella mediopunctata* which is synonymized with *K. adaroi* in this paper.

As pointed out by Fourtanier (1987, p. 107-108), there is some doubt that the holotype specimen of *Cussia praepaleacea* Schrader chosen by Schrader (1973) may be *Koizumia adaroi*. Despite the original statement that *C. praepaleacea* has a hyaline valve face (absence of areolae), the photographed holotype seems to have circular areolae between the transapical costae on the valve face. However, I cannot assert the presence of areolae with confidence because of the rather poor picture of the holotype.

Koizumia akibae Yanagisawa sp. nov.

Figures 8-8—11; 12-1—7.

Synonyms.—*Rossiella praepaleacea* (Schrader) Gersonde, Akiba *et al.*, 1982, pl. 3, fig. 93. *Rossiella praepaleacea* (Schrader) Gersonde et Schrader, Akiba, 1986, p. 445, pl. 19, fig. 6.

Description.—Valve linear-lanceolate, 28-50 μm long, 7-10 μm wide. Apices not rostrate. Transapical costae, 7-8 in 10 μm , rarely branching and almost continuous, not broken. A faint longitudinal costa present one areola apart from a margin. Marginal ridge of fused type with two longitudinal rows of subrounded pores occluded by cribrum-like layers (type 4). A subcentral rimoportula, one per cell, located near the valve edge as the simple rimoportula with its lip-shaped internal inner aperture opening diagonally to the apical axis and its external pore being flush with the marginal ridge surface. Cingulum consisting of two or three bands punctated with a row of small puncta.

Holotype.—Figure 8-9 (GSJF14590 deposited in the Geological Survey of Japan).

Type sample.—DSDP Hole 438A, Core 50, Section 6, Interval 20-24 cm, 40°37.79'N, 143°14.15'E, northwest Pacific, off Honshu, Japan.

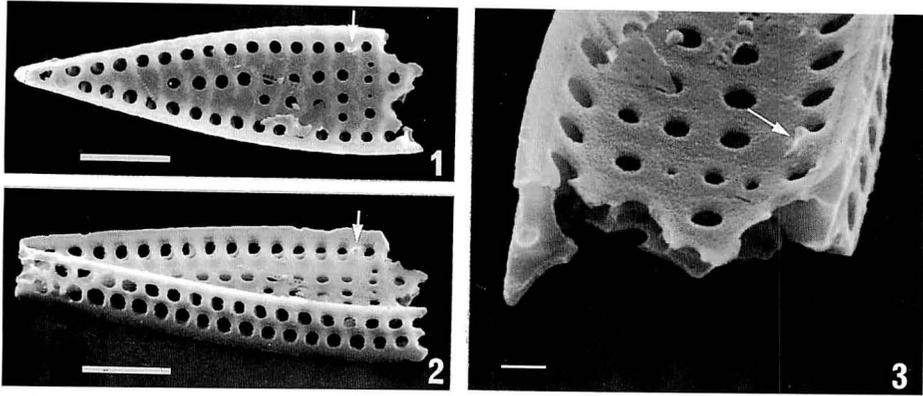


Figure 9. SEM photomicrographs of *Koizumia adaroi* (Azpeitia) Yanagisawa comb. nov. Sample M32, Isozaki Formation, Ajigaura area, Japan. Broad and narrow scale bars equal $5\ \mu\text{m}$ and $1\ \mu\text{m}$, respectively. Arrows indicate rimoportulae. **1.** Inner view of valve. **2.** Oblique view. **3.** Enlarged view of a destroyed valve.

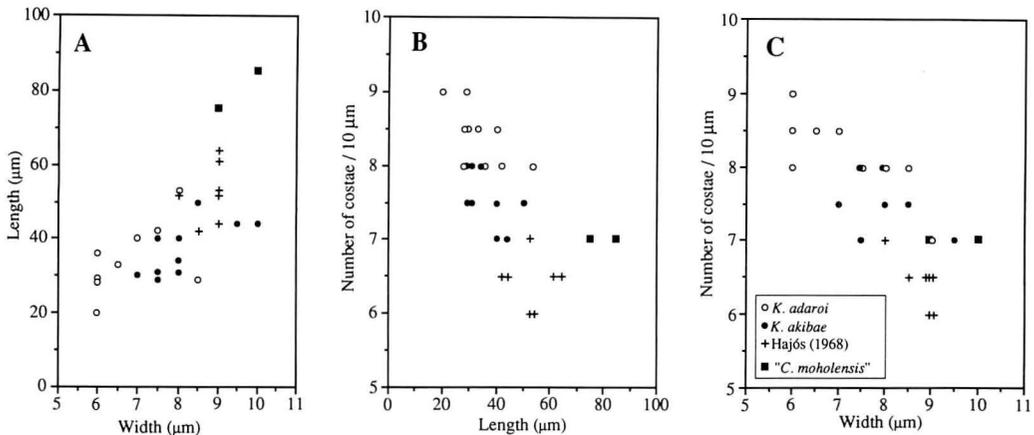


Figure 10. Size variation in *Koizumia adaroi* (Azpeitia) Yanagisawa comb. nov. and *K. akibae* Yanagisawa sp. nov. **A.** Scatter plot of valve width versus length. **B.** Scatter plot of valve length versus the number of transapical costae in $10\ \mu\text{m}$. **C.** Scatter plot of valve width versus the number of transapical costae in $10\ \mu\text{m}$. Samples from no. 1, 5, 8 in Table 1. Pluses indicate the size of *Rhaphoneis mediopunctata* Hajós and *R. mediopunctata* var. *matraensis* Hajós (Hajós, 1968). Closed squares indicate the size of *Cussia moholensis* Schrader (Schrader, 1974a).

Type level.—Late Miocene in age, *Thalassionema schraderi* Zone (NPD 6B).

Comparison.—*Koizumia abibae* resembles *K. adaroi*, but is distinct from the latter in having nearly continuous transapical costae, a longitudinal costa (Figure 5), slightly broader valve width and slightly broader spacing of transapical costae (Figure 10). The species is similar to *K. tatsunokuchiensis*, but differs from the latter mainly by non-

rostrate apices and nearly continuous transapical costa. The species has been reported as *Rossiella praeapaleacea* by Akiba *et al.* (1982) and Akiba (1986), but *K. akibae* has areolae on the valve face whereas *B. praeapaleacea* completely lacks areolae.

Stratigraphic range.—In the North Pacific, the species occurs from the upper part of the *Denticulopsis katayamae* Zone (NPD 6A) to the middle part of the *Rouxia californica*

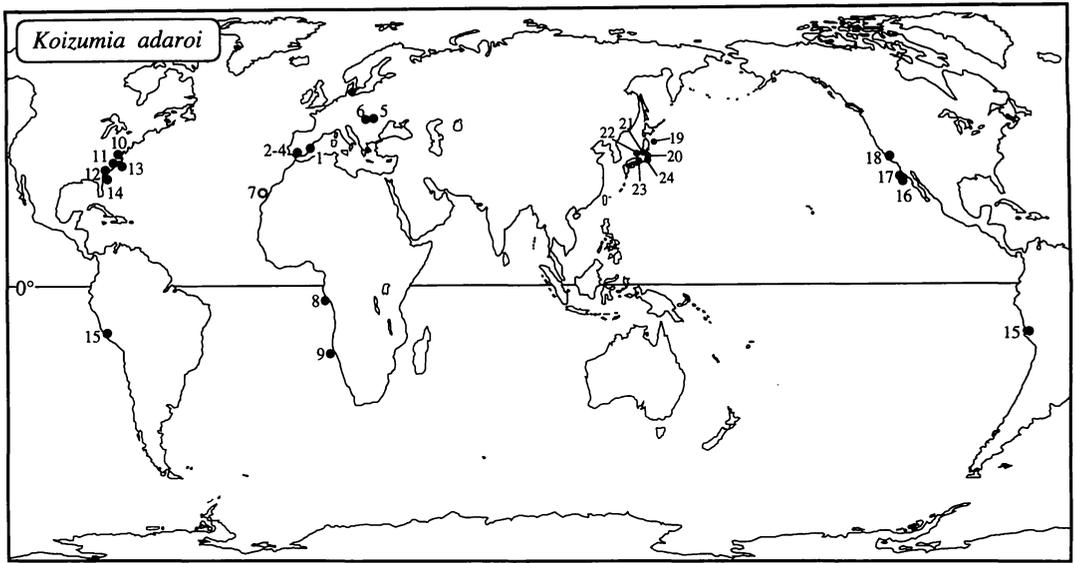


Figure 11. Geographic distribution of *Koizumia adaroi* (Azpeitia) Yanagisawa comb. nov. Closed circles : localities reported with figures. Open circle : locality reported without figures. 1. Lorca, Spain (Azpeitia, 1911; Pastor, 1991; Gersonde and Schrader, 1984). 2. Puente Gentil, Guadalquivir Basin, Spain (Monjanel, 1987). 3. Aguilar, Guadalquivir Basin, Spain (Monjanel, 1987). 4. San Felix, Guadalquivir Basin, Spain (Monjanel, 1987). 5. Szurdokpüspöki, Hungary (Hajós, 1968). 6. Szokolya, Hungary (Hajós, 1977, 1986). 7. DSDP Hole 369A, eastern north Atlantic margin off northwest Africa (Schrader, 1977). 8. Cores ANG 1 and ANG 2, South Atlantic off Angola (Fourtanier, 1987). 9. DSDP Hole 363, South Atlantic off Namibia (Fourtanier, 1987). 10. Petersburg, Virginia, U.S.A. (Andrews, 1980). 11. Pungo River Formation, RA-13-GRL, Beaufort County, North Carolina, U.S.A. (Abbott and Ernissee, 1983). 12. Hawthorn Formation, Dawsons Landing, South Carolina, U.S.A. (Abbott and Andrews, 1979). 13. Pungo River Formation, Onslow Bay continental shelf cores OB 108 and OB 95, off North Carolina (Powers, 1988). 14. Drill core AMCOR 6002, off Georgia, U.S.A. (Abbott, 1980). 15. Pisco Formation, Pisco, Peru (Fourtanier and Macharé 1988; Fourtanier, 1987). 16. DSDP Hole 470, northeast Pacific off Baja California (Barron, 1981a; Fourtanier, 1987). 17. Experimental Mohole Drilling Guadalupe Site, northeast Pacific off Baja California (Schrader, 1974a). 18. Monterey Formation, Lompoc, California, U.S.A. (Barron, 1975). 19. DSDP Hole 438A, northwest Pacific off Japan (this study; Fourtanier, 1987). 20. M32, Izozaki Formation, Ajigaura, Ibaraki, Japan (this study). 21. Nishimyo Formation, Sumon, Niigata, Japan (this study). 22. Otokawa Formation, Endo, Toyama, Japan (Yanagisawa, 1990b). 23. Oidawara Formation, Mizunami, Gifu, Japan (this study). 24. Nabuto Formation, Kamogawa, Chiba, Japan (this study).

Zone (NPD 7A) (Figures 6, 7).

Geographic distribution.—At present, this species is found only in DSDP Hole 438A (Akiba, 1986, this study) and from the Omatsuzawa Formation in Matsushima area, Japan (Akiba *et al.*, 1982) (Figure 13). It is probably a middle-latitude species following the distribution pattern of the related species *K. adaroi* and *K. tatsunokuchiensis*.

Etymology.—This new species is named in honor of Mr. Fumio Akiba, who first figured

this species (Akiba *et al.*, 1982; Akiba, 1986).

***Koizumia tatsunokuchiensis* (Koizumi)
Yanagisawa comb. nov.**

Figures 8-14—25, 14-1—9.

Basionym.—*Rhaphoneis tatsunokuchiensis* Koizumi, 1972, p. 394, pl. 42, figs. 3, 4

Synonyms.—*Rhaphoneis tatsunokuchiensis* Koizumi; Koizumi, 1973, pl. 20, figs. 14, 15; 1975a,

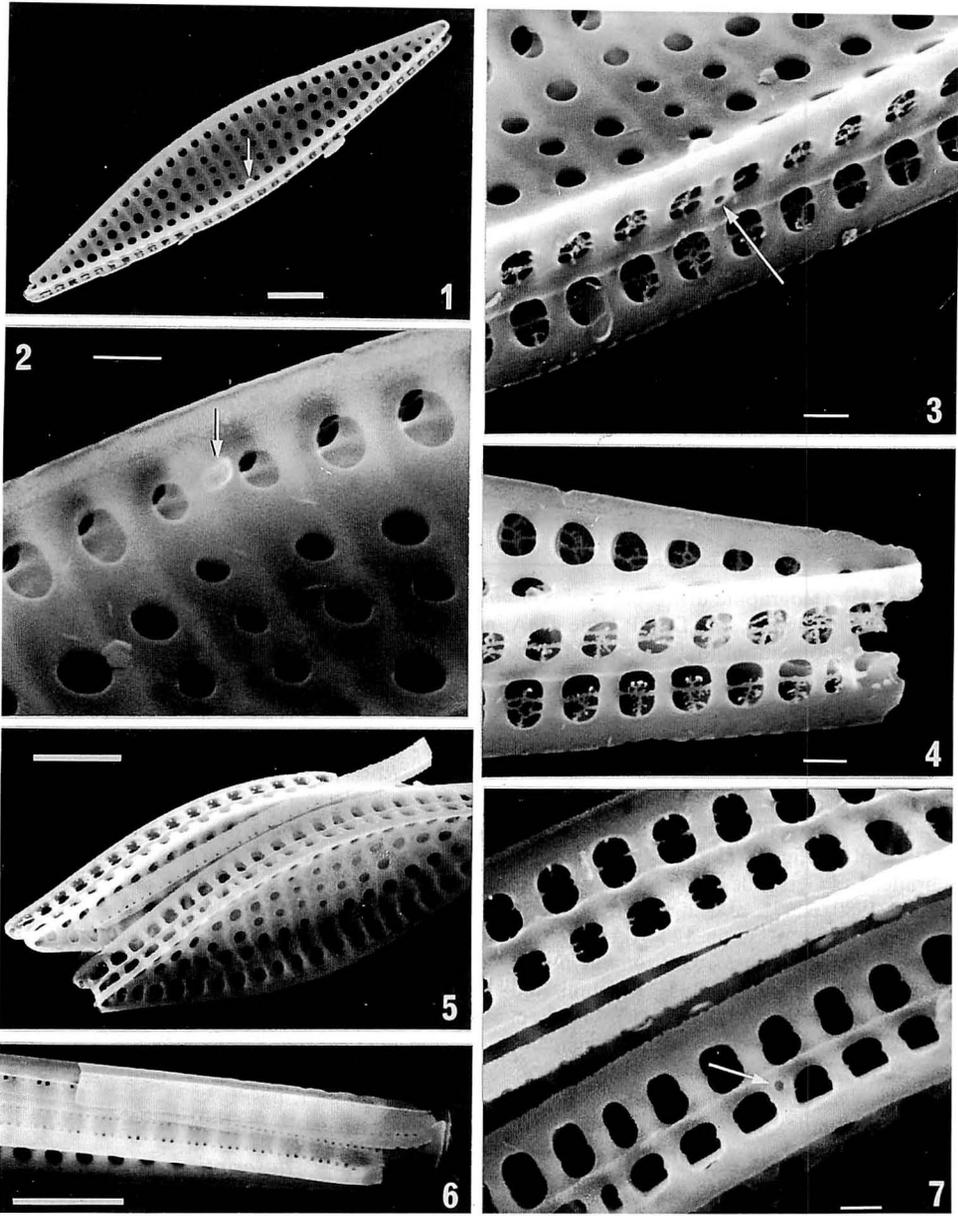


Figure 12. SEM photomicrographs of *Koizumia akibae* Yanagisawa sp. nov. DSDP Hole 438A, 53–2, 30–31 cm. Broad and narrow scale bars equal $5\ \mu\text{m}$ and $1\ \mu\text{m}$, respectively. **1, 2.** Inner views of a valve. Arrows indicate rimoportulae. **3.** Enlarged view of marginal ridge, showing a rimoportula (arrow) and cribrum-like siliceous layers across the pores of marginal ridge. Note a suture line between two sibling valves. **4.** Enlarged view of an apex. **5.** Two sets of fused sibling valves. **6.** Marginal ridge with cingulum bands. **7.** Enlarged view of Fig. 12-5, showing the external opening of a rimoportula (arrow).

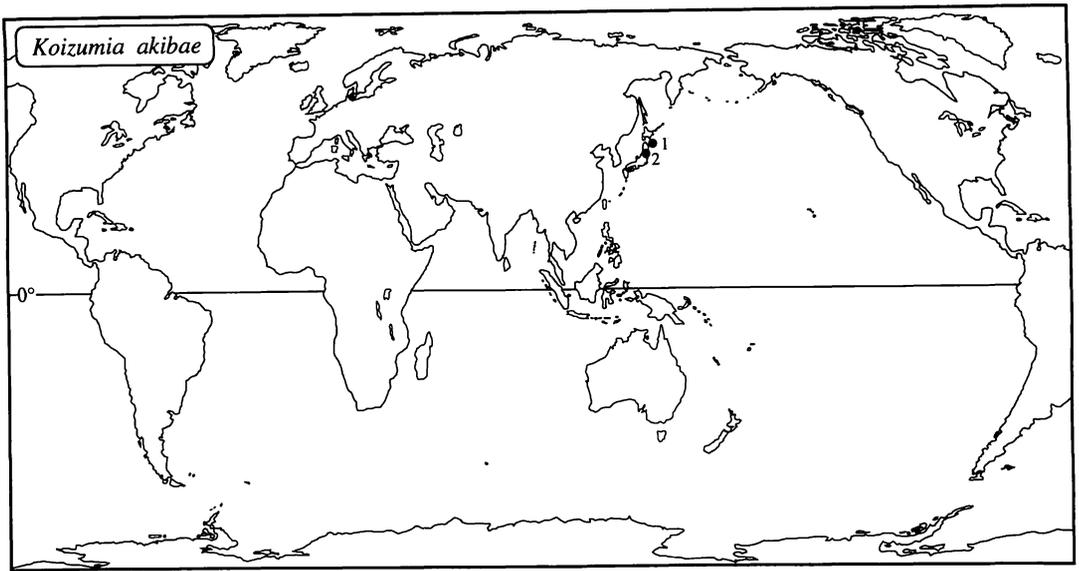


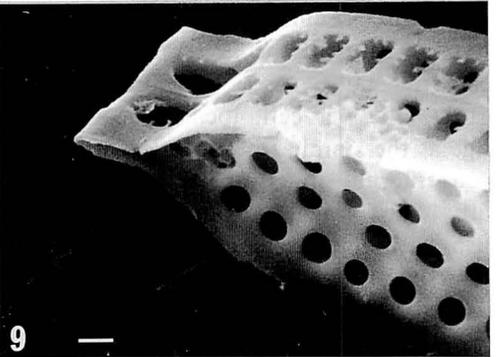
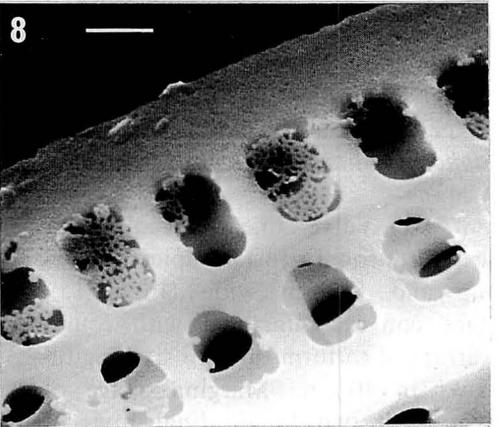
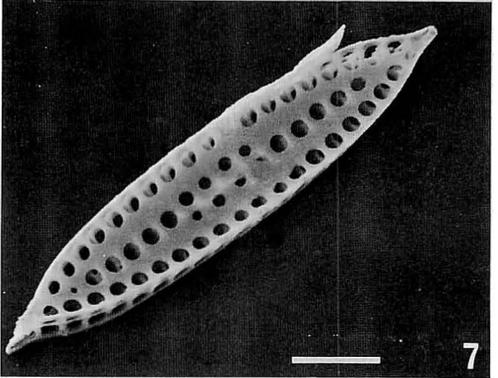
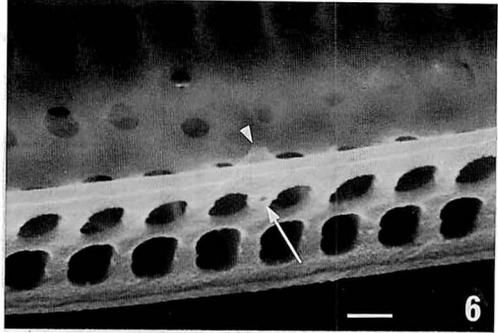
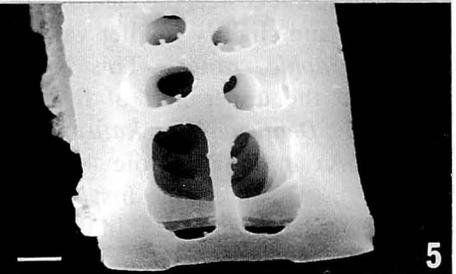
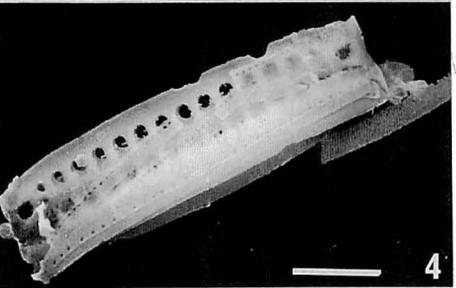
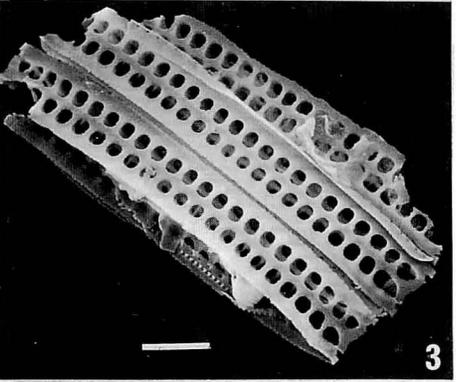
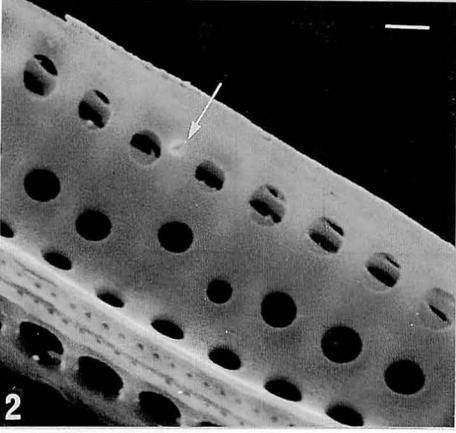
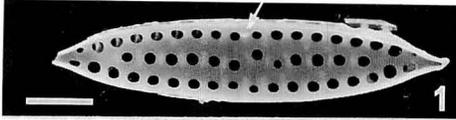
Figure 13. Geographic distribution of *Koizumia akibae* Yanagisawa sp. nov. Closed circles: localities reported with figures. 1. DSDP Hole 438A, northwest Pacific off Japan (this study; Akiba, 1986). 2. Omatsuzawa Formation, Matsushima, Miyagi, Japan (Akiba *et al.*, 1982).

p. 804; *Cussia tatsunokuchiensis* (Koizumi) Schrader, 1974a, p. 543, figs. 1-6, 1-7; Schrader, 1974b, p. 914; Koizumi, 1975b, p. 876, pl. 4, figs. 33-35; 1975c, p. 619, pl. 1, fig. 23; Koizumi and Ujiié, 1976, pl. 12, fig. 7; Harper, 1977, pl. 3, fig. 7; Schrader and Gersonde, 1978, p. 151, pl. 2, fig. 5; Barron, 1980, p. 672, pl. 1, fig. 31, pl. 4, fig. 3; Kulm *et al.*, 1981, pl. 1, fig. 12; Akutsu, 1982, pl. 20, fig. 2099; *Bogorovia tatsunokuchiensis* (Koizumi) Jousé, 1976, p. 1233; Koizumi and Tanimura, 1985, pl. 1, fig. 19; Bodén, 1992, p. 135, pl. 2, figs. 2, 3; *Bogorovia mediopunctata* (Hajós) Jousé, 1976, p. 1233, fig. 4; Jousé *ed.*, 1977, pl. 45, fig. 31; *Rossiella tatsunokuchiensis* (Koizumi) Gersonde, Akiba *et al.*, 1982, pl. III, figs. 90, 91; Desikachary *et al.*, 1984, p. 338 pl. 1, fig. 7; Barron, 1985, p. 790, fig. 9.8; Hirayama and Uemura, 1985, pl. 1, fig. 7; Ito, 1986, pl. 3, fig. 11; Taketani *et al.*, 1986, pl. 3, figs. 10, 11;

Fourtanier and Macharé, 1988 pl. 3, fig. 40; *Rossiella tatsunokuchiensis* (Koizumi) Gersonde et Schrader, 1984, p. 106; Koizumi, 1986, pl. 1 fig. 5; Akiba, 1986, p. 445, pl. 19, figs. 7-9; Akiba, 1987, pl. 2, fig. 15; Yanagisawa, 1987, pl. 5, figs. 1, 2; Taketani *et al.*, 1990, pl. 10, figs. 15, 16; Watanabe, 1990, pl. 1, fig. 10; Yanagisawa *et al.*, 1991, pl. 24, fig. 4; "*Cussia*" *mediopunctata* (Hajós) Schrader, Akiba *et al.*, 1982, pl. 3, fig. 92; *Rossiella* cf. *tatsunokuchiensis* (Koizumi) Gersonde et Schrader, Akiba, 1986, p. 445, pl. 19, figs. 10-12; *Rossiella praepaleacea* Schrader et Gersonde, Schrader and Castaneda, 1990, pl. 1, figs. 1-3.

Original description.—Valve lanceolate-rhombic or lanceolate, with produced apices. The length of apical axis 20-36 μm ,

→ **Figure 14.** SEM photomicrographs of *Koizumia tatsunokuchiensis* (Koizumi) Yanagisawa comb. nov. (1-4, 6, 7) Sample Ya 185, Tatsunokuchi Formation, Matsushima area, Japan. (5, 8, 9) DSDP Hole 438A, 50-6, 20-24 cm. Broad and narrow scale bars equal 5 μm and 1 μm , respectively. 1, 2. Inner views of a process valve. Arrow indicates a rimoportula. 3. Short colony chain composed of three sets of fused sibling valves. 4. Marginal ridge with cingulum bands. 5. Enlarged view of an apex. 6. Enlarged view of marginal ridge. Arrow head and arrow indicate a rimoportula and its outer opening, respectively. 7. Inner view of a non-process valve. 8. Enlarged view of marginal ridge, showing cribrum-like siliceous layers covering the pores of marginal ridge. 9. Oblique view of a set of fused sibling valves. Note a suture line between the two valves.



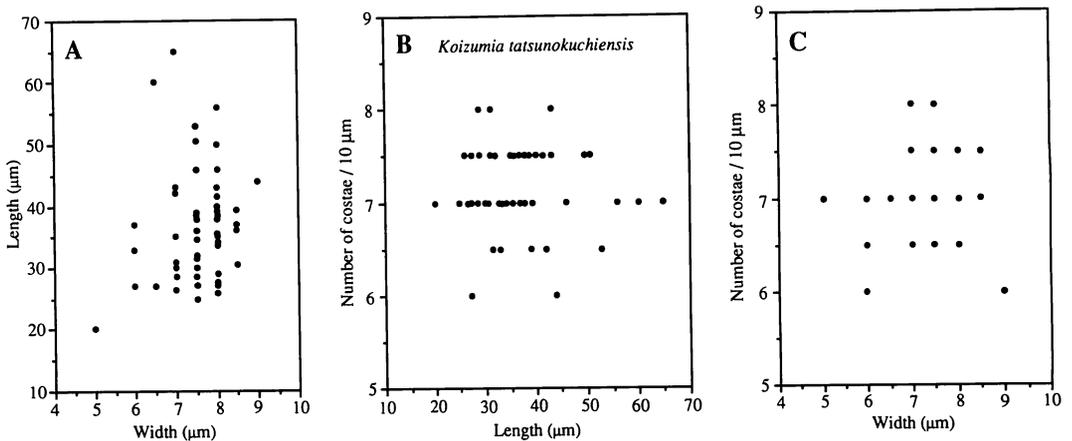


Figure 15. Size variation in *Koizumia tatsunokuchiensis* (Koizumi) Yanagisawa comb. nov. **A.** Scatter plot of valve width versus length. **B.** Scatter plot of valve length versus the number of transapical costae in 10 μm . **C.** Scatter plot of valve width versus the number of transapical costae in 10 μm . Samples from no. 1-4, 9 in Table 1.

tranapical axis 5–10 μm . Valve surface flat, covered with large sub-rectangular puncta, 6–8 in 10 μm . Puncta in weakly radiating curved lines on both sides of a narrowed linear pseudoraphe, and are interrupted by the sub-marginal hyaline line extending parallel to the valve margin. The number of longitudinal parallel rows of puncta is about 6 (as *Rhaphoneis tatsunokuchiensis* Koizumi, 1972, p. 349).

Observation.—Valve linear-lanceolate or rhombic with strongly rostrate apices, 20–64 μm long and 5–9 μm wide (Figure 15). Valve face convex, punctated with round areolae arranged to form three to six longitudinal rows in 10 μm . Marginal ridge of fused type with two longitudinal rows of subrounded pores occluded by cribrum-like layers (type 4), though the layers have been dissolved in many cases. A subcentral rimoportula, one per cell, located near the valve edge as the simple rimoportula with its lip-shaped internal inner aperture opening diagonally to the apical axis and its external pore flush with the marginal ridge surface. Cingulum consisting of several bands, each of which is perforated by a row of small puncta.

Holotype.—Koizumi, 1972, pl. 42, fig. 4,

Slide no. 6717, position England Finder T44-4, deposited in Dr. Koizumi's personal diatom collections.

Type sample.—Sample Tomioka 36, Tomioka Town, Futaba district, Fukushima Prefecture, northeast Honshu, Japan.

Type level.—Late Pliocene in age, the *Neodenticula koizumii*-*Neodenticula kamtschatica* Zone (NPD 8). The type sample of this species was originally assigned to the Tatsunokuchi Formation in the lower Sendai Group (Koizumi, 1972), but it is now included in the Dainenji Formation in the upper Sendai Group (Yanagisawa, 1990a).

Comparison.—This species closely resembles *K. adaroi*, but differs by the strongly rostrate apices (Figure 5). *Koizumia tatsunokuchiensis* is distinguished from *K. akibae* by having strongly rostrate apices, discontinuous transapical costae, the lack of a longitudinal costa and slightly smaller valve size.

Stratigraphic range.—This species first occurs in the upper part of the early Late Miocene *Denticulopsis katayamae* Zone (NPD 6A) in DSDP Hole 438A (Table 2, Figure 6). However, the first occurrence of this species has been placed in the middle part of the *Neodenticula kamtschatica* Zone

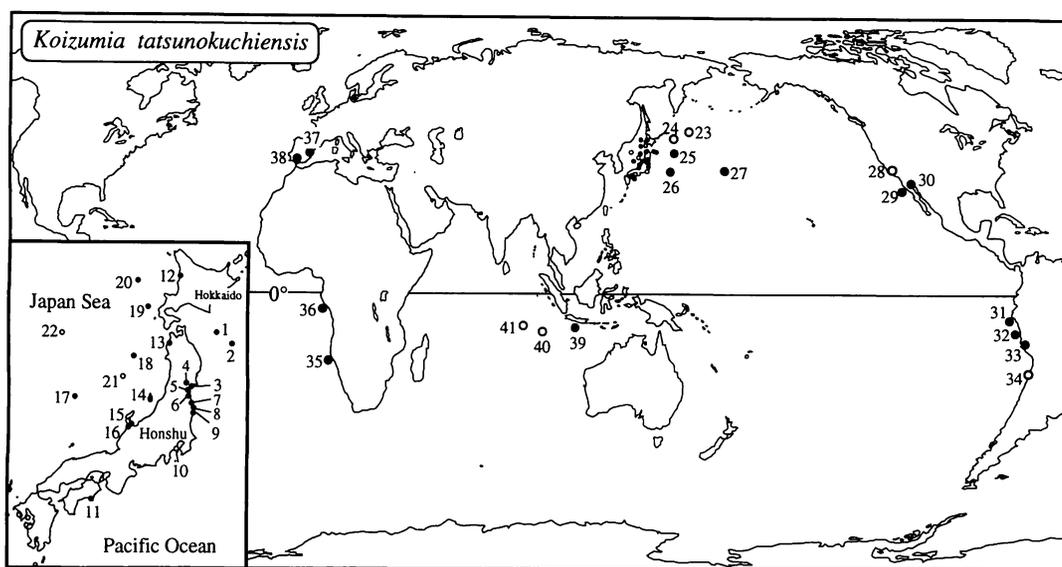


Figure 16. Geographic distribution of *Koizumia tatsunokuchiensis* (Koizumi) Yanagisawa comb. nov. Closed circles : localities reported with figures. Open circles : localities reported without figures. 1. DSDP Hole 438A, northwest Pacific off Japan (this study ; Barron, 1980 ; Akiba, 1986 ; Fourtanier, 1987). 2. DSDP Hole 584, northwest Pacific off Japan (Akiba, 1986). 3. Tatsunokuchi Formation, Matsushima, Miyagi, Japan (Akiba *et al.*, 1982 ; this study). 4. Omatsuzawa Formation, Matsushima, Miyagi, Japan (Akiba *et al.*, 1982). 5. Tatsunokuchi Formation, Sendai, Miyagi, Japan (Koizumi, 1973 ; Yanagisawa, 1990a). 6. Tatsunokuchi Formation, Iwanuma, Miyagi, Japan (Akutsu, 1982 ; Yanagisawa, 1990a ; this study). 7. Dainenji Formation (Tomioka F.), Tomioka, Fukushima, Japan (Koizumi, 1972 ; Taketani *et al.*, 1986 ; Yanagisawa *et al.*, 1989 ; Yanagisawa, 1990a ; this study). 8. Taga Group, Hirono, Fukushima, Japan (Koizumi, 1975c). 9. Yotsukura Formation, Iwaki, Fukushima, Japan (Taketani *et al.*, 1990). 10. Ikego and Zushi Formations, Ikego, Zushi, Kanagawa, Japan (Maruyama, 1993a, b). 11. Nobori Formation, Kochi, Shikoku, Japan (Koizumi and Ujiie, 1976). 12. Enbetsu Formation, Shosanbetsu, Hokkaido, Japan (Harper, 1977). 13. Akaishi and Mado Formations, Ajigasawa, Aomori, Japan (Hirayama and Uemura, 1985 ; Akiba and Hiramatsu 1988). 14. Nakayama Formation, Sado Island, Niigata, Japan (Akiba, 1987). 15. Ao Formation, Himi, Toyama, Japan (Watanabe, 1990). 16. Takakubo Mudstone, Tsuribe, Ishikawa, Japan (Ito, 1986). 17. DSDP Hole 797B, Japan Sea (Koizumi, 1992). 18. DSDP Hole 794A, Japan Sea (Koizumi, 1992). 19. DSDP Hole 796A, Japan Sea (Koizumi, 1992). 20. DSDP Hole 795A, Japan Sea (Koizumi, 1992). 21. DSDP Hole 299, Japan Sea (Koizumi, 1975a). 22. DSDP Hole 301, Japan Sea (Koizumi, 1975a). 23. DSDP Hole 581, northwest Pacific (Koizumi and Tanimura, 1985). 24. DSDP Hole 580, northwest Pacific (Koizumi and Tanimura, 1985). 25. DSDP Hole 579, northwest Pacific (Koizumi and Tanimura, 1985). 26. DSDP Hole 578, northwest Pacific (Koizumi and Tanimura, 1985 ; Bodén, 1992). 27. DSDP Hole 310, northwest Pacific (Koizumi, 1975b). 28. Sisquoc Formation, Harris Grade, Santa Barbara, California, U. S.A. (Barron and Baldauf, 1986). 29. Experimental Mohole Drilling Guadalupe site, northeast Pacific off Baja California (Schrader, 1974a). 30. San Felipe, Baja California, Mexico (this study). 31. Dredge sample 7,706 from sea floor off Peru (Kulm *et al.*, 1981). 32. Delfin well off Peru (Schrader and Castaneda, 1990). 33. Pisco Formation, Pisco, Peru (Fourtanier and Macharé, 1988). 34. Caleta Herradura de Mejillones, Antofagasta, Chile (Koizumi, 1990). 35. DSDP Hole 362, South Atlantic off Namibia (Fourtanier, 1987). 36. Cores ANG 1 and ANG 2, South Atlantic off Angola (Fourtanier, 1987). 37. Lorca, Spain (Gersonde, 1980). 38. San Felix, Spain (Monjanel, 1987). 39. Dredge sample D-1, equatorial Indian Ocean off Java, Indonesia (Yanagisawa, 1987 ; this study). 40. DSDP Hole 213, equatorial Indian Ocean (Schrader, 1974b ; Desikachary *et al.*, 1984). 41. DSDP Hole 215, equatorial Indian Ocean (Schrader, 1974b).

(NPD 7B) near the Miocene/Pliocene boundary (Barron, 1980, 1985; Akiba, 1986; Koizumi, 1985; Koizumi and Tanimura, 1985) and estimated at 5.26 Ma (Barron, 1992). This large discrepancy may be due to the extremely sporadic and sparse occurrence of this species below the Miocene/Pliocene boundary. Probably the occurrence of this species in the Upper Miocene interval may have been overlooked by earlier researchers because of the scarcity of this species. The increase in abundance of this species around the Miocene/Pliocene boundary (Figure 7) is coincident with the previously reported first occurrence of this species.

In DSDP Hole 472 (northeast Pacific, off Baja California, Mexico), Barron (1981a) reported the first occurrence of this species at the base of the *Thalassiosira antiqua* Zone, which can be estimated at 7.6 Ma (Barron, 1992), and so slightly later than in Hole 438A.

In the South Atlantic, the first occurrence of this species falls in the *Coscinodiscus yabei* Zone (NTD 10) (Fourtanier, 1987), which is almost synchronous to that in North Pacific DSDP Hole 438A (Figure 7).

The last occurrence of this species in the middle- to high-latitude North Pacific has been reported in the upper part of the *Neodenticula koizumii*—*N. kamtschatica* Zone (NPD 8) (Barron, 1980, 1985) and estimated at 2.5–2.55 Ma by Barron (1992). In the tropical Indian Ocean, the last occurrence of *R. tatsunokuchiensis* lies near the top of the *Nitzschia jouseae* Zone (NTD 14) according to Schrader (1976). However, *K. tatsunokuchiensis* was illustrated from the C Subzone of the *Rhizosolenia praebergonii* Zone (NTD 15C, latest Pliocene in age) in dredge samples obtained from the Sunda Forearc off Java Island (Yanagisawa, 1987), suggesting that its last occurrence may range up at least to the latest Pliocene in this area (Figure 7). In the South Atlantic, the species last occurs in the uppermost *Nitzschia jouseae* Zone (NTD 14) which coincides with that in the tropical Indian Ocean (Fourtanier, 1987).

Thus the first and last occurrences of this species appear largely diachronous regionally. However, combination of all data available indicates that the species first appeared in the early Late Miocene and disappeared near the end of the Pliocene (Figure 7).

Geographic distribution.—*Koizumia tatsunokuchiensis* has been reported from numerous areas of the world (Figure 16). The species seems to be distributed mainly in the middle latitudes, but it also occurs in low and high latitudes. The species has been recorded more commonly from on-land sequences than from purely oceanic sediments. Moreover, this species occurs fairly commonly in intrabay sediments such as the Tatsunokuchi Formation. These occurrences imply that this species flourished in near-shore shallow environments.

Etymology.—The species name is derived from the Tatsunokuchi Formation from which the species was firstly described. However, the type material of this species is not from the formation, but from the Dainenji Formation as discussed above.

Conclusion

A new fossil marine diatom genus *Koizumia* Yanagisawa is proposed for three fossil species. The morphology of the genus is characterized by cribrum-like siliceous layers across the pores of the marginal ridge, the suture line on the marginal ridge and the presence of transapical and longitudinal rows of areolae on the valve face. Such features are unique to the genus and never present in its related genera *Rossiella* and *Bogorovia*. *Koizumia* is distributed mainly in near-shore or upwelling regions of the middle latitudes, and thus shows significantly different distribution pattern from *Rossiella* and *Bogorovia*, both of which are essentially oceanic and tropical to subtropical genera. Such morphological uniqueness and differing geographic distribution pattern of the genus are

considered to be distinctive enough to establish a new genus. Some features of this genus such as the colony chain formation connected by marginal ridges, a rimoportula in the pattern of "one per cell" and the presence of apical pore field suggest that the genus can be placed in the family Cymatosiraceae Hasle, von Stosch et Syvertsen.

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大松沢, Otokawa 音川, Sado 佐渡, Sendai 仙台, Shosanbetsu 初山別, Sumon 守門, Tatsnokuchi 竜の口, Tomioka 富岡, Yotsukura 四倉, Zushi 逗子.

海生化石無縦溝珪藻の新属 *Koizumia* 属: 化石無縦溝珪藻の新属 *Koizumia* を, *K. tatsunokuchiensis* (Koizumi) Yanagisawa, *K. adaroi* (Azpeitia) Yanagisawa および *K. akibae* Yanagisawa の3種を基に設立した。本属は, 近縁の *Rossiella* 属および *Bogorovia* 属に似るが, 縁どり隆起 (marginal ridge) の小穴が篩模様の薄膜に覆われること, 胞紋が切頂列および縦走列を作ることなどの独特な形質によって, それらの属とは明瞭に区別される。本属を構成する3種は, いずれも浅海性種で, 主として中緯度地域の沿岸または湧昇域に多産するが, 外洋域には少ない。この点でも本属は, 基本的に外洋性で熱帯-亜熱帯に分布の中心を持つ *Rossiella* 属および *Bogorovia* 属とは全く異なる。*Koizumia* 属は, 縁どり隆起によって長い鎖状群体を作ること, apical pore field を持つこと, さらに各被殻に1つの唇状突起を持つことなどの形質から, キマトシラ科に属するものとみられる。柳沢幸夫

978. CARBONIFEROUS FORAMINIFERS FROM THE EXOTIC LIMESTONE BLOCKS IN THE ITSUKAICHI DISTRICT, SOUTHERN KANTO MOUNTAINS, JAPAN*

FUMIO KOBAYASHI

Institute of Natural and Environmental Sciences, Himeji Institute of Technology, Sanda, Hyogo, 669-13

Abstract. Sixty-five species referable to 36 genera of Carboniferous foraminifers are discriminated from the exotic limestone blocks embedded in the Jurassic accretionary complexes of the Itsukaichi district, southern Kanto Mountains. These foraminifers are *Eostaffella*, *Profusulinella*, and many others which have not yet been described in the Kanto Mountains. *Endothyra igo*, *Eostaffella kamiyoawensis*, *Profusulinella hinodensis* and *Pseudoendothyra musashiensis* are newly proposed herein.

Key words. Carboniferous foraminifers, exotic limestone blocks, Jurassic accretionary complexes, Itsukaichi, Kanto Mountains

Introduction

Fusulinacean limestones in the Kanto Mountains are mostly Middle Carboniferous to Middle Permian in age (e.g. Huzimoto, 1936; Morikawa, 1955; Ishii, 1962; Kobayashi, 1988). Lower Carboniferous and Upper Permian limestones are rare in these mountains. Igo and Kobayashi (1974, 1980) reported Carboniferous limestones from 12 localities in the Itsukaichi district, southern Kanto Mountains. They described Namurian conodonts and corals from nodular or lenticular limestones and cherts from some of these localities, and briefly noted the occurrence of such primitive fusulinaceans as *Millerella*, *Eostaffella*, and *Profusulinella*. Subsequently, these limestones and cherts have been considered to be exotic blocks embedded in the Jurassic accretionary complexes (Takashima and Koike, 1984; Ozawa and Kobayashi, 1986; Sakai, 1987).

Limestone blocks in the Itsukaichi district

yield more than 100 species of foraminifers ranging in age from late Early Carboniferous to Late Permian. The Carboniferous limestone blocks contain such primitive fusulinaceans as *Eostaffella*, *Profusulinella*, *Akiyoshiella*, and *Pseudostaffella*, and various forms referable to Endothyridae and other families. Most of them are rarely known from the Kanto Mountains and Outer Zone of Southwest Japan.

Late Paleozoic foraminifers have been inactively investigated recently in comparison with the peak time of the 1950's and 1960's in Japan. Collision-accretion tectonics and the 1980's radiolarian studies reveal that the Late Paleozoic foraminifer limestones are exotic to the surrounding arenaceous and pelitic rocks and are inappropriate as an instrument for consideration of age and structure of accretionary complexes. On the other hand, the fauna and facies of the limestones and other associated rocks, widely distributed in the Japanese Islands, are an important source of information available for reconstructions of the paleobiogeographic province and the

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travel history of the lost oceanic plate.

This paper announces the occurrence of Carboniferous foraminifers from the limestone blocks embedded in the Jurassic accretionary complexes of the Itsukaichi district. Eight species, including 4 new, are described. All the specimens illustrated in this paper are stored in the collection of the Division of Earth Sciences, Museum of Nature and Human Activities, Hyogo.

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Geologic setting

Carboniferous foraminifers in the southern Kanto Mountains have been described or illustrated from the Raidenyama Paleozoic Belt (Huzimoto, 1932) or the Kitaosogi Formation (Ozawa, 1975) west of Ome (Huzimoto, 1936; Ozawa, 1975), and from the Shiromaru Paleozoic Belt (Huzimoto, 1932) or the Ogawadani Formation (Ozawa and Kobayashi, 1986) west of Itsukaichi (Huzimoto, 1936; Kobayashi, 1988). Additionally, Igo and Kobayashi (1974) showed rather extensive distribution of Carboniferous limestones in the Itsukaichi district. Fossiliferous Carboniferous limestones have been reported at 36 localities, including 12 by Igo and Kobayashi (1974). Among them, 27 are assignable to the Kamiyazawa Formation, 5 to the Takamizuyama Group, and 4 to the Shomaru Formation (Figure 1) based on the subdivision of the Jurassic accretionary complexes by Ozawa and Kobayashi (1986). However, the subdivision in the Itsukaichi district varies among authors (Takashima and Koike, 1984; Ozawa and Kobayashi 1986; Sakai, 1987).

According to Ozawa and Kobayashi (1986), the Kamiyazawa Formation is distinguished from the Shomaru Formation by the difference of chronologic distribution of exotic blocks and age of the surrounding pelitic rocks. On the basis of distribution,

geologic structure and lithologic assemblages, the Takamizuyama Group forms a nappe overlying the Kamiyozawa, Shomaru and Kawai Formations, which constitute the Musashi Group, and the Nishitama Group. The Nishitama Group in the Itsukaichi district is a coherent stratigraphic unit of the Upper Permian to Upper Triassic, partly ranging to Lower Jurassic, and yields such diagnostic index genera as *Palaeofusulina*, *Ophiceras*, *Halobia*, *Monotis* and many others. Late Paleozoic foraminiferal limestones are entirely lacking in the Kawai Formation.

Limestones of the Kamiyozawa and Shomaru Formations are diverse in lithologies, ages, forms, sizes, chaotically embedded within sheared pelitic rocks. Exotic blocks of the Jurassic Torinosu-type limestone are included in the Kamiyozawa Formation. Pillow lava and mafic hyaloclastite enclosing numerous small blocks of limestone are also observable. Most of the Paleozoic limestones are poor or lacking in fossils, and consist of fine-grained packstone. Occasionally, they suffer from weak dolomitization. Occurrence of well-preserved foraminifers is limited to relatively coarse-grained packstone and grainstone containing various kinds of fossils, especially crinoids and algae.

Exotic blocks of the Takamizuyama Group are characterized by laterally well-traceable, highly thick, bedded cherts. Two different kinds of limestones are recognizable in this group. One is nodular or lenticular limestones, which are embedded within basaltic pyroclastics and lava situated at the base of thick cherts. In places, they are prolific in conodonts in addition to megafossils, as indicated by Igo and Kobayashi (1974) and others. The other is thin-layered limestones interbedded with cherts. Those exposed around Mts. Hinode and Asou, and Mitake Railway Station suffer remarkable dolomitization, some of them being altered to dolostone. These two types of limestones are best displayed at Mitsuzawa, about 3 km NW of

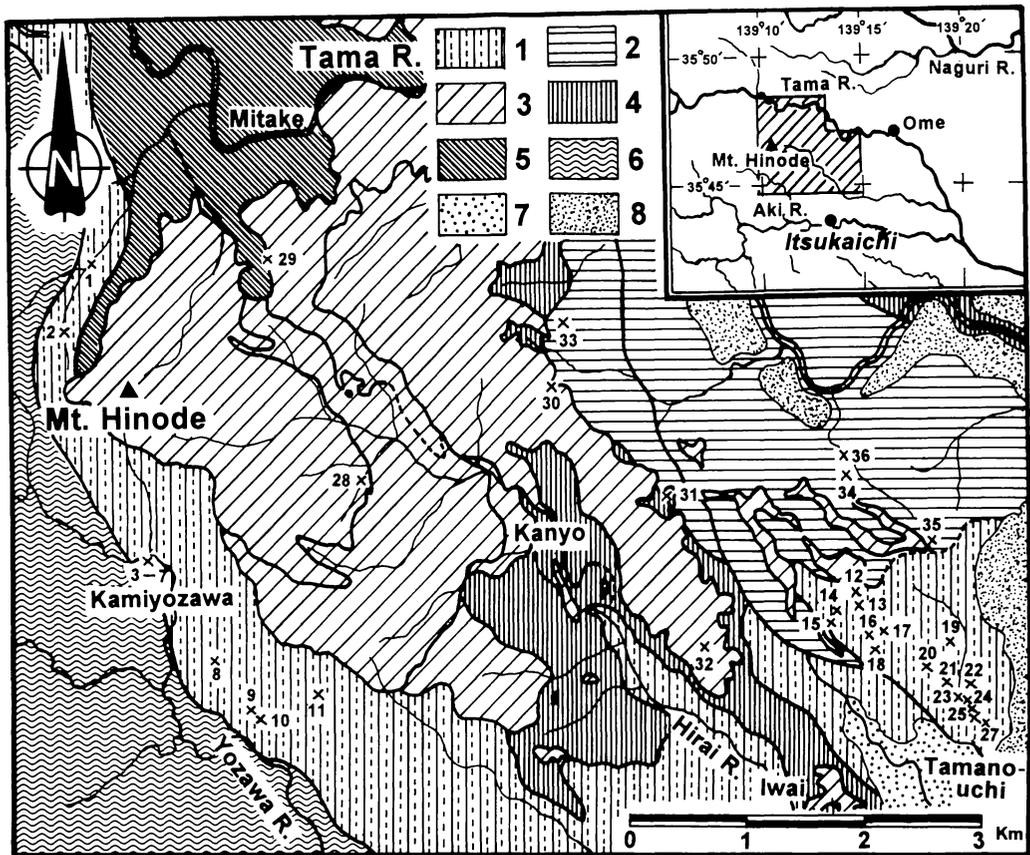


Figure 1. Geologic map of the Itsukaichi district indicating fossil localities studied herein. 1, 2, 5: Musashi Group (1: Kamiyozawa Formation; 2: Shomaru Formation; 5: Kawai Formation). 3: Takamizuyama Group. 4: Nishitama Group. 6: Tamagawa Group. 7: Neogene formations. 8: Quaternary deposits.

Musashi-itsukaichi Railway Station (Igo and Kobayashi, 1974).

Most species of the Carboniferous foraminifers in the Itsukaichi district occur in the Kamiyozawa Formation, yielding such primitive fusulinaceans as *Eostaffella*, *Profusulinella*, *Akiyoshiella* and *Pseudostaffella*, and various forms referable to the Endothyridae and other families (Table 1). They are rarely known from the Kanto Mountains and Outer Zone of Southwest Japan. *Obsoletes obsoletus* (Schellwien), *Fusiella* sp. and *Eoschubertella* sp. are restricted to the Shomaru Formation. Carboniferous as well as Permian foraminifers are scarce in the

Takamizuyama Group. Some species of *Eostaffella*, *Endothyra* and others are yielded by the limestones in which two Namurian conodont assemblages of different ages are discriminated (Igo and Kobayashi, 1974).

Systematic description

Superfamily Endothyracea Brady, 1884
 Family Endothyridae Brady, 1884
 Genus *Endothyra* Phillips, 1846
Endothyra igoi Kobayashi, n. sp.

Figures 3-1-7

Materials studied.—About 200 variously

oriented specimens.

Diagnosis.—Large-sized *Endothyra* having shallowly depressed septal suture and well-developed secondary deposits, consists of streptospirally coiled inner 2 to 3 whorls and involute, partly evolute, planispirally coiled terminal whorl.

Description.—Test discoidal with 4 whorls, broadly rounded periphery and umbilical depressions. Longer diameter of test about 0.57 to 0.77 mm. Proloculus, 0.04 to 0.06 mm in its outside diameter, followed by streptospirally coiled inner 2 to 3 whorls with abrupt changes of plane of coiling. The terminal whorl is coiled planispirally and involute, partly evolute. Chambers a few in early stages, 9 or 10 in the terminal whorl.

Wall usually with three layers, thin dark outer and inner layers and their intermediate thicker fibrous or alveolar layer in outer whorls. Septa inclined anteriorly. Septal sutures shallowly depressed. Secondary deposits well developed on the chamber floor and marginal part of chamber in form of nodes, ridges or hooks.

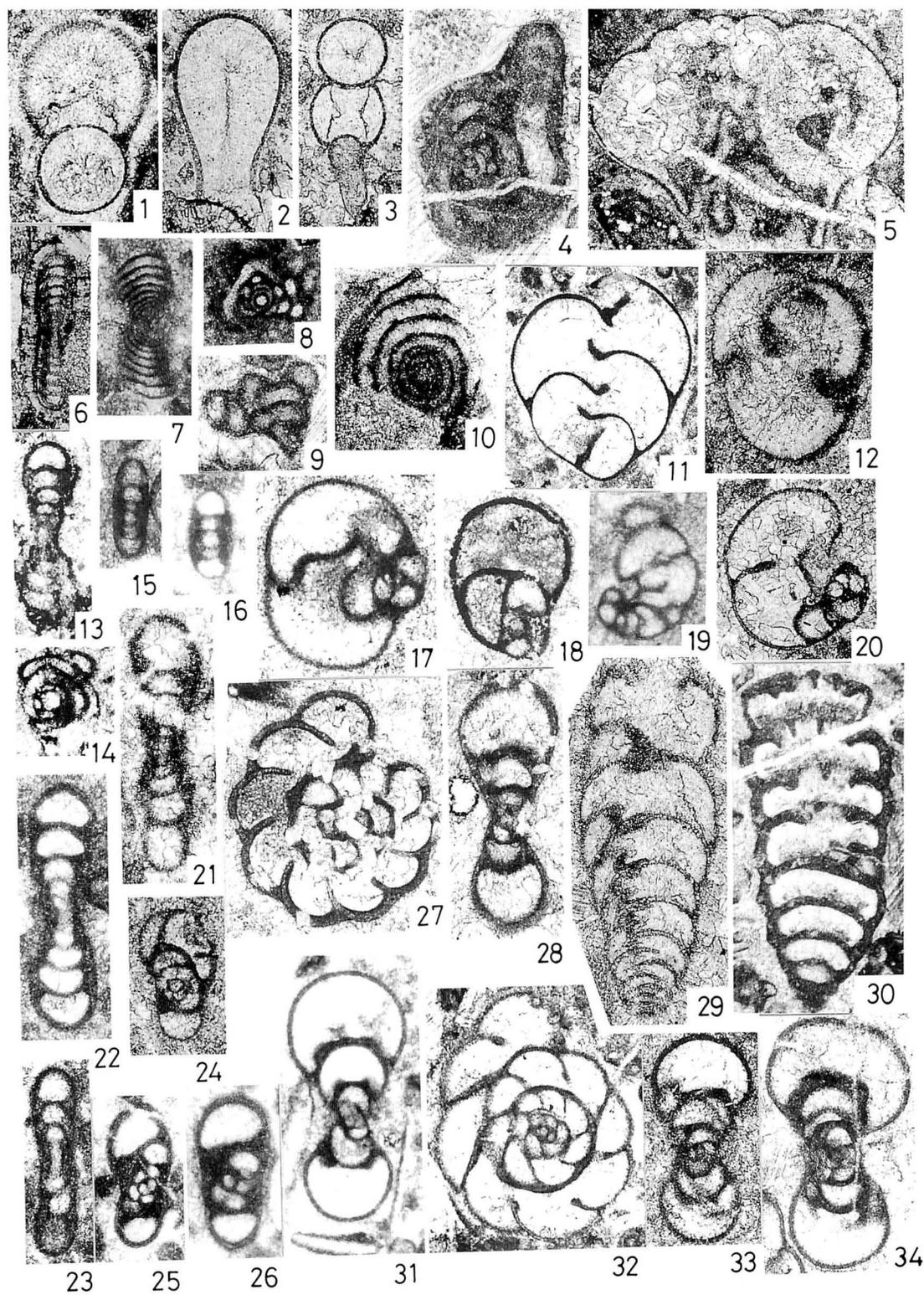
Remarks.—The present new species resembles *Endothyra excellens* (Zeller) described from the Clore Limestone of the type Chesterian of Illinois (Zeller, 1953) in mode of coiling, well-developed secondary deposits and a

large test. However, the former has more chambers in the terminal whorl, shallower septal sutures and longer septa than does the latter. This species is closely similar to *Endothyra rotayi* Lebedeva originally described from the Lower Carboniferous of the Kuznets Basin (Lebedeva, 1954), but differs from the latter in longer septa, more irregular and more rapid coiling and a larger ratio of greatest width to diameter. *Endothyra granularis* Rozovskaya from the Tula, Aleksin and Mikhailov Horizons of the Russian Platform (Rozovskaya, 1963) is also similar to the present new species in some respects, but the latter has a smoother test outline, more chambers and deeper septal sutures. *Endothyra mutabilis* Reytlinger proposed from the Bashkirian of the central Volga area (Reytlinger, 1961) has a smaller test and smaller number of chambers in the terminal whorl than the present new species.

Endothyra is most prolific in the Viséan of the Russian Federation and Ukraine (Bogush and Yeferev, 1962; Rozovskaya, 1963). The present new species seems to differ from the Viséan species of *Endothyra* by its larger test and greater number of chambers.

Endothyra sp. A in this paper is easily distinguished from the present new species by its smaller test and the slower expansion of

→ **Figure 2.** 1-3. *Tuberitina* spp., lateral sections, 1: Loc. 17; D2-1342a, 2: Loc. 12; D2-1311, 3: Loc. 25; D2-1574, ×80. 4. *Glomospiroides* sp., lateral section, Loc. 3, D2-1732, ×60. 5. Tuberitinidae gen. and sp. indet., lateral section, Loc. 26, D2-1580, ×40. 6, 7. *Eolasiodiscus donbassicus* Reytlinger, tangential sections, Loc. 3, 6: D2-1761b; ×80, 7: D2-1733; ×100. 8, 14. *Pseudoglomospira* sp., lateral sections, 8: Loc. 1; D2-2198b, 14: Loc. 21; D2-1266, ×60. 9. *Quasilituotuba* sp., lateral section, Loc. 4, D2-1779, ×60. 10, 21-23. *Pseudoammodiscus* sp., 10: transverse section; Loc. 16: D2-1282; ×60, 21-23: tangential sections, Loc. 27, 21: D2-1202a, ×80, 22: D2-1209c; ×80, 23: D2-1212; ×60. 11. *Biseriella* sp., lateral section, Loc. 2, D2-2228, ×40. 12. *Globivalvulina* sp. B, lateral section, Loc. 18, D2-1706, ×60. 13. *Planoarchaediscus* ? sp., axial section, Loc. 21, D2-1267b, ×80. 15, 16. *Mediocris breviscula* (Ganelina), axial sections, 15: Loc. 3; D2-1728a; ×80, 16: Loc. 27; D2-1208; ×100. 17-20. *Biseriella kamensis* (Reytlinger), lateral sections, 17: Loc. 22; D2-1464; ×80, 18: Loc. 21; D2-1272b; ×80, 19: Loc. 26; D2-1583; ×50, 20: Loc. 26; D2-1633; ×60. 24-26. *Endothyra* sp. A, 24: oblique section; Loc. 22; D2-1463, 25: axial section; Loc. 27; D2-1204b, 26: tangential section; Loc. 27; D2-1207a, ×60. 27, 28. *Planoendothyra* sp. B, 27: sagittal section; D2-1258a, 28: tangential section; D2-1258b, Loc. 21, ×60. 29. *Climacammina* sp. C, lateral section, Loc. 18, D2-1705c, ×50. 30. *Climacammina* sp. A, longitudinal section, Loc. 17, D2-1342b, ×20. 31-34. *Planoendothyra* sp. A, 31: tangential section; Loc. 27; D2-1207b; ×60, 32: sagittal section, Loc. 3; D2-1775d; ×50, 33: axial section; Loc. 26; D2-1588; ×60, 34: tangential section; Loc. 21; D-1259a; ×60. (All specimens in this Figure are from the Kamiyozawa Formation)



each whorl.

Etymology.—This new species is named in honor of Dr. Hisayoshi Igo, Professor of the University of Tsukuba in recognition of the his eminent work on fusulinaceans of Japan and Southeast Asia.

Occurrence.—Common at Loc. 21, and rare at Locs. 3, 4, 15, 16, 21, 24, 26, 27, 28A.

Reg. numbers.—Holotype : D2-1267a (Figure 3-1), Paratypes : D2-1254 (Figure 3-2); D2-1272a (Figure 3-3); D2-1271 (Figure 3-4); D2-1267c (Figure 3-5); D2-1261 (Figure 3-6); D2-1259b (Figure 3-7).

Genus *Planoendothyra* Reytlinger, 1959

Planoendothyra sp. A

Figures 2-31-34

Materials studied.—Four illustrated and additionally several tens of variously oriented specimens.

Description.—Test discoidal, broadly and deeply umbilicated on both sides with shallowly depressed septal sutures, consisting of 4 whorls. Periphery and lateral sides broadly rounded. Longer diameter of test about 0.63 to 0.80 (?) mm. Proloculus minute, about 0.03 mm in its outside diameter. Inner one or two whorls streptospirally coiled, with sharp changes of plane of coiling, subsequent outer ones planispirally coiled and completely evolute.

Wall thin, microgranular, commonly appears to be undifferentiated. Septa medium to long, hooklike, curved anteriorly,

8 or 9 in the last whorl. Distinct secondary deposits developed at basal and marginal parts of chambers.

Remarks.—The present unnamed species is characterized by a thin wall, compared with size of test, and distinct secondary deposits. It is similar to *Planoendothyra spirilliniformis* (Brazhnikova and Potievskaya) illustrated in pl. 19, fig. 1 by Potievskaya (in Wagner *et al.* eds, 1979) from the Bashkirian of the Donets Basin in mode of coiling, broadly and deeply umbilicated poles, thinner wall and development of secondary deposits, except for the larger test of the former. *Planoendothyra mameti* Igo and Adachi from the Ichinotani Formation (Igo and Adachi, 1981) is also similar to the present unnamed species, but the latter has a larger test and more rapidly expanding outer whorls.

Occurrence.—Rare to common at Locs. 3, 4, 21, 26, 27, 28B.

Reg. numbers.—D2-1207b (Figure 2-31), D2-1775d (Figure 2-32), D2-1588 (Figure 2-33), D2-1259a (Figure 2-34).

Superfamily Fusulinacea von Möller, 1878

Family Ozawainellidae Thompson
and Foster, 1937

Genus *Eostaffella* Rauser-Chernousova, 1948

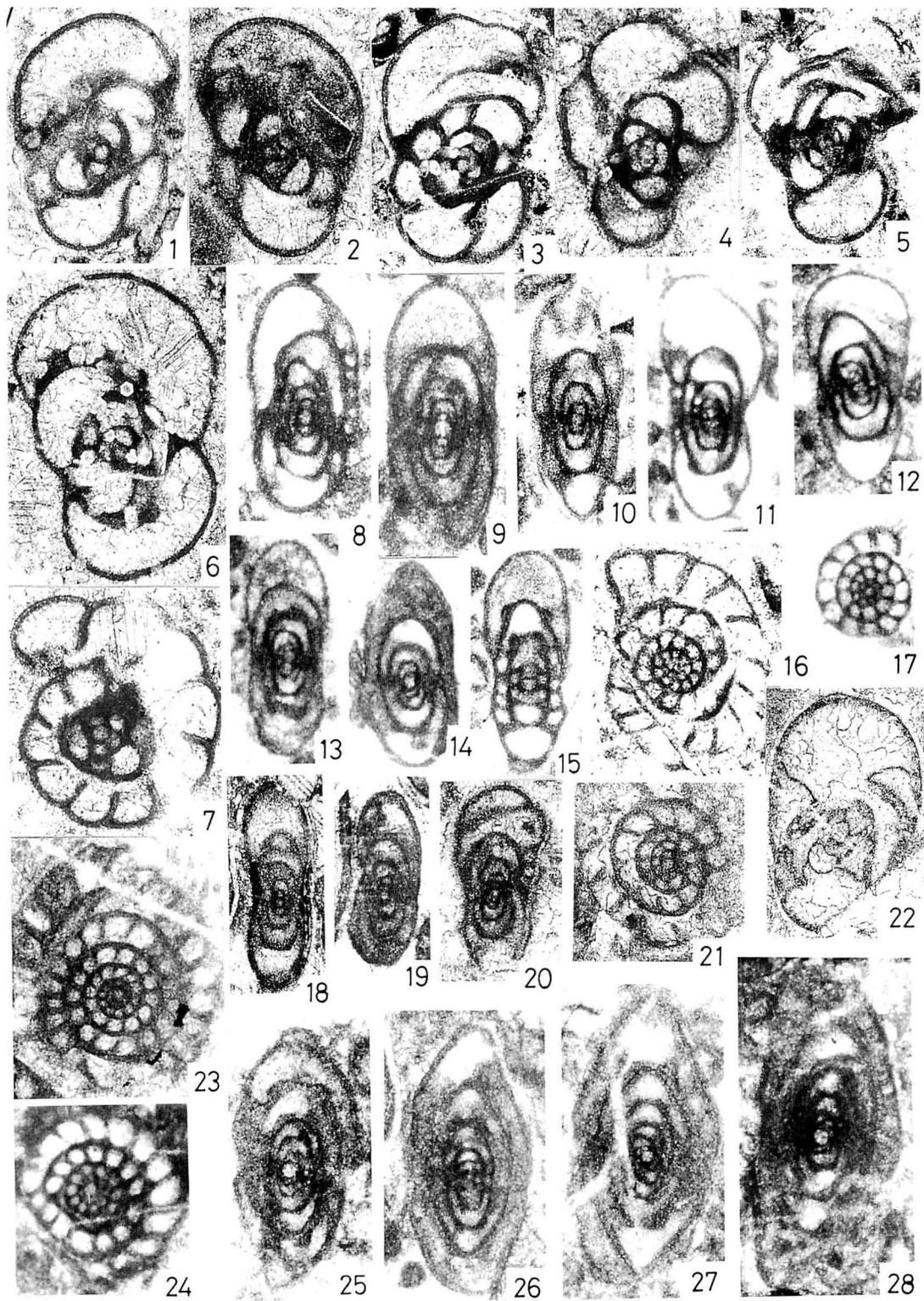
Eostaffella kamiyozaensis

Kobayashi, n. sp.

Figures 3-23-28

Materials studied.—Six illustrated specimens and several others.

→ **Figure 3.** 1-7. *Endothyra igoi* Kobayashi, n. sp., 1, 3: axial sections; 2, 5: tangential sections; 4, 6: oblique sections; 7: sagittal section, 1, 3-7: Loc. 21; 2: Loc. 24, 1: D2-1267a (holotype); 2-7: D2-1254; D2-1272a; D2-1271; D2-1267c; D2-1261; D2-1259b (paratypes), 1, 2, 4, 6, 7: $\times 60$; 3, 5: $\times 50$. 8-17. *Eostaffella yowarensis* (Ota), 8-10, 13, 14: axial sections; 11, 12, 15: tangential sections; 16, 17: sagittal sections, 8-13, 15: Loc. 27; 14, 16: Loc. 3; 17: Loc. 21, 8: D2-1209a; 9: D2-1209b 2 10: D2-1205; 11: D2-1206; 12: D2-1207c; 13: D2-1202b; 14: D2-1731; 15: D2-1211a; 16: D2-1766; 17: D2-1269, 8, 9: $\times 80$; 10-15, 17: $\times 60$; 16: $\times 50$. 18-21. *Eostaffella etoi* Ota, 18-20: axial sections; 21: sagittal section, Loc. 3, 18: D2-1762; 19: D2-1760; 20: D2-1750; 21: D2-1761a, $\times 60$. 22. *Bradyina* sp. A, axial section, Loc. 11, D2-1906, $\times 40$. 23-28. *Eostaffella kamiyozaensis* Kobayashi, n. sp., 23, 24: sagittal sections; 25, 27, 28: axial sections; 26: tangential section, Loc. 4, 27: D2-1777 (holotype), 23-26, 28: D2-1775a; D2-1776a; D2-1776b; D2-1775b; D2-1775c (paratypes), $\times 60$. (All specimens in this Figure are from the Kamiyoza Formation)



Diagnosis.—Large-sized species of *Eostaffella* characterized by a bluntly pointed periphery, nearly straight lateral sides, somewhat protruded poles, asymmetrical, low and massive chomata, and weak secondary deposits in polar regions.

Description.—Shell large for the genus, lenticular in shape with a bluntly pointed periphery, straight to slightly convex lateral sides and somewhat protruded poles. Mature shell of 5 to 6 volutions, and 0.32 to 0.38 (?) mm in axial length, 0.72 to 0.83 (?) mm in median width. Form ratio about 0.5.

Proloculus small, spherical and 0.03 to 0.05 mm in its outside diameter. Inner one or two volutions slightly askew to planispirally coiled succeeding outer ones. The first to fifth volutions of the holotype: 0.03, 0.03, 0.05, 0.11 and 0.16 mm in half length; 0.04, 0.08, 0.11, 0.18 and 0.31 mm in radius vector; 0.6, 0.4, 0.4, 0.6 and 0.5 in form ratio, respectively.

Spirotheca rather thick for the genus, composed of three layers, a thin tectum and lower and upper tectoria in outer volutions, but undifferentiated in the first volution. Its maximum thickness in the fifth volution about 0.02 mm in the holotype. Septa unfluted and slightly inclined anteriorly. Septal counts from the first to fifth volutions 5 or 6, 10 or 11, 11 or 12, 13 to 16 and 19 (?), respectively.

Weak secondary deposits developed in polar regions. Chomata asymmetrical, low and massive. Tunnel angle variable in volutions as well as specimens, but less than 20 degrees in most of outer volutions.

Remarks.—Periphery, lateral sides and polar regions of the present new species appear to be more similar to *Ozawainella* than to *Eostaffella*. However, this species is assignable to *Eostaffella* based on poorly developed chomata, a smaller shell, and fewer septa and volutions. The present new species is most similar to species of the *Eostaffella ikensis* group such as *E. ikensis* Vissarionova, *E. ikensis tenebrosa* Vissarionova and *E. proikensis* Rauser-Chernousova

in many respects, but the former differs from the latter Viséan forms by its larger shell, more number of volutions and more rapidly expanded outer volutions. This new species closely resembles *Eostaffella pespicabila* Grozdilova and Lebedeva, which also belongs to the *Eostaffella ikensis* group described from the Viséan of the Perm district (Grozdilova and Lebedeva, 1954). However, *E. pespicabila* has poorly developed chomata and prominent umbilicated depressions. Three forms of *Eostaffella mirifica* Brazhnikova proposed from the Namurian of the Dnieper-Donets Basin (Brazhnikova *et al.*, 1967) are distinct from this new species in having a smaller shell, narrower tunnel and more pointed periphery.

Eostaffella kamiyozawensis resembles *Eostaffella quasiample* Sheng, *E. subsolana* Sheng and *E. intermedia* Sheng described from the "Taitzeho" (Taizihe) Valley of Liaoning, North China (Sheng, 1958). However, the present new species has a larger shell and longer radius vectors in the corresponding volution. This new species is also similar to *Ozawainella japonica* Sada from the Akiyoshi Limestone (Sada, 1975), but the latter has a straight tunnel, more massive chomata and more septa.

Etymology.—Species name comes from the local geographical name Kamiyozawa, located northwest of Itsukaichi.

Occurrence.—Common at Loc. 4.

Reg. numbers.—Holotype: D2-1777 (Figure 3-27), Paratypes: D2-1775a (Figure 3-23); D2-1776a (Figure 3-24); D2-1776b (Figure 3-25); D2-1775b (Figure 3-26); D2-1775c (Figure 3-28).

Eostaffella yowarensis (Ota, 1971)

Figures 3-8—17

Millerella yowarensis Ota, 1971, p. 66, 67, pl. 12, figs. 1-19; Ota, 1975, pl. IIE-4, figs. 11a, 11b (not described, fig. 11a is same as pl. 12, fig. 8 of Ota, 1971); Sashida, 1981, p. 10, 11, pl. 3, figs. 1-7; Matsusue, 1986, pl. 6, figs. 13 (not described); Ueno, 1989, pl. 1, fig. 17 (not described).

Millerella toriyamai Ota, 1971, p. 67, 68, pl. 13, figs. 1-15; Matsusue, 1986, pl. 6, fig. 14 (not described).
Eostaffella yowarensis (Ota), Ozawa and Kobayashi, 1990, pl. 2, figs. 1, 2 (not described).

Materials studied.—Ten illustrated and several other specimens.

Description.—Shell lenticular to discoidal with narrowly to broadly rounded periphery, straight to convex lateral sides and slightly depressed umbilical regions. The first volution evolute, subsequent ones generally involute, and the outermost one involute to slightly evolute. Mature shell composed of 4 to 5 volutions gradually increasing in height. Expansion of shell and outline of each volution vary considerably.

Length 0.18 to 0.24 mm, width 0.45 to 0.63 mm, and form ratio 0.3 to 0.4 in 9 axial sections. Proloculus minute, spherical and 0.02 to 0.04 mm in outside diameter. Spirotheca commonly less than 0.01 mm in thickness, composed of a tectum, lower tectorium and very thin, partly lacking, upper tectorium in outer volutions. Septa plane and slightly curved anteriorly. Septal count 14 or 15 in the terminal volution. Chomata low and poorly developed. Tunnel path narrow and generally straight, but highly irregular in specimens.

Remarks.—The species belonging to *Millerella*, as represented by the type species, have a completely evolute shell, while some species referable to *Eostaffella* have an involute or partly evolute last volution, such as *E. designata* (Zeller), *E. pinguis* (Thompson), *E. pressa* (Thompson), *E. mutabilis* Rauser-Chernousova, and *E. postmosquensis* Kireeva.

Millerella yowarensis and *M. toriyamai* were described from the same locality of the Akiyoshi Limestone (Ota, 1971). Based on the coiling of the shell, expansion of the outer volutions, and other characteristics, they are assignable to *Eostaffella*. The holotypes of the two mentioned species are dissimilar in the thickness of the spirotheca, shape of the periphery, lateral sides and umbilication of the poles. However, many specimens illus-

trated by Ota show wide variation and *E. toriyamai* is considered to be conspecific with *E. yowarensis*.

The Itsukaichi specimens are identical with *E. yowarensis*, but they have a somewhat smaller shell and thinner spirotheca than do the original specimens. *E. yowarensis* differs from *Eostaffella bigemmicula* (Igo) in having a larger shell. It is probably distinguished from *E. kanmerai* (Igo) by the completely involute coiling of the latter. This species shows some resemblance to *Eostaffella mixta* (Rauser-Chernousova) and *E. pseudostruvei* (Rauser-Chernousova and Beljaev) var. *chomatifera* Kireeva from the Bashkirian of the Russian Platform and adjacent regions (Rauser-Chernousova *et al.*, 1951) and Dnieper-Donets Basin (Manukalova-Grebenyuk *et al.*, 1969), respectively, but differs from the latter two in having thinner spirotheca and obscure and discontinuous chomata.

Occurrence.—Common at Loc. 27 and rare at Locs. 3, 15, 21-24, 26.

Reg. numbers.—D2-1209a (Figure 3-8), D2-1209b (Figure 3-9), D2-1205 (Figure 3-10), D2-1206 (Figure 3-11), D2-1207c (Figure 3-12), D2-1202b (Figure 3-13), D2-1731 (Figure 3-14), D2-1211a (Figure 3-15), D2-1766 (Figure 3-16), D2-1269 (Figure 3-17).

Family Fusulinidae von Möller, 1878
 Genus *Profusulinella* Rauser-Chernousova
 and Beljaev, 1936
Profusulinella hinodensis
 Kobayashi, n. sp.

Figures 4-3-7, 6-5

Materials studied.—Five illustrated and several other specimens.

Diagnosis.—Inflated fusiform to fusiform *Profusulinella*, having unfluted septa throughout the shell, and a rather high irregular tunnel path.

Descripton.—Shell inflated fusiform to fusiform in shape with a broadly arched periphery, straight lateral sides and bluntly

pointed poles. Mature shell of 5 to 6 volutions, 1.34 to 1.68 mm in axial length and 0.83 to 1.10 mm in median width, giving a form ratio of 1.5 to 1.9. The holotype of 5½ volutions, 1.62 mm in axial length, 1.10 mm in median width, with a form ratio of 1.5.

Proloculus subspherical, small, and 0.07 to 0.09 mm in longer diameter, 0.08 mm in the holotype. Inner one or two volutions tightly coiled, subsequent ones gradually increase in length and width. The first to fifth volutions of the holotype are: 0.06, 0.12, 0.34, 0.55 and 0.73 mm in half length; 0.08, 0.12, 0.19, 0.32 and 0.47 mm in radius vector; 0.8, 0.9, 1.8, 1.7 and 1.6 in form ratio, respectively.

Spirotheca very thin and probably undifferentiated in inner one or one and a half volutions. Beyond the second volution, spirotheca gradually thickened, composed of a tectum and thin lower and upper tectoria. Septa unfluted throughout shell. Septal counts from the second to fifth volutions: 11, 14, 15 and 19 (?) in the specimen illustrated in Figure 4-6, 10, 13, 15 and 18 in Figure 4-7.

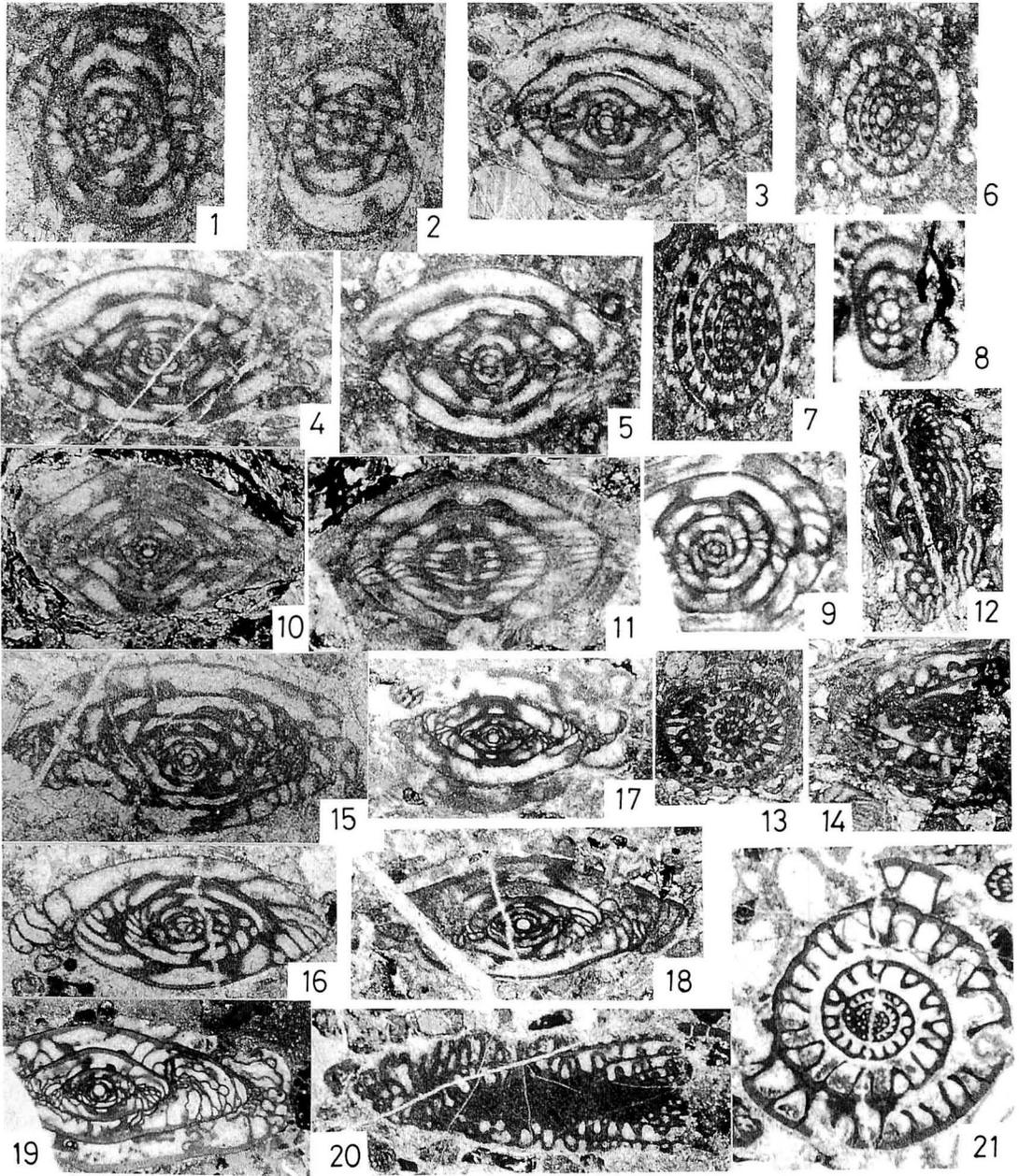
Chomata low, gently sloping toward polar regions in inner volutions, becoming higher in tunnel regions of outer volutions. Tunnel rather high, half to one-third as high as chambers. Tunnel path narrow in inner volutions, and highly variable in outer ones. Tunnel angle of some specimens attains more than 70 degrees in outer volutions.

Remarks.—*Profusulinella hinodesis* resembles *P. fukujiensis* Igo from the Ichinotani

Formation (Igo, 1957) and *P. beppensis* Toriyama from the Akiyoshi Limestone (Toriyama, 1958). Many topotype specimens from Ichinotani and Akiyoshi are examined for the sake of better understanding of the intraspecific variation of these two species (Figure 6). They show wide variation especially in size of shell, shape of lateral sides and poles, and development of chomata. The present new species can be distinguished from *P. fukujiensis* in less prominent chomata, a larger shell and larger form ratio, and from *P. beppensis* in weaker development of chomata, more slowly expanded outer volutions, a smaller shell and larger form ratio. *Profusulinella omiensis* Watanabe, described from the Omi Limestone (Watanabe, 1974), has weakly fluted septa in the polar regions, whereas septa of the present new species are unfluted throughout shell. *P. hinodesis* is easily distinguished from *P. daiyamensis* Hasegawa originally described from the Akiyoshi Limestone (Hasegawa, 1967) in having slightly concave lateral sides and by the smaller proloculus of the latter. *Profusulinella* n. sp. illustrated by Ishii (1985) from the Yura area, Kii Peninsula, is considered to be identical with the present new species, but the former has not been described.

The present new species is allied to *Profusulinella ovata* Rauser-Chernousova and *P. aljutovica* Rauser-Chernousova, both of which were originally described from the

→ **Figure 4.** **1, 2.** *Pseudostaffella composita* Grozdilova and Lebedeva, 1: axial section; D2-1978a; ×50, 2: tangential section; D2-1978b; ×60, Loc. 5. **3-7.** *Profusulinella hinodesis* Kobayashi, n. sp., 3-5: axial sections; 6, 7: sagittal sections, Loc. 6, 3: D2-1832 (holotype); 4-7: D2-1833; D2-1835; D2-1834; D2-1841 (paratypes), ×25. **8, 9.** *Pseudostaffella kanumai* Igo, axial sections, 8: Loc. 1; D2-2196; ×60, 9: Loc. 7C; D2-1808; ×30. **10, 11.** *Profusulinella rhomboides* (Lee and Chen), 10: axial section; D2-2195, 11: tangential section; D2-2198a, Loc. 1, ×25. **12-14.** *Akiyoshiella ozawai* Toriyama, 12, 14: tangential sections; 13: oblique section, Loc. 7B. 12: D2-1813a; 13: D2-1813b; 14: D2-1813c, ×15. **15, 16.** *Fusulinella itadorigawensis* Ishii, 15: axial section; D2-1905, 16: oblique section; D2-1904, Loc. 11, ×20. **17, 18.** *Montiparus matsumotoi* (Kanmera), axial sections, Loc. 12, 17, : D2-1305; 18: D2-1306, ×15. **19.** *Triticites ozawai* Toriyama, axial section, Loc. 19, D2-1556, ×10. **20.** *Quasifusulina longissima* (Möller), axial section, Loc. 13, D2-1325, ×15. **21.** *Carbonoschwagerina* sp., sagittal section, Loc. 14. D2-1667, ×15. (All specimens in this Figure are from the Kamiyozawa Formation)



Lower Moscovian of Samara Bend (Rauser-Chernousova, 1938). However, *P. hinodensis* differs from the former by its larger proloculus, more loosely coiled inner volutions and wider tunnel, and from the latter by its more inflated shell. *P. primitiva* Grozdilova and Lebedeva from the Bashkirian of the Kolva-Vishera region (Grozdilova and Lebedeva, 1954) is also close to the present new species. Some major differences between the two species are that the former has a smaller shell, narrower tunnel and more pointed axial ends. *P. hinodensis* is distinguished from *P. decora* Thompson and *P. munda* Thompson described from the *Profusulinella* Zone of Texas (Thompson, 1948) by its smaller shell, larger tunnel angles and more irregular tunnel path.

Etymology.—This species is named for Mt. Hinode, northwest of Itsukaichi.

Occurrence.—Common to rare at Loc. 6.

Type specimens.—Holotype: D2-1832 (Figure 4-3), Paratypes; D2-1833 (Figure 4-4); D2-1835 (Figure 4-5); D2-1834 (Figure 4-6); D2-1841 (Figure 4-7).

Genus *Obsoletes* Kireeva, 1950

Obsoletes obsoletus (Schellwien, 1908)

Figures 7-8—14

Fusulina obsoleta Schellwien, 1908, p. 167, 168, pl. 19, figs. 5-7.

Neofusulinella obsoleta (Schellwien), Lee, 1927, p. 18, 19, pl. 2, fig. 19.

Fusulinella obsoleta (Schellwien), Putrja, 1940, p. 54-56, pl. 2, figs. 6-9.

Protriticites obsoletus (Schellwien), Putrja, 1948, p. 94, pl. 1, figs. 7; Rozovskaya, 1950, p. 10, 11, pl. 1, figs. 1-4; Da and Sun, 1983, p. 38, 39, pl. 7, fig. 2.

Obsoletes obsoletus (Schellwien), Rauser-Chernousova and Fursenko, 1959, pl. 7, fig. 8 (same as pl. 1, fig. 2 of Rozovskaya, 1950); Rozovskaya, 1975, pl. 12, figs. 5, 6 (fig. 5: same as pl. 19, fig. 7 of Schellwien, 1908; fig. 6: same as pl. 1, fig. 2 of Rozovskaya, 1950); Niikawa, 1978, p. 562, 563, pl. 12, figs. 1, 2; Ozawa and Kobayashi, 1990, pl. 3, figs. 16-18 (not described); Ozawa, Kobayashi and Watanabe, 1991, Fig. 3. 1, 2 (same as pl. 3, figs. 16, 18 of Ozawa and Kobayashi, 1990).

Obsoletes obsoleta (Schellwien), Loeblich and Tappan, 1988, pl. 267, figs. 10-12 (same as pl. 19, figs. 6, 7, 5 of Schellwien, 1908).

Protriticites obsoletus cylindrica Da, in Da and Sun, 1983, p. 38, pl. 7, fig. 1.

Protriticites aff. *obsoletus* (Schellwien), Sheng, 1958, p. 36, 37, 95, 96, pl. 10, fig. 12.

? *Obsoletes* cf. *obsoletus* (Schellwien), Ueno, 1991, p. 818, figs. 4-9—13.

non. *Protriticites obsoletus* (Schellwien), Chen and Wang, 1983, p. 40, pl. 5, figs. 8, 9, 12.

Materials studied.—Five axial and two sagittal sections illustrated.

Description.—Shell subcylindrical to elongate fusiform with a broadly arched periphery, straight to slightly convex lateral sides and rounded poles. Mature shell of 5 to 6 volutions, 5.09 to 5.62 (?) mm in axial length and 1.45 to 1.55 mm in median width. Form ratio 3.5 to 3.6.

Proloculus spherical to subspherical, 0.08 to 0.12 mm in outside major diameter. Inner three volutions fusiform and tightly coiled. Outer two to three volutions, elongate fusiform to subcylindrical and loosely coiled compared with inner cones. The first to fifth volutions of the specimen shown in Fig. 7-8: 0.12, 0.41, 0.75, 1.36 and 2.59 mm in half length; 0.11, 0.18, 0.32, 0.50 and 0.85 mm in median width; 1.1, 2.3, 2.4, 2.7 and 3.0 in form ratio, respectively.

Spirotheca thin, composed of a tectum and lower and upper tectoria in inner three volutions. Lower tectorium partly seems to be diaphanotheca. In outer volutions, spirotheca consists of a tectum and protheca with alveolar structure. Upper tectorium obscure or lacking. Thickness of spirotheca from the first to fifth volutions of the specimen shown in Figure 7-8: 0.013, 0.015, 0.023, 0.023 and 0.028 mm, respectively.

Septa weakly fluted in polar and axial regions. Septal counts of the first to sixth volutions of the specimen shown in Fig. 7-13: 8, 11, 13, 15, 16 and 21, respectively.

Chomata massive, asymmetrical, nodelike to hooklike, one-third to two-thirds as high as chambers, but discontinuous and poorly

developed in the terminal volution. Tunnel angle 20 to 35 degrees in inner volutions, but highly variable and occasionally attains more than 50 degrees in outer ones. Tunnel path not straight.

Remarks.—The present specimens have about twice as large a shell and more strongly fluted septa than the original ones described from the Upper Carboniferous of the Donbass (Schellwien, 1908). However, they present striking similarities in other characters such as thin spirotheca and massive chomata.

The Itsukaichi specimens bear the closest resemblance to those described from the Upper Carboniferous of the Moscow Basin by Rozovskaya (1950).

This species shows considerable but continuous variation. However, there are remarkable differences between the Akiyoshi specimens described by Ueno (1991) and previously described ones in thickness of spirotheca, septal fluting and development of chomata. It is doubtful whether the Ueno's specimens are referable to the present species and assign-

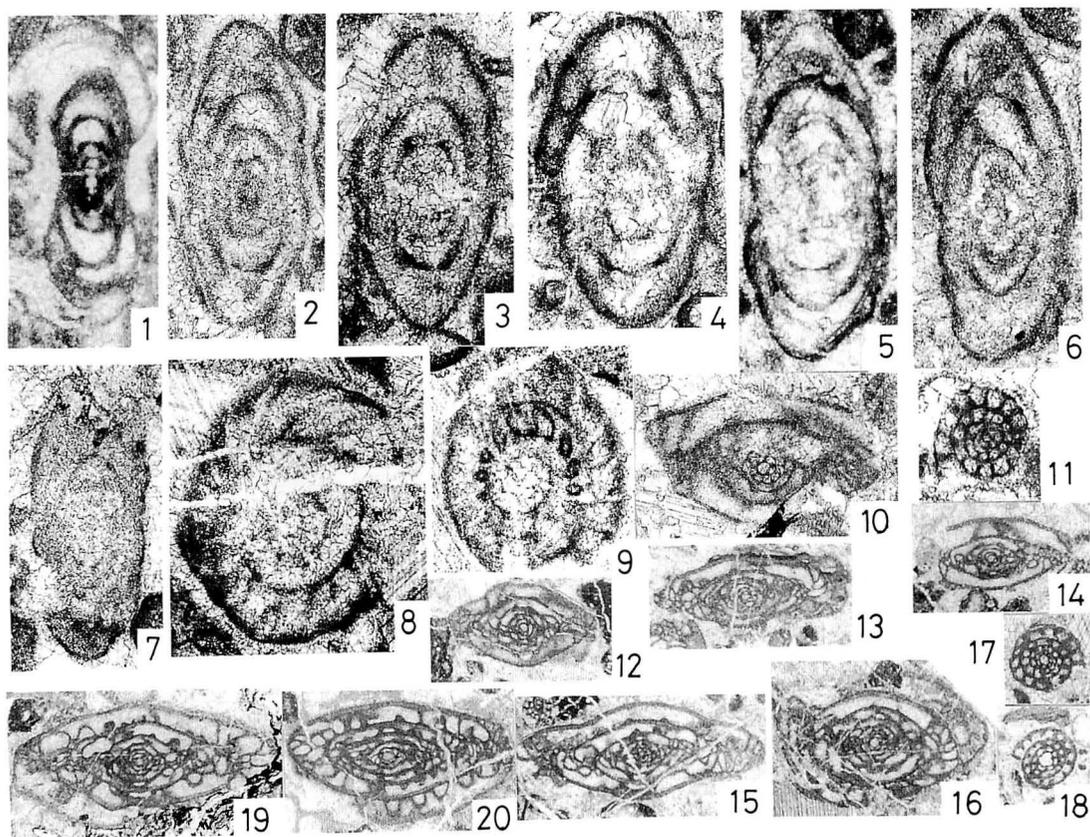


Figure 5. 1. *Millerella* sp., axial section, Loc. 27, D2-1204c, $\times 60$. 2-9. *Pseudoendothyra musashiensis* Kobayashi, n. sp., 2-7: axial sections; 8, 9: sagittal sections, 2-4, 6-9: Loc. 3; 5: Loc. 27, 2: D2-1746 (holotype); 3-9: D2-1735; D2-1737; D2-1211b; D2-1738; D2-1756; D2-1728b; D2-1759 (paratypes), 2, 4, 6-9: $\times 50$; 3, 5: $\times 60$. 10, 11. *Schubertella* sp., 10: axial section; Loc. 12; D2-1299, 11: sagittal section; Loc. 13, D2-1318, $\times 40$. 12-18. *Triticites nakatsugawensis* Morikawa, 12-16: axial sections; 17, 18: sagittal sections, 12, 13, 15-17: Loc. 13; 14, 18: Loc. 18, 12: D2-1321; 13: D2-1324; 14: D2-1705a; 15: D2-1322a; 16: D2-1319; 17: D2-1322b; 18: D2-1705b, $\times 15$. 19, 20. *Triticites* sp., axial sections, Loc. 14, 19: D2-1669; 20: D2-1668, $\times 15$. (All specimens in this Figure are from the Kamiyozawa Formation)

able to *Obsoletes* based on the dissimilarities of these diagnostic characters. Three specimens described from the Maping Limestone of Guangxi by Chen and Wang (1983) do not belong to this species. These have rather symmetrical chomata, straight tunnel path, and thicker spirotheca in outer volutions, compared to the original as well as to other previously described materials.

Occurrence.—Common to rare at Loc. 36.

Reg. numbers.—D2-3163a (Figure 7-8), D2-3169 (Figure 7-9), D2-3173 (Figure 7-10), D2-3172a (Figure 7-11), D2-3174a (Figure 7-12), D2-3175 (Figure 7-13), D2-3164a (Figure 7-14).

Family Schwagerinidae Dunbar
and Henbest, 1930

Genus *Montiparus* Rozovskaya, 1948
Montiparus matsumotoi (Kanmera, 1955)

Figures 4-17, 18

Triticites matsumotoi Kanmera, 1955, p. 184, 185, pl. 11 figs. 6-25; Choi, 1972, p. 483-486, pl. 7, figs. 1-9; Ota, 1975, pl. IIE-4, figs. 9a, 9b (not described).

Protriticites (Protriticites) matsumotoi (Kanmera); Ozawa, 1975, pl. 8, figs. 29-31 (not described).

Protriticites aff. *matsumotoi* (Kanmera); Yamagiwa and Kubota, 1980, figs. 1-3 (not described).

Triticites matsumotoi kattoi Suyari, 1962, p. 15, 16, Pl. 5, figs. 1-3.

Triticites matsumotoi suitaensis Suyari, 1962, p. 17, 18, pl. 5, figs. 4-6.

Montiparus matsumotoi (Kanmera): Ozawa and Kobayashi, 1990 pl. 4, figs. 4, 5 (not described); Ozawa, Kobayashi and Watanabe, 1991, figs. 3-7, 8 (not described, fig. 3-8 is same as pl. 4, fig. 5 of Ozawa and Kobayashi, 1990).

Remarks.—Spirothecal structure of the

present form is: undifferentiated in the first volution; composed of a tectum, thicker lower tectorium showing appearance of protheca and thinner, occasionally indistinct, upper tectorium in the second and third ones; and made up of a tectum and finely alveolar keriotheca in the succeeding ones. The Itsukaichi specimens closely resemble *Montiparus*

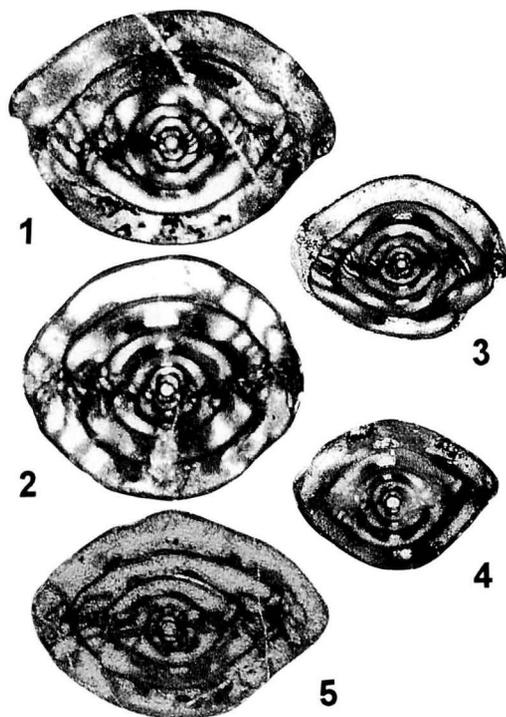
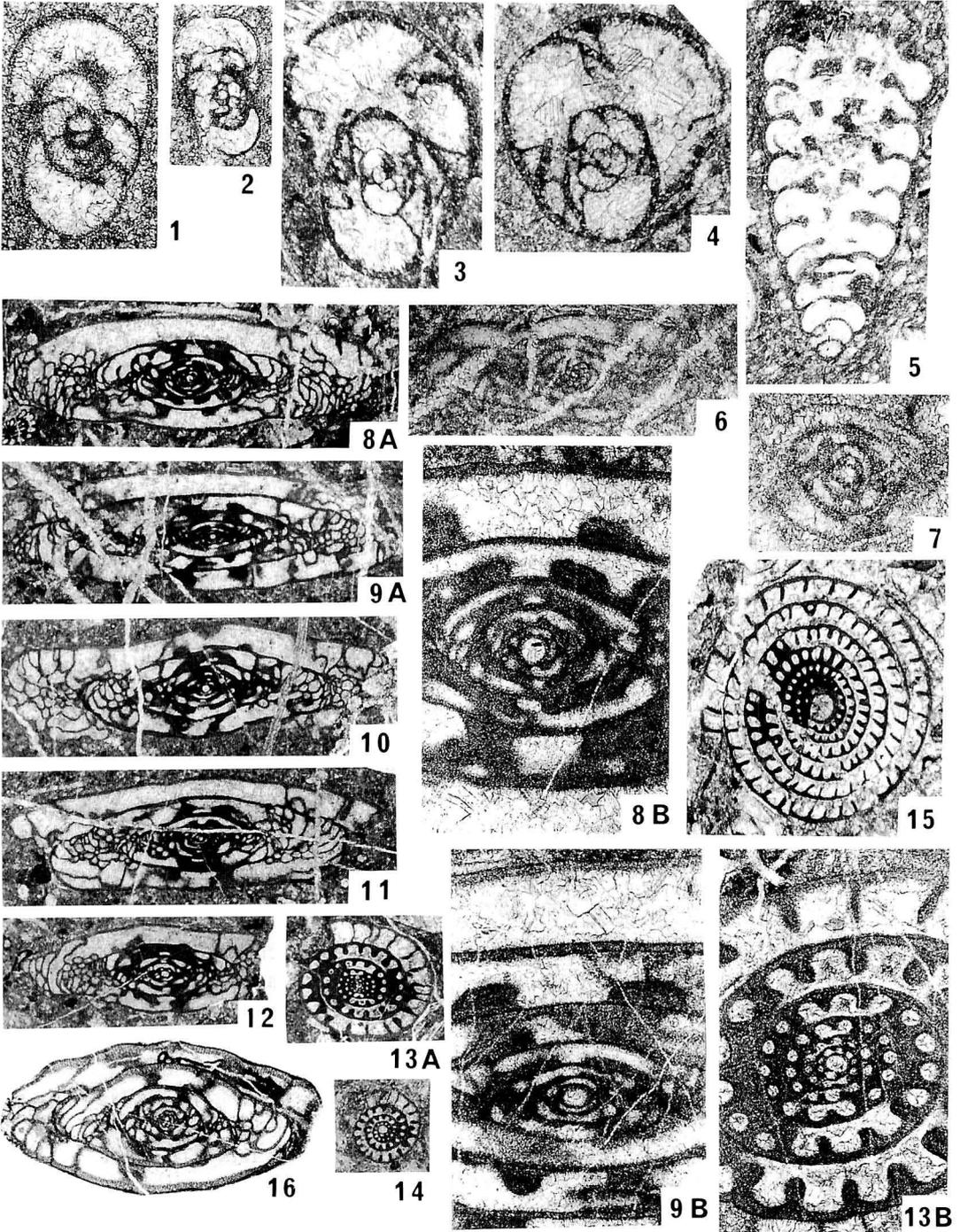


Figure 6. 1, 2. *Profusulinella beppensis* Toriyama, topotype specimens from the Akiyoshi Limestone. 3, 4. *Profusulinella fukujiensis* Igo, topotype specimens from the Ichinotani Formation. 5. *Profusulinella hinodensis* Kobayashi, n. sp., holotype specimen from the Kamiyozawa Formation. All are $\times 25$.

→ **Figure 7.** 1, 2. *Endothyra* sp. B, 1: tangential section; D2-3171, 2: axial section; D2-3174b, Loc. 36, $\times 60$. 3, 4. *Bradyina* sp. B, 3: axial section; D2-3172b, 4: lateral section; D2-3164b, Loc. 36, $\times 30$. 5. *Climacammina* sp. D, longitudinal section, Loc. 36, D2-3167, $\times 15$. 6. *Fusiella* sp., axial section, Loc. 36, D2-3163b, $\times 40$. 7. *Eoschubertella* sp., axial section, Loc. 36, D2-3165, $\times 60$. 8-14. *Obsoletes obsoletus* (Schellwien), 8-12: axial sections, 13, 14: sagittal sections, Loc. 36, 8: D2-3163a; 9: D2-3169; 10: D2-3173; 11: D2-3172a; 12: D2-3174a; 13: D2-3175; 14: D2-3164a, 8A, 9A, 10-12, 13A, 14: $\times 11$; 8B, 9B, 13B: $\times 40$. 15. *Beedeina* sp., sagittal section, Loc. 34, D2-3084, $\times 15$. 16. *Triticites* sp. B, axial section, Loc. 32, D2-3221, $\times 15$. (All specimens in this Figure are from the Shomaru Formation, except for 16 from the Takamizuyama Group)



matsumotoi (Kanmera) in tightly coiled inner volutions, massive chomata and weakly fluted septa in polar regions, in addition to spirothecal structure; nevertheless, the terminal volution is incompletely preserved. Although the original specimens from the Yayamadake Limestone were assigned to the genus *Triticites* (Kanmera, 1955), the expansion of the shell, development of chomata, and thickness and composition of the spirotheca of this species are more like *Montiparus* than *Triticites*.

Two subspecies proposed by Suyari (1962) from Shikoku are considered to be synonymous with *Montiparus matsumotoi*, because the Shikoku specimens are not clearly marked off from the original Yayamadake ones, there being only slight differences of development of chomata, form ratio, and other features.

Occurrence.—Common to rare at Loc. 12.

Reg. numbers.—D2-1305 (Figure 4-17), D2-1306 (Figure 4-18).

Family Staffellidae Miklukho-Maklay, 1949

Genus *Pseudoendothyra* Mikhaylova, 1939

Pseudoendothyra musashiensis

Kobayashi, n. sp.

Figures 5-2—9

Materials studied.—Eight illustrated specimens.

Diagnosis.—*Pseudoendothyra* with a lenticular shell, weakly recrystallized in its outer part and more remarkably recrystallized in its inner part, consisting of 4 to 5 volutions, minute proloculus, rather thick spirotheca compared with size of shell and indistinct chomata.

Description.—Shell medium to small for the genus, lenticular in shape, weakly recrystallized in its outer part and more remarkably recrystallized in its inner part. Periphery bluntly pointed to narrowly rounded, lateral sides convex to nearly straight, polar regions almost parallel-sided with shallow umbilical depressions. Coiling subinvolute throughout growth. Mature specimens of 4 to 5

volutions, 0.27 to 0.38 mm in axial length, 0.66 to 0.77 mm in median width, giving a form ratio of 0.4 to 0.6. Proloculus minute and spherical. Inner one to two volutions tightly coiled compared with the subsequent gradually expanding ones. Prolocular size, half length and radius vector of each volution not exactly measured.

Spirotheca rather thick compared with size of shell and composed of a tectum and inner thick translucent layer in outer volutions. Septa recrystallized as well as spirotheca, unfluted and curved anteriorly. Chomata indistinct, rudimentarily developed at both sides of a low, straight and narrow tunnel.

Remarks.—The present new species resembles *Pseudoendothyra yakoyamai* (Sada) from the *Profusulinella* Zone of the Taishaku Limestone (Sada, 1972) in shape and degree of recrystallization of the shell. However, the former has a smaller shell and fewer volutions. Although the radius vector and half length of the present new species are not exactly measured, they are likely to be smaller than the corresponding volutions of *P. yakoyamai* (Sada).

Various forms of *Pseudoendothyra*, assigned to 14 species and six subspecies, are described from the Middle Viséan to Lower Moscovian of the Moscow Basin and elsewhere (Rozovskaya, 1963). Some of them are closely similar to the present new species, but *P. musashiensis* has a more remarkably recrystallized shell, especially in its inner part and indistinct chomata. By its smaller shell for about the same number of volutions, this species is apparently distinguished from *Pseudoendothyra mathildae* (Dutkevich) originally described from the Kasimovian of the Middle Urals (Dutkevich, 1934) and *P. vlerki* (Ginkel) and its allied species described from the Vereyan of the Cantabrian Mountains, Spain (Ginkel, 1965).

Etymology.—Species name is derived from the ancient geographical name, Musashi, for the western part of Tokyo Prefecture.

Occurrence.—Common at Loc. 3 and rare

at Locs. 4 and 27.

Reg. numbers.—Holotype: D2-1746 (Figure 5-2), Paratypes: D2-1735 (Figure 5-3); D2-1737 (Figure 5-4); D2-1211b (Figure 5-5); D2-1738 (Figure 5-6); D2-1756 (Figure 5-7); D2-1728b (Figure 5-8); D2-1759 (Figure 5-9).

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関東山地南部, 五日市地域の石灰岩ブロック産石炭紀有孔虫化石: 関東山地南部, 五日市地域のジュラ紀付加体に含まれる石灰岩のブロックは前期石炭紀末から後期ペルム紀の有孔虫化石を産する。識別された石炭紀の有孔虫化石は 36 属 65 種に及ぶ。これらのうち, *Eostaffella*, *Profusulinella* など, バシキリアン以前の有孔虫類は関東山地や西南日本外帯では稀にしか産しない。 *Endothyra igoi*, *Eostaffella kamiyozawensis*, *Profusulinella hinodensis*, *Pseudoendothyra musashiensis* の 4 新種を含む 8 種の有孔虫化石を記載した。 小林文夫

979. THE SHELL STRUCTURE OF THE CARAPACE IN *XESTOLEBERIS HANAI* ISHIZAKI (CRUSTACEA, OSTRACODA)*

MICHIAKI YUMOTO

Department of Environmental Science, Graduate School of Science
and Technology, Kumamoto University, Kumamoto, 860

Abstract. The development of carapace shell structure during ontogeny of *Xestoleberis hanai* Ishizaki, 1968 was investigated with the aid of a scanning electron microscope (SEM). Photographs of broken sections of carapaces ranging from the second instar (the adult-7 instar) to adult reveal that the carapace is composed of four distinct layers: 1) an organic fibrous layer that is characterized by a network of organic fibers with few calcite grains; 2) a foliated layer formed by an aggregation of plate-like grains; 3) a granular layer consisting of an aggregation of granular grains; and 4) a prismatic layer constructed of an aggregation of columnar grains extending perpendicularly to the valve surface. Three of the layers, i.e., all but the organic fibrous layer, are distinguished by the shape and arrangement of calcite grains. The calcified procuticle of adult specimens is composed of an outer organic fibrous, a middle granular, and an inner prismatic layer. That of juvenile specimens in the second to fourth instars consists of only the foliated layer. That of juvenile specimens in the fifth and sixth instars develops outer granular and inner prismatic layers. The seventh and eighth instar juveniles possess a procuticle of the same three layers as in the adult. During growth, the shell structure of this species thus undergoes a change in its constructional design between molt stages, particularly from fourth instar to fifth instar and from sixth instar to seventh instar.

Key words. Ostracoda, shell structure, ostracod carapace, ontogeny, *Xestoleberis hanai*.

Introduction

In the past, research on ostracod valves has extensively been carried out solely on the basis of their outward morphology. However, anatomical information recorded within the hard tissue can be decoded, if we know the relationship between the hard tissue and the cellular tissue. For example, in work of extreme importance to those working on phylogenetic reconstruction, Okada (1981, 1982) pointed out that the reticulation pattern of the carapace surface of *Bicornucythere*

bisanensis (Okubo, 1975) corresponds to the arrangement of epidermal cells; thus the surface structure of the carapace is in some sense a reflection of the underlying cellular tissue. The distribution of normal pore canals on the carapace may reflect the arrangement of nervous tissue, since the pore canals are a part of the sensory organ and the sensory hair connects with the nerve cells (Tsukagoshi, 1989). The ontogenetic changes of these organs provide useful information for taxonomy and phylogenetic reconstruction. Phylogenetic relations of specific and generic groups of ostracods have been estimated based on the ontogenetic change of the distributional pattern of pore systems (Ikeya and Tsukagoshi,

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1988; Tsukagoshi, 1990; Tsukagoshi and Ikeya, 1991; Irizuki, 1993).

What shell structure makes ostracod valves such excellent "recorders"? The outer lamellar cuticle, often simply called the "ostracod shell," is divided into three different layers: outer epicuticle, middle procuticle and inner membranous layer. The epicuticle is not calcified (Bate and East, 1972), and this layer of *Bicornucythere bisanensis* is made up of three layers, discriminated by TEM observation (Okada, 1982). The procuticle is composed of small calcareous grains enclosed by an organic membrane (Jørgensen, 1970). Sylvester-Bradley and Benson (1971) called the procuticle the "foliated layer" because it contains flattened grains. Langer (1973) was able to distinguish different types of structural arrangements of the grains in some Ordovician to Recent ostracods. He classified the grains into three grades; 1) Unregelmäßig polyedrische Kristallite, 2) Plattige Kristallite, 3) Prisma-artige, irreguläre grob-oder dünn-säulige Kristallite. Sohn and Kornicker (1988) investigated the shell structure of carapaces in myodocopid ostracods, and reported five primary components and some combinations of each of these primary components. They discussed the taxonomic distribution of the primary components. The studies of Langer (1973) and Sohn and Kornicker (1988) suggest the procuticle may not be merely a single type of foliated layer, but in fact varies. The inner membranous layer, unknown in detail in its structure, is non-calcified. In this paper the terms of these three layers in the outer lamellar cuticle are after Okada (1982).

During growth, ostracods molt their carapaces until adulthood. The shell structure in juveniles has been discussed by Sohn and Kornicker (1988). They suggested that the valves of juveniles of two different sizes have the same combination of primary components. Up till now, observations of the shell structure of all instar juveniles have not been

reported. This paper addresses the question of whether the shell structure of the carapace of juveniles in each instar is, in fact, the same structure as in the adult.

In this paper the shell structure of carapace of *X. hanaii* is described with respect to the calcified procuticle and its ontogenetic variations.

Material and methods

Xestoleberis hanaii Ishizaki, 1968 is common in near-shore habitats of the Japanese Islands. Its kidney-shaped carapace has a smooth surface without ornamentation (Figure 1-1). Sexual dimorphism is distinct, i.e., the posterior of the female is more roundish than the male. The female holds several eggs and juveniles of the first and second instars in its posterior body cavity (Figure 1-3). Earlier instars of egg-laying ostracods are hard to recover. Even if we find earlier instars of ostracods in sediment samples, it may be difficult to identify them. It is easy to obtain the first and second instar juveniles of *X. hanaii*, however, because *X. hanaii* is ovoviviparous. Therefore, *X. hanaii* is a suitable species for ontogenetic study. The first instar of *X. hanaii* has antennules and antennae, but does not have a carapace; the carapace is formed at the second instar (Okubo, 1984).

In this study the animals were taken from two locations, near Kameshima Island and Hikisakamatsubara Beach on the northeastern side of Amakusa Shimoshima Island, Ariakekai Bay, western Kyushu, Japan (Figure 2). In the laboratory, live *Xestoleberis hanaii* were sorted and fixed in 4% glutaraldehyde solution immediately after collection. Some females with eggs were picked up before treatment and cultured in a petri dish. After leaving the mother specimens, the second instar juveniles were used as experimental material. The animals were killed by formaldehyde solution and washed in distilled water, and then the soft parts were removed

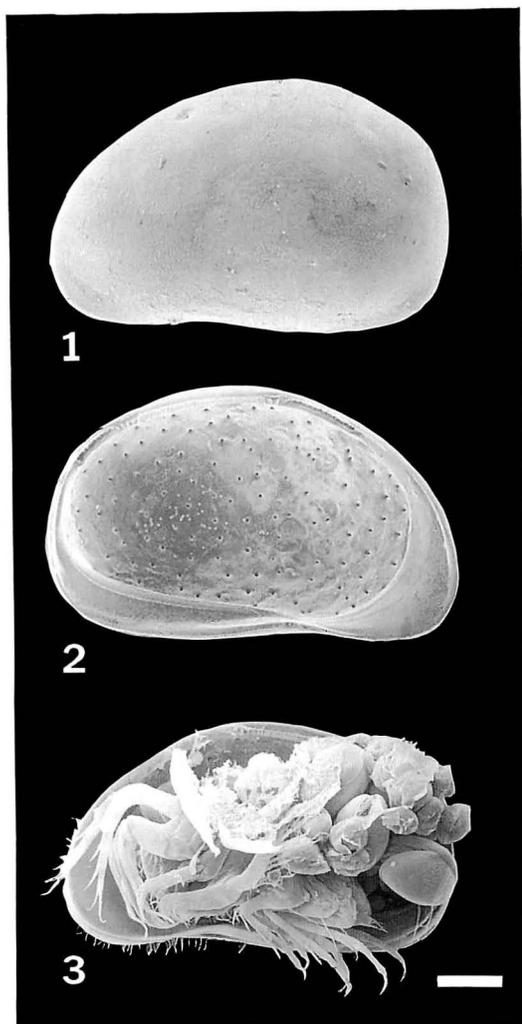


Figure 1. *Xestoleberis hanaii* Ishizaki, 1968. Female. **1.** Lateral view of left valve. **2.** Internal view of left valve. **3.** Internal view with soft part, eggs, the first and the second instars. Scale bar = 100 μm .

from the carapace.

The valves of the adult and older juveniles in the seventh and eighth instars were broken into several pieces with a razor. The fractured surface of each valve fragment was etched using 4% EDTA-2Na, then washed in distilled water. Samples were prepared for SEM photography by freeze drying, submerging in liquid nitrogen for several minutes, and

drying under vacuum for about three hours. The valves of younger juveniles than the sixth instar were freeze-dried before they were cut, to avoid a loss of very small fractured valve fragments during preparation.

Shell structure of carapace in *Xestoleberis hanaii*

Shell structure in adult : The outer lamellar cuticle, not counting the marginal zone of the valve, has a thickness of about 17 μm in the adult. The outer lamellar cuticle of *X. hanaii* is divided into three layers; outer epicuticle, middle procuticle and inner membranous layer (Figure 3). The epicuticle is 1 μm thick. It is divided into a homogenous outer layer and an inner layer with a network structure. The procuticle, under the epicuticle, is the thickest layer in the outer lamellar cuticle. SEM observations show that the calcified procuticle is composed of three layers. The organic fibrous layer in the outer part is seen to be a network of organic matter (OF in Figure 4-1). This layer, as stained by hematoxylin-eosin, is distinguished by a thin layer from the other layers (arrow OF in Figure 4-2). Figure 4-1 shows organic fibers connecting to the outer epicuticle, and branching off and binding to each other to form a network. In specimens treated by EDTA, no grains appear in the organic fiber network. The middle layer of the procuticle, the granular layer, is composed of an aggregation of irregularly shaped granules (G in Figure 4-1). Each grain is less than 1 μm in diameter. The interstices between the grains are filled with organic matter forming the network of thin membrane. The organic fibers in this part are finer than those in the above-mentioned organic fibrous layer. The inner part of the procuticle, the prismatic layer, is occupied by columnar grains. Each grain is arranged perpendicular to the inner surface of the carapace. There are two types of prismatic grains: one is thin and foliated (P in Figure 4-1); the other has a rod-like shape

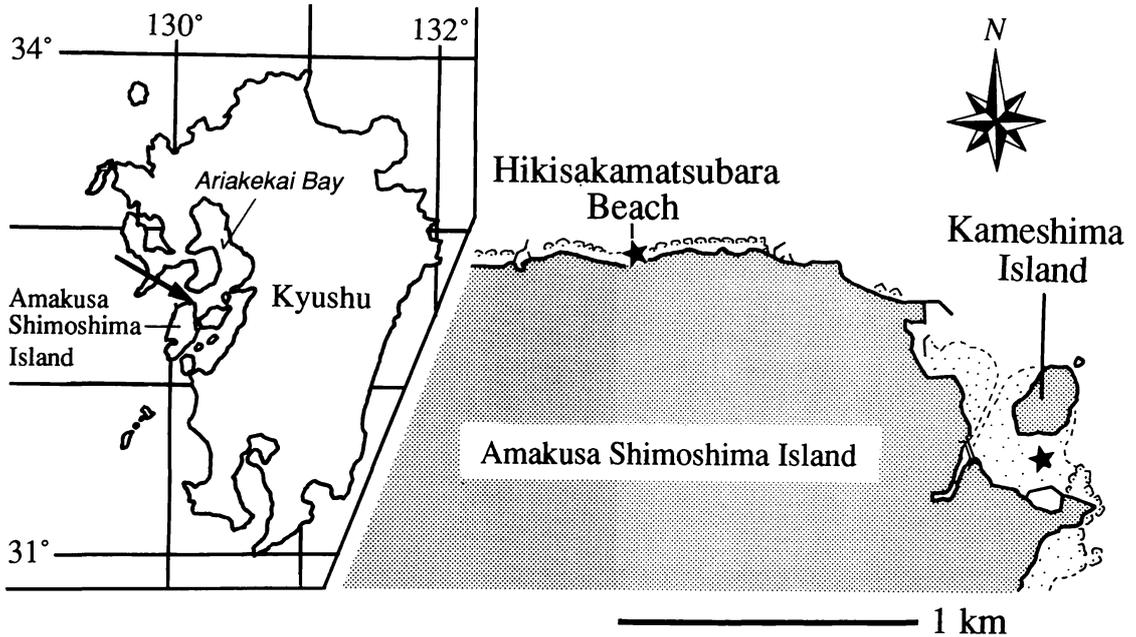


Figure 2. Map of northeastern corner of Amakusa Shimoshima Island showing two sampling locations indicated by star marks. One near Kameshima Island, lat. 32°32.1'N, long. 130°11.9'E, sandy bottom overgrown with eel grass *Zostera*. Another at Hikisakamatsubara Beach, lat. 32°32.8'N, long. 130°10.1'E, bottom containing calcareous algae. Water depth of both locations about 20 cm at low-tide.

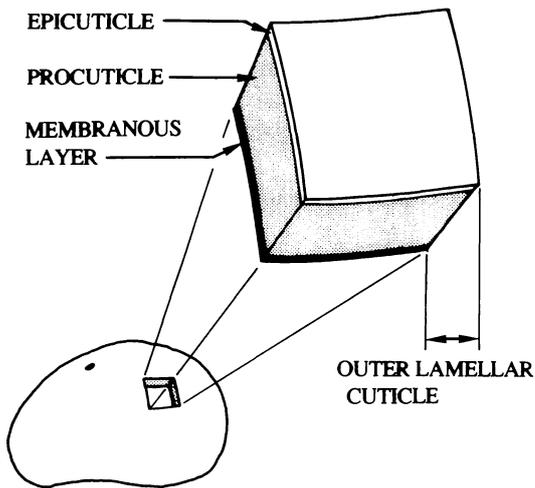


Figure 3. Diagram of the ostracod valve and terminology.

(P in Figure 4-3). Quantity of the organic matter is less in the prismatic layer than in the outer two layers. The procuticle of adult specimens is made up of three component layers: organic fibrous, granular and prismatic. The membranous layer is the thinnest in the outer lamellar cuticle. The membranous layer continues to the wall of pore canals, but its detailed structure cannot be seen in SEM observation.

In the muscle attachment area (Figure 5-1) the shell structure does not show a combination of three components. The organic membrane extends from the margin of the scar to the epicuticle (Figure 5-2). Fine fibrous filaments run in various directions and many granular and a few prismatic grains occupy this area.

Newly formed cuticle: Ostracods shed their carapaces for growth. Growing individual must prepare the next (new) cuticle under the old cuticle before molting. Most

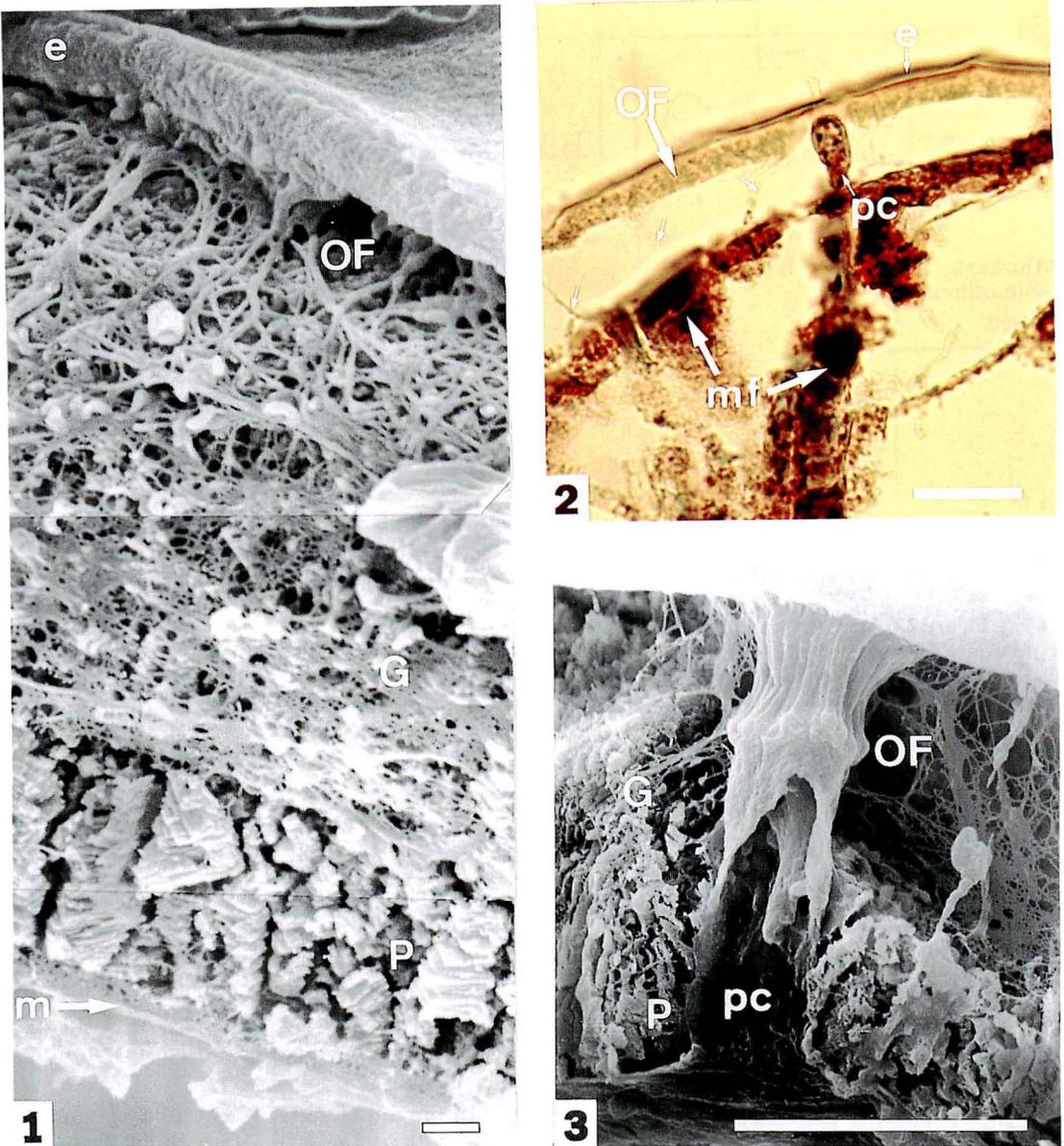


Figure 4. Shell structure of ostracod carapace in adult. **1.** Edge view at a break in the outer lamellar cuticle. The procuticle can be seen between epicuticle and membranous layer. **2.** Light micrograph of adductor muscle fibers and a pore canal in transverse section of a specimen embedded in paraffin. Three small arrows in cuticle indicate the pan structure. **3.** Vertical section at a pore canal. Scale bars: 1 = 1 μm ; others = 10 μm . e: epicuticle, m: membranous layer, mf: adductor muscle fiber, pc: pore canal, OF: organic fibrous layer, G: granular layer, P: prismatic layer.

crustaceans reabsorb calcium from the old cuticle before molting. However, Turpen and Angell (1971) found neither resorption of calcium from the old cuticle nor calcium storage in the living tissues of the ostracod *Heterocypris*. This suggests that ostracods obtain calcium from the surrounding water and/or their foods when they need it.

The dorsal part of the left valve of the eighth instar was cut out (Figure 5-4), so that the new outer lamellar cuticle of adulthood, full of wrinkles, was exposed. The external shapes of the new pores had already been formed on the surface of the new cuticle (Figure 5-3). The fractured surface of the newly formed cuticle shows granules, about 2 μm in diameter, underlying the new epicuticle (Figure 5-6). These granules may be epidermal cells making the new procuticle. It is notable that the membranous layer of the old valve is still present in spite of the growth of premolt tissues (arrow m in Figure 5-5). The membranous layer is dissolved in many crustaceans before molting, to reabsorb calcium from the old cuticle. However, the presence of the membranous layer before molting in ostracods supports the statement of Turpen and Angell (1971) that ostracods do not reabsorb calcium from the old carapace before molting.

Ontogenetic changes of shell structure: During growth ostracods shed their smaller old carapaces. Eight clusters of specimen sizes are recognized in *X. hanaii*, interpreted as eight ontogenetic stages. As the first instar juvenile does not have the carapaces (Okubo, 1984), specimens in the smallest cluster are identified as juveniles in the second instar that have been released from their mothers. This species molts eight times before adulthood.

The procuticle of younger juveniles from the second to fourth instars consists only of plate-like crystals arranged parallel to the surface of the carapace. This structure, called the foliated layer, is similar to the foliated layer of Sylvester-Bradley and Benson

(1971), but much thinner (Figures 6-1, 2, 3).

The procuticle of the fifth instar shows quite different structure than the fourth instar. Its procuticle is formed of outer granular and inner prismatic layers, not the foliated layer (Figure 6-4). The grains of the outer part are arranged irregularly. Short prismatic grains are concentrated in the middle and inner parts of the procuticle. Based on this type of structure, the fifth instar is considered to have already an adult-type shell construction. The sixth instar juvenile also has the procuticle being constructed by granular and prismatic layers (Figure 6-5). The rod-like crystals of the prismatic layer clearly appear in this stage.

In the procuticle of seventh-instar juveniles the organic fibrous layer is recognized under the epicuticle (Figure 6-6), although the fibers do not show full development of the organic fibrous layer as in adulthood. The organic fibrous layer first appears in the seventh instar. In the eighth instar the procuticle is exactly the same as in the adult (Figure 6-7).

Discussion

In the procuticle of *X. hanaii*, there are three different grain shapes: foliated, granular and prismatic. Jørgensen (1970) noted that the grains in the cuticle are enclosed by an organic membrane. It has been reported that this organic structure is an organic framework of chitin fibers (Bate and East, 1972, 1975), an irregular space lattice structure of chitinous fibers (Langer, 1973), a piled membranous structure with many spaces between the undulating membranes (Okada, 1982), and a net-like counterpart of each "primary component" (Sohn and Kornicker, 1988). The shape of the calcareous grains seems to be similar to the spaces in the organic structure. These observations may show the shell compositions, which are the organic fibrous, the foliated, the granular and the prismatic layers in this paper, in the procuticle to be regulated

by the organic structure, as the shell composition is an aggregation of calcite grains.

The shell structure in the muscle attachment area suggests a close connection between the shape of calcite grains and the organic structure (Figure 5-2). The adductor muscle fibers connect to the central muscle scars. This central muscle scar area seems to receive the force when valves are closed. The relations between the outer lamellar cuticle and the adductor muscle fibers have been discussed in detail by Okada (1983). He revealed the three-dimensional shell structure of the cuticle of the muscle scars in *B. bisanensis*. In the procuticle, the filamentous network extends outward to the surface of the cuticle near the margin of each scar, which he named the "pan structure". The pan, as Okada pointed out, made use of the filamentous network as an anchor in the mass of grains in the procuticle. In *X. hanaii* variations in the organic structure of the procuticle cause local variations in the shell structure of the muscle attachment area.

The mechanism of cuticular formation is known for the carapace of decapods. The carapace contains four discrete layers: the epicuticle, the exocuticle, the endocuticle and the membranous layer. The exo- and endocuticles are secreted by the organic matrix before and after molting. Both cuticles are calcified after molting. Although both the exocuticle and endocuticle have many lamellae, the two cuticles differ in their lamellar spacing, with the interlamellar distance being less in the exocuticle than in the endocuticle (Roer and Dillaman, 1984).

In ostracods, a new carapace is formed before and after molting. The epicuticle and

outer part of the procuticle are secreted before molting. After the old carapace is cast off, ostracods make a strong and thick carapace in a short time. According to Turpen and Angell (1971), the calcification of the carapace in the ostracod *Heterocypris* occurs within seven hours after molting. In *X. hanaii* the new carapace hardened within 24 hours after molting (Okubo, 1984). The inner part of the procuticle must be secreted and calcified immediately after molting for rapid shell formation. The primary function of the prismatic layer may be for the quick and efficient secretion and calcification of the procuticle.

There are three steps in the ontogenetic development of the shell structure of the procuticle: the first step, with only a foliated layer from the second to fourth instars; the second step, with granular and prismatic layers in the fifth and sixth instars; and the last step, with organic fibrous, granular and prismatic layers from the seventh instar to adult. The shell structure thus undergoes a discontinuous change in its constructional design from the fourth to the fifth instars. The change of the shell structure from the sixth to seventh instars is gradual, adding the organic fibrous layer. As the organic structure controls the layers, it seems that this species changes the mechanism of formation of the organic structure when it reaches the fifth instar and seventh instar.

Figure 7 shows the relationship between the thickness of the outer lamellar cuticle and instar number. The younger instars possess a very thin cuticle. Although the rate of increase in the thickness is rapid between the eighth instar and the adult, it is constant and

→ **Figure 5.** Shell structure of muscle attachment area and newly formed cuticle. **1.** Inner surface of central muscle scars of left valve. **2.** Shell structure in vertical section of muscle attachment area. **3.** Wrinkly new outer lamellar cuticle and two sieve type pores (s) on its surface. **4.** The anterior dorsal view of 8th instar juvenile in which the dorsal part of left valve was removed. Wrinkly new outer lamellar cuticle was already formed before next molting. **5.** Old and new outer lamellar cuticles. The membranous layer of old cuticle (arrow m) and surface of the new outer lamellar cuticle (arrow n). **6.** Vertical section of new procuticle. Granules show epidermal cells. Scale bars: 1 and 4 = 100 μm ; 3 = 1 μm ; others = 10 μm . g: granules, m: membranous layer, n: new outer lamellar cuticle, o: old outer lamellar cuticle.

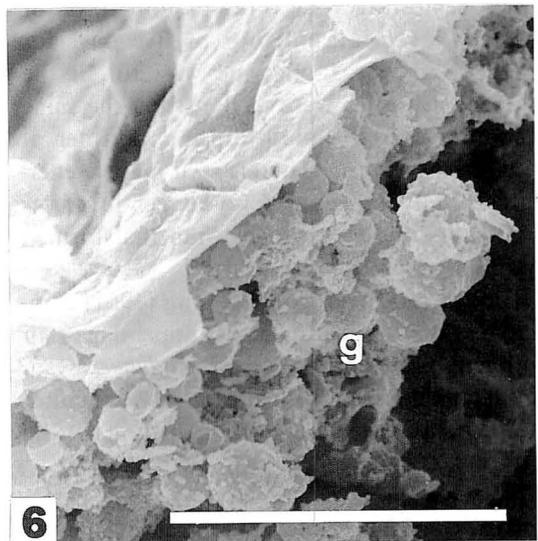
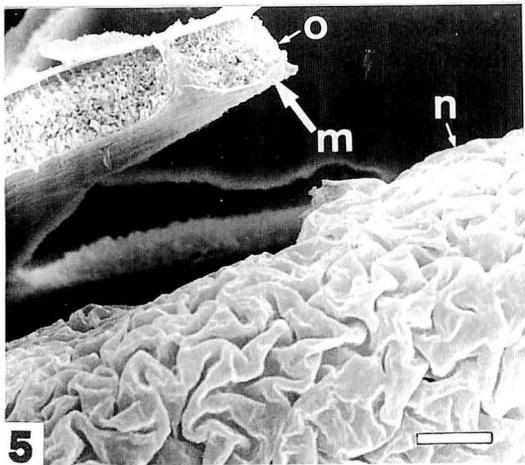
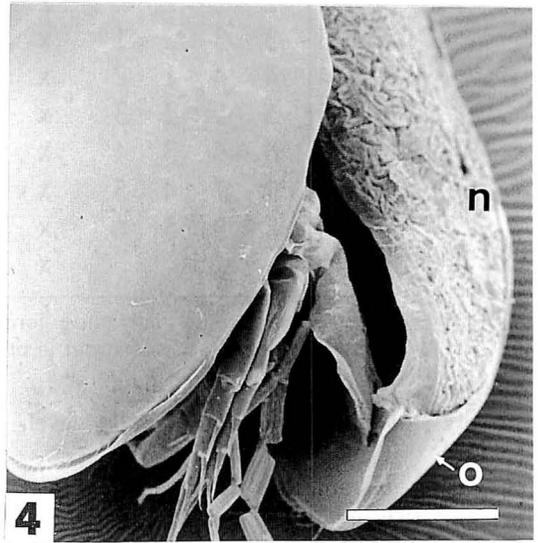
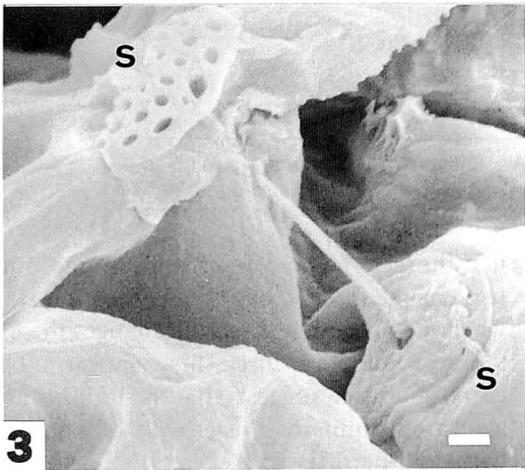
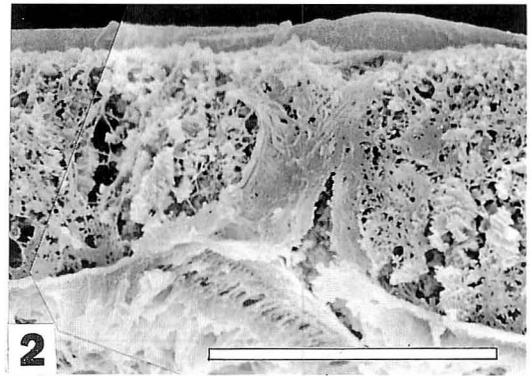
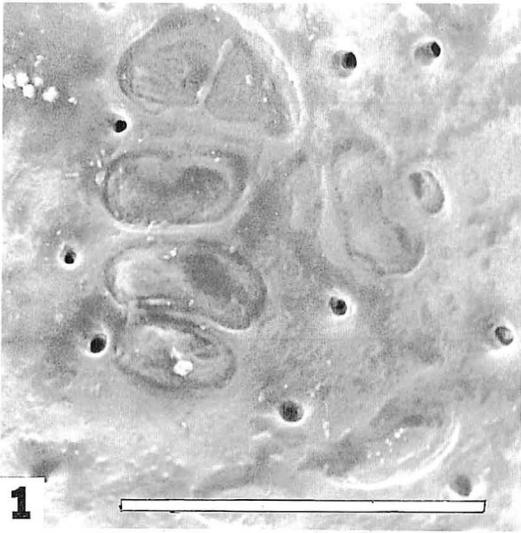


Table 1. Morphological features of ostracods occurring in different molt stages (modified from Kesling, 1961, Q20).

		Taxon					Appendages									
		Cypridacea	Cytheracea	<i>Xestoleberis</i> sp.	Cypridinidae	<i>Conchoecia</i> sp.	Antennule	Antenna	Mandible	Maxilla	1st thoracic leg	2nd thoracic leg	3rd thoracic leg	Gonads	Genitalia	Furca
Instar Number	1	1	1	x	x	x	a
	2	2	2	x	x	x	A	A
	3	3	3	..	1	x	x	x	x	A
	4	4	4	1	2	x	x	x	x	A	a	A
	5	5	5	2	3	x	x	x	x	x	A	a	x
	6	6	6	3	4	x	x	x	x	x	x	A	a	x
	7	7	7	4	5	x	x	x	x	x	x	x	A	a	..	x
	8	8	8	5	6	x	x	x	x	x	x	x	x	A	..	x
		Adult					x	x	x	x	x	x	x	x	x	x

x, structure present indefinite form; A, anlage always present; a, anlage present in some species, but not in others; .., no trace of structure found.

relatively slow during earlier juvenile development.

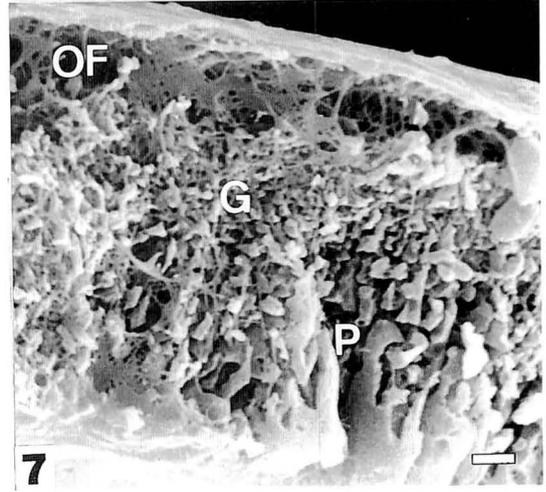
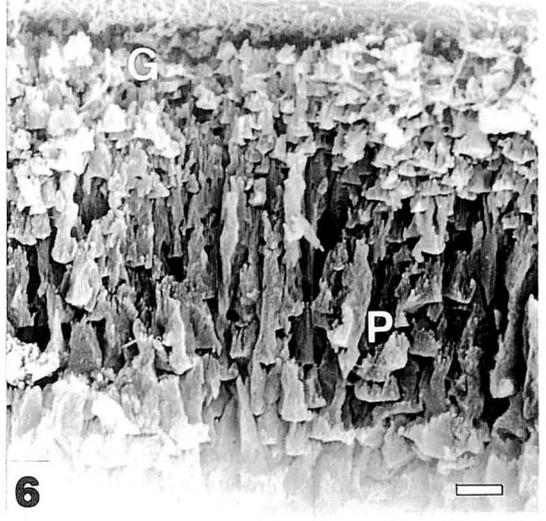
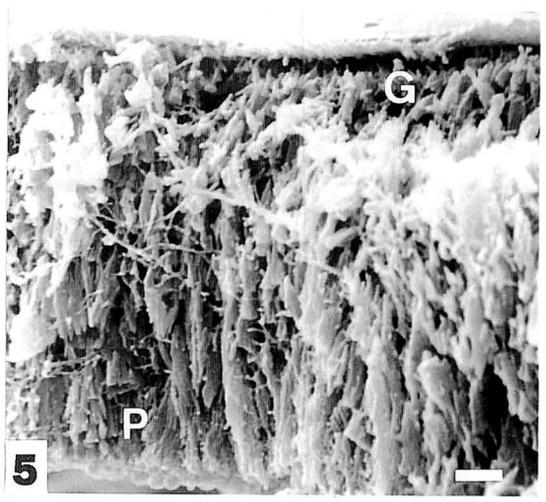
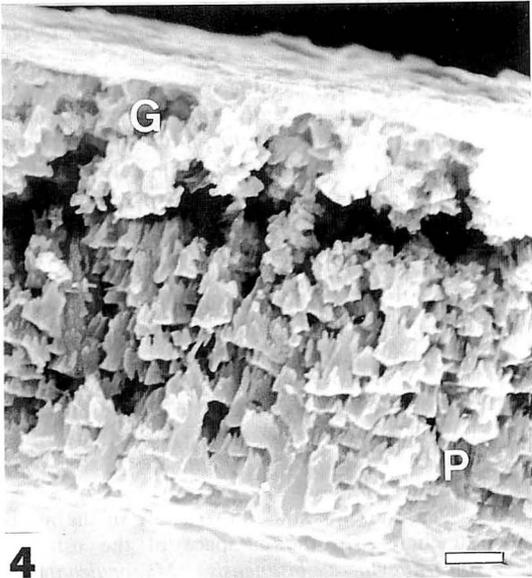
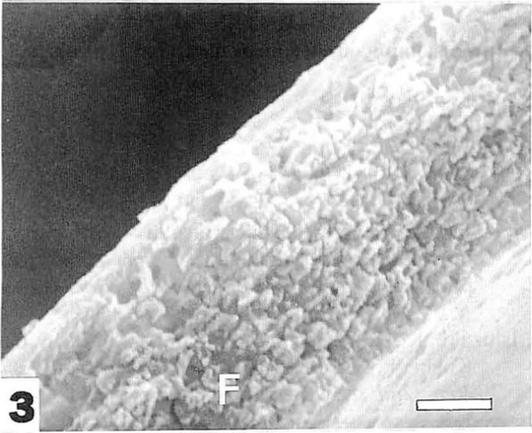
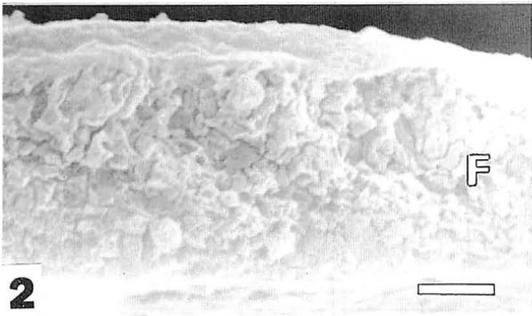
In earlier instars the molting interval is short and the juveniles have a thin cuticle. According to Okubo (1984), the intervals between molting were three or four days for younger juveniles and four or five days for older juveniles. It may be wasteful, if the younger juveniles were to construct the same procuticle as in the adult for the short interval between moltings. Therefore, it may be energetically advantageous for younger juveniles to form a simpler carapace than that formed by older juveniles and adults.

Table 1 modified from Kesling (1961) summarizes the appearance of appendages in ontogeny. Juveniles of *Xestoleberis* sp. younger than the fifth instar have neither thoracic legs nor furca. In the fifth instar the

first thoracic leg and furca appear, and other legs emerge in later stages. At the molt stage when the procuticle structure changes the first thoracic leg and furca first appear. This correspondence suggests that the fifth instar is a turning point for the growth of both soft parts and hard tissue.

It is shown that the shell structure of Bivalvia may be a conservative feature and therefore may be an effective characteristic for recognizing phylogenetic relationships (Shimamoto, 1986). Although the shell structure of the ostracod carapace is anatomically very different, it may also be the case that phylogenetic relationships in ostracods can be enshrined in the types of procuticle structure and layers.

→ **Figure 6.** Shell structure of ostracod carapace in each instar. 1. 2nd instar. 2. 3rd instar. 3. 4th instar. 4. 5th instar. 5. 6th instar. 6. 7th instar. 7. 8th instar. All scale bars = 1 μm. F: foliated layer, G: granular layer, OF: organic fibrous layer, P: prismatic layer.



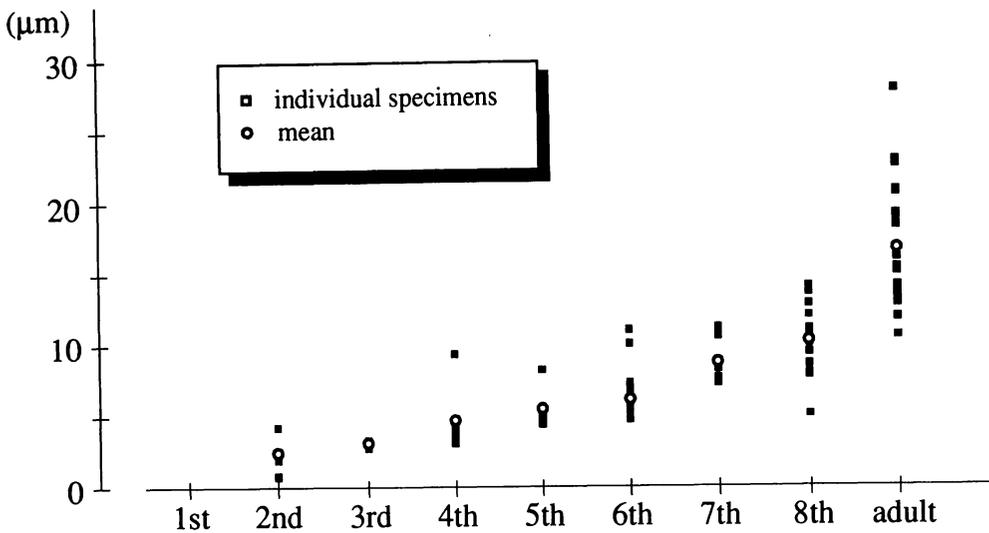


Figure 7. Thickness of outer lamellar cuticle in each instar among 66 specimens measured. Squares represent individual specimens; circles show mean values.

Acknowledgments

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Amakusa Shimoshima Island 天草下島, Ariakekai Bay 有明海, HIKISAKAMATSUBARA 引坂松原, Kameshima Island 亀島.

Xestoleberis hanaii Ishizaki (甲殻類, 介形虫) の殻構造: 日本の沿岸域に生息する介形虫の1種 *Xestoleberis hanaii* Ishizaki, 1968 について, 殻の破断面を走査電顕で観察した。成体および幼生の殻の原クチクラは, 4つの構造—有機質繊維構造・葉状構造・粒状構造・柱状構造—によって構成される。有機質繊維構造を除く3つの構造は, 方解石粒の形態により区別できる。成体の原クチクラは外側から有機質繊維, 粒状, 柱状構造の順に配列するが, 幼生では2齢から4齢の原クチクラは葉状構造だけからなる。5齢と6齢の原クチクラでは, 外側に粒状構造が, 内側に柱状構造が発達する。7齢および8齢の原クチクラでは, 成体と同じ構造の配列となる。本種の殻構造は, 4齢から5齢に脱皮するときと6齢から7齢に脱皮するときに原クチクラの構成を変化させることが示された。 湯本道明

980. AN INQUIRY INTO THE MECHANICS OF TRIGONIID HINGE SYSTEM*

YOSHIO YUKI

NHK ; Japan Broadcasting Corporation
Jinnan, Shibuya-ku, Tokyo, 150

Abstract. The gear-like intricate dentition of the Trigoniidae appears to fix the axis of valve opening and closing movement, while the opening and closing forces must be generated independently by the ligament and adductor muscles. As a result of experiments and moment analysis on living specimens of *Neotrigonia margaritacea* (Lamarck), it was found that the three axes determined by dentition, ligament and adductor muscles are largely different from one another in orientation. Provided that minimum friction is required for the smooth hinge movement, the opening force by ligament and closing force by adductor muscles have to compensate each other, and the axis of their resultant force may coincide with the dentition axis. The relatively short ligament in trigoniids seems to enable such a remote valve movement axis from the postero-dorsal margin as well as the formation of remarkably pennate shells like *Pterotrigonia*.

Key words. Trigoniidae, *Neotrigonia margaritacea*, dentition axis, ligament axis, closing moment axis.

Introduction

The adaptive morphology of trigoniids has attracted the attention of many paleontologists and malacologists because this group exhibits various peculiar morphological features. In particular, the dentition of trigoniids is very unique and stable, and the walls of hinge teeth and sockets are invariably carved by a number of curvilinear striae, termed secondary dentition (Stanley, 1977, 1978).

As pointed out by Makiyama (1926), the striae must represent the traces of the opening and closing movement of the valves. Because the striated teeth and sockets act as intricate gears, it is difficult for us to open an articulated specimen of *Neotrigonia margaritacea* (Lamarck) without recognizing the

direction of its rotation axis. This axis does not seem to coincide with the direction of the ligament (or the postero-dorsal margin of shell), though the actual valve rotation of living bivalves must be controlled by the total of ligament force and adductor force (Trueman, 1969). The valve opening and closing movement of bivalves, in general, is directly related with such essential behaviors for life as respiration, feeding, reproduction, locomotion and protection.

The aim of this study is to evaluate the mechanics of the valve opening and closing movement by estimating the axes, which are independently inferred from the analyses of ligament force and resultant adductor force. Because the actual valve rotation axis can be strictly determined by the dentition, trigoniids are regarded as convenient material for this analytical study.

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Materials

Living materials.—Living shells of *Neotrigonia margaritacea* (Lamarck) were used for the observation and analysis of morphology. They were obtained on May 24, 1991, from sandy mud substrata at 6–10 m depth in Western Port Bay, Victoria, Australia. Some shells of infaunal bivalves preserved in the University Museum, University of Tokyo, were also used for the present comparative study.

Fossil materials.—The following specimens were used: *Nipponitrigonia kikuchiana* (Yokoyama) from the Lower Cretaceous Miyako Group in northeast Honshu; *Pterotrigonia eufaulensis* (Gabb) from the Upper Cretaceous Ripley Formation in Tennessee, U.S.A.; *Yaadia ainuana* (Yabe and Nagao) from the Upper Cretaceous Middle Yezo Group in central Hokkaido; silicone replica of a specimen of *Trigonioides tetoriensis* Maeda from the Lower Cretaceous Tetori Group in central Honshu.

Procedures and results

Procedure 1. Valve rotation axis

The hinge teeth of post-Triassic trigoniids are surprisingly stable in spite of the great variability in the shell outline and surface sculpture (Cox, 1952; Cox *et al.*, 1969), though a polyphyletic origin of this family has been suggested by some authors (Newell and Boyd, 1975). The anterior and posterior walls of two strong teeth of the right valve and those of corresponding sockets of the left valve have about a dozen of the characteristic curvilinear striae. As Makiyama (1926) pointed out, these striae seem to be concentric circles if observed perpendicularly to the wall. He mentioned further that they represent the traces of loci on the tooth and socket surface in the process of valve rotation (Figure 1).

Makiyama's insight is here developed to a method to estimate the unique rotation axis

from the dental structure. Because the walls of every tooth and socket are planar, the striae must look nearly straight and parallel to one another when they are observed from the direction perpendicular to the exact rotation axis.

The measuring device introduced here is to quantify the straightness of the striae (Figure 2). The striated teeth of a right valve of *Neotrigonia margaritacea* (Lamarck) was viewed from the ventral side and enlarged twenty times with the aid of a profile projector (Nikon V-16D). Then, both ends of each curved stria were linked by a straight line, and the area enclosed by the curved and straight lines was measured by counting the number of dots on the display of a personal computer. Of course, the less total area means the closer approach to the direction perpendicular to the rotation axis.

As shown in Figure 3, the total of the areas enclosed by curved and straight lines becomes minimum when the hinge teeth is viewed from the direction of 57 degrees with the postero-dorsal margin of shell. This means that the actual valve rotation axis in *N. margaritacea* is 33 degrees away from the postero-dorsal margin.

The same method can be applied to fossil trigoniids and trigonioidids if the hinge teeth are well exposed. Suitable specimens may be rare, but I could examine some specimens of *Nipponitrigonia kikuchiana* (Yokoyama), *Pterotrigonia eufaulensis* (Gabb), *Yaadia ainuana* (Yabe and Nagao) and *Trigonioides tetoriensis* Maeda and determine the approximate direction of their rotation axes (Figure 4).

Procedure 2. Relative length of ligament

The ligament of trigoniids and many heterodont bivalves (e.g. lucinids, cardiids and venerids) is opisthodontic and external. Cox *et al.* (1969: N81) mentioned, "When there is a ligamental nymph, its upper surface will usually indicate the direction of the [hinge] axis." This may be true as to many heterodont bivalves with long external liga-

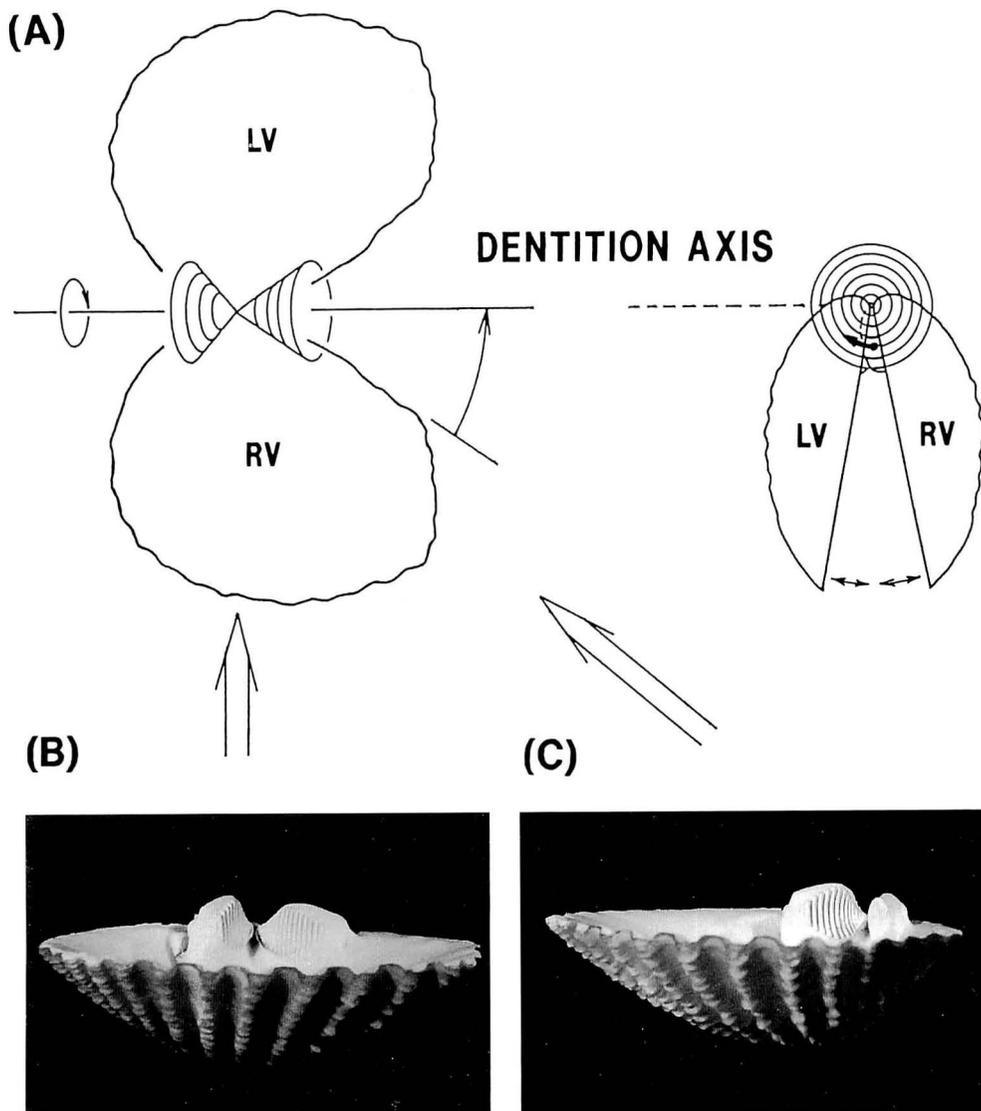


Figure 1. Geometrical model for valve rotation movement. A: When the valves rotate around a hinge axis, each locus on the teeth scribes a circle bound in a plane perpendicular to the axis. B: Ventral view of a right valve of *Neotrigonia margaritacea* (Lamarck) ($\times 2$), in which the striae on the tooth walls look straight and parallel. C: Postero-ventral view of the same specimen, in which the striae look curved. Arrows indicate the direction of views.

ment. In trigoniids, however, the axis of valve rotation and prolongation of the ligament (or postero-dorsal margin of shell) are obviously discordant, as were ascertained by Procedure 1. Intuitively, the degree of the discordance is related to the relative length of the ligament. The ligament length of some

trigoniids and heterodont bivalves were measured and standardized in accordance with the radius of an equivalent circle, the area of which is equal to the shell surface in lateral view.

The relative length of the ligament is about 31% of the radius of equivalent circle in *N.*

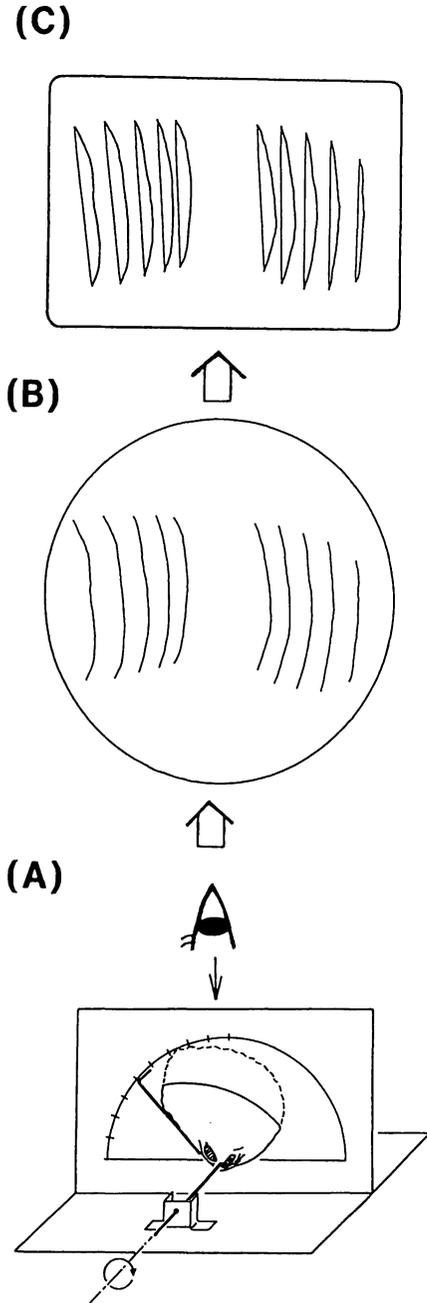


Figure 2. Measuring the "straightness" of the striae on the tooth walls. A: Measuring device contrived with a silicone replica of a right valve of *Neotrignia margaritacea* (Lamarck). B: The striae are projected and enlarged on the screen of a profile projector. C: Traces of the striae are bridged, and the total of enclosed areas is measured by the number of dots on the screen of a personal computer.

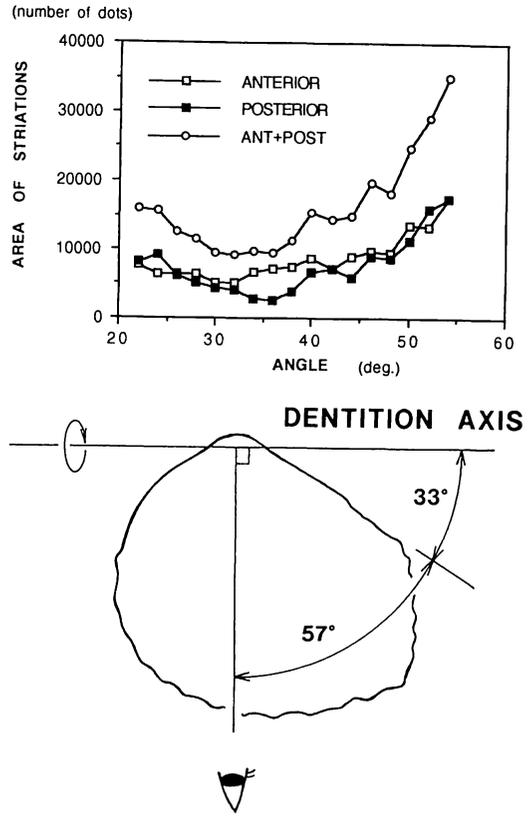


Figure 3. Results of the procedure 1 (see also Figure 2). The "straightness" of the striae becomes optimal, when the hinge is viewed from the direction of about 57° away from the postero-dorsal margin. This means that the dentition axis intersects the margin at an angle of about 33°.

margaritacea and about 25% in *Pterotrignia eufaulensis* (Figure 5). These values are notably smaller than other heterodont bivalves (except for the Cardiidae).

Procedure 3. Valve opening axis by ligament force

The main function of ligament is to open the valves when the adductor muscles relax, and it also serves to unite the dorsal margin of the valves (Trueman *in* Cox *et al.*, 1969). The axis of valve opening force can be examined by measuring the gape between the two valves when the force is applied perpendicularly to the commissure plane (Figure 6). In order to evaluate the effect caused only by the ligament, all the hinge teeth and soft part

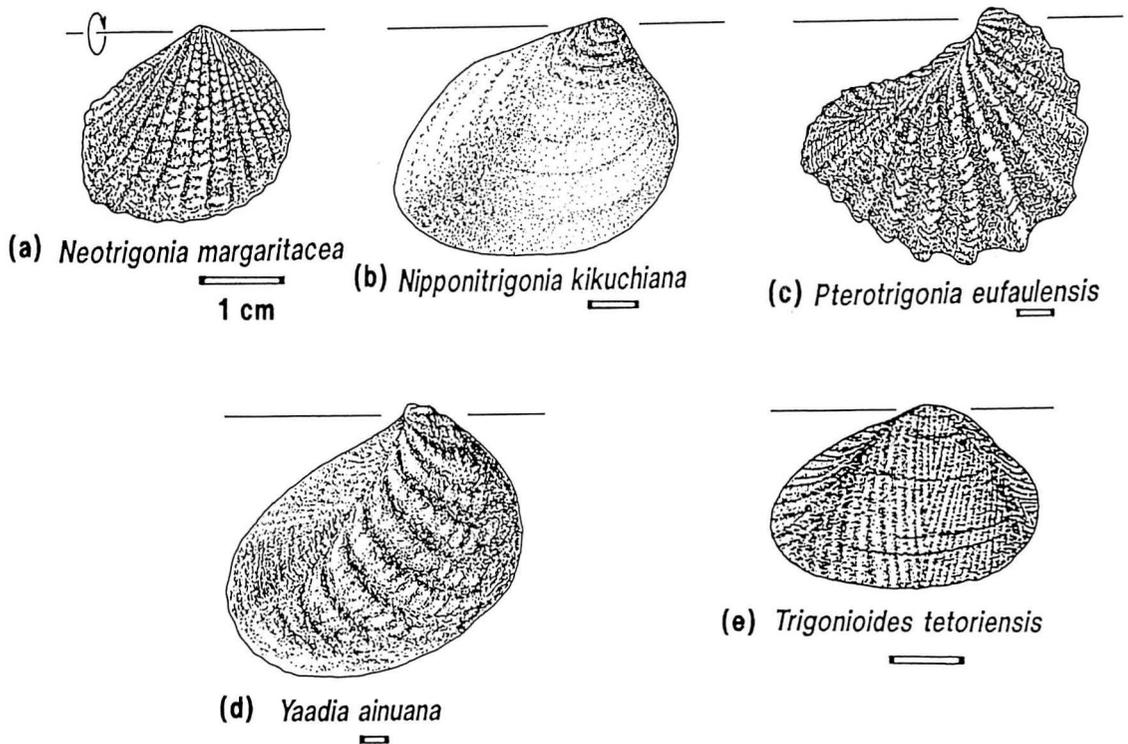
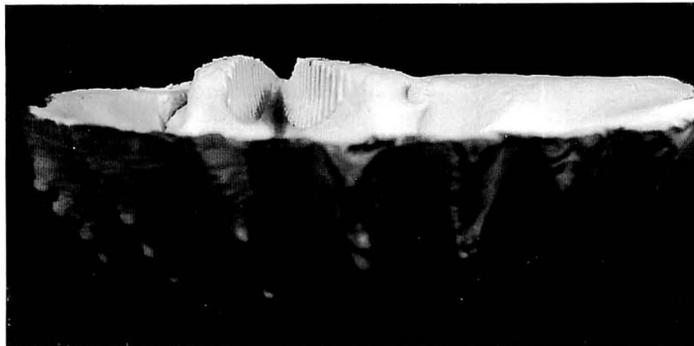
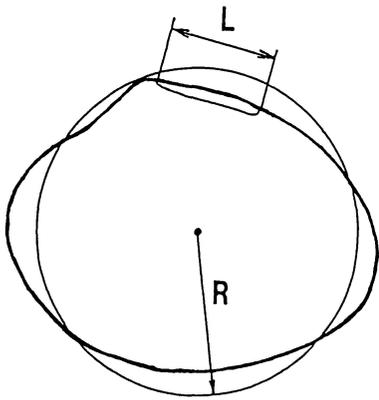
(A)**(B)**

Figure 4. A : Dentition axes of some trigoniid and trigonioidid bivalves : *Neotrigonia margaritacea* (Lamarck), *Nipponitrigonia kikuchiana* (Yokoyama), *Pterotrigonia eufaulensis* (Gabb), *Yaadia ainuana* (Yabe and Nagao), *Trigonioides tetoriensis* Maeda. B : Ventral view of the hinge of *Pterotrigonia eufaulensis*, showing nearly straight striae on the tooth walls.



$$\text{STDeD LIGAMENT LENGTH} = \frac{L}{R}$$

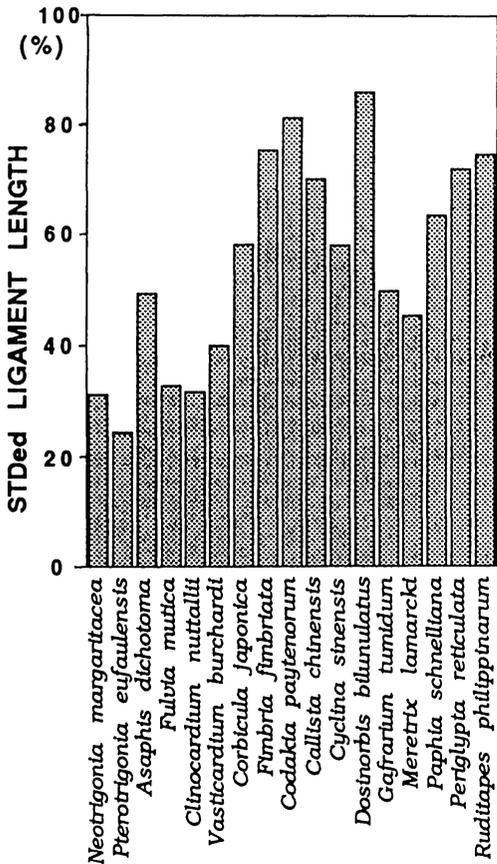


Figure 5. Comparison of relative ligament length, which is standardized by the radius of an equivalent circle. Trigoniids reveal shorter ligament than most heterodont bivalves.

of a living specimen of *N. margaritacea* were eliminated. The ligament was kept wet with sea water during the experiment. First, a compressive force was operated perpendicularly to the commissure plane at a certain point F on the ventral margin. The fixed point U at the umbo (proximal end of ligament) was linked with the point F, and the perpendicular line to FU through the point U is termed a "temporary ligament axis." The angle between this axis and the extension of the postero-dorsal shell margin was measured. Then, the points A and P were set at the

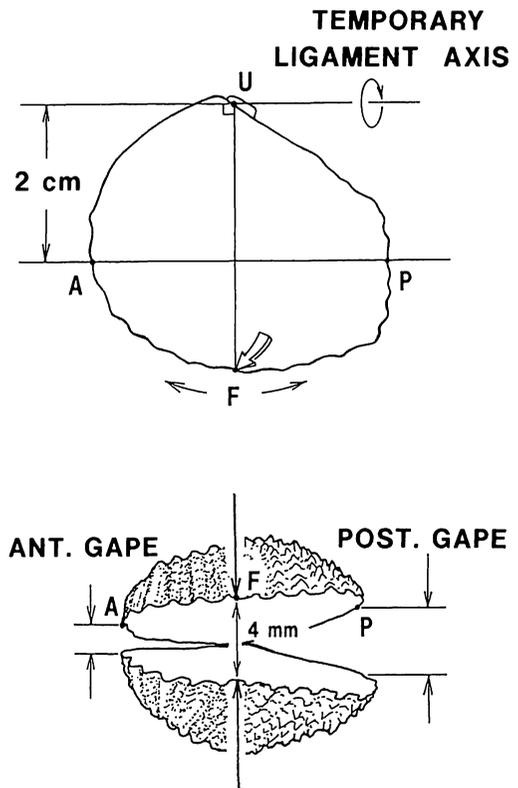


Figure 6. Estimating method of the valve opening axis by ligament, using a living specimen of *N. margaritacea*, the teeth and soft part of which are completely eliminated. A perpendicular compressive force is applied at an optional point (F), and the "temporary ligament axis" is drawn to set two points (A and P). U is a fixed point throughout the valve rotation. The gapes are measured at A and P, when the gape at F becomes 4.0 mm.

anterior and posterior margins of the shell with distances of 20 mm from the temporary ligament axis. When the gape between the valves at the point F became 4 mm, the gapes at the points A and P were measured. This experiment was repeatedly performed by shifting the point F along the ventral margin. When the gapes at the points A and P were identical, the temporary ligament axis was regarded as representing the real valve opening axis by the ligament force alone.

The valve opening force by ligament in *N. margaritacea* holds an axis at about 48 degrees away from the postero-dorsal margin of shell (Figure 7). Although this experiment can be performed only in living bivalves with active ligament, it should be emphasized that this axis does not agree with the pron-

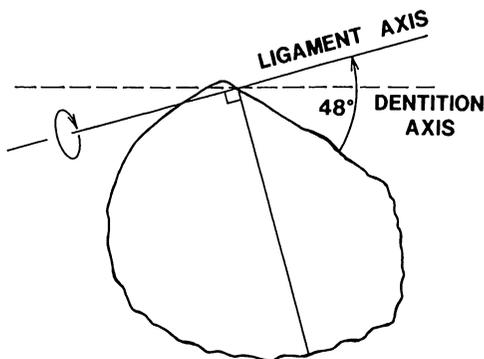
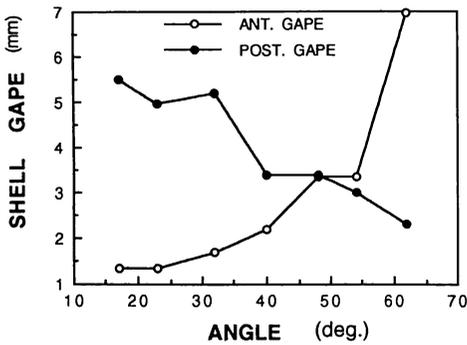


Figure 7. Results of serial experiments in the procedure 3 (see also Figure 6). The shell gapes at A and P become equal when the “temporary ligament axis” intersects the postero-dorsal margin at an angle of about 48°.

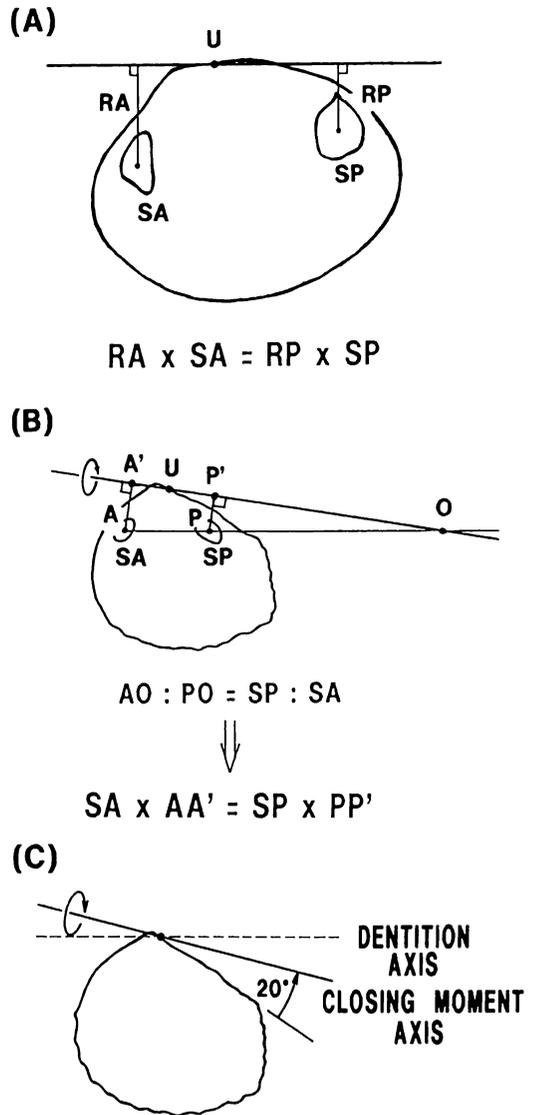


Figure 8. Estimating method of the closing moment axis. A: The valve closing axis is determined by the balance of two moments by the anterior and posterior adductor muscles. SA, SP: Areas of anterior and posterior adductor muscle scars in perpendicular views to the commissure. RA, RP: Distances between the valve closing axis and the center of each muscle scar (A, P). B: Geometrical diagram to determine the closing moment axis on the prolongation line AP, and the point O is set where the reversed areal ratio SP/SA equals AO/PO. Then, AA' : PP' equals SP : SA, because of the similarity between $\triangle OAA'$ and $\triangle OPP'$, and the two moments become equal. C: Closing moment axis of *N. margaritacea*, intersecting the postero-dorsal shell margin at an angle of about 20°.

gation of ligament on the postero-dorsal margin.

Procedure 4. Valve closing moment axis by adductor muscles

A moment on a rotation axis is generally calculated by the product of the strength of a force by the distance between the operating point and the rotation axis. The relative contractile forces of the two adductor muscles in a given specimen may be most reasonably estimated by measuring the areas of the muscle scars. Stanley (1972) noted a similar procedure to evaluate two contractile forces of pedal retractors. The expected valve closing axis by the resultant force of adductor muscles has to lie in the direction where the moments of the two muscles are equal to each other (Figure 8A). This axis can be determined by introducing a simple geometry (Figure 8B).

The closing moment axis of *N. margaritacea* intersects the postero-dorsal margin of shell at an angle of about 20 degrees (Figure 8C).

Discussions

By the procedure 1-4, the orientations of three different axes were estimated independently by the analysis of curvilinear striae on the walls of teeth, the experiment of ligament force and the moment calculation of the contraction of adductor muscles. They are here called the dentition axis, ligament axis and closing moment axis, respectively.

It is notable, at least in the Trigoniidae, that the dentition axis is coincident neither with the prolongation of ligament nor with the postero-dorsal margin of the shell, though the valve opening force must be generated only by the ligament. If the prolongation of ligament (or postero-dorsal margin) were coincident with the rotation axis, the animal could not open the valves in such a pennate form as *Pterotrigonia* and *Aptotrigonia*. On the other hand, no physical problem occurs if the actual axis of rotation is apart from the

postero-dorsal margin. This condition is actually ascertained in *Pterotrigonia eufaulensis* (Gabb) (Figure 9). As evidenced by the procedure 2, *Neotrigonia margaritacea* (Lamarck) (and probably all the other post-Triassic trigoniids) has decidedly shorter ligament in comparison with many heterodont bivalves with parivincular ligament (Figure 5). Only some species of the Cardiidae share relatively short ligament with the Trigoniidae.

Most bivalves have more or less prosogyrous umbones which are coiled forward (Stanley, 1975, 1978). The prosogyrous or orthogyrous shell commonly results in a nearly straight postero-dorsal margin, and this condition is compatible with a relatively long ligament. The opisthogyrous shell coiling of *Pterotrigonia* (and some other genera of the Trigoniidae) would produce a pronouncedly concave postero-dorsal shell margin and would not allow a long ligament.

Generally, in many heterodont bivalves

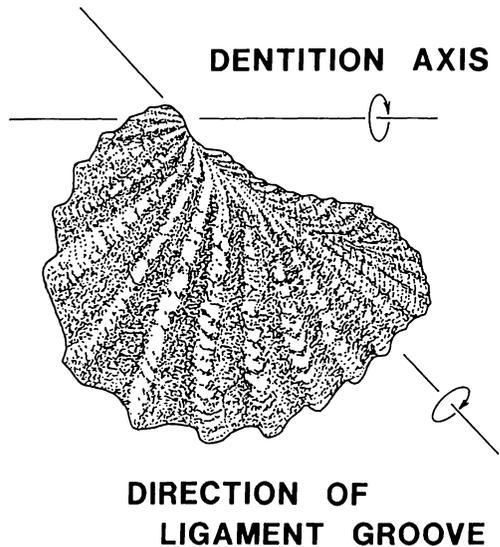
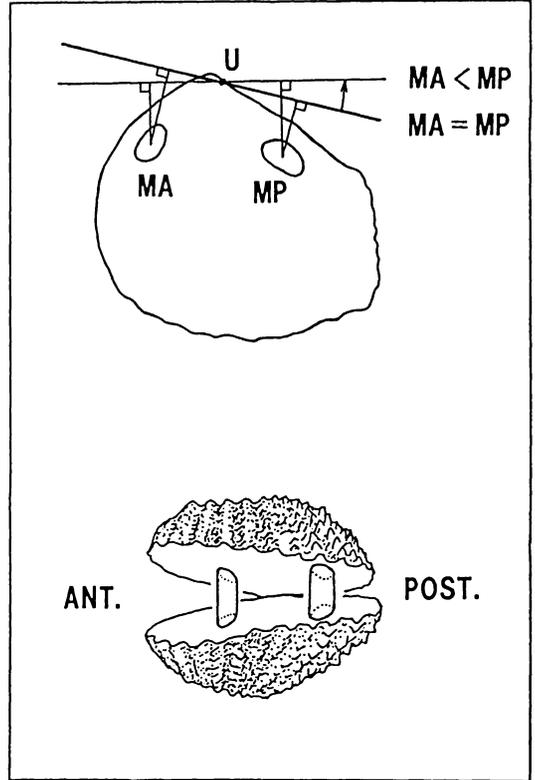
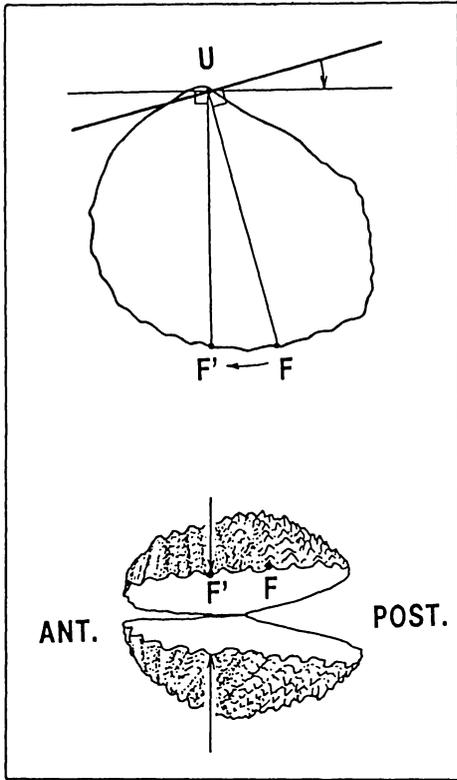


Figure 9. Dentition axis and the prolongation of ligament groove in a pennate trigoniid *Pterotrigonia eufaulensis* (Gabb). If the ligament groove were coincident with the valve rotation axis, valve opening would be impossible because of the collision of the posterior ends of the two valves.

(A) LIGAMENT

(B) CLOSING MOMENT



(C)

COMPENSATION

CLOSING MOMENT AXIS

DENTITION AXIS

LIGAMENT AXIS

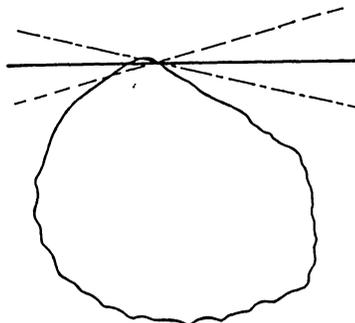


Figure 10. Relation between the dentition axis and the balance of forces by the ligament and adductor muscles. The ligament axis (A) and the closing moment axis (B) are largely discordant in orientation, but the two forces seem to compensate each other to form a "balanced axis (C)". The "balanced axis" has to coincide with the dentition axis, because minimum dental friction is required for the smooth movement of valves. MA, MP: Moments of anterior and posterior adductor muscles.

without such intricate teeth as trioniid dentition, two independent forces by ligament and adductor muscles may operate in order to open and close the valves in opposite directions. The relative movement of the two valves is determined by the balance of these two forces (Trueman *in* Cox *et al.*, 1969). In view of the analysis of ligament in *N. margaritacea*, it is noticeable that the ligament axis is further apart from the postero-dorsal shell margin than the dentition axis which is the actual rotation axis of the valves (Figure 7). On the contrary, the closing moment axis in *N. margaritacea* is close to the postero-dorsal margin than the actual valve rotation axis (Figure 8C).

The opening and closing forces of the valves may have their own axes but seem to compensate each other to form a "balanced axis." When the operating point F shifts to F' so that the "temporary axis" approaches the dentition axis, the posterior gape between the two valves becomes wider than the anterior gape (Figure 10A). On the contrary, if the closing moment axis were coincident with the dentition axis, the posterior closing moment would become larger than the anterior, and the anterior gape would become wider than the posterior gape (Figure 10B).

Because the actual valve rotation is determined by the interaction of the forces of ligament and adductor muscles, the "balanced axis" must lie between the ligament axis and the closing moment axis. Although its quantitative dynamic analysis is difficult at present, this condition seems to be realized in the morphology of *N. margaritacea*. Provided that minimum dental friction is required for the smooth movement of the valves, it is reasonable to consider that the "balanced axis" coincides with the dentition axis (Figure 10C).

Conclusion

The valve rotation axis of trioniids can be uniquely determined by the curvilinear striae

on the walls of teeth and sockets; the striae must look nearly straight and parallel, if they are observed from the direction perpendicular to the axis.

The postero-dorsal margin of a bivalve does not necessarily correspond to the valve rotation axis. Particularly in the Trioniidae, the rotation axis is far apart from the postero-dorsal margin. Such a remote axis enables a highly pennate shell form like *Pterotrionia*. The relatively short ligament of *Neotrionia margaritacea* (Lamarck) (and probably all the other species of the Trioniidae) is compatible with the rotation axis much apart from the prolongation of ligament.

The valve rotation movement in *N. margaritacea* must be determined by the interaction of two independent forces generated by the ligament and adductor muscles. The present analysis proved that the axes of the two forces are largely different from each other in orientation. The gear-like intricate dentition of trioniids indicates that the actual valve movement axis is almost strictly fixed, and that the "balanced axis" of the two forces substantially coincides with the dentition axis.

Acknowledgements

I am especially grateful to Professors I. Hayami and K. Tanabe for their kind guidance during the course of this study and critical reading of the manuscript. Special thanks are due to Dr. K. Bandel and S. Isaji who provided fossil specimens. Dr. T. Daragh and Mr. J. Austin kindly supported my field work in Australia. Thanks are extended to Drs. K. Abe, T. Oji and Y. Shigeta and Mr. T. Ubukata, who provided me with helpful suggestions in the laboratory works.

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トリゴニア科の蝶番メカニズムについての考察: 二枚貝の殻の開閉は靱帯と閉殻筋が独立に生み出す力で決まる。しかしトリゴニア科の二枚貝の持つ複雑な鋸歯は、きつく咬み合って殻の開閉運動の回転軸を固定しているように見える。現生 *Neotrigonia margaritacea* での実験とモーメント解析の結果として、次の3つの軸: 歯の構造から決まる軸; 靱帯による開く力の中心軸; 閉殻筋の閉じる力の中心軸、のそれぞれの軸の方向は大きく異なっていることがわかった。滑らかな蝶番の動きのために、靱帯による開く力と閉殻筋の閉じる力がうまくバランスをとり開閉運動を行い、その結果として決まる軸は歯の構造から決まる軸とよく一致している。また、トリゴニア科の比較的短い靱帯は殻の後背縁から離れた開閉軸を可能にし、*Pterotrigonia* に見られるような特異なしゃもじ型の殻の形成も可能にしていることが示唆される。

結城 仁夫

981. DIVERSITY OF *CHLAMYS* (BIVALVIA) FROM THE PLIOCENE OGIKUBO FORMATION, CENTRAL JAPAN*

KAZUTAKA AMANO

Department of Geoscience, Joetsu University of Education,
Joetsu, Niigata Prefecture, 943

Abstract. Many specimens of *Chlamys* were obtained from the Early Pliocene Ogikubo Formation in northern Nagano Prefecture, central Honshu. These are identified with the following six species: *Chlamys (Chlamys) cosibensis* (Yokoyama), *C. (C.) ingeniosa tanakai* Akiyama, *C. (C.) foeda* (Yokoyama), *C. (C.) insolita* (Yokoyama), *C. ("C.") lioica shigaramiensis* Amano et Karasawa and *C. (Leochlamys) tanassevitschi* (Khomenko). The last species has hitherto also been known as *Chlamys daishakaensis* Masuda et Sawada or *C. iwakiana* (Yokoyama).

The diversity of this chlamid fauna is attributed to the distributional pattern and geologic ranges of the species. *Chlamys lioica shigaramiensis* and *C. tanassevitschi* are confined to the northwest flank of the Orihashi Syncline, which was deeper and colder than the southeast flank area where *C. foeda* occurred.

Chlamys ingeniosa tanakai, *C. insolita* and *C. lioica shigaramiensis* are Miocene relict forms. They survived in the studied area to the Middle Pliocene, owing to the cold-water embayment conditions. The mixture of Miocene and Pliocene type species accounts for the diversity of *Chlamys* from the Ogikubo Formation.

Key words. Diversity, *Chlamys*, Pliocene, Ogikubo Formation.

Introduction

In Nagano Prefecture, central Japan, many molluscan fossils occur in the Pliocene Ogikubo Formation (Amano and Karasawa, 1993). The fauna is very important for examining the Mio-Pliocene succession of shallow sea molluscan fauna in the Japanese Neogene because the Ogikubo Formation may be the only embayment setting of Japan Sea borderland in the Early Pliocene. Moreover, it has been known as a mixed fauna including typical Miocene and Pliocene species (Amano and Karasawa, 1993).

Pectinids including *Chlamys* are common

bivalves in the Japanese Neogene as well as from this formation (Masuda, 1962a), and are suitable for examining the Mio-Pliocene faunal change in Japan because of their fast rate of evolution (Stanley, 1986). The genus *Chlamys* is abundant in the Ogikubo Formation and was studied by some previous authors (Yokoyama, 1925b; Akiyama, 1958; Masuda, 1962a; Amano and Karasawa, 1986; Amano *et al.*, 1991). When he summarized the taxonomy of Japanese Neogene pectinids, Masuda (1962a) described the following species from the "Shigarami Formation" including the Ogikubo: *Chlamys cosibensis cosibensis* (Yokoyama), *C. c. turpicula* (Yokoyama), *C. daishakaensis* Masuda et Sawada, *C. insolita* (Yokoyama) and *C. tanakai* Akiyama. Later, Amano

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and Karasawa (1986) proposed a new subspecies, *shigaramienseis* of *C. lioica* (Dall). Amano *et al.* (1991) described *C. foeda* (Yokoyama) and discussed its ecology and evolution. However, "*C. daishakaenseis*" from this formation has never been illustrated or described. Little is known about the exact distribution of the above species in the formation.

It is noteworthy that few deposits in Japan yield a high diversity of *Chlamys* in the Neogene. However, there is no discussion in the literature on the causes of the high diversity of *Chlamys* in the Ogikubo Formation.

Therefore, the purpose of this paper is to taxonomically reexamine some species of *Chlamys* and to discuss the reasons why so many species of *Chlamys* could live in the studied area.

Geological and paleoecological settings

The Ogikubo Formation crops out to the west of Nagano City in the northern part of Nagano Prefecture (Figure 1). It has been folded by the Orihashi Syncline and shows finer-grained facies on the northwest flank than in the southeast. On the northwest flank, the formation mainly consists of siltstone and mudstone associated with sandstone. On the southeast flank, it is chiefly composed of fine-grained sandstone with siltstone and conglomerate. The Ogikubo Formation unconformably covers the Arakurayama Formation. The upper part of the Ogikubo is an isochronous deposit to the lower part of the Sarumaru Formation (Amano and Karasawa, 1993). Amano and Karasawa (*op. cit.*) also assigned an age of 3–4 Ma to the Ogikubo based on the planktonic foraminifers and K/Ar dating.

Amano and Karasawa (1993) recognized four associations in the Ogikubo molluscan fauna: *Mya-Macoma*, *Mizuhopecten-Chlamys*, *Conchocele*, and *Chlamys-Tridonta* associations (Figure 1). Among these, *Mya-Macoma* association is restricted to the inter-

tidal zone on the southeast flank. The last two associations, which occurred at lower sublittoral and upper bathyal depths, are on the northwest flank. The upper sublittoral *Mizuhopecten-Chlamys* association occurred on both flanks of the Orihashi Syncline.

From the above-noted lithofacies change and the distribution of molluscan associations, it is obvious that part of the formation on the northwest flank was deposited in deeper water than that on the southeast one.

Localities of *Chlamys*

Many molluscan fossils were obtained from 25 localities of the Ogikubo Formation (Amano and Karasawa, 1993; Figure 2). From 16 of these localities, the following five species of *Chlamys* were collected: *Chlamys* (*Chlamys*) *cosibensis* (Yokoyama), *C.* (*C.*) *foeda* (Yokoyama), *C.* (*C.*) *ingeniosa tanakai* Akiyama, *C.* ("*Chlamys*") *lioica shigaramienseis* Amano et Karasawa and *C.* (*Leochlamys*) *tanassevitschi* (Khomeiko). Unfortunately, *Chlamys insolita* (Yokoyama) could not be obtained, but I had an opportunity to examine the holotype (monotype) of the species.

The total number of localities and specimens herein treated are listed below: *C. ingeniosa tanakai*, 15 localities (Loc. nos. 2, 4, 6, 7, 8, 10, 15, 16, 17, 18, 19, 21, 22, 24, 25), 130 specimens; *C. cosibensis*, 6 localities (Loc. nos. 5, 6, 17, 21, 22, 24), 12 specimens; *C. lioica shigaramienseis*, 2 localities (Loc. nos. 21, 22), 5 specimens; *C. foeda*, 1 locality (Loc. no. 10), 2 specimens; *C. tanassevitschi*, 1 locality (Loc. no. 22), 2 specimens.

Almost all the specimens occurred as single valves and mainly from fine- to medium-grained sandstone (Loc. nos. 2, 4, 5, 6, 7, 8, 10, 17, 18) and tuffaceous muddy fine- to medium-grained sandstone (Loc. nos. 15, 16, 19, 22, 24, 25). At Loc. 21, three species of *Chlamys* occur in a granule-bearing fine-grained sandstone.

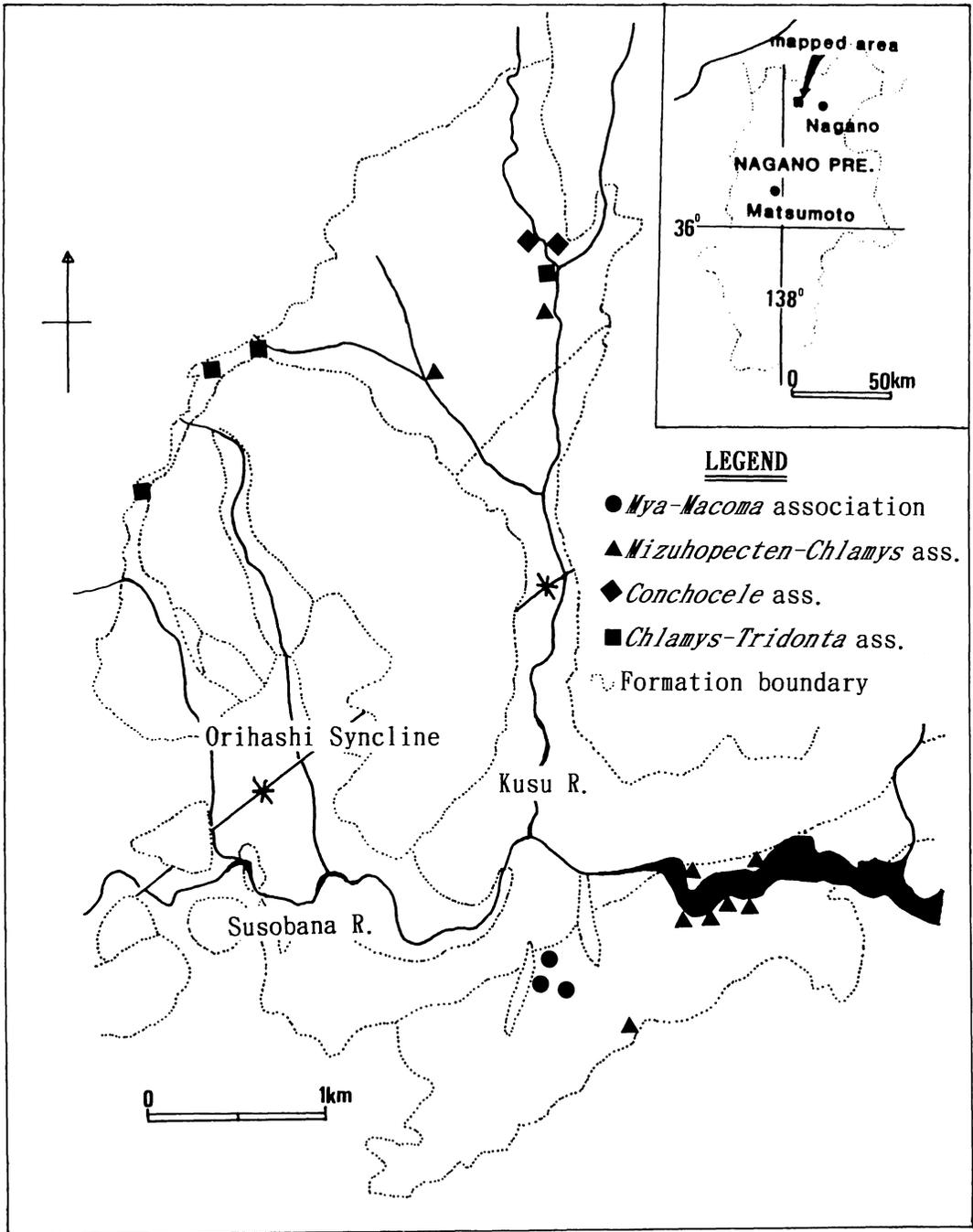


Figure 1. Distribution of molluscan associations in the Ogikubo Formation.

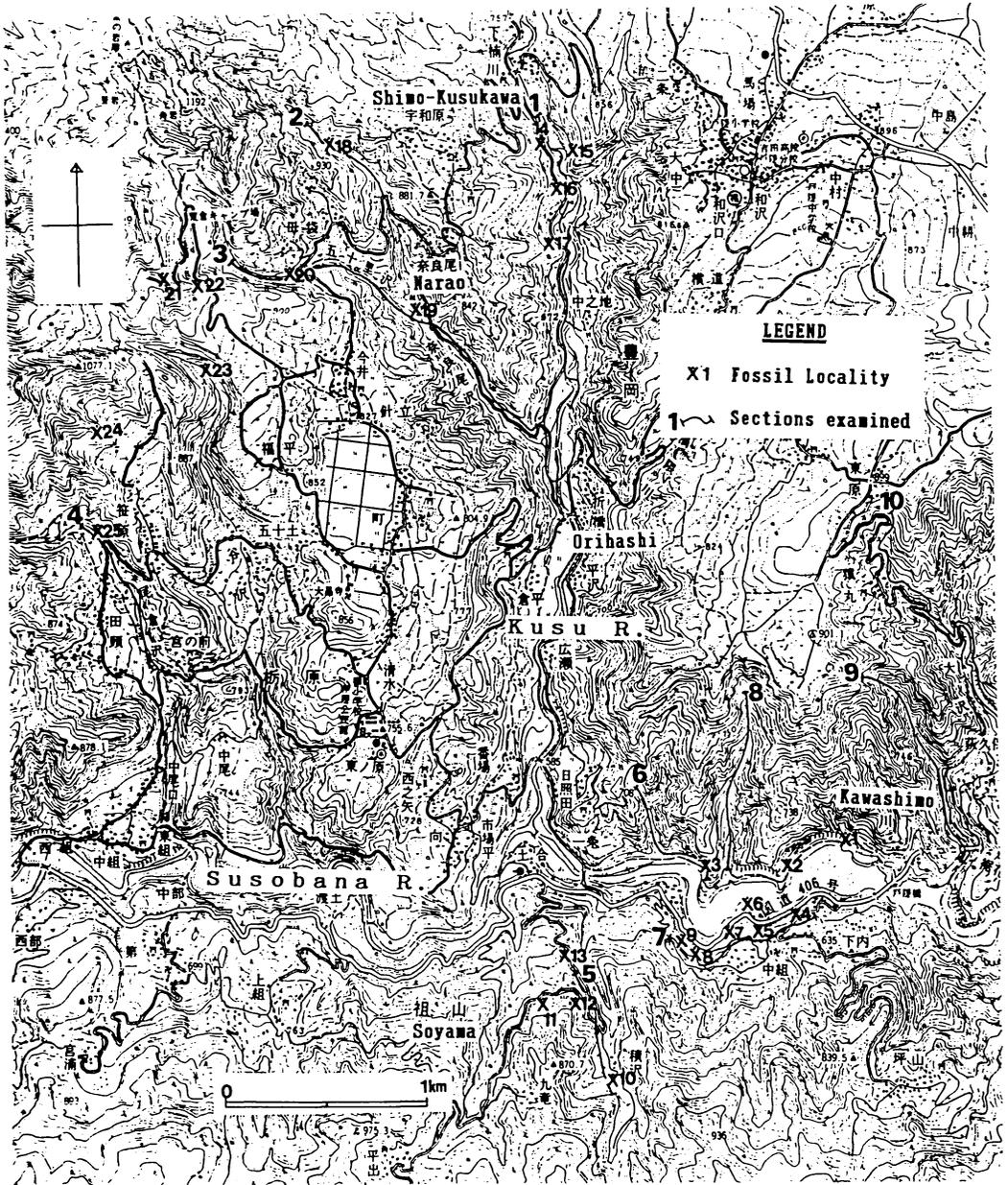


Figure 2. Localities of fossils (after Amano and Karasawa, 1993; using the topographical maps of “Togakushi” and “Shinano-Nakajo” scale 1 : 25,000 published by Geographical Survey Institute of Japan).

Systematic notes on some species of *Chlamys*

Chlamys cosibensis, *C. foeda* and *C. lioica shigaramiensis* were taxonomically examined

in detail by Masuda (1973), Amano and Karasawa (1986), and Amano *et al.* (1991). Therefore, in this section, the following three species will be examined; *Chlamys ingeniosa tanakai*, *C. insolita* and *C. tanassevitschi*.

Family Pectinidae Rafinesque, 1815

Subfamily Chlamydiae Korobkov, 1960

Genus *Chlamys* [Röding, 1798]

Subgenus *Chlamys* [Röding, 1798]

Chlamys (Chlamys) ingeniosa tanakai

Akiyama, 1958

Figures 3-1, 3, 9

Chlamys sp., Kuroda, 1931, p. 37-38, pl. 2, fig. 9, pl. 3, fig. 10; Tomizawa, 1958, p. 326, pl. 3, figs. 4a, b.

Chlamys ingeniosa tanakai Akiyama, 1958, p. 243-245, pl. 36, figs. 1, 2a, b, 3a, b.

Chlamys obesa Akiyama, 1958, p. 245-246, pl. 36, figs. 4a, b, 5a, b, 6a, b.

Chlamys (Chlamys) tanakai Akiyama. Masuda, 1962a, p. 186, pl. 22, figs. 4-7; Amano and Karasawa, 1986, pl. 4, figs. 2, 8.

Type locality.—Kawashita (Kawashimo?), Togakushi-mura, Kamiminochi-gun, Nagano Prefecture. TKD, Reg. no. 5334.

Remarks.—*Chlamys ingeniosa tanakai* is of moderate size and the valves are moderately inflated. There are 24 to 28 dichotomous granulated radial ribs with interstitial riblets on the right valves and 23 to 27 granulated radial ribs with one or two interstitial riblets on the left valves.

The present subspecies was proposed by Akiyama (1958) based on specimens from the Ogikubo Formation. At that time, he also proposed another species, *Chlamys obesa* from a locality near the type locality of the present subspecies. Thereafter, Masuda (1962) considered the latter as a synonym of the former.

Before the proposal by Akiyama, Kuroda (1931) described and illustrated the present subspecies as *Chlamys* sp. from Shimosoyama (Ogikubo Formation). However, the figured specimens are internal casts; none of the shell remains. Its rubber mold (Figure 3-3) shows the same characteristics as the present subspecies.

Comparison.—*Chlamys ingeniosa tanakai* is slightly different from *C. i. ingeniosa* (Yokoyama) from the Miocene Nanao Forma-

tion, Ishikawa Prefecture (Figure 3-8, holotype; Figure 3-5, topotype) by having a smaller apical angle, later splitting radial ribs, stronger intercalated riblets, and a smaller resilial pit on the right valve. *Chlamys ingeniosa ingeniosa* flourished in early Middle Miocene age and may be an ancestor of *C. i. tanakai*.

As already pointed out by Akiyama (1958), the present subspecies is related to the Recent *Chlamys islandica* group. Among them, *Chlamys hindsi* (Carpenter) is the most allied to the present one. However, the left valve of *hindsi* has tricarinate radial ribs which have never been observed in this subspecies.

Distribution.—Pliocene Arakurayama and Ogikubo Formations.

Chlamys (Chlamys) insolita
(Yokoyama, 1925)

Figures 3-2, 7

Pecten insolitus Yokoyama, 1925b, p. 18, pl. 5, fig. 3.
Chlamys (Chlamys) insolita (Yokoyama). Masuda, 1962a, p. 171.

Chlamys anapleus (Woodring). Gladenkov *et al.*, 1984, p. 187, pl. 35, figs. 2, 6 (*non* pl. 34, fig. 8, pl. 37, figs. 1, 3).

Type locality.—Shigarami, Togakushi-mura, Kami-minochi-gun, Nagano Prefecture. CM22634.

Remarks and comparison.—*Chlamys insolita* was proposed on the basis of one right valve from Shigarami (Ogikubo Formation) by Yokoyama (1925b). The present species is characterized by 21 broad radial ribs with interstitial riblets and a narrow byssal fasciole.

When they described molluscan fossils from the Miocene Kakert Suite in western Kamchatka, Gladenkov *et al.* (1984) illustrated some specimens as *Chlamys anapleus*. As the result of examination of their specimens stored at the Geological Institute of the Russian Academy of Sciences in Moscow, it has become clear that they differ from Woodring's species by having more numerous

radial ribs. The specimen collected by Dr. Sinelnikova from the Etolon Suite (Figure 3-7) also shows the same characteristics as the present species.

Chlamys anapleus (Woodring) and *C. strategus* (Dall) are allied to this species, but *anapleus* has 11 radial ribs and *strategus* has about 7 ribs.

Distribution.—Miocene Kakert and Etolon Suites in Kamchatka; Pliocene Ogikubo Formation in Honshu.

Subgenus *Leochlamys* MacNeil, 1967

Chlamys (*Leochlamys*) *tanassevitschi*
(Khomenko, 1934)

Figures 4-1, 2, 4, 5, 6, 7, 5-1, 2, 3, 4

Pecten tanassevitschi Khomenko, 1934, p. 33-34, pl. 3, figs. 4, 5, pl. 4, figs. 1-5, pl. 5, figs. 3, 4, pl. 6, figs. 1, 2, pl. 7, fig. 1

Pecten (*Pecten*) *iwakianus* Yokoyama, Nomura and Hatai, 1935, p. 102-103, pl. 12, fig. 3, pl. 13, fig. 8.

Pecten (*Chlamys*) *tanassevitschi* Khomenko, Slodkewitsch, 1938, p. 108, pl. 20, fig. 5, pl. 21, figs. 1-3, pl. 22, fig. 1.

Chlamys (*Chlamys*) *iwakiana* (Yokoyama). Kanehara, 1942, p. 137-138, pl. 15, fig. 6, pl. 16, fig. 5; Omori, 1977, p. 68, fig. 5.

Chlamys hastata iwakiana (Yokoyama). Kubota, 1950, p. 14, figs. 52, 64.

Chlamys iwakiana (Yokoyama). Itoigawa, 1958, pl. 1, fig. 12.

Chlamys daishakaensis Masuda and Sawada, 1961, p. 23-25, pl. 4, figs. 8, 9; Ogasawara *et al.*, 1986, pl. 52, figs. 18, 19; Akamatsu and Suzuki, 1990, pl. 1, fig. 8; Akamatsu and Suzuki, 1992, pl. 3, fig. 9.

Chlamys (*Chlamys*) *farreri nipponensis* Kuroda. Krishtofovich, 1964, p. 139-141, pl. 19, figs. 2, 3, pl. 24, fig. 3 (non pl. 17, fig. 1); Zhidkova *et al.*, 1968, p. 84, pl. 24, figs. 1, 2.

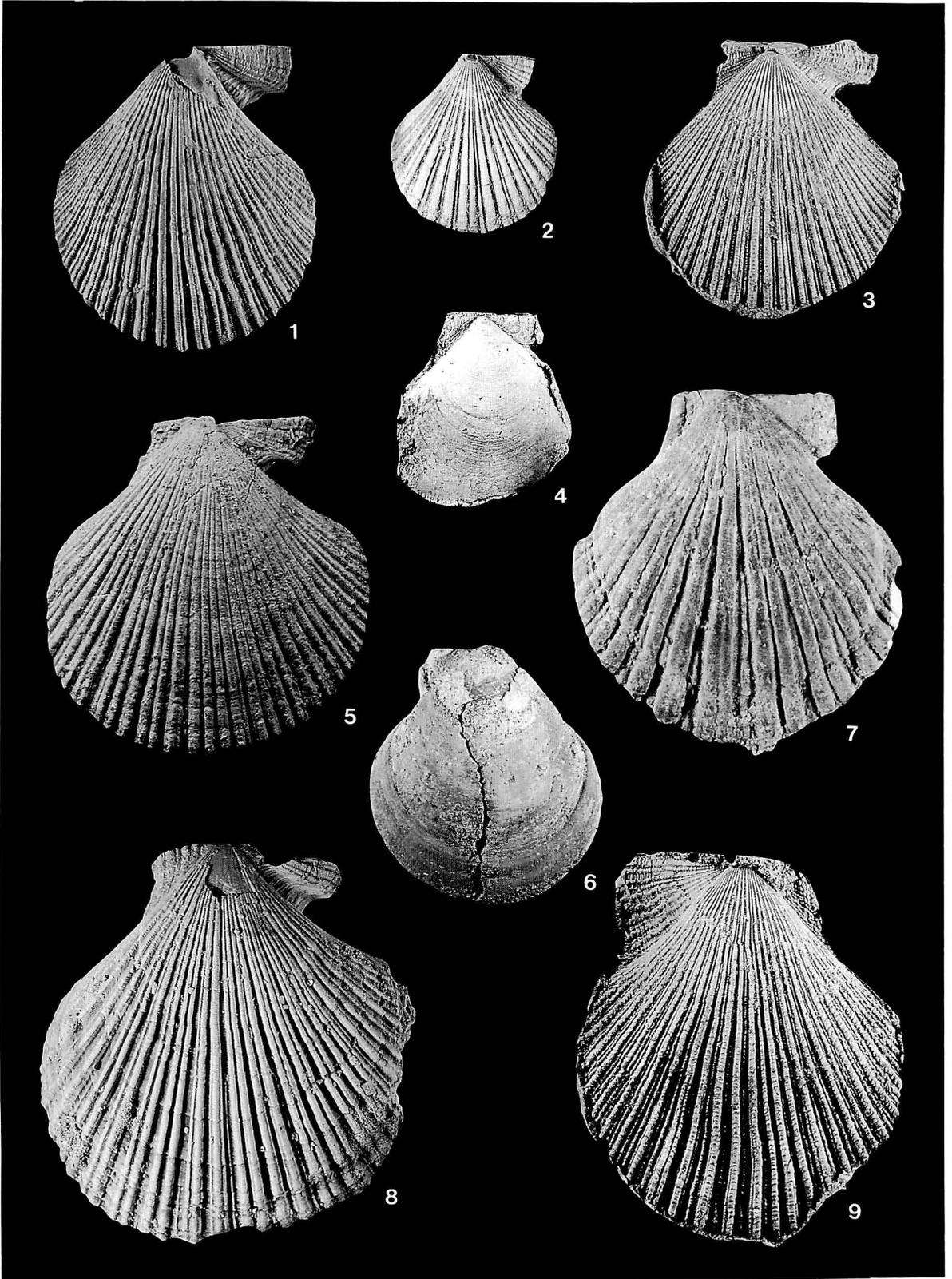
Chlamys (*Chlamys*) *sawanensis* Omori, 1977, p. 68, pl. 2, figs. 7a, b.

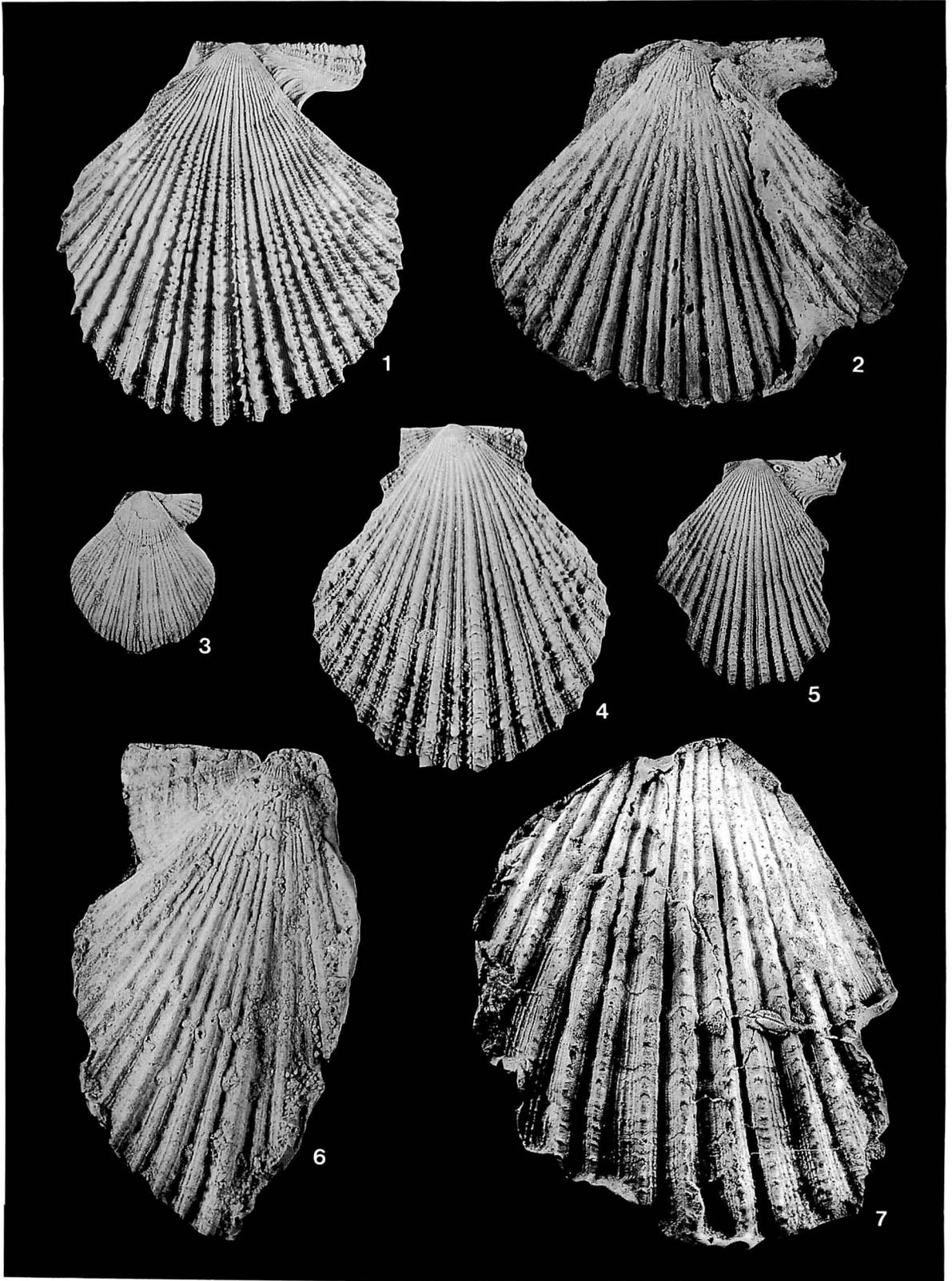
Chlamys (*Chlamys*) *daishakaensis* Masuda and Sawada. Uozumi *et al.*, 1986, pl. 20, fig. 10.

Type locality.—Exposure along the coast to the south of Piltuk River, western part of Schmidt Peninsula, Sakhalin. Lectotype no. 30/5043.

Original description.—"Shell thick, inequilateral, inequivalve; both valves moderately inflated in same extent. Anterior auricle nearly twice as long as posterior one; byssal notch deep, ctenolium considerably variable. Upper half of anterior auricle of right valve ornamented with five rough grooves between imbricated and rounded ribs, becoming more wide toward upper; surface of lower half of auricle sculptured by deep growth lines. Anterior auricle of left valve with 12 deeply rounded and imbricated ribs, these ribs nearly equal or finer ribs intercalated with stronger ones in places; growth lines also distinct. Posterior auricle of both valves less massive, and their sculpture considerably fine: except for many narrowly arranged growth lines, four fine weakly imbricated radial ribs separated by equal interspaces, with two fine radial threads. Number of ribs 22, nearly equal or different from each other to some extent. Ribs high and rounded with many fine imbrications; interspaces deep, usually broader than ribs, but sometimes equal, very rarely narrower than ribs. Besides concentric sculpture due to growth, interspaces of ribs with fine and weakly imbricated secondary riblets; number of secondary riblets attaining three in large sample; secondary riblets situated on both sides or one side of main ribs in some cases, separated from main ribs in another cases;

→ **Figure 3.** 1, 3, 9: *Chlamys* (*Chlamys*) *ingeniosa tanakai* (Akiyama). 1; Loc. 7, JUE no. 15429. 3; rubber mold (Kuroda, 1931, pl. 2, fig. 9, JC610038), JUE no. 15430. 9; Loc. 10, JUE no. 15431. 2, 7: *Chlamys* (*Chlamys*) *insolita* (Yokoyama). 2; holotype (CM22634). 7; Etolon Suite, West Kamchatka, deposited in Geological Institute, Moscow. 4: *Chlamys* ("Chlamys") *lioica shigaramiensis* Amano et Karasawa. Loc. 22, JUE no. 15432. 5, 8: *Chlamys* (*Chlamys*) *ingeniosa ingeniosa* (Yokoyama). 5: topotype collected by Dr. N. Matsuura. 8; holotype (CM25519). 6: *Chlamys* ("Chlamys") *lioica lioica* (Dall). Loc. Bolishoi Cape, Etolon Suite, deposited in Geological Institute, Moscow (N670/82). All figures are natural in size.





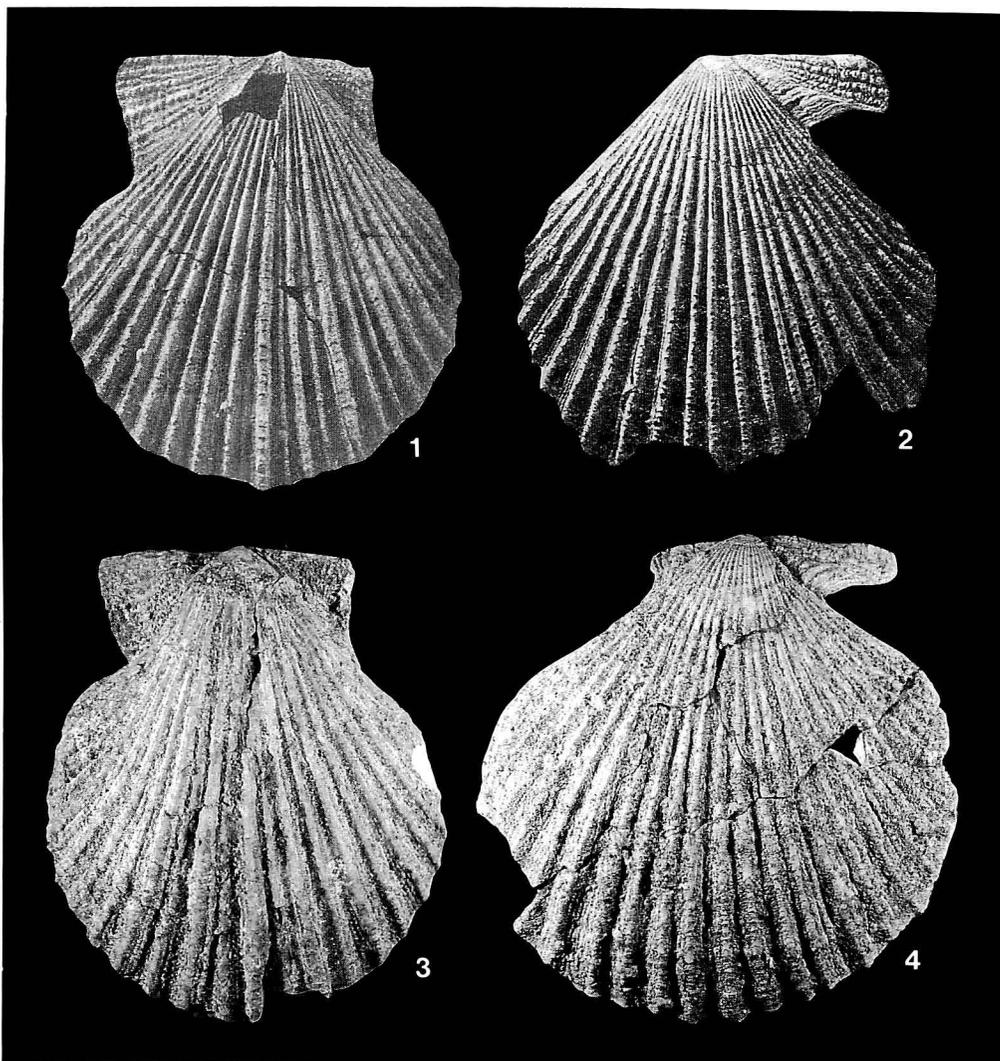


Figure 5. Type specimens of *Chlamys* (*Leochlamys*) *tanassevitschi* (Khomenko) and “*Chlamys daishakaensis* Masuda et Sawada”. **1, 2:** syntypes of *Chlamys* (*Leochlamys*) *tanassevitschi* (Khomenko), $\times 0.75$, Nos. 24, 30/5043, (reproduced from Khomenko, 1934, pl. 4, fig. 2, pl. 7, fig. 1). **3:** topotype of “*Chlamys daishakaensis* Masuda et Sawada”, $\times 0.5$, IGPS no. 15410. **4:** holotype of “*Chlamys daishakaensis* Masuda et Sawada”, $\times 0.55$, IGPS no. 90708.

wide range of variation usually recognized on secondary ribs. (Originally in Russian, translated into English”).

Remarks.—*Chlamys tanassevitschi* (Syn- types, Figures 5–1, 2) is characterized by its large shell size (maximum length 112 mm,

← **Figure 4.** **1, 2, 4, 5, 6, 7:** *Chlamys* (*Leochlamys*) *tanassevitschi* (Khomenko). **1;** $\times 0.75$, Loc. 2 km upstream bank of Soibetsu River, Hokkaido, Setana Formation, JUE no. 15433. **2, 6, 7;** $2, \times 1, 6, 7 \times 0.8$; Loc. 22, JUE nos. 15434~15436. **4, 5;** $\times 1$, Loc. Kaidate, Niigata Pref., Sawane Formation, JUE nos. 15437-1~15437-2. **3:** *Chlamys* (*Chlamys*) *cosibensis* (Yokoyama). $\times 1$, Loc. 6, JUE no. 15438.

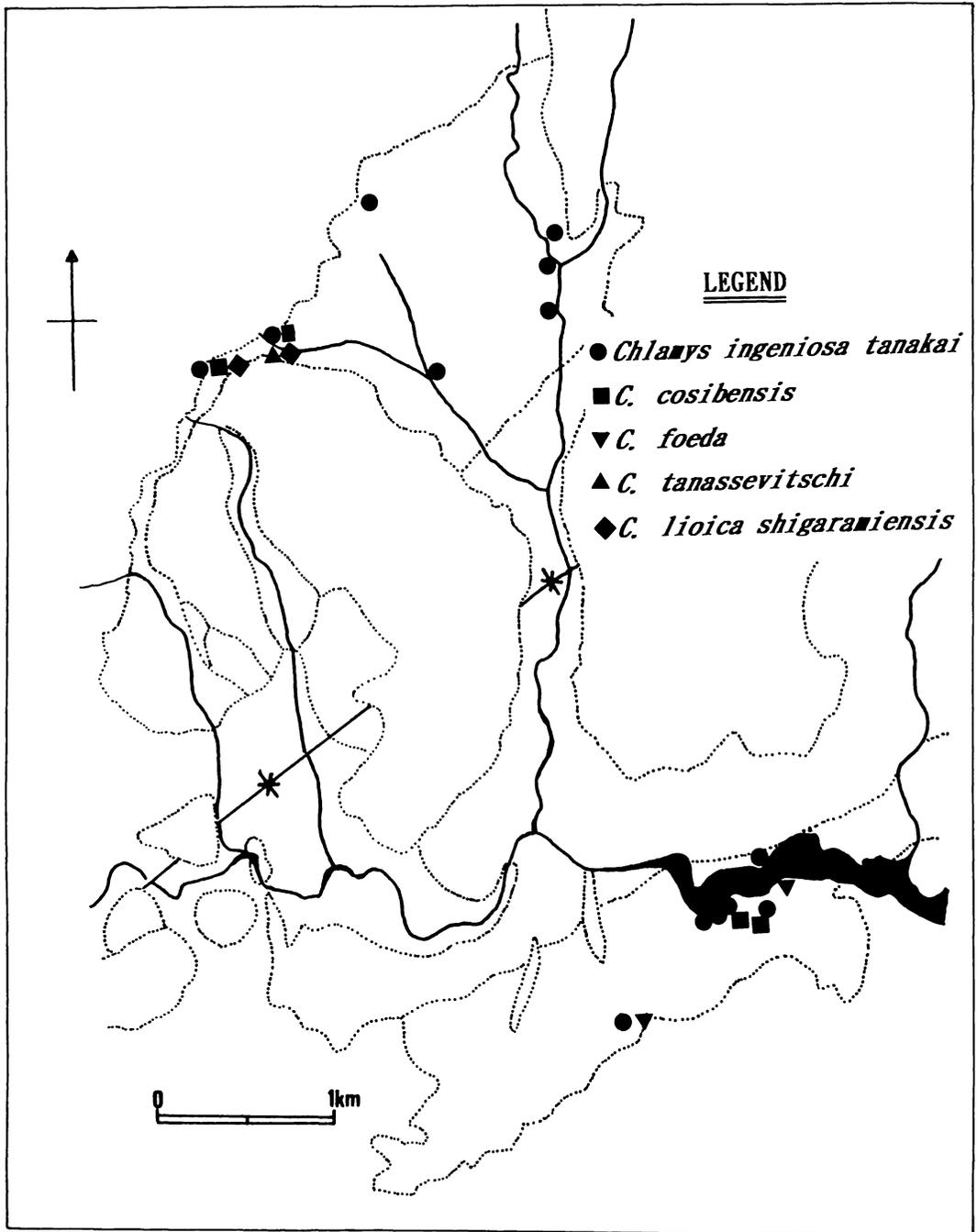


Figure 6. Distribution of *Chlamys* in the Ogikubo Formation.

according to Khomenko, 1934), narrowly elongated anterior auricle of right valve ornamented with four radial ribs, and 22 to 24 imbricated radial ribs on its shell surface with a few intercalated radial threads.

The Ogikubo specimens are large in size (maximum length 126.9 mm) and have similar auricular characters. Although they have less numerous radial ribs (about 20), these ribs are scaled with fine radial threads on both flanks and three radial threads in each interspace. Therefore, the Ogikubo specimens are clearly identifiable with the present species.

Krishtofovich (1964) and Zhidkova *et al.* (1968) misjudged the present species as a synonym of the Recent species *Chlamys farreri nipponensis* Kuroda. However, it is easy to distinguish *tanassevitschi* from the Recent species by the larger shell, narrowly elongate anterior auricle of right valve and less numerous ribs on the auricles of both valves.

When Masuda and Sawada (1961) proposed *Chlamys daishakaensis* (Holotype, Figure 5-4), based on specimens from the Early Pleistocene Daishaka Formation, they did not compare it with the present species. As the result of examination of the type specimens, some topotype specimens and some specimens from the Setana Formation in Hokkaido (Figure 4-1), I can consider *Chlamys daishakaensis* to be a synonym of *C. tanassevitschi* because of its large shell size, similar shell shape and nearly equal number of ribs.

Many previous authors frequently identified the present species with *Chlamys iwakiana* established by Yokoyama (1925a). As already pointed by Masuda and Sawada (1961), *Chlamys iwakiana* differs from *C. tanassevitschi* by having a less inflated left valve and less elevated radial ribs.

According to Omori (1977), his new species, *Chlamys sawanensis* slightly differs from "*C. iwakiana*" (= *C. tanassevitschi*) by having fewer secondary radial threads.

However, his two specimens are smaller (maximum length, 66 mm) than the present species. Moreover, some specimens from the Sawane Formation (Figures 4-5, 5) show the same characteristics as the present one in shell sculpture and other features.

Comparison.—The present species is allied to *Chlamys* (*Leochlamys*) *tugidakensis* MacNeil (1967) from the Pliocene? of the Tugidak Island in its narrowly elongate shape of auricle, and in similar form and number of radial ribs to the present species. The development of secondary riblets is the most obvious difference between *Chlamys tanassevitschi* and *C. tugidakensis*. Interstitial riblets are rarely present on the right young valves of *tugidakensis*.

The Recent species, *Chlamys* (*Leochlamys*) *farreri* (Jones et Preston) is another allied species to the present one. As pointed out above, the *farreri* has a broader anterior ear of right valve, more numerous radial ribs on the anterior auricle (about six to seven on right valve, about twenty on the left), and lower radial ribs on the shell surface of both valves.

Distribution.—Pliocene Pomyr Suite in northern Sakhalin, Early Pleistocene Shimonopporo, Setana and Tomikawa Formations in Hokkaido, Plio-Pleistocene Daishaka, Sasaoka, Haizume, Sawane, and Ogikubo Formations in Honshu.

Diversity of *Chlamys* and its causes

The following chlamids are recorded from the Ogikubo Formation; *Chlamys ingeniosa tanakai*, *C. cosibensis*, *C. foeda*, *C. insolita*, *C. lioica shigaramiensis* and *C. tanassevitschi*. In addition to these *Chlamys* species, the Ogikubo also yields *Swiftopecten swiftii* (Bernardi), *Mizuhopecten yamasakii* (Yokoyama) and *Yabepecten tokunagai* (Yokoyama) (Amano and Karasawa, 1988). Other than the Setana, Na-arai and Ogikubo Formations, there are no Plio-Pleistocene formations in Japan which yield more than

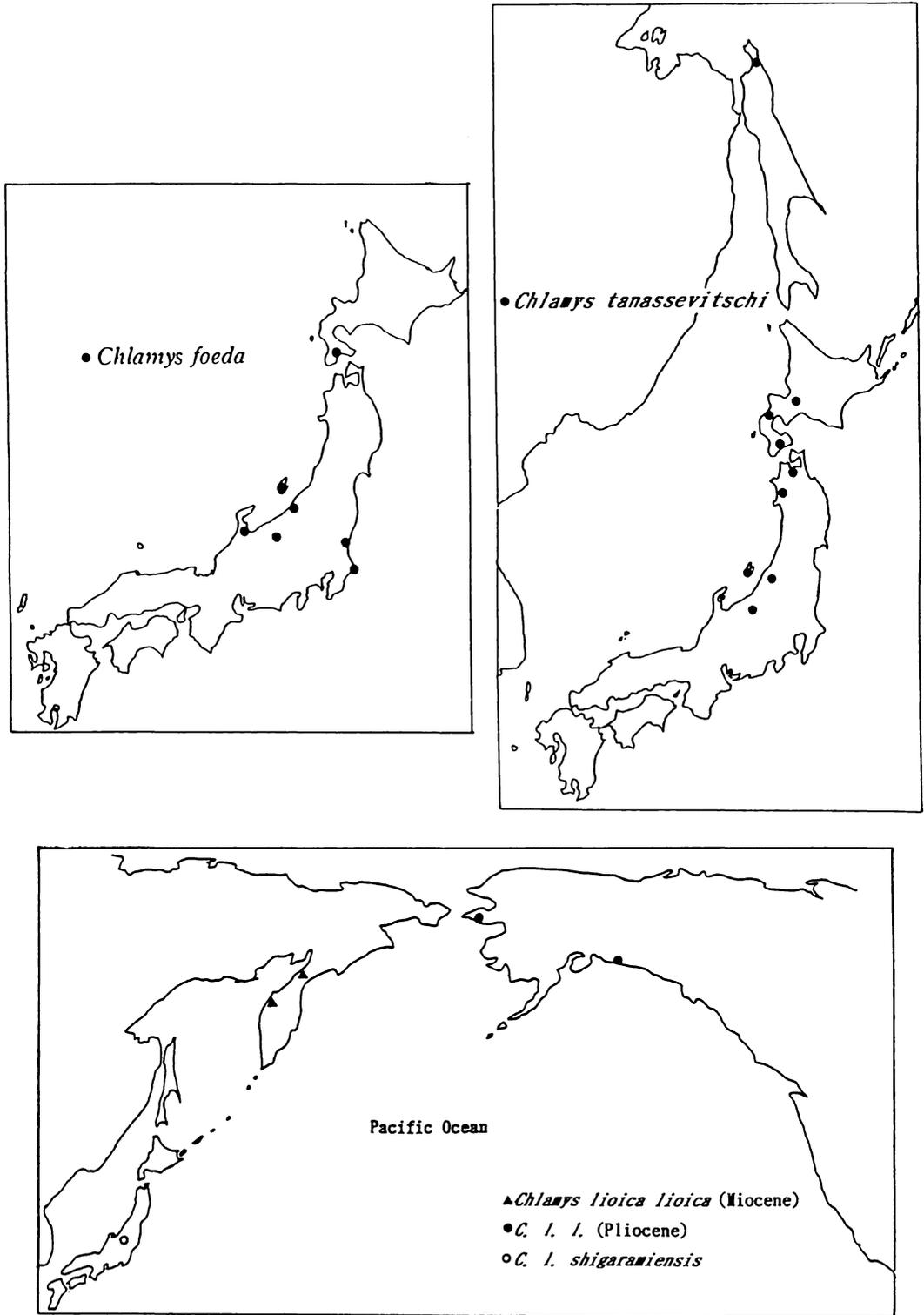


Figure 7. Geographical distribution of *Chlamys foeda*, *C. tanassevitschi* and *C. lioca* group.

Table 1. Epifaunal bivalves other than pectinids from the Ogikubo Formation

Species name	depth (m)*	bottom**
<i>Arca boucardi</i> Josseume	0-20	R
<i>Porterius dalli</i> (Smith)	0	R
<i>Mytilus (Crenomytilus) grayanus</i> (Dunker)	0-20	R
<i>Modiolus difficilis</i> Kuroda et Habe	0-20	R
<i>Solamen spectabilis</i> (A. Adams)	30-300	fS
<i>Acesta goliath</i> (Sowerby)	100-1,390	sM
<i>Anomia chinensis</i> Philippi	0-20	R, fgS
<i>Monia macroschisma</i> (Deshayes)	0-40	R
<i>Neopycnodonte musashiana</i> (Yokoyama)	20-500	M, R
<i>Crassostrea gigas</i> (Thunberg)	0	M, R

*** chiefly after Habe (1977): ** R, Rock; fS, fine sand; fgS, fine pebble-bearing sand; sM, sandy mud; M, mud.

six chlamids (Masuda, 1962b; this study). Some taxonomical problems of *Chlamys* from the Setana Formation are pointed out by Shikama and Ikeya (1964) and Uozumi and Akamatsu (1975). Thus the Ogikubo Formation represents one of very few Plio-Pleistocene deposits yielding a diverse pectinid fauna.

Other than the *Chlamys islandica* group, many Recent *Chlamys* live in the warm waters around Japan (Higo and Goto, 1993). Despite its boreal-type fauna (Tomizawa, 1958; Amano and Karasawa, 1993), the Ogikubo Formation yields a high diversity of chlamids. The high diversity of chlamids can not be attributed to the climate. Alternatively, the isolation of habitat between each species and some Miocene relict species may make the diversity of chlamids of the Ogikubo Formation high.

The above six species are not always collected together, but instead occur separately in the studied area (Figure 6). Two common species, *Chlamys ingeniosa tanakai* and *C. cosibensis* occur on both flanks of the Orihashi Syncline and are found in both upper and lower sublittoral associations (*Mizuhopecten-Chlamys* and *Chlamys-Tridonta* associations).

The occurrence of *Chlamys foeda* is

confined to the southeast flank while *C. lioica shigaramiensis* and *C. tanassevitschi* occur in the northwest. *C. foeda* might have preferred shallower water than the latter two. Judging from the distribution of the above species (Figure 7), the northern limit of the latter two species is located further north than that of *foeda*, and therefore they probably lived in colder water. This estimation is supported by the following species association. The latter two chlamids are frequently accompanied by *Tridonta alaskensis* (Dall) and *Yabepecten tokunagai* (Yokoyama) which originated in northern Pacific waters and had migrated southward by the Pliocene (Ogasawara, 1986; Masuda, 1986).

Of the six chlamids, *Chlamys cosibensis*, *C. tanassevitschi*, and *C. foeda* are commonly recognized in the Pliocene and Early Pleistocene Omma-Manganji fauna (Otuka, 1939). Especially, *Chlamys foeda* and *C. tanassevitschi* have never been found in any Miocene faunas, but are characteristic elements of the Omma-Manganji fauna (Masuda, 1980).

The Ogikubo Formation also yields the following three species which are confined to the Pliocene strata around the studied area. *Chlamys ingeniosa tanakai* most abundantly occurs from the formation and is derived from

the Miocene ancestor, *C. ingeniosa ingeniosa*. *C. lioica shigaramiensis* is also derived from Miocene *C. lioica lioica* in Kamchatka. *Chlamys insolita* has been commonly found from the Miocene Kakert and Etolon Suites in Kamchatka (Gladenkov *et al.*, 1984) while the Pliocene occurrence is confined to the Ogikubo Formation. Therefore, these species are relicts of the Miocene faunas in Honshu and Kamchatka. Another reason for the high diversity of chlamids are attributed to these three Miocene relicts in addition to Omma-Manganjian species.

As above noted, the Miocene relicts might have lived on the sublittoral sandy bottom. There is a problem remaining unsolved about the reason why some Miocene relict species of *Chlamys* survived in these habitats which are vulnerable for epifaunal species.

Other than *Swiftopecten swiftii*, the eight pectinid species from the Ogikubo Formation are all extinct. By contrast, all epifaunal bivalves in this formation other than pectinids are extant forms (Table 1). Other than *Acesta goliath*, which lives in the lower sublittoral to upper bathyal zones where predators are rare, almost all the species are now living on hard bottoms of the intertidal and upper sublittoral zones.

Stanley (1986) suggested the extraordinary high rate of extinction of pectinaceans results from the heavier predation pressure on the subtidal soft bottom than on the intertidal hard bottom where many other epifauna lived.

In discussing the characteristics of the extinct bivalve genera of the Plio-Pleistocene Omma-Manganji fauna, Amano and Tanaka (1992) pointed out that the monospecific genera inhabiting sublittoral sandy bottoms suffered extinction while those inhabiting the rocky shores and the deep water survived. Conclusively, the sublittoral sandy bottom is a vulnerable place for infaunal bivalves as well as for epifauna including *Chlamys*.

One possible cause why the Miocene relicts survived under such vulnerable conditions is

the cold embayment in the studied area. Vermeij (1986) pointed out that cold water can act as an ecological refuge. A representative Pliocene index fossil, *Fortipecten takahashii* (Yokoyama) occurred in the cold-water embayments, where it was a recliner. Its mode of life is rare among late Cenozoic bivalves but was common among Mesozoic epifaunas (Hayami and Hosoda, 1988). Like *Fortipecten takahashii*, the relict Miocene chlamids could not survive too long and became extinct by Middle Pliocene time.

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Nagano 長野, Ogikubo 荻久保, Orihashi 折橋, Shigarami 柵, Arakurayama 荒倉山, Setana 瀬棚, Daishaka 大釈迦。

鮮新統荻久保層産 *Chlamys* 属 (二枚貝) の多様性: 長野県北部の下部鮮新統荻久保層から数多くの *Chlamys* が採集された。これらの標本は、次の6種に同定される。すなわち、*Chlamys* (*Chlamys*) *cosibensis* (Yokoyama), *C. (C.) ingeniosa tanakai* Akiyama, *C. (C.) foeda* (Yokoyama), *C. (C.) insolita* (Yokoyama), *C. ("C.") lioica shigaramiensis* Amano et Karasawa, *C. (Leochlamys) tanassevitschi* (Khomenko) である。このうち、*Chlamys tanassevitschi* は従来 *C. daishakaensis*, *C. iwakiana* とされてきた種であり、荻久保層からは今回初めて図示された。

この様に種が多く見られる理由として、その分布パターンや生存期間が考えられる。*Chlamys lioica shigaramiensis* や *C. tanassevitschi* はより深く、寒冷であったと考えられる折橋向斜構造の北西翼地域に限られ、*C. foeda* は南東翼に限られている。また、6種中、*Chlamys ingeniosa tanakai*, *C. insolita*, *C. lioica shigaramiensis* は中新世の遺存種で、鮮新世中期まで本地域周辺の寒冷な内湾域に生きのびた。以上のような種の棲み分け、中新世型の種と鮮新世型の種の混合により、本地域の *Chlamys* の多様性が高くなっている。

天野和孝

SHORT NOTES

**32. TAXONOMIC NOTE ON THE STROMATOPOROID
AND RUGOSE CORAL GENERA *LABECHIELLA*,
LABECHIELLATA AND *MAZAPHYLLUM****

KEI MORI

Institute of Geology and Paleontology,
Tohoku University, Sendai, 980

The history of the proposal of the genus *Labechiella* is confusing. It was proposed as a subgenus of *Labechia* by Yabe and Sugiyama (1930, p. 54) and *Labechia serotina* Nicholson (1886) from the Silurian of England was chosen as the type species. Sugiyama (1939, p. 443) proposed *Labechiella* again without commenting on the previous study of Yabe and Sugiyama (1930) and described a new type species, *Labechiella regularis* from the Silurian of Japan. The next year the same description of the genus *Labechiella* and *L. regularis* was published by Sugiyama (1940, p. 111). It is evident that *Labechiella* Sugiyama (1939) is a junior homonym of *Labechiella* Yabe and Sugiyama (1930). In 1941 Sugiyama (1941, p. 75) wrote the following concerning the genus *Labechiellata*: "In a recent paper, the writer established a new stromatoporoid, *Labechiellata* based upon *Labechiellata regularis* from the Middle Gotlandian deposits of the Kitakami Mountainland." Although *Labechiellata* has long been considered to be simply a *lapsus memoriae* for the genus *Labechiella* (Galloway, 1957, Flügel and Flügel-Kahler, 1968 and Mori, 1973), the proposal of this new generic name produced further confusion.

Yabe and Sugiyama (1930) in the paper proposing the subgenus *Labechiella*, also

proposed the species *Labechia regularis* from the Ordovician of China. Judging from the gross skeletal structures of the holotype (IGPS coll. cat. no. 37684, monotypic), it does not belong to *Labechia*, but to *Labechiella*, because the horizontal structure is dominantly composed of horizontal cysts. In the genus *Labechiella*, the specific name *regularis* is therefore preoccupied by Sugiyama's (1939) use of the name for the Silurian species. Thus *Labechiella regularis* Sugiyama (1939) became a secondary homonym of *Labechiella regularis* (Yabe and Sugiyama, 1930). To resolve the homonymy, Webby (1979) proposed the new name *Labechiella sugiyamai* for the former (Silurian) species. Through the reexamination of the holotype specimen of *Labechiella sugiyamai* (IGPS coll. cat. no. 50593), however, it became evident that the type specimen is not a stromatoporoid, but a fragment of a rugose coral which was described as *Mazaphyllum mirum* Kato (Kato, 1982, p. 390, pl. 61, figs. 1, 2; text-fig. 1A-C). Both specimens come from exactly the same locality; Higuchizawa, Hikoroichi, Ofunato City, Iwate Prefecture. The rugose coral genus *Mazaphyllum* was first proposed by Crook (1955) and was based on *M. cortisjonesi* from the Silurian of New South Wales. The specimens described by Kato (1982) as a cystiphyllid coral from Japan certainly belong to the same group described by Crook (1955). Therefore, fol-

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lowing the code of nomenclature, it is concluded that (1) *Labechiella sugiyamai* Webby is invalid as a stromatoporoid species, (2) contrary to the previous opinions, the specific name *Labechiellata regularis* is valid and *M. mirum* becomes a junior subjective synonym of the former, and (3) the generic name *Mazaphyllum* is a synonym of *Labechiellata*. Thus it is unfortunate that *Labechiellata*, once proposed as a stromatoporoid genus, must be used as a genus of rugose corals, and that the type specimens of *Labechiellata regularis* comprise a collection of small pieces of the corallum and do not show all the features of a complete cystiphyllid rugose coral.

I thank Professor M. Kato, Hokkaido University and Professor Colin W. Stearn, McGill University, for their comments and reviewing the manuscript.

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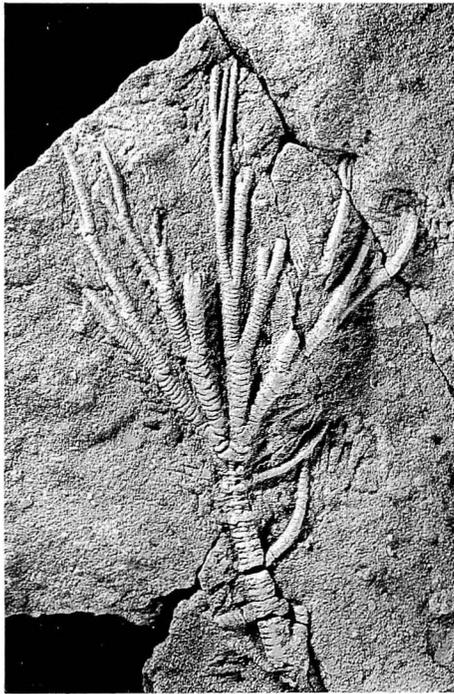
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The calligraphy on the cover for the Japanese title “Nihon Koseibutsu-gakkai Hokoku Kiji” is the work of Dr. Matajiro Yokoyama, a fatherly figure in Japanese paleontology, who was Professor of Stratigraphy and Paleontology at the Geological Institute, Imperial University of Tokyo.

The fossil on the cover is *Isocrinus (Chladocrinus) hanaii* Oji, an Early Cretaceous (Aptian) crinoid, which was described from the Hiraiga Formation exposed at Haipe, Tanohata-mura, Shimo-Hei County, Iwate Prefecture, Northeast Japan. (University Museum of the University of Tokyo coll. cat. no. ME6950, paratype specimen, length about 11 cm).

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行事予定

◎学会創立 60 周年にあたる 1995 年の年会・総会は、1995 年 2 月 2 日～4 日に名古屋大学理学部で開催されます。

1995 年年会総会では、シンポジウム「哺乳類の系統進化研究の現状と将来展望」(世話人：瀬戸口烈司，富田幸光，小澤智生)が予定されています。

◎1995 年例会(第 144 回例会)は、横須賀市自然博物館および横須賀市文化会館で 6 月 24 日，25 日に開催の予定です。講演申込は 4 月 30 日(必着)です。講演申込と予講集原稿の書き方については、「化石」54 号をご覧ください。

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長谷川四郎

森 啓

棚部 一成

石崎 国熙

小笠原憲四郎

富田 幸光

加瀬 友喜

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