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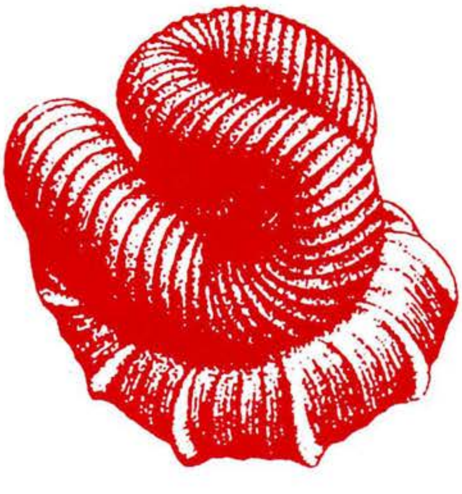

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Cover : Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Conodont faunas across the Mid-Carboniferous boundary in the Hina Limestone, Southwest Japan

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Abstract. The Hina Limestone yields abundant conodont elements that range from early Visean to late Bashkirian in age. These conodont faunas permit detailed examination of the successive changes across the Mid-Carboniferous boundary. Six conodont zones can be recognized in ascending order: the *Gnathodus bilineatus*, *Declinognathodus inaequalis*-*Gnathodus bilineatus*, *Declinognathodus noduliferus*, *Neolochriea nagatoensis*, *Neolochriea koikei*, and *Neognathodus symmetricus* Zones. The Mid-Carboniferous boundary in the Hina Limestone can be identified by the base of the *Declinognathodus inaequalis*-*Gnathodus bilineatus* Zone. A remarkable faunal transition occurs within the *Declinognathodus inaequalis*-*Gnathodus bilineatus* and *Declinognathodus noduliferus* Zones, in which Mississippian conodonts go extinct and several new typical Pennsylvanian taxa appear. Three *Declinognathodus* species, *Declinognathodus inaequalis*, *D. noduliferus*, and *D. japonicus*, successively appear in the order given. A new genus, *Neolochriea*, with *Neolochriea hisaharui*, sp. nov. as the type species and two other new species, *N. hisayoshii* and *N. koikei*, are described in addition to eight other species of conodonts. All *Neolochriea* species occur in the stratigraphic level between the extinction of Mississippian conodonts and the appearance of *Neognathodus symmetricus*.

Key words: Biostratigraphy, conodont, *Declinognathodus*, Hina Limestone, Mid-Carboniferous boundary, *Neolochriea*

Introduction

In the late nineteenth century the Carboniferous System was subdivided into the Mississippian and Pennsylvanian Systems in the United States because of the presence of a sedimentary and faunal gap in the middle part of the Carboniferous in eastern North America. Subsequently, the Mississippian and Pennsylvanian were retained as Subsystems and their mutual boundary designated as the Mid-Carboniferous boundary.

In 1983, the Subcommission on Carboniferous Stratigraphy of the International Union of Geological Sciences approved a recommendation that the Mid-Carboniferous boundary should be placed at the level of the first appearance of the conodont *Declinognathodus noduliferus* in some continuously deposited sequence of rocks. This position coincides approximately with the *Eumorphoceras*-*Homoceras* ammonoid zonal transition (Lane and Manger, 1985). At the instigation of the Subcommission on Carboniferous Stratigraphy, the Mid-Carboniferous Boundary Working Group was organized to select a Mid-Carboniferous boundary stratotype in 1985. The working group has provided much new biostratigraphic information on faunal and floral changes of many marine and terrestrial fossil groups across the Mid-Carboniferous boundary (e.g., Ramsbottom *et al. eds.*, 1982; Lane *et al.*, 1985; Riley *et al.*, 1987; Rui *et al.*, 1987; Wang *et al.*, 1987b; Nemirovskaya, 1987; Nemirovskaya *et al.*, 1990; Varker *et al.*, 1990; Nigmadganov and Nemirovskaya, 1992). In a later decision the Arrow Canyon section in Nevada was selected as the stratotype of the Mid-Carboniferous boundary (Lane *et al.*, 1994; Lane, 1995; Brenckle *et al.*, 1997).

After the first report of Japanese Carboniferous conodonts by Igo and Koike (1964) from the Omi Limestone, many studies on Japanese Carboniferous conodonts have been carried out; these are summarized by Igo (1994). Koike (1967) established a Carboniferous conodont zonation based on faunas from the Atetsu Limestone. This conodont zonation has been used as the standard one in the Japanese Carboniferous. The *Gnathodus bilineatus*-*Declinognathodus noduliferus* Zone of the Atetsu Limestone is unique, because typical "Mississippian" taxa co-occur with "Pennsylvanian" species. Koike (1967) correlated this zone to the uppermost Chesterian of North America and the lower Namurian of Europe. However, *Gnathodus bilineatus* and *Declinognathodus noduliferus* have never been found together within the same stratigraphic level in Europe and North America. Therefore, the geological age assignment of the *Gnathodus bilineatus*-*Declinognathodus noduliferus* Zone of the Atetsu Limestone has been questioned by

European and North American conodont researchers (Webster, 1969 ; Lane and Straka, 1974 ; Higgins, 1975).

However, this conodont assemblage, recognized in the Atetsu Limestone, has been described not only from Japan (Haikawa, 1988) but also in Malaysia (Igo and Koike, 1968 ; Metcalfe, 1980) and China (Wang *et al*., 1987b). Haikawa (1988) suggested that *Lochriea commutata* and *Declinognathodus noduliferus* co-occurred in the Uzura Quarry in the

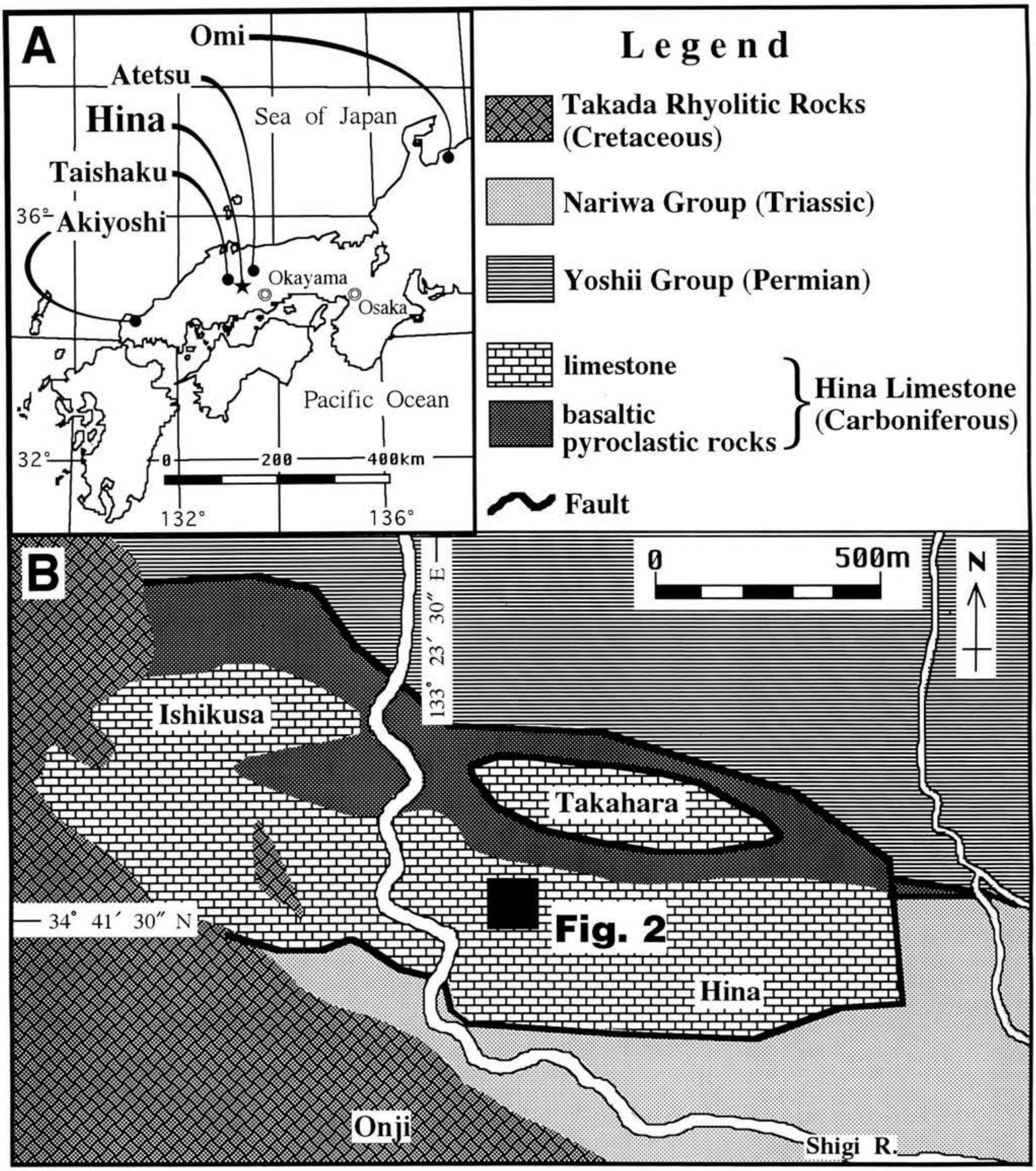


Figure 1. Location map of Hina in southwest Japan (A), and geological map of the Hina Limestone (B).

western part of the Akiyoshi Plateau although details of the stratigraphic relationship between them were not given. Up to the present, students of the Japanese Carboniferous have been uncertain about the details of the conodont faunal changes across the Mid-Carboniferous boundary.

In order to resolve this uncertainty, I have restudied the conodont faunal successions in the Akiyoshi, Omi, Atetsu, Taishaku, and Hina Limestones, all of which are exposed as isolated plateaus in the Inner Zone of southwest Japan (Figure 1-A). These consist mainly of pure, massive limestones that conformably overlie alkaline basalt flows or volcaniclastic rocks. This volcanic-limestone succession is interpreted to be a carbonate reef complex that formed on an oceanic seamount in Panthalassa during Late Paleozoic time (Kanmera and Nishi, 1983; Sano and Kanmera, 1988).

Recently, I discovered a new section of the Hina Limestone, in which the conodont faunas and the biostratigraphic succession across the Mid-Carboniferous boundary are excellently preserved. The present paper aims (1) to describe in detail the conodont succession and to propose a new conodont zonation across the Mid-Carboniferous boundary for the Hina Limestone, (2) to correlate these zones with those of other Japanese limestone untis, namely the Atetsu and Akiyoshi Limestones, with the important Mid-Carboniferous boundary section at Arrow Canyon, and also with the Stonehead Beck, Aksu-I, Zhelvakovaya Valley, and Luosu sections, and (3) to discuss the conodont faunas across the Mid-Carboniferous boundary in the Japanese Carboniferous.

Geologic setting

The Hina Limestone, located in the western part of Okayama prefecture, is a Carboniferous limestone mass in the Inner Zone of southwest Japan. The limestone and associated basaltic pyroclastic rocks are exposed over 2 km in an east-west direction and 0.8 km in a north-south direction. This limestone is overthrust the Permian Yoshii and Triassic Nariwa Groups and forms a klippe (Sada *et al.*, 1979).

Hase and Yokoyama (1975) subdivided the Hina Limestone into four foraminiferal zones, in ascending order, the *Endothyra, Eostaffella-Millerella, Pseudostaffella*, and *Profusulinella* Zones. They also reported some brachiopods from this

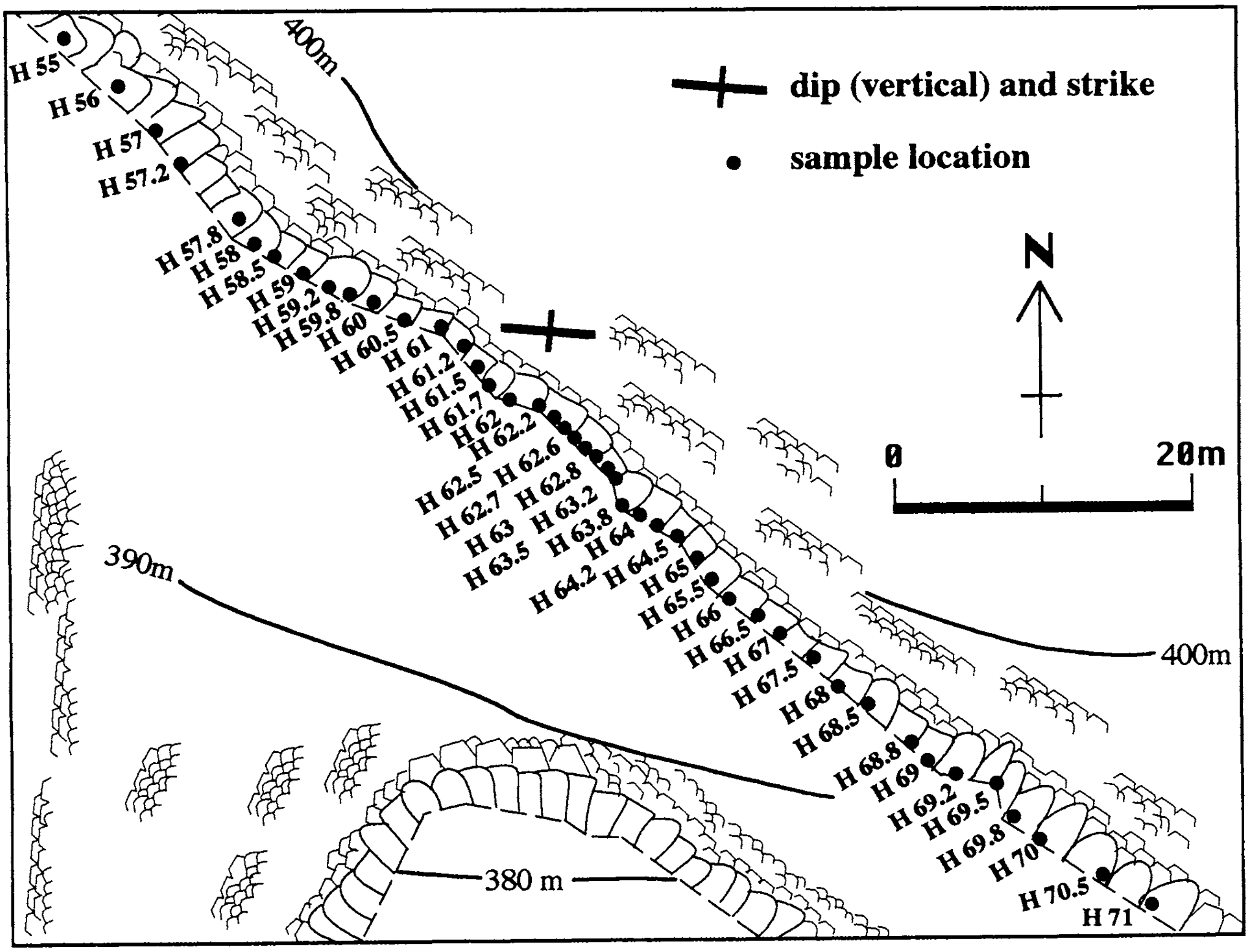


Figure 2. Sampling points in the examined section of the Hina Limestone.

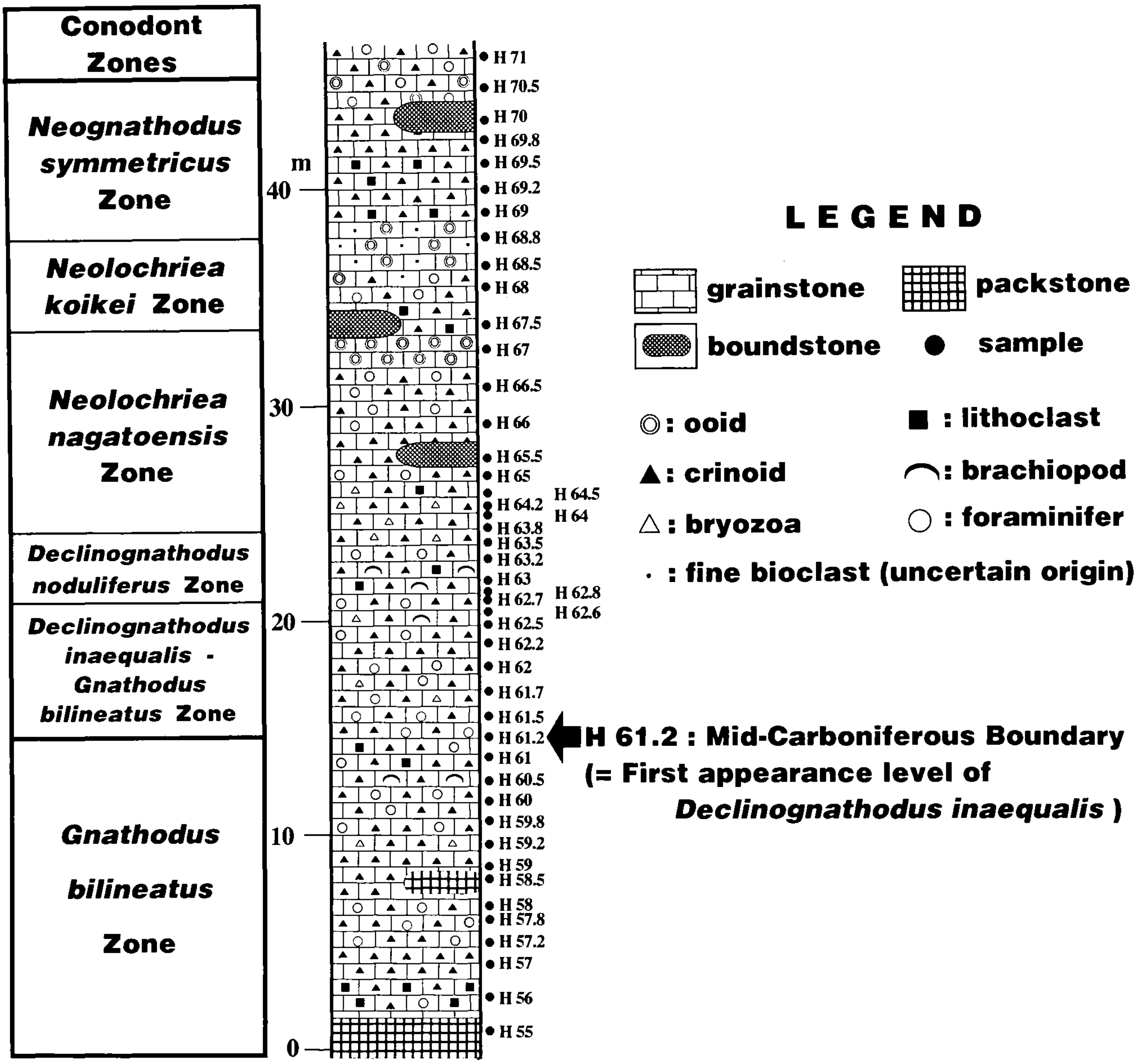


Figure 3. Geologic column of the measured section with indications of sampling levels and conodont zones established in this paper. The proposed Mid-Carboniferous boundary position (H 61.2) defined by the first appearance of *Declinognathodus inaequalis*.

limestone and assigned the *Endothyra* and *Eostaffella-Millerella* Zones to the early and late Visean of the European standard, respectively. Recently, Fujimoto and Sada (1994) studied the foraminiferal biostratigraphy of the Hina Limestone. However, the Mid-Carboniferous boundary in this limestone still remained ambiguous.

The measured limestone section in this study crops out in an abandoned limestone quarry of Kokan Kogyo Co., Ltd. in the eastern part of the Hina Limestone, Takahara area, and is about 50 m thick (Figures 1-B and 2). It corresponds to the middle part of the *Eostaffella-Millerella* Zone of Hase and Yokoyama (1975). The measured section represents a continuous succession composed mainly of massive, pure, shallow-marine limestones (Figure 3). Bioclastic (crinoidal-foraminiferal-bryozoan) grainstone predominates, with subordinate amounts of bioclastic packstone, oolitic grainstone, crinoidal-lithoclastic grainstone, and algal-coral boundstone. No distinctive physical breaks were observed in the section, and conodonts were obtained from most samples.

Conodont biostratigraphy

As shown in Figure 2, 45 samples were collected systematically for conodonts. I processed 2 to 5 kg of limestone

Table 1. Distribution of conodonts in the measured section of the Hina Limestone. Numerals show the number of conodont specimens per 1 kg limestone sample. Generic abbreviations : *D.-Declinognathodus, G.-Gnathodus, N.-Neolochriea.*

SAMPLE **TAXA**	H 55	H 56	H 57	H 57.2	H 57.8	H 58	H 58.5	H 59	H 59.2	H 59.8	H 60	H 60.5	H 61	H 61.2	H 61.5	H 61.7	H 62	H 62.2	H 62.5	H 62.6	H 62.7	H 62.8	H 63	H 63.2	H 63.5	H 63.8	H 64	H 64.2	H 64.5	H 65	H 65.5	H 66	H 66.5	H 67	H 67.5	H 68	H 68.5	H 68.8	H 69	H 69.2	H 69.5	H 69.8	H 70	H 70.5	H 71
Gnathodus bilineatus			2	11	8	5	6	3	9	2	17	6	1	2	1	2	1	5	1																										
Vogelgnathus campbelli				1							1	2			1																														
Vogelgnathus akiyoshiensis		1	1	1	1			1	3	1	1	2																																	
Cavusgnathus unicornis		1	1	5		1	6		1	2	2		2	1	1		1																												
***Cavusgnathus* sp. indet.**				2	1		2		1	2				1		1																													
Hindeodus minutus							2	2	2	2	2	1	1	1		1	1	1			1				1		1	1	1						1		1	1							
Declinognathodus inaequalis														1			1	4	1	1	8	5	4	4								2													
Declinognathodus noduliferus																					1	3	6	8	11	3	1			1		3	1												
Declinognathodus japonicus																								2	8	6	2			1		4		1	1	3	1	2	1			7	2	2	2
Lochriea commutata		1	4	4	3	3	3		1		2							1	1		5	7	4																						
Lochriea nodosa														1																															
Neolochriea nagatoensis																										16	21	3					1												
***Neolochliea hisayoshii* sp. nov.**																													4	1		1													
***Neolochriea hisaharui* sp. nov.**																															20		3												
***Neolochriea koikei* sp. nov.**																																			1		1	1	1			1			2
Neognathodus symmetricus																																						1	1				1	1	1
Conodont Zone	***Gnathodus bilineatus* Zone**													***D. inaequalis - G. bilineatus* Zone**							***D. noduliferus* Zone**					***Neolochriea nagatoensis* Zone**									***N. koikei* Zone**			***Neognathodus symmetricus* Zone**							

from each level in the measured section. A total of 16 conodont species were identified. Table 1 shows the distribution of conodonts in the measured section and the number of conodont elements extracted per 1 kg of limestone sample.

Based on the first appearance of biostratigraphically significant species, the following six conodont zones were established across the Mid-Carboniferous boundary for the Hina Limestone in ascending order: the *Gnathodus bilineatus, Declinognathodus inaequalis-Gnathodus bilineatus, Declinognathodus noduliferus, Neolochriea nagatoensis, Neolochriea koikei*, and *Neognathodus symmetricus* Zones.

The *Gnathodus bilineatus* Zone is the lowest conodont zone in the measured section and is at least 15 m thick (sample no. H 55-H 61.2). Typical Mississippian conodonts, including *Gnathodus bilineatus*, *Lochriea commutata, Vogelgnathus campbelli* (Figure 11-7), *V. akiyoshiensis* (Figure 11-6), and *Cavusgnathus unicornis* (Figure 11-4a, b) occur characteristically from this zone. Except for *V. akiyoshiensis*, which disappears at the upper part of this zone (H 60.5 level), all the species survive into the overlying zone. *L. commutata* is common in the lower part of this zone.

The *Declinognathodus inaequalis-Gnathodus bilineatus* Zone is 6 m thick (H 61.2-H 62.7). Its base is defined by the first appearance of *Declinognathodus inaequalis* and the top is defined by the first appearance of *D. noduliferus*. The conodont assemblage of this zone is characterized by the co-occurrence of typical "Mississippian" species with the "Pennsylvanian" species *D. inaequalis*. Except for *Lochriea commutata*, most of the "Mississippian" conodonts become extinct in this zone. *L. nodosa* was obtained only from the H 61.2 level, at the base of this zone.

The *Declinognathodus noduliferus* Zone is about 4 m thick (H 62.7-H 63.8). Its base is defined by the first appearance of *Declinognathodus noduliferus* and the upper limit is defined by the first appearance of *Neolochriea nagatoensis. Lochriea commutata* is still found in this zone (H 62.7, H 62.8, and H 63). *D. inaequalis* occurs together with the nominate species through this zone. On the other hand, *D. japonicus* first appears in the upper part of this zone (H 63.2).

The *Neolochriea nagatoensis* Zone is 9 m thick (H 63.8-H 67.5). It is defined as the stratigraphic interval between the first appearances of *Neolochriea nagatoensis* and *N. koikei* sp. nov.; the latter is the defining species of the overlying zone. The conodont fauna of this zone is characterized by the occurrence of *Neolochriea* gen. nov. *N. nagatoensis*, which occurs abundantly from the H 63.8 and H 64 levels, is also found from H 64.2 and H 66.5. *N. hisayoshii* sp. nov. first appears from H 64.5 and is found up to H 66. *N. hisaharui* sp. nov. occurs abundantly in H 65.5 and is found up to H 66.5. These three *Neolochriea* species have short stratigraphic ranges in comparison with other conodonts in the Hina Limestone.

In addition to the index species, *Declinognathodus inaequalis, D. noduliferus, D. japonicus, N. hisayoshii* sp. nov., and *N. hisaharui* sp. nov. occur from the *Neolochriea nagatoensis* Zone. *D. inaequalis* is very rare and occurs only from H 66. *D. noduliferus* occurs up to the H 66.5 level in this zone. In contrast to other *Declinognathodus* species, *D. japonicus* occurs commonly throughout this zone.

The *Neolochriea koikei* Zone is 5 m thick (H 67.5-H 68.8). Its base is marked by the first appearance of *Neolochriea koikei* sp. nov. In addition to the index species, *Hindeodus minutus* and *Declinognathodus japonicus* occur from this zone. *D. inaequalis* and *D. noduliferus* were not recovered from this zone.

The *Neognathodus symmetricus* Zone is the uppermost conodont zone in the measured section and is at least 8 m in thickness (H 68.8 and higher). The lower limit is defined

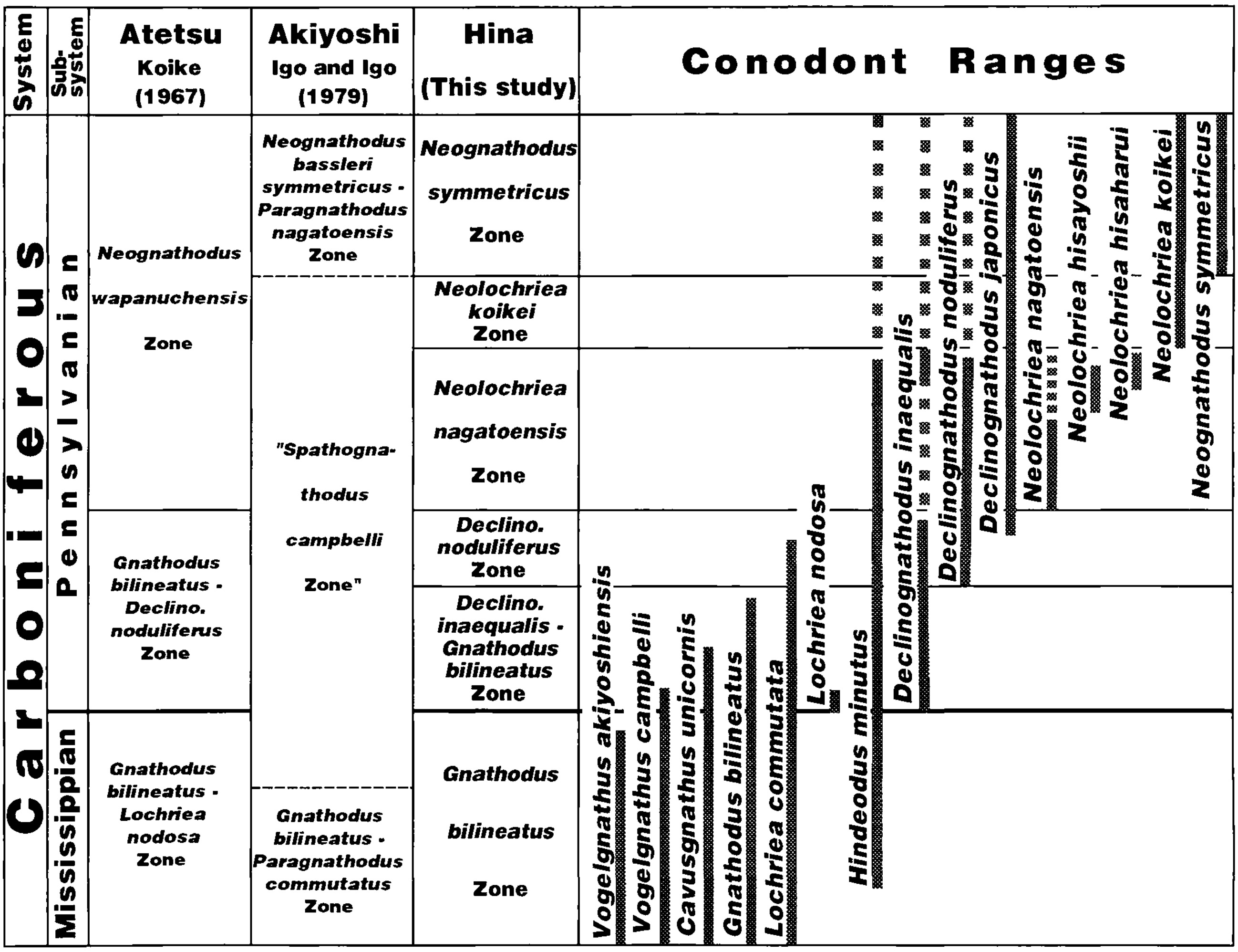


Figure 4. Range chart of conodont species in the measured section of the Hina Limestone. Generic abbreviation : *Declino.-Declinognathodus*.

by the first appearance of *Neognathodus symmetricus*, a well-known index species for the lower Bashkirian. *Declinognathodus japonicus* and *Neolochriea koikei* sp. nov. occur in this zone and are also found from stratigraphically higher levels in the measured section.

Correlation with Japanese Limestone

1. Atetsu Limestone

Koike (1967) established seven Carboniferous conodont zones in the Nagoe and Kodani Formations of the Atetsu Limestone. Recently, some of the zones were revised by Igo (1994). According to him, three conodont zones across the Mid-Carboniferous boundary are recognized in ascending order (Figure 4).

(1) *Gnathodus bilineatus-Lochriea nodosa* Zone

This zone is characterized by *Gnathodus bilineatus, Lochriea commutata, L. nodosa*, and *Vogelgnathus campbelli*, typical Mississippian conodont species. Except for the presence of *L. nodosa*, this fauna is almost the same as the conodont fauna of the *Gnathodus bilineatus* Zone in the Hina Limestone. *L. nodosa* is very rare in the Hina Limestone and was not obtained from the *G. bilineatus* Zone.

(2) *Gnathodus bilineatus-Declinognathodus noduliferus* Zone

Declinognathodus noduliferus first appears from the base of this zone in association with Mississippian conodonts. The specimen assigned to *Gnathodus nodulifera* by Koike (1967, pl. 3, fig. 10) has four distinctive outer nodes and can be included in *D. inaequalis*. Therefore, this zone in the Atetsu Limestone can be correlated with the *Declinognathodus inaequalis-Gnathodus bilineatus* Zone in the Hina Limestone.

(3) *Neognathodus wapanuckensis* Zone

This zone is defined by the total range of *Neognathodus wapanuckensis*. *Declinognathodus noduliferus, Paragnathodus ? nagatoensis* and other taxa are also abundant in the *Neognathodus wapanuckensis* Zone (Igo, 1994, p. 101). However, *N. wapanuckensis* was not reported from the lower part of this zone in the Atetsu Limestone (e.g., Koike, 1967, localities 37a, 38, 40, 123, 124). At these localities, *D. noduliferus* and *P. ? nagatoensis* occur abundantly and

Mississippian conodonts become extinct below this zone. *P.* ? *nagatoensis* can be assigned to *Neolochriea* spp. including *N. nagatoensis* in the Hina Limestone. Therefore, the *N. wapanuckensis* Zone in the Atetsu Limestone can be correlated with the *Neolochriea nagatoensis* to *N. symmetricus* Zones in the Hina Limestone.

2. Akiyoshi Limestone

Igo and Igo (1979) established the following three conodont zones across the Mid-Carboniferous boundary in the lower part of the Akiyoshi Limestone (Figure 4). Besides this, Haikawa (1988) established five Lower Carboniferous conodont zones below the Mid-Carboniferous boundary.

(1) *Gnathodus bilineatus-Paragnathodus commutatus* Zone

This zone includes the *Gnathodus bilineatus-Cavusgnathus charactus* Zone and *Lochriea nodosa* Zone by Haikawa (1988). It is characterized by typical Mississippian conodonts and can be correlated with the *G. bilineatus* Zone in the Hina Limestone.

(2) "*Spathognathodus campbelli* Zone"

This zone was established in the Shishidedai area in the northeastern part of the Akiyoshi Limestone Plateau (Igo and Igo, 1979). *Vogelgnathus campbelli* [=*Spathognathodus campbelli* in Igo and Igo, 1979] is particularly abundant and ranges up to the uppermost part of this zone, whereas *V. akiyoshiensis* disappears in the lower part of this zone. In the Akiyoshi Limestone this zone cannot be determined exactly because the occurrence of conodonts is rare.

(3) *Neognathodus bassleri symmetricus-Paragnathodus nagatoensis* Zone

This zone was established in the Uzura quarry in the western part of the Akiyoshi Limestone Plateau (Igo and Igo, 1979). *Neognathodus bassleri symmetricus* [=*Neognathodus symmetricus*], *Paragnathodus nagatoensis*, *Idiognathoides opimus*, and *Hindeodus minutus* are found in this zone. Based on the occurrence of *Lochriea commutata* and *Declinognathodus noduliferus* Haikawa (1988) supposed an earliest Pennsylvanian age for the quarry. However, the exact stratigraphic levels of *L. commutata*, *D. noduliferus*, and *N. symmetricus* have not been made clear in the Uzura quarry. Using the occurrence of *N. symmetricus*, this zone can be correlated with the *Neognathodus symmetricus* Zone in the Hina Limestone. Further investigation, however, will be necessary to settle the detailed correlation of conodont zones between the Akiyoshi Limestone and the Hina Limestone.

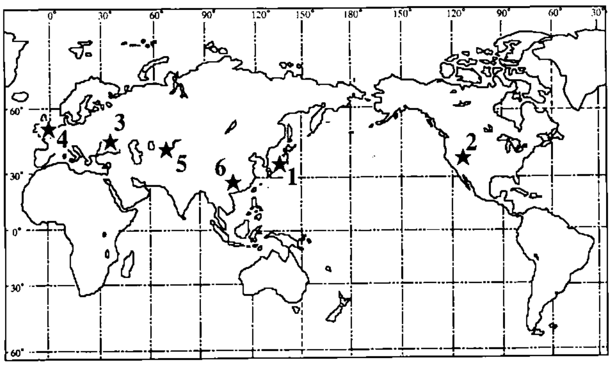


Figure 5. Map showing important localities of the Mid-Carboniferous boundary sections: 1. Hina Limestone (Japan), 2. Arrow Canyon section (U.S.A.), 3. Donets Basin (Ukraine), 4. Stonehead Beck section (England), 5. Aksu-I section (Uzbekistan), 6. Luosu section (China).

International correlation

1. Arrow Canyon section (U.S.A.)

This section is located in the Arrow Canyon Range about 80 km northeast of Las Vegas, Nevada. Recently, this section was selected as boundary stratotype of the Mid-Carboniferous boundary because of the complete exposure of marine deposits across the boundary (Lane, 1995; Brenckle *et al.*, 1997). According to Baesemann and Lane (1985), four conodont zones across the Mid-Carboniferous boundary are recognized in the ascending order (Figure 6).

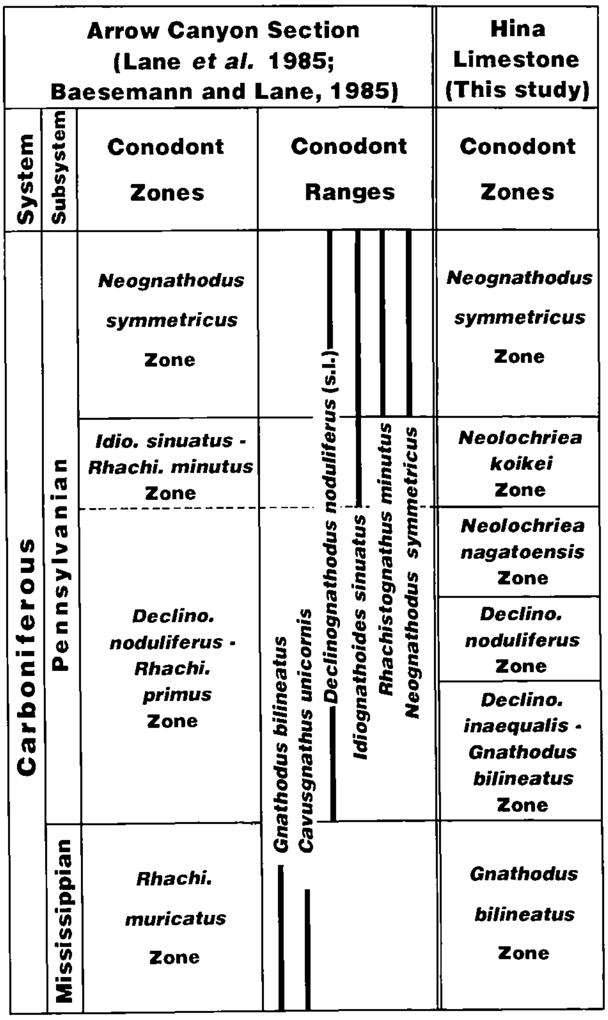


Figure 6. Range chart of conodont species in the Arrow Canyon section and comparison with the Hina Limestone. Generic abbreviations: *Declino.*-*Declinognathodus*, *Idio.*-*Idiognathoides*, *Rhachi.*-*Rhachistognathus*.

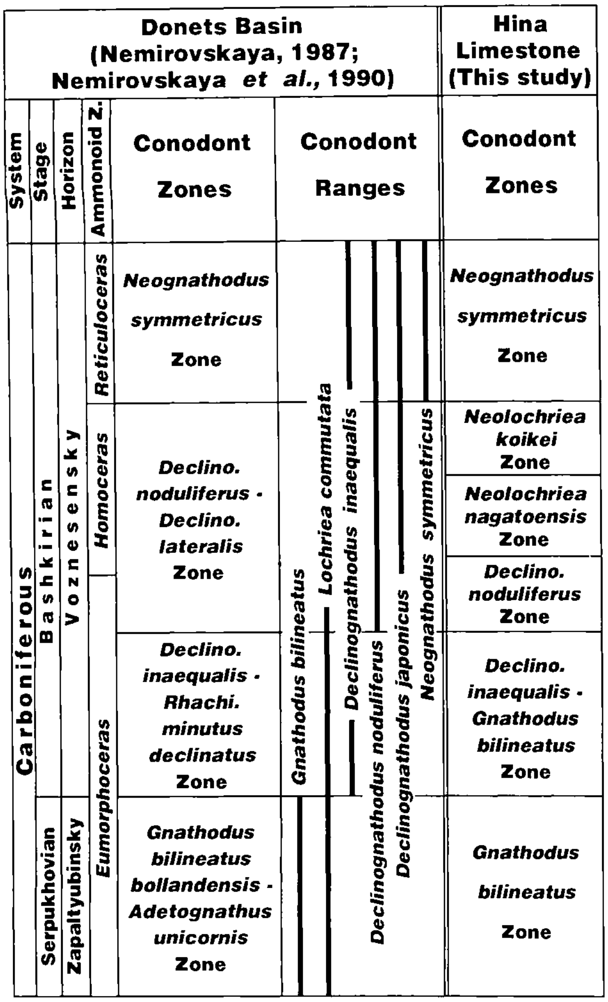


Figure 7. Range chart of conodont species in the Donets Basin and comparison with the Hina Limestone. Generic abbreviations: *Declino.*-*Declinognathodus*, *Rhachi.*-*Rhachistognathus*.

(1) *Rhachistognathus muricatus* Zone

This zone is the latest Mississippian conodont zone in the Arrow Canyon section. In addition to the index species, *Gnathodus bilineatus* and *Cavusgnathus unicornis* are found. Therefore, this zone is correlated with the *Gnathodus bilineatus* Zone in the Hina Limestone.

(2) *Declinognathodus noduliferus*-*Rhachistognathus primus* Zone

The Mid-Carboniferous boundary is placed at the base of this zone (61B level) where *Declinognathodus noduliferus* (s.l.) first appears (Brenckle *et al.*, 1997). The specimens of *D. noduliferus* (s.l.) obtained from Sample 61B and Sample 62 are illustrated in Brenckle *et al.* (1997, pl. 1, figures 2-4). However, these are quite similar to *D. inaequalis*. Using the first appearance of *D. inaequalis*, the lower part of this zone can be correlated with the *Declinognathodus inaequalis*-*Gnathodus bilineatus* Zone in the Hina Limestone.

(3) *Idiognathoides sinuatus*-*Rhachistognathus minutus* Zone

The base of this zone is defined by the first appearance of *Idiognathoides sinuatus*. As *I. sinuatus* and *Rhachistognathus minutus* have not been found in the Hina Limestone, this zone could not be recognized in it. The equivalent stratigraphic interval of the *Declinognathodus noduliferus*, *Neolochriea nagatoensis*, and *Neolochriea koikei* Zones in the Hina Limestone may correspond to the *D. noduliferus*-*Rhachistognathus primus* plus *Idiognathoides sinuatus*-*R. minutus* Zones in the Arrow Canyon section.

(4) *Neognathodus symmetricus* Zone

The lower limit of this zone is defined by the first appearance of *Neognathodus symmetricus*. Therefore, the base of this zone is referable to the base of the same zone in the Hina Limestone.

2. Donets Basin (Ukraine)

Nemirovskaya *et al.* (1990) proposed the Zhelvakovaya Valley section along the Kal'mius River in the Donets Basin for the Mid-Carboniferous boundary stratotype. This section is also the stratotype of the Zapaltyubinsky Horizon (uppermost Serpukhovian Stage) and of the Voznesensky Horizon (lowermost Bashkirian Stage). The conodont zones across the Mid-Carboniferous boundary in this section are as follows (Figure 7). The conodont fauna observed in the Zhelvakovaya Valley section is quite similar to that observed in the Hina Limestone.

(1) *Gnathodus bilineatus bollandensis*-*Adetognathus unicornis* Zone

This zone is characterized by typical Mississippian conodont species. Except for *Lochriea commutata*, the "Mississippian" conodonts are restricted to this zone. Therefore, this zone can be correlated with the *Gnathodus bilineatus* Zone in the Hina Limestone.

(2) *Declinognathodus inaequalis*-*Rhachistognathus minutus declinatus* Zone

The Mid-Carboniferous boundary is placed at the base of this zone where *Declinognathodus inaequalis* first appears in the Donets Basin. Using the first appearance of *D. inaequalis*, this zone can be correlated with the *Declinognathodus inaequalis*-*Gnathodus bilineatus* Zone in the Hina Limestone.

(3) *Declinognathodus noduliferus*-*Declinognathodus lateralis* Zone

The base of this zone is defined by the first appearance of *Declinognathodus noduliferus*. *Lochriea commutata* ranges up to this zone. The first appearance datum of *D. japonicus* is found in this zone. Therefore, this zone can be correlated with the *Declinognathodus noduliferus* Zone in the Hina Limestone.

(4) *Neognathodus symmetricus* Zone

In the Donets Basin, *Neognathodus symmetricus* first appears with *Reticuloceras* from the base of this zone (Nemirovskaya, 1987). Because of the occurrence of *N. symmetricus*, this zone can be correlated with the same zone in the Hina Limestone.

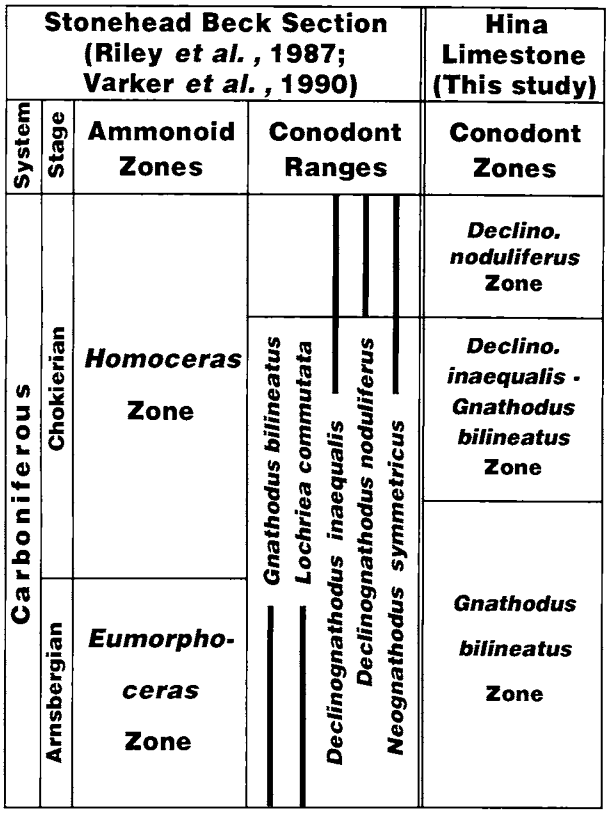


Figure 8. Range chart of conodont species in the Stonehead Beck section and comparison with the Hina Limestone. Generic abbreviation: *Declino.*-*Dèclinognathodus*.

3. Stonehead Beck section (England)

The Stonehead Beck section is located in the Craven Basin at the northwestern end of the Pendle Monocline, about 35 km west-northwest of Leeds, England. This section covers the *Eumorphoceras* Zone (Arnsbergian Stage) and the *Homoceras* Zone (Chokierian Stage) (Varker *et al.*, 1990). Riley *et al.* (1987) and Varker *et al.* (1990) reported the distribution of ammonoids, conodonts, and miospores in the Stonehead Beck section, however, conodont recovery has been poor in the strata across the Arnsbergian/Chokierian boundary (Figure 8).

(1) *Eumorphoceras* Zone

Mississippian conodonts are restricted in the *Eumorphoceras* Zone in the Stonehead Beck section. Therefore, this zone almost corresponds to the *Gnathodus bilineatus* Zone in the Hina Limestone.

(2) *Homoceras* Zone

Neognathodus symmetricus appears together with *Declinognathodus inaequalis* from 9.4 m above the base of this zone. After their appearance, *D. noduliferus* first appears from 9.8 m above the base of this zone (Figure 8). *D. japonicus* has not been found in the Stonehead Beck section.

Neognathodus symmetricus occurs with *Declinognathodus japonicus* from the *Reticuloceras* Zone in the Donets Basin (Figure 7) (Nemirovskaya, 1987). On the other hand, in England *D. japonicus* first appears at the base of the Alportian Stage (upper *Homoceras* Zone) and is abundant at the Marsdenian Stage (*Reticuloceras* Zone) in the Namurian of the Central Province (Higgins, 1975). Therefore, *N. symmetricus* might appear earlier in the Stonehead Beck section than in the Donets Basin.

Because of the first appearance of *Declinognathodus noduliferus* and the absence of *D. japonicus*, the lower part of the *Declinognathodus noduliferus* Zone in the Hina Limestone can be correlated with the *Homoceras* Zone in the Stonehead Beck section. The equivalent stratigraphic level of the *D. inaequalis*-*Gnathodus bilineatus* Zone in the Hina Limestone may correspond to the stratigraphic level up to the first occurrence of *D. noduliferus* in the Stonehead Beck section.

4. Aksu-I section (Uzbekistan)

The Aksu-I section is located at the south point of the Surkhantau Ridge, which belongs to the southwestern part of the Gissar Ridge, South Tienshan, Uzbekistan. The Aksu-I section represents deep-water deposits across the Mid-Carboniferous boundary and five conodont zones are recog-

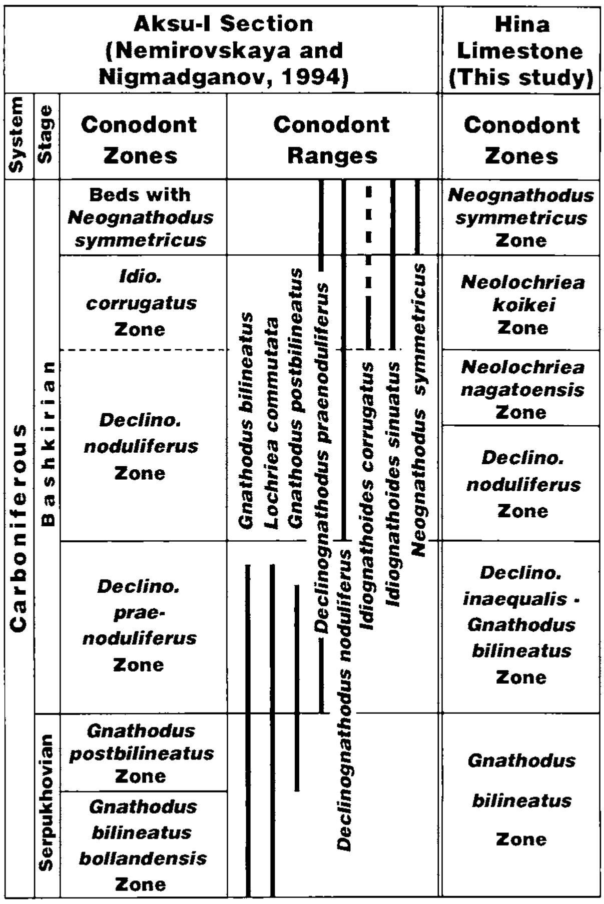


Figure 9. Range chart of conodont species in the Aksu-I section and comparison with the Hina Limestone. Generic abbreviations: *Declino.*-*Declinognathodus*, *Idio.*-*Idiognathoides*.

nized (Figure 9) (Nemirovskaya and Nigmadganov, 1994).

(1) *Gnathodus bilineatus bollandensis* Zone

(2) *Gnathodus postbilineatus* Zone

These two zones are characterized by Mississippian conodont species. Therefore, these zones can be correlated with the *Gnathodus bilineatus* Zone in the Hina Limestone.

(3) *Declinognathodus praenoduliferus* Zone

Nemirovskaya and Nigmadganov (1994) defined the Mid-Carboniferous boundary as lying at the base of this zone. They considered that *Declinognathodus praenoduliferus* phylogenetically arose from *Gnathodus bilineatus* and is the first representative of *D. noduliferus* (s.l.). They considered also that this species is the index of the Mid-Carboniferous boundary (oral communication with Nemirovskaya, 1996). A few Mississippian conodonts including *Gnathodus bilineatus* and *Lochriea commutata* range up to the uppermost level of this Zone. Therefore, this zone can be correlated with the *Declinognathodus inaequalis*-*Gnathodus bilineatus* Zone in the Hina Limestone.

(4) *Declinognathodus noduliferus* Zone

The base of this zone is defined by the first appearance of *Declinognathodus noduliferus*. Therefore, the base of this zone is referable to the base of the same zone in the Hina Limestone.

(5) *Idiognathoides corrugatus* Zone

Idiognathoides corrugatus and *I. sinuatus* occur before the appearance of *Neognathodus symmetricus* in the Aksu-I section. This zone could not be recognized in the Hina Limestone. However, *I. sinuatus* appears earlier than *Neognathodus symmetricus* as shown in the Arrow Canyon section (Baesemann and Lane, 1985). Accordingly, the equivalent stratigraphic interval of the *Declinognathodus noduliferus, Neolochriea nagatoensis*, and *N. koikei* Zones in the Hina Limestone may correspond to *D. noduliferus* plus *Idiognathoides corrugatus* Zone in the Aksu-I section.

5. Luosu section (China)

The Luosu section, which ranges from early Carboniferous (Tatangian Stage) to early Permian (Chihsian Stage), is exposed along the Wangmo-Luodian highway, located about 7 km southwest of Luosu, southern Guizhou Province, south China. Many conodont elements have been reported in this section (e.g., Rui *et al.*, 1987 ; Wang *et al.*, 1987b ; Wang and Higgins, 1989). According to Wang *et al.*, (1987b), the conodont zones across the Mid-Carboniferous boundary in the Luosu section are as follows (Figure 10).

(1) *Gnathodus bilineatus bollandensis* Zone

This zone in the Luosu section is correlated to the *Gnathodus bilineatus* Zone in the Hina Limestone.

(2) *Declinognathodus noduliferus* Zone

Wang *et al.* (1987b) defined the base of this zone as the Mid-Carboniferous boundary. In the Luosu section, Mississippian and Pennsylvanian conodonts co-occur obviously in this zone. On the other hand, they co-occur in the same or lower horizons (*Declinognathodus inaequalis*-*Gnathodus bilineatus* Zone) in the Hina Limestone. Following the proposal of the Madrid Congress in 1983 (Lane and Manger, 1985), the Mid-Carboniferous boundary in the Luosu section can be correlated to the base of the *D. inaequalis*-*G. bilineatus* Zone in the Hina Limestone. However, there is another possibility, namely, that the Mid-Carboniferous boundary exists below the base of the *D. noduliferus* Zone in the Luosu section. This is because *D. inaequalis* was found very rarely in the Luosu section. This species was obtained only from the *Idiognathoides sulcatus*-*I. corrugatus*-*I. sinuatus* Zone.

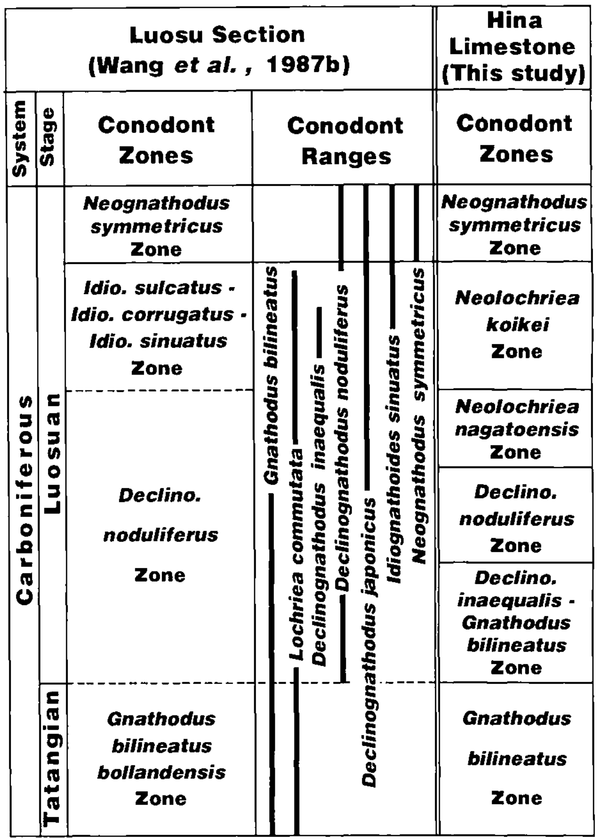


Figure 10. Range chart of conodont species in the Luosu section and comparison with the Hina Limestone. Generic abbreviations : *Declino.*-*Declinognathodus, Idio.*-*Idiognathoides.*

(3) *Idiognathoides sulcatus*-*I. corrugatus*-*I. sinuatus* Zone

Based on the occurrence of *Idiognathoides sinuatus*, the equivalent stratigraphic level of this zone may be below the *Neognathodus symmetricus* Zone in the Hina Limestone.

(4) *Neognathodus symmetricus* Zones

This zone in the Luosu section is correlated to the same zone in the Hina Limestone.

Discussion

1. Notes on Mid-Carboniferous boundary

Table 2 shows the international correlation of conodont zones in the Hina Limestone across the Mid-Carboniferous boundary. As shown above, the *Declinognathodus* species are the most important elements in defining the Mid-Carboniferous boundary in each section.

Table 2. Correlation of conodont zones established in the Hina Limestone with those in five important sections of the Mid-Carboniferous boundary. Generic abbreviations: *Declino.-Declinognathodus, I.-Idiognathoides, Rhachi.-Rhachistognathus*.

<table>
<tr><th rowspan="2"></th><th rowspan="2" colspan="2">U.S.A.</th><th rowspan="2">Western Europe</th><th rowspan="2">Eastern Europe</th><th>U. S. A.
Arrow Canyon Section
Lane *et al.* (1985)
Baesemann & Lane (1985)</th><th>ENGLAND
Stonehead Beck Section
Riley *et al.* (1987)
Varker *et al.* (1990)</th><th>UKRAINE
Donets Basin
Nemirovskaya (1987)
Nemirovskaya *et al.* (1990)</th><th>UZBEKISTAN
Aksu-I Section
Nemirovskaya & Nigmadganov (1994)</th><th>CHINA
Luosu Section
Wang *et al.* (1987b)</th><th>JAPAN
Hina Limestone
(This Study)</th></tr>
<tr><th>Conodont Zones</th><th>Ammonoid Zones</th><th>Conodont Zones</th><th>Conodont Zones</th><th>Conodont Zones</th><th>Conodont Zones</th></tr>
<tr><td rowspan="7">Carboniferous</td><td rowspan="5">Pennsylvanian</td><td rowspan="5">Morrowan</td><td>Kinderscoutian</td><td rowspan="5">Bashkirian</td><td>*Neognathodus symmetricus* Zone</td><td></td><td>*Neognathodus symmetricus* Zone</td><td>Beds with *Neognathodus symmetricus*</td><td>*Neognathodus symmetricus* Zone</td><td>*Neognathodus symmetricus* Zone</td></tr>
<tr><td rowspan="2">Alportian</td><td>*I. sinuatus - Rhachi. minutus* Zone</td><td rowspan="5">*Homoceras* Zone</td><td rowspan="3">*Declino. noduliferus - Declino. lateralis* Zone</td><td>*I. corrugatus* Zone</td><td>*I. sulcatus - I. corrugatus - I. sinuatus* Zone</td><td>*Neolochriea koikei* Zone</td></tr>
<tr><td rowspan="3">*Declino. noduliferus - Rhachi. primus* Zone</td><td rowspan="2">*Declino. noduliferus* Zone</td><td rowspan="3">*Declino. noduliferus* Zone</td><td>*Neolochriea nagatoensis* Zone</td></tr>
<tr><td rowspan="3">Chokierian</td><td>*Declino. noduliferus* Zone</td></tr>
<tr><td>*Declino. inaequalis - Rhachi. minutus declinatus* Zone</td><td>*Declino. praenoduliferus* Zone</td><td>*Declino. inaequalis - Gnathodus bilineatus* Zone</td></tr>
<tr><td rowspan="2">Mississippian</td><td rowspan="2">Chesterian</td><td rowspan="2">Serpukhovian</td><td rowspan="2">*Rhachi. muricatus* Zone</td><td rowspan="2">*Gnathodus bilineatus bollandensis - Adetognathus unicornis* Zone</td><td>*Gnathodus postbilineatus* Zone</td><td rowspan="2">*Gnathodus bilineatus bollandensis* Zone</td><td rowspan="2">*Gnathodus bilineatus* Zone</td></tr>
<tr><td>Arnsbergian</td><td>*Eumorphoceras* Zone</td><td>*Gnathodus bilineatus bollandensis* Zone</td></tr>
</table>

Higgins (1975) subdivided *Declinognathodus noduliferus* into three subspecies, *Idiognathoides noduliferus inaequalis*, *I. n. noduliferus* (s.s.), and *I. n. japonicus*. He showed that these subspecies form a transition series characterized by the reduction of the nodes of the outer lateral platform. It has been considered that *I. n. inaequalis* and *I. n. noduliferus* appear together from the same stratigraphic level.

In the Hina Limestone, *Declinognathodus inaequalis, D. noduliferus* and *D. japonicus* appear successively from the H 61.2, H 62.7, and H 63.2 levels, respectively (Table 1 and Figure 4). It is evident that these species appear successively not only in the Hina Limestone but also in the Zhelvakovaya Valley section of the Donets Basin (Figure 7). Therefore, I treat these three subspecies as independent species because of their different form and different stratigraphic appearance.

At the 13th International Congress on Carboniferous-Permian, Mizuno and Ueno (1995) proposed placing the Mid-Carboniferous boundary at the base of *Declinognathodus noduliferus* Zone (H 62.7 level) in the Hina Limestone because the Mid-Carboniferous boundary should be defined as the first appearance datum of *Declinognathodus noduliferus* (s.s.). However, the Mid-Carboniferous Boundary Working Group concluded that the occurrence of any "*Declinognathodus noduliferus*" (s.l.) could become the index of the Mid-Carboniferous boundary. "*D. noduliferus*" (s.l.) here includes not only *D. inaequalis* but also *D. praenoduliferus* from the Aksu-I section in Uzbekistan (oral communication, Nemirovskaya, 1996).

I suppose that such ambiguities in the definition of "*Declinognathodus noduliferus*" gave rise to inconsistency in determining the Mid-Carboniferous boundary. Following the Mid-Carboniferous Boundary Working Group conclusion, in this paper I place provisionally the Mid-Carboniferous boundary in the Hina Limestone at the base of the *Declinognathodus inaequalis-Gnathodus bilineatus* Zone (H 61.2 level). However, more detailed examination in other Mid-Carboniferous sections is necessary to resolve this inconsistency.

2. Notes on *Declinognathodus* species

Many conodont workers argue that the ancestor of *Declinognathodus* species including *D. inaequalis* and *D. praenoduliferus* is not *Gnathodus girtyi simplex* but *G. bilineatus* (e.g., Grayson *et al.*, 1990; Nemirovskaya and Nigmadganov, 1994). In contrast, North American workers have considered *G. girtyi simplex* as the ancestor (e.g., Dunn, 1970, 1971; Lane and Straka, 1974; Lane *et al.*, 1985; Brenckle *et al.*, 1997). Except for the Arrow Canyon section, *G. g. simplex* has not been recorded across the Mid-Carboniferous boundary. On the other hand, *G. bilineatus* is recorded in all sections including the Arrow Canyon and Japanese sections. As *G. g. simplex* is not recorded either in the Hina Limestone or in the Atetsu Limestone, I presume that the ancestor of *Declinognathodus* species is *G. bilineatus*.

3. Co-occurrence of Mississippian and Pennsylvanian conodonts

Precise observations on the stratigraphic occurrence of conodont faunas across the Mid-Carboniferous boundary in the Hina Limestone reveal that "Mississippian" conodonts co-occur with *Declinognathodus* species (see Table 1 and Figure 4). Koike (1967) had already reported this unique conodont composition in his *Gnathodus bilineatus-Declinognathodus noduliferus* Zone in the Atetsu Limestone. However, Lane and Straka (1974) did not approve of the co-occurrence of Mississippian conodonts and *Declinognathodus* species in the Atetsu Limestone and they assigned *D. noduliferus* (="*Gnathodus nodulifera*" by Koike, 1967) to *G. girtyi simplex*.

The holotype of *Gnathodus girtyi simplex* Dunn (1965, pl. 140, fig. 3a) has only one large node in the posterior half of the platform, while the specimen of "*G. nodulifera*" shown by Koike (1967, pl. 3, fig. 10) has four distinctive nodes. Therefore, Koike's "*G. nodulifera*" should be taxonomically included in *Declinognathodus inaequalis*.

Co-occurrence of Mississippian conodonts and *Declinognathodus* species across the Mid-Carboniferous boundary is not peculiar in Japan but widespread in several regions; e.g., in the Aksu-I and Luosu sections (see Figures 9 and 10).

4. Notes on *Neolochriea* gen. nov.

Above the Mid-Carboniferous boundary in the Hina Limestone, a new conodont genus *Neolochriea* appears (described later). *Neolochriea nagatoensis* first appears at the H 63.8 level, that is, slightly higher than the last occurrence datum of *Lochriea commutata* (H 63). Above H 63.8, three new species of *Neolochriea* appear. Except for *N. koikei* sp. nov. the stratigraphic ranges of *Neolochriea* species are very short. The occurrence of *N. nagatoensis, N. hisayoshii* sp. nov., and *N. hisaharui* sp. nov. are restricted to the *Neolochriea nagatoensis* Zone in the Hina Limestone. On the other hand, *N. koikei* first appears at the H 67.5 level and ranges upto the H 71 level in the Hina Limestone.

Neolochriea koikei sp. nov. closely resembles some of the *Idiognathoides* species, such as *I. pacificus* and *I. convexus*, but the former differs from the latter by the absence of the sulcus. The *Idiognathoides* species are dominant in the Late Carboniferous. They survived at the stratigraphically higher level in the measured section. *Lochriea, Neolochriea*, and *Idiognathoides* species occur successively also from other seamount limestones in the Akiyoshi Terrane of southwest Japan. Considering the resemblance of form and the successive faunal appearance of these species in the Hina Limestone, I suppose that the *Neolochriea* species may be a transitional form which is derived from *Lochriea* and evolves into *Idiognathoides*. More detailed examination in other seamount limestones are necessary to confirm this hypothesis.

Conclusions

1. The following six conodont zones are established in the uppermost Mississippian and lowermost Pennsylvanian strata in the Hina Limestone in ascending order.
    (1) *Gnathodus bilineatus* Zone
    (2) *Declinognathodus inaequalis-Gnathodus bilineatus* Zone
    (3) *Declinognathodus noduliferus* Zone
    (4) *Neolochriea nagatoensis* Zone
    (5) *Neolochriea koikei* Zone
    (6) *Neognathodus symmetricus* Zone
2. According to the conventional boundary definition, the base of the *Declinognathodus inaequalis-Gnathodus bilineatus* Zone (the first appearance level of *Declinognathodus inaequalis*) is provisionally defined as the Mid-Carboniferous boundary level in the Hina Limestone. However, the definition of the Mid-Carboniferous boundary should be revised by detailed faunal analyses in the future.
3. Successive faunal changes characterized by the extinction of most Mississippian conodonts and introduction of several new elements typical of the Pennsylvanian occur in the conodont fauna across the Mid-Carboniferous boundary in the Hina Limestone.
4. Co-occurrence of Mississippian conodonts with Pennsylvanian conodonts is recognized in the *Declinognathodus inaequalis-Gnathodus bilineatus* Zone to the *Declinognathodus noduliferus* Zone in the Hina Limestone.
5. A new genus *Neolochriea*, which appears above the Mid-Carboniferous boundary, may be a transitional form from *Lochriea* which evolved into *Idiognathoides*.

Systematic paleontology

All of the conodont specimens figured in the present paper are registered and stored in the collections of the Department of Earth Sciences, Faculty of Science, Chiba University (DESC).

Genus **Declinognathodus** Dunn, 1966

Type species.—Cavusgnathus nodulifera Ellison and Graves, 1941

Declinognathodus inaequalis (Higgins, 1975)

Figures 12-1—5

Idiognathoides noduliferus inaequalis Higgins, 1975, p. 53, pl. 12, figs. 1-7, 12, pl. 14, figs. 11-13, pl. 15, figs. 10, 14; Metcalfe, 1980, p. 306, pl. 38, figs. 10-12, 15.

Gnathodus nodulifera (Ellison and Graves). Koike, 1967, p. 297, 298, pl. 3, fig. 10 (only).

Idiognathoides noduliferus (Ellison and Graves). Igo and Koike, 1968, p. 28, 29, pl. 3, figs. 8, 9 (only).

Declinognathodus noduliferus (Ellison and Graves). Grayson *et al.*, 1985, p. 163, pl. 1, figs. 1, 5, 10 (only); Nigmadganov and

Nemirovskaya, 1992, pl. 3, figs. 5, 8 (only); Brenckle *et al.*, 1997, pl. 1, figs. 2-4.

Declinognathodus noduliferus inaequalis (Higgins). Higgins, 1985, pl. 6.2, figs. 11, 12, 14, pl. 6.3, figs. 1, 4; Li *et al.*, 1987, pl. 1, figs. 3, 4; Nemirovskaya, 1987, pl. 1, figs. 6, 10, 13, 14; Wang *et al.*, 1987a, p. 126, 127, pl. 3, figs. 1, 2, pl. 6, fig. 10; Wang *et al.*, 1987b, pl. 2, fig. 1; Wang and Higgins, 1989, p. 276, pl. 13, figs. 5, 12; Nemirovskaya *et al.*, 1990, pl. 4, figs. 3-18, 20-22, 24, 28.

Declinognathodus noduliferus noduliferus (Ellison and Graves). Higgins, 1985, pl. 6.3, fig. 7 (only).

Declinognathodus inaequalis (Higgins). Riley *et al.*, 1987, pl. 3, figs. 28-40; Kulagina *et al.*, 1992, pl. 30, figs. 5, 6, 11.

Declinognathodus noduliferus (Ellison and Graves). Grayson *et al.*, 1990, p. 363, 364, pl. 1, fig. 22 (only).

Description.—Blade is as long as platform or slightly longer than it. It is straight or slightly curved inward, and continues onto platform as a carina. Carina bends slightly on the anterior part of the unit and straightens on the posterior end. Parapet is well developed along the inner lateral platform and fuses with the carina to form transverse ridges on posterior part of unit. Median trough is rather deep. Nodes are developed along the anterior part of outer lateral platform and form a straight line. Four or more nodes are present.

Remarks.—*Declinognathodus inaequalis* was originally described by Higgins (1975) from the *Homoceras subglobosum* Zone of the central Pennines region in England. It is characterized by having four or more nodes on the outer lateral platform. The Hina specimens are quite congruent with the original ones.

Gnathodus nodulifera described by Koike (1967) from the Atetsu Limestone seems to be divisible into three species of *Declinognathodus* by the difference in the number of outer nodes. The specimen illustrated in plate 3, figure 10 of Koike (1967) has four nodes and can be included in *D. inaequalis*.

Two specimens of *Idiognathoides noduliferus* illustrated by Igo and Koike (1968) from the Panching Limestone, west Malaysia, also have four nodes. Metcalfe (1980) restudied the conodont faunas of the Panching Limestone and established the *Idiognathoides noduliferus inaequalis*-*Gnathodus commutatus* Subzone in the lower part of this limestone. He reported that the Mississippian conodonts and *D. inaequalis* occur together in samples of this subzone. In the Hina Limestone, *D. inaequalis* also occurs with Mississippian conodonts from the *Declinognathodus inaequalis*-*Gnathodus bilineatus* Zone to the *D. noduliferus* Zone. The first appearance of *D. inaequalis* defines the Mid-Carboniferous boundary in the Hina Limestone.

Materials.—DESC-95347 from H 62.7, DESC-95348 from H 62.8, DESC-95349 from H 62.7, DESC-95352 from H 66, DESC-96006 from H 61.2.

Declinognathodus japonicus (Igo and Koike, 1964)

Figures 12-9—12

Streptognathodus japonicus Igo and Koike, 1964, p. 188, 189, pl. 28, figs. 5-23.

Declinognathodus nevadensis Dunn, 1966, p. 1300, pl. 158, figs. 4, 8.

Idiognathoides aff. *noduliferus* (Ellison and Graves). Lane, 1967, p. 938, pl. 123, figs. 9-11, 13, 16, 17.

?*Gnathodus nodulifera* (Ellison and Graves). Koike, 1967, p. 297, 298, pl. 3, fig. 9 (only).

Gnathodus japonicus (Igo and Koike). Higgins and Bouckaert, 1968, p. 35, 36, pl. 4, figs. 1, 2, 4.

Idiognathoides noduliferus (Ellison and Graves). Igo and Koike, 1968, p. 28, 29, pl. 3, figs. 10, ?12 (only); Thompson, 1970, p. 1046, pl. 139, figs. 2, 3, 5, 6, 20 (only).

Streptognathodus noduliferus (Ellison and Graves). Webster, 1969, p. 48, 49, pl. 4, fig. 7 (only).

Idiognathoides noduliferus japonicus (Igo and Koike). Higgins, 1975, p. 54, pl. 14, figs. 7-10; Metcalfe, 1980, p. 306, pl. 38, figs. 14, 17.

Declinognathodus noduliferus (Ellison and Graves). Grayson *et al.*, 1985, p. 163, pl. 1, figs. 13, 18, 25 (only); Lane *et al.*, 1985, figs. 7-D, E, F, G; Nigmadganov and Nemirovskaya, 1992, pl. 3, figs. 3, 9, 11, 13, 14, 17 (only).

Declinognathodus noduliferus japonicus (Igo and Koike). Higgins, 1985, pl. 6.3, figs. 2, 9; Nemirovskaya, 1987, pl. 1, figs. 12, 15, 19; Wang and Higgins, 1989, p. 276, pl. 1, figs. 6-9.

Declinognathodus praenoduliferus Nigmadganov and Nemirovskaya, 1992, pl. 2, figs. 10, 11, pl. 3, fig. 2 (only).

Declinognathodus japonicus (Igo and Koike). Kulagina *et al.*, 1992, pl. 30, figs. 12-15, 17.

Description.—Blade is almost as long as platform. It is slightly curved inward, and continues onto platform as a carina. Carina is slightly bent on the anterior part of unit and curves slightly inward on the posterior end. A parapet is developed along inner lateral platform. Median trough is shallow and extends between the carina and parapet to near the posterior end of platform. Only a single node is developed at anterior part of outer lateral platform.

Remarks.—This species is characterized by having a single node on the outer lateral platform. The presence of a thick carina ornamented with node-like ridges, a distinctive single node, and a small ridge on the outer side of the carina were illustrated on the holotype of *Declinognathodus japonicus*. All specimens listed in synonymy have a single distinctive node on the outer side of the carina. The holotype of *D. nevadensis* of Dunn (1966), *Idiognathoides* aff. *noduliferus* of Lane (1967), and *Streptognathodus noduliferus* of Webster (1969) also have a single distinctive node on the outer side of the carina. Therefore, they can be assigned to *D. japonicus*.

The specimen of *Gnathodus nodulifera* illustrated by Koike (1967, pl. 3, fig. 9) has a single node but it is very small. This small specimen may be an immature form and therefore is questionably included as a synonym. Three specimens illustrated as *Declinognathodus praenoduliferus* by Nigmadganov and Nemirovskaya (1992, pl. 2, figs. 10, 11, and pl. 3, fig. 2) have a distinctive single node on the outer side of the carina. They closely resemble the Hina specimens. For this reason they are placed in *D. japonicus*.

Materials.—DESC-95374 from H 63.5, DESC-95376 from H 63.5, DESC-96008 from H 63.2, DESC-96009 from H 63.2.

Declinognathodus noduliferus (Ellison and Graves, 1941)

Figures 12-6—8

Cavusgnathus nodulifera Ellison and Graves, 1941, p. 4, pl. 3, figs. 4, 6.

Gnathodus nodulifera (Ellison and Graves). Koike, 1967, p. 297, 298, pl. 3, figs. 11, 12 (only).

Gnathodus noduliferus (Ellison and Graves). Higgins and Bouckaert, 1968, p. 33, 34, pl. 2, figs. 6, 12.

Idiognathoides noduliferus (Ellison and Graves). Igo and Koike, 1968, p. 28, 29, pl. 3, figs. 7, 11 (only); Thompson, 1970, p. 1046, pl. 139, figs. 8, 16 (only); Lane and Straka, 1974, p. 85-87, figs. 35. 1-15; figs. 41. 15-17.

Streptognathodus noduliferus (Ellison and Graves). Webster, 1969, p. 48, 49, pl. 4, fig. 8 (only).

Declinognathodus noduliferus (Ellison and Graves). Dunn, 1970, p. 330, pl. 62, figs. 1, 2; Grayson *et al.*, 1985, p. 163, pl. 1, figs. 9, 15 (only); Riley *et al.*, 1987, pl. 3, figs. 41-47; Nigmadganov and Nemirovskaya, 1992, pl. 3, figs. 4, 6, 7, 10, 12, 15, 16 (only); Kulagina *et al.*, 1992, pl. 30, figs. 2-4, 7-10.

Idiognathoides noduliferus noduliferus (Ellison and Graves). Higgins, 1975, p. 54, pl. 14, figs. 15, 16; Metcalfe, 1980, p. 306, pl. 38, figs. 16, 18.

Declinognathodus noduliferus noduliferus (Ellison and Graves). Higgins, 1985, pl. 6.2, fig. 13 (only); Li *et al.*, 1987, pl. 1, fig. 1; Nemirovskaya, 1987, pl. 1, figs. 7, 9, 11, 20, 21; Wang *et al.*, 1987a, p. 127, pl. 3, figs. 3-5, pl. 7, fig. 1; Wang *et al.*, 1987b, pl. 1, figs. 4, 5, 8; Wang and Higgins, 1989, p. 276, 277, pl. 2, figs. 5-9.

"Declinognathodus" noduliferus (Ellison and Graves). Grayson *et al.*, 1990, p. 363, 364, pl. 1, fig. 21 (only).

Description.—Blade is almost as long as platform. It is slightly curved inward, and continues onto platform as a carina. Carina is slightly bent at anterior part of unit and curves slightly inward on the posterior end. A parapet is developed along the inner lateral platform. Median trough is rather deep in anterior part of platform and rather shallow in posterior part. Two or three nodes are well developed at anterior part of outer lateral platform.

Remarks.—*Declinognathodus noduliferus* was first described by Ellison and Graves (1941). According to them, three nodes commonly extend in a row posteriorly from the junction of the blade and outer side of the platform. The specimens identified as *D. noduliferus* in this study are characterized by having two or three nodes on the outer lateral platform. All of the specimens mentioned in synonymy have also two or three nodes on the outer side of the carina.

The specimens described by Koike (1967) as *Gnathodus nodulifera* have from one to four nodes. Among them, only two specimens illustrated with two nodes (pl. 3, fig. 11) and three nodes (pl. 3, fig. 12) are assigned to *Declinognathodus noduliferus*.

Materials.—DESC-95362 from H 62.8, DESC-95365 from H 62.8, DESC-96007 from H 62.7.

Genus ***Gnathodus*** Pander, 1856

Type Species.—*Polygnathus bilineatus* Roundy, 1926

Gnathodus bilineatus (Roundy, 1926)

Figures 11-1—3.

Polygnathus bilineatus Roundy, 1926, p. 13, pl. 3, figs. 10a-c.

Gnathodus bilineatus (Roundy). Hass, 1953, p. 78, pl. 14, figs. 25-28; Higgins, 1961, pl. 10, fig. 5; Koike, 1967, p. 296, pl. 1, figs. 9-11; Wirth, 1967, p. 205, pl. 19, figs. 6-9; Igo and Koike, 1968, p. 29, pl. 3, figs. 6; Rhodes *et al.*, 1969: p. 94, 95, pl. 18, figs. 14a-17d; Igo, 1973, p. 193, pl. 29, figs. 1-5 (only); Igo and Kobayashi, 1974, p. 419, 420, pl. 56, figs. 1-3; Watanabe, 1975, p. 163, pl. 14, figs. 1-5; Metcalfe, 1980, p. 302, pl. 38, figs. 5, 8, 9; Metcalfe, 1981, pl. 3, figs. 2a-4d; von Bitter and Plint-Geberl, 1982, pl. 6, figs. 8-11; Haikawa, 1988, pl. 6, fig. 11, pl. 7, figs. 3, 4; Grayson *et al.*, 1990, p. 361, 362, pl. 1, fig. 1.

Gnathodus bilineatus bilineatus (Roundy). Bischoff, 1957, p. 21, 22, pl. 3, figs. 11, 15-20, pl. 4, fig. 1; Higgins and Bouckaert, 1968, p. 29, pl. 3, fig. 9; Higgins, 1975, p. 28, 29, pl. 11, figs. 1-4, 6, 7; Higgins, 1985, pl. 6.1, figs. 1, 2; Li *et al.*, 1987, pl. 1, fig. 12; Riley *et al.*, 1987, pl. 2, figs. 2, 4; Wang *et al.*, 1987a, p. 128, pl. 1, fig. 6; Wang *et al.*, 1987b, pl. 3, fig. 12; Wang and Higgins, 1989, p. 277, 278, pl. 6, figs. 7-11; Varker *et al.*, 1990, pl. 1, fig. 1; Kulagina *et al.*, 1992, pl. 28, figs. 4-7; Nigmadganov and Nemirovskaya, 1992, pl. 1, fig. 3.

Gnathodus modocensis Rexroad, 1957, p. 30, 31, pl. 1, figs. 15-17; Rexroad, 1958, p. 17, 18, pl. 1, figs. 1, 2.

Gnathodus smithi Clarke, 1960, p. 26, 27, pl. 4, figs. 13, 14, pl. 5, figs. 9, 10.

Gnathodus bilineatus bollandensis Higgins and Bouckaert, 1968, p. 29, 30, pl. 2, figs. 10, 13, pl. 3, figs. 4-8, 10; Higgins, 1975, p. 29, pl. 11, figs. 5, 8-13; Higgins, 1985, pl. 6.1, figs. 4, 5; Li *et al.*, 1987, pl. 1, fig. 11; Riley *et al.*, 1987, pl. 2, figs. 5-8, 12; Wang *et al.*, 1987a, p. 128, pl. 1, figs. 7-10; Wang *et al.*, 1987b, pl. 2, figs. 9, 12; Wang and Higgins, 1989, p. 278, pl. 12, figs. 8-11; Varker *et al.*, 1990, pl. 1, figs. 2-12; Kulagina *et al.*, 1992, pl. 28, figs. 8, 9, 12; Nigmadganov and Nemirovskaya, 1992, pl. 1, figs. 1, 2, 4; Nemirovskaya and Nigmadganov, 1993, pl. 2, fig. 1.

Gnathodus postbilineatus Nigmadganov and Nemirovskaya, 1992, pl. 1, figs. 7-9, pl. 2, figs. 1, 2, 4 (only).

Remarks.—Many workers have subdivided this species into two subspecies: *G. bilineatus bilineatus* (s.s.) and *G. b. bollandensis*. Higgins (1975) stated that distinctive characters of *G. b. bollandensis* are a narrow, rectangular to semiovate outer platform and the lack of a posterior lateral row of nodes adjacent to the carina, which is a common feature of *G. b. bilineatus*.

The Hina specimens are the nearest to *Gnathodus bilineatus bollandensis* (see Higgins, 1975, pl. 11, figs. 5, 8-13). However, some of their features seem to be in the range of variation of *G. b. bilineatus*. Although additional taxonomic study is necessary, I treated *G. b. bilineatus* (s.s.) and *G. b. bollandensis* by Higgins (1975) as a single species, *G. bilineatus*.

This species closely resembles *Gnathodus postbilineatus*, but it is distinguished from the latter by having a parapet without fusing in the carina. Six of the specimens of *G. postbilineatus* described by Nigmadganov and Nemirovskaya (1992) may be identical with *G. bilineatus*.

Materials.—DESC-95250 from H 57.2, DESC-96001 from H

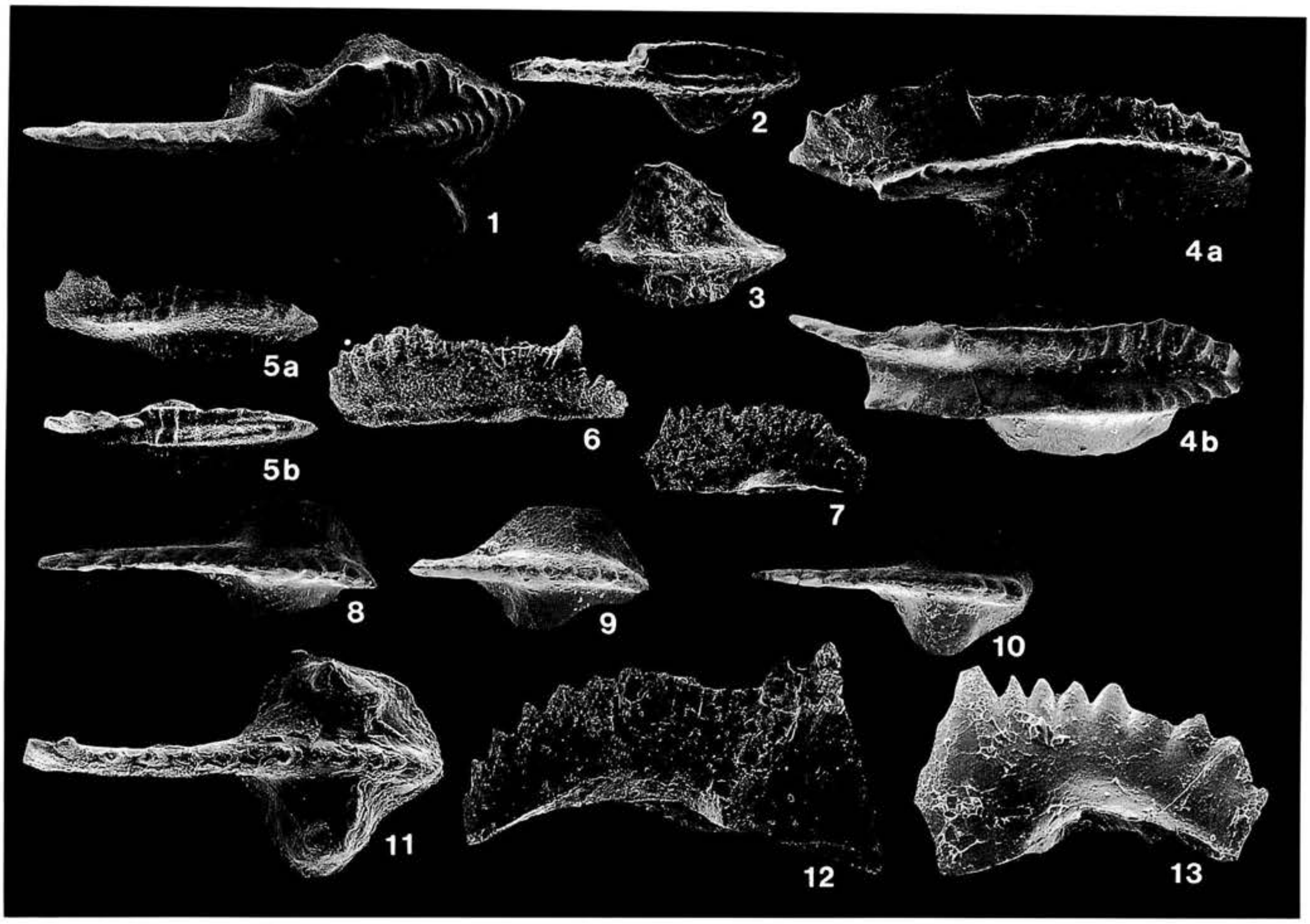


Figure 11. **1-3.** *Gnathodus bilineatus* (Roundy). 1 : DESC-95250 from Loc. H 57.2, upper view, ×40, 2 : DESC-96001 from Loc. H 61.7, upper view, ×60, 3 : DESC-96002 from Loc. H 62.5, upper view, ×60. **4a, 4b.** *Cavusgnathus unicornis* Youngquist and Miller, DESC-95258 from Loc. H 61. 4a : oblique upper view, ×60, 4b : upper view, ×60. **5a, 5b.** *Cavusgnathus* sp. indet., DESC-95261, from Loc. H 58.5. 5a : oblique upper view, ×60, 5b : upper view, ×60. **6.** *Vogelgnathus akiyoshiensis* (Igo), DESC-96003, from Loc. H 60, lateral view, ×60. **7.** *Vogelgnathus campbelli* (Rexroad), DESC-96004, from Loc. H 61.5, lateral view, ×60. **8-10.** *Lochriea commutata* (Branson and Mehl), 8 : DESC-95289 from Loc. H 62.7, upper view, ×60, 9 : DESC-95291 from Loc. H 62.8, upper view, ×60, 10 : DESC-95293 from Loc. H 63, upper view, ×60. **11.** *Lochriea nodosa* (Bishoff), DESC-95281 from Loc. H 61.2, upper view, ×60. **12, 13.** *Hindeodus minutus* (Ellison). 12 : DESC-96005 from Loc. H 59.2, lateral view, ×60, 13 : DESC-95274 from Loc. H 64, lateral view, ×60.

61.7, DESC-96002 from H 62.5.

Genus **Lochriea** Scott, 1942

Type species.—*Spathognathodus commutatus* Branson and Mehl, 1941

Lochriea commutata (Branson and Mehl, 1941)

Figures 11-8—10

Spathognathodus commutatus Branson and Mehl, 1941, p. 98, pl. 19, figs. 1-4 ; Clarke, 1960, p. 19, pl. 3, figs. 4, 5.

Gnathodus inornatus Hass, 1953, p. 80, pl. 14, figs. 9-11 ; Stanley, 1958, p. 465, pl. 68, figs. 5, 6.

Gnathodus commutatus commutatus (Branson and Mehl). Bischoff, 1957, p. 22, pl. 4, figs. 2-6, 15 ; Koike, 1967, p. 269, 267, pl. 1, figs. 12-16 ; Wirth, 1967, p. 206, pl. 19, figs. 10, 11.

Gnathodus commutatus var. *commutatus* (Branson and Mehl). Higgins, 1961, p. 212, 213, pl. 10, fig. 6.

Gnathodus commutatus (Branson and Mehl). Stibane, 1967, p. 334, pl. 36, figs. 25-28 ; Higgins and Bouckaert, 1968, p. 30, pl. 2, fig. 5 ; Webster, 1969, p. 31, pl. 5, fig. 13 ; Rhodes *et al*., 1969, p. 95, 96, pl. 19, figs. 9a-12d ; Igo, 1973, p. 193, pl. 29, figs. 8-13 ; Igo and Kobayashi, 1974, p. 420, 421, pl. 56, figs. 6, 7 ; Watanabe, 1975, p. 164, pl. 14, figs. 8-11 ; Metcalfe, 1980, p. 309, pl. 38, figs. 3, 4 ; Metcalfe, 1981, p. 21, 23, pl. 7, figs. 6, 7.

Paragnathodus commutatus (Branson and Mehl). Higgins, 1975, p. 70, 71, pl. 7, figs. 7-9, 11, 13, 16, 20, 21 ; Belka, 1982, pl. 1, fig. 11 ; Grayson *et al*., 1985, p. 169, pl. 1, fig. 24, pl. 2, fig. 19 ; Riley *et al*., 1987, pl. 2, figs. 1, 3 ; Wang *et al*., 1987a, p. 130, 131, pl. 2, fig. 12 ; Wang *et al*., 1987b, pl. 2, fig. 2, pl. 3, fig. 10 ; Kulgina *et al*., 1992, pl. 29, figs. 1, 2 ; Haikawa, 1988, pl. 6,

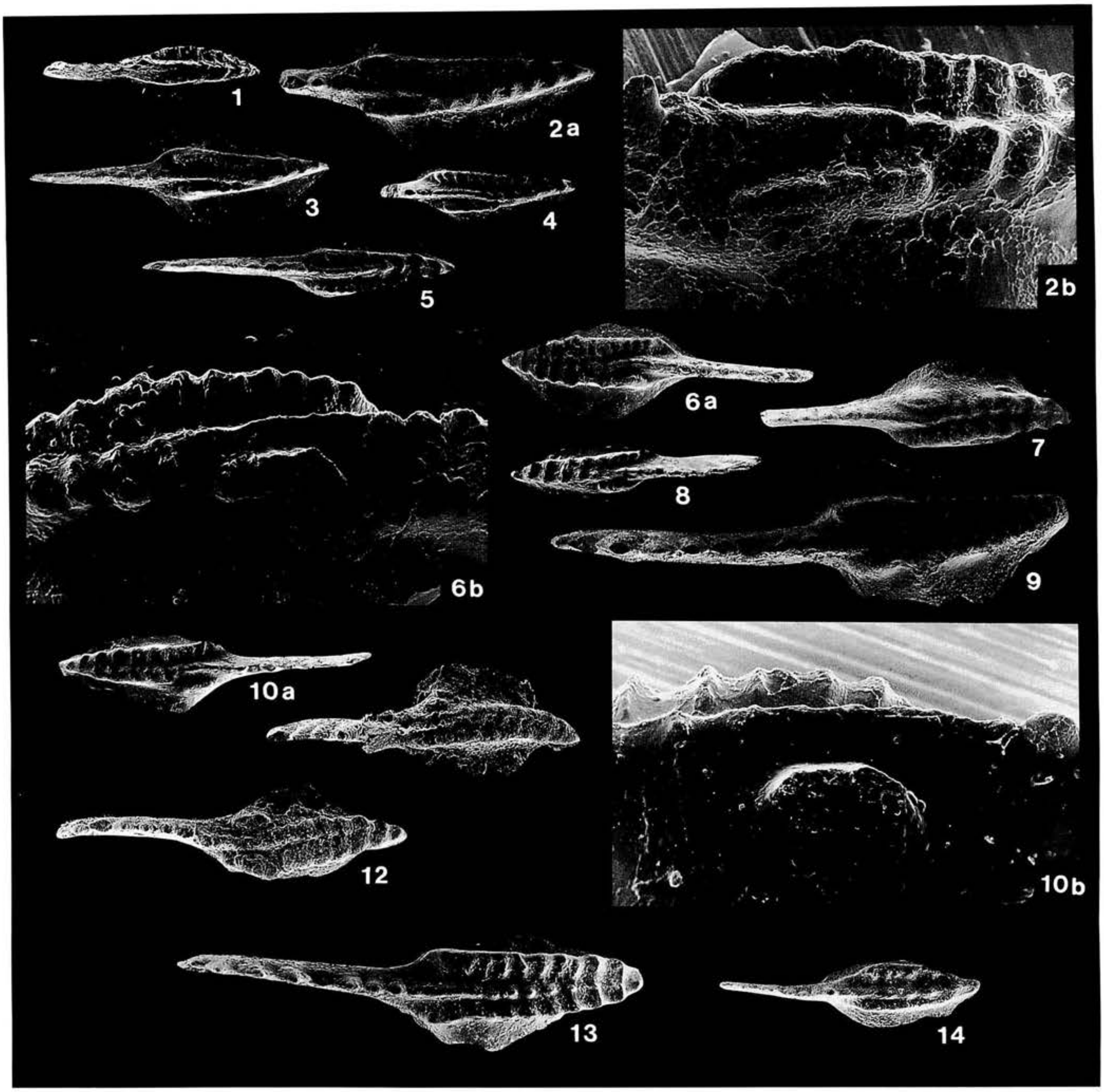


Figure 12. **1-5.** *Declinognathodus inaequalis* (Higgins). 1 : DESC-96006 from Loc. H 61.2, upper view, ×60, 2a, b : DESC-95349 from Loc. H 62.7, 2a : upper view, ×60, 2b : oblique upper view, x 180, 3 : DESC-95347 from Loc. H 62.7, upper view, ×60, 4 : DESC-95348 from Loc. H 62.8, upper view, ×60, 5 : DESC-95352 from Loc. H 66, upper view, ×60. **6-8.** *Declinognathodus noduliferus* (Ellison and Graves). 6a, b : DESC-95362 from Loc. H 62.8, 6a : upper view, ×60, 6b : oblique upper view, ×180, 7 : DESC-95365 from Loc. H 62.8, upper view, ×60, 8 : DESC-96007 from Loc. H 62.7, upper view, ×60. **9-12.** *Declinognathodus japonicus* (Igo and Koike). 9 : DESC-96008 from Loc. H 63.2, upper view, ×60, 10a, b : DESC-96009 from Loc. H 63.2, 10a : upper view, ×60, 10b : oblique upper view, ×300, 11 : DESC-95374 from Loc. H 63.5, upper view, ×60, 12 : DESC-95376 from Loc. H 63. 5, upper view, ×60. **13, 14.** *Neognathodus symmetricus* (Lane). 13 : DESC-95390 from Loc. H 70.5, upper view, ×60, 14 : DESC-95389 from Loc. H 68.8, upper view, ×60.

figs. 1, 2. ; Wang and Higgins, 1989, p. 285, pl. 8, figs. 4, 5 ; Nemirovskaya *et al.*, 1990, pl. 3, fig. 4.

Lochriea commutata (Branson and Mehl). Higgins, 1985, pl. 6.1, fig. 10 ; Varker and Sevastopulo, 1985, pl. 5.5, figs. 11, 12 ; Rexroad and Horowitz, 1990, p. 508, 509, pl. 2, figs. 18-23 [Pa element] ; Nemirovskaya *et al.*, 1994, pl. 2, fig. 1.

Remarks.—This species has an unornamented platform that is broadly ovate in oral view and a carina that includes laterally expanded denticles with a curious polygonal pattern on part of its surface. The carina of *Lochriea commutata* is similar to that of *Neolochriea nagatoensis* in shape, but the denticles of the former are like thick needles, whereas those of the latter are less sharp and similar to spherical knolls.

This species was originally described by Branson and Mehl (1941) from the Chesterian Pitkin Limestone in North America. Grayson *et al.*, (1985) reported that it occurs together with *Declinognathodus noduliferus* in the Rhoda Creek Formation of Oklahoma, and ranges up to the uppermost part of their surveyed section (the *Declinognathodus noduliferus* Zone). In the Hina Limestone, this species is found commonly in the lower part of the *Declinognathodus noduliferus* Zone. In the Zhelvakovaya Valley section, this species also occurs with *D. noduliferus* in strata above the Mid-Carboniferous boundary (Nemirovskaya *et al.*, 1990). Therefore, the range of *Lochriea commutata* extends beyond the Mid-Carboniferous boundary.

Materials.—DESC-95289 from H 62.7, DESC-95291 from H 62.8, DESC-95293 from H 63.

Lochriea nodosa (Bischoff, 1957)

Figure 11-11

Gnathodus commutatus nodosus Bischoff, 1957, p. 23, 24, pl. 4, figs. 12, 13 ; Higgins, 1961, p. 213, pl. 10, figs. 7, 8 ; Koike, 1967, p. 297, pl. 1, fig. 19 ; Wirth, 1967, p. 207, pl. 19, figs. 13-18.

Gnathodus commutatus var. *nodosus* Bischoff. Higgins, 1961, p. 213, pl. 10, figs. 7, 8.

Gnathodus nodosus (Bischoff). Higgins and Bouckaert, 1968, pl. 2, fig. 2 (only) ; Rhodes *et al.*, 1969, p. 104, 105, pl. 19, figs. 16a-20c ; Igo, 1973, p. 194, pl. 29, figs. 14-17 ; Igo and Kobayashi, 1974, p. 421, pl. 56, figs. 8-12 ; Watanabe, 1975, p. 164, pl. 14, figs. 12-16 ; Metcalfe, 1980, p. 304, pl. 38, fig. 2 ; Metcalfe, 1981, pl. 6, figs. 1-5.

Paragnathodus nodosus (Bischoff). Higgins, 1985, pl. 6.1, fig. 9 ; Li *et al.*, 1987, pl. 1, fig. 7 ; Riley *et al.*, 1987, pl. 2, figs. 10, 11, 13, 14 ; Wang *et al.*, 1987a, p. 131, pl. 1, figs. 3-5 ; Haikawa, 1988, pl. 7, figs. 8, 9 ; Wang *et al.*, 1987b, pl. 1, fig. 9, pl. 2, fig. 10 ; Wang and Higgins, 1989, p. 285, 286, pl. 8, figs. 6, 7 ; Nemirovskaya *et al.*, 1990, pl. 3, figs. 3, 9 ; Kulagina *et al.*, 1992, pl. 29, fig. 13.

Lochriea nodosa (Bischoff). Nemirovskaya *et al.*, 1994, pl. 1, fig. 8, pl. 2, fig. 6.

Remarks.—This species differs from *Lochriea commutata* in having a platform ornamented with several nodes or ridges. Recently, Nemirovskaya *et al.* (1994) stated that *L. commutata* and *L. cracoviensis*, both having simple unornamented platforms, are the earliest representatives of the genus *Lochriea*. They also stated that *Lochriea* species with ornamented platforms first appear during the late Visean or earliest Serpukhovian, and may be valuable for correlation. They recognized eight species in total of *Lochriea* with ornamented platforms : *L. mononodosa*, *L. nodosa*, *L. cruciformis*, *L. multinodosa*, *L. monocostata*, *L. costata*, *L. ziegleri*, and *L. senckenbergica*.

Among the Japanese *Lochriea* specimens, species with ornamented platforms are less common. Their biostratigraphic significance is unclear at present. In this study, I treat these forms with ornamented platforms from the Hina Limestone as *L. nodosa*.

Material.—DESC-95281 from H 61.2.

Genus **Neognathodus** Dunn, 1970

Type species.—*Polygnathus bassleri* Harris and Hollingsworth, 1933

Neognathodus symmetricus (Lane, 1967)

Figures 12-13, 14

Gnathodus bassleri symmetricus Lane, 1967, p. 935, pl. 120, figs. 2, 13, 14, 17, pl. 121, figs. 6, 9.

Gnathodus wapanuckensis (Harlton). Koike, 1967, p. 300, pl. 1, figs. 22-25.

Gnathodus bassleri (Harris and Hollingsworth). Webster, 1969, p. 29, pl. 5, fig. 14 (only).

Neognathodus bassleri (Harris and Hollingsworth). Dunn, 1970, p. 336, pl. 64, figs. 1a-c, 12 (only).

Neognathodus bassleri symmetricus (Lane). Lane and Straka, 1974, p. 96, figs. 37. 22, 31, 32, 37-39, figs. 39. 16-18, 21-24.

Neognathodus symmetricus (Lane). Grayson, 1984, p. 51, pl. 2, fig. 7 ; Li *et al.*, 1987, pl. 1, fig. 6 ; Wang *et al.*, 1987a, p. 130, pl. 3, figs. 6, 7, pl. 7, figs. 3, 4, 8, 12, pl. 8, figs. 2-5 ; Wang *et al.*, 1987b, pl. 2, fig. 6, pl. 3, fig. 4 ; Wang and Higgins, 1989, p. 282, 283, pl. 2, figs. 1-4 ; Grayson *et al.*, 1990, p. 377, 378, pl. 3, fig. 23 ; Nigmadganov and Nemirovskaya, 1992, pl. 4, figs. 1, 7.

Description.—Platform is almost symmetrical in oral view and consists of prominent straight carina and two well developed parapets. Carina is nodular and extends near posterior end of platform. Two parapets are ornamented by transversely ridged nodes.

Remarks.—This species differs from *Neognathodus bassleri* in being a nearly symmetrical platform and in having the carina centered between the margins of the platform.

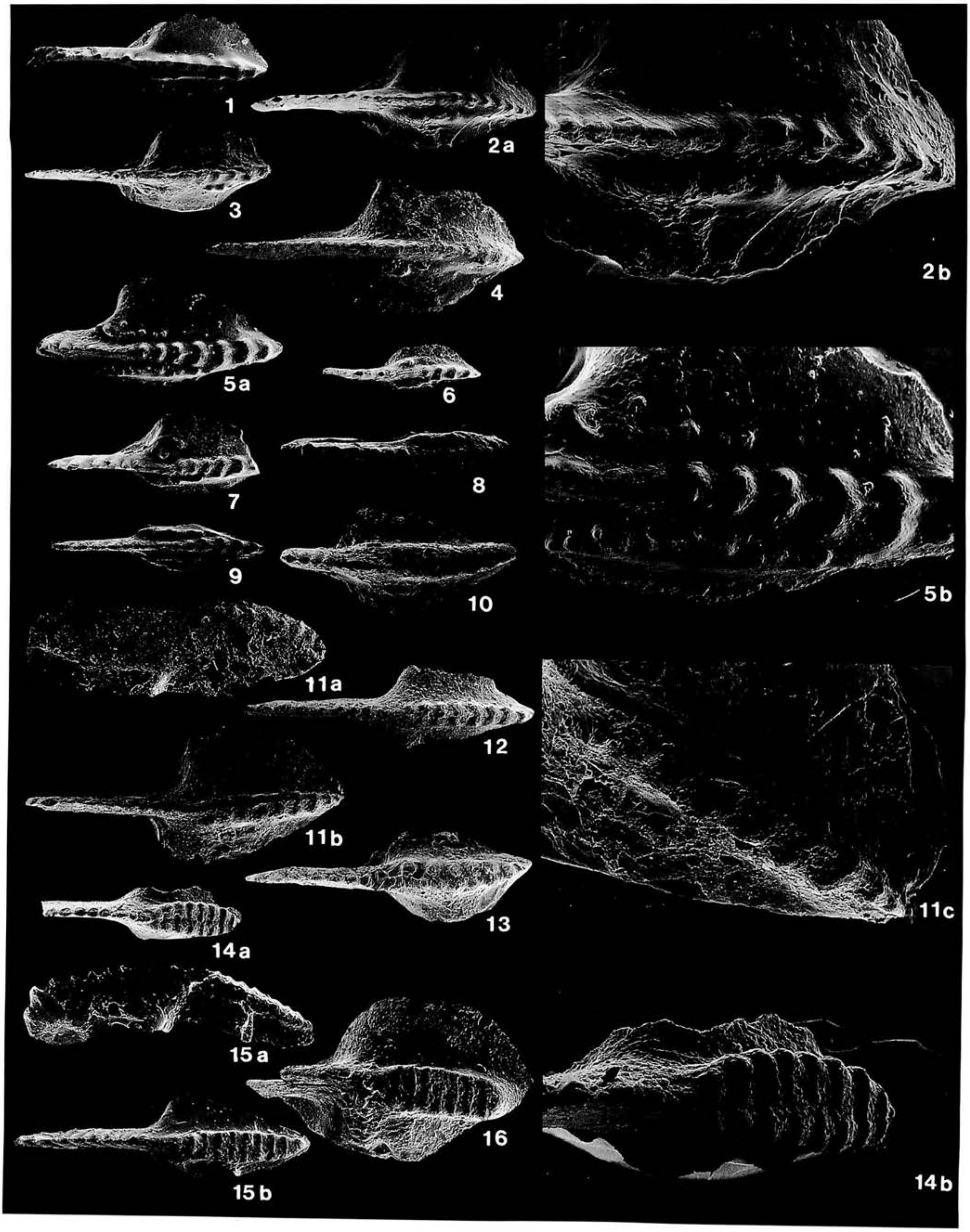
The specimens of *Gnathodus wapanuckensis* described by Koike (1967) from the Kodani Formation of the Atetsu Limestone have a narrow symmetrical platform, and are here assigned to *Neognathodus symmetricus*.

Materials.—DESC-95389 from H 68.8, DESC-95390 from H 70.5.

Genus **Neolochriea** gen. nov.

Type species.—*Neolochriea hisaharui* Mizuno gen. et sp. nov.

Diagnosis.—Scaphate pectiniform elements with free


1
2a
2b
3
4
5a
5b
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7
8
9
10
11a
12
11b
11c
13
14a
15a
16
14b
15b

blade, smooth platform, and nodular carina. Blade is about half element length and possesses low denticles. Platform is oval or elliptical in form. Carina is long, ornamented with weakly nodes or ridges, and extends to posterior end of platform. Basal cavity is large.

Remarks.—*Neolochriea* gen. nov. differs from *Lochriea* Scott, 1942 in having a long and pointed posterior platform, from *Ferganaegnathodus* Nemirovskaya and Nigmadganov, 1993 in having a nodular carina, and from *Idiognathoides* Harris and Hollingsworth, 1933 in absence of a sulcus at the anterior part of the platform. The following four species are referable to the genus *Neolochriea*: *N. nagatoensis, N. hisayoshii* sp. nov., *N. hisaharui* sp. nov., and *N. koikei* sp. nov. I have recovered these *Neolochriea* species from other seamount limestones in the Akiyoshi Terrane of southwest Japan, such as the Akiyoshi, Taishaku, Atetsu, and Omi Limestones. All of the *Neolochriea* species appear between the last occurrence of *Lochriea* species and the first occurrence of *Idiognathoides* species. Therefore, *Neolochriea* gen. nov. may derive from *Lochriea* and evolve into *Idiognathoides* during the Early Pennsylvanian.

Etymology.—From *neo* (Greek) meaning "new" and *lochriea*, referring to the genus *Lochriea*, therefore "new" *Lochriea*.

Geological age.—Earliest Late Carboniferous or earliest Pennsylvanian.

Neolochriea hisaharui sp. nov.

Figures 13-10—13

Gnathodus commutatus nagatoensis Igo and Koike, 1965, p. 89, pl. 9, fig. 10 (only); Koike, 1967, p. 297, pl. 1, fig. 18 (only).

Diagnosis.—Blade is as long as platform or slightly longer than it and continues as a carina. Carina bends slightly on the anterior part of the platform and straightens on the posterior end. Long straight carina continues to posterior end of platform as narrow, low, and node-like denticles. Outer and inner surfaces of platform are smooth.

Description.—In upper view, the unit is elliptical and pointed at posterior end of platform. Long blade continues posteriorly as a carina. Carina is long, relatively thick, straight, rising above smooth platform, and ornamented with two rows of nodes. A very shallow groove curves between the rows toward the posterior part of the carina. The groove vanishes about two-thirds of the distance from the anterior part of the carina, where the nodes fuse into a single row.

In lateral view, blade is high and long. Denticles of blade are very low. One of the anterior denticles is slightly higher and pointed. Underside of platform is flat and upper side is slightly arched.

In aboral view, the basal cavity is deep and widely flaring anteriorly.

Remarks.—*Neolochriea hisaharui* sp. nov. is similar to *N. nagatoensis*, but can be distinguished from the latter by the difference in width of the carina. This new species has a thickened carina with a very shallow groove, whereas *N. nagatoensis* has a narrow carina without the groove. Among the specimens illustrated as *N. nagatoensis*, one specimen of Igo and Koike (1965, pl. 9, fig. 10) and another specimen of Koike (1967, pl. 1, fig. 18) have a thickened carina with a shallow groove. They are considered to be identical with the present new species.

Neolochriea hisaharui sp. nov. is similar to *Gnathodus glaber* described by Wirth (1967) from the Quinto Real of the Western Pyrenees in Spain, but the former differs from the latter in having an elliptical platform and a relatively thick carina. In *N. hisaharui* sp. nov. the carina is ornamented by two rows of nodes, but in *G. glaber* the carina comprises only a single narrow row of nodes.

Etymology.—The specific name is dedicated to Professor Hisaharu Igo, Department of Astronomy and Earth Sciences, Tokyo Gakugei University, who has contributed much to the progress of Late Paleozoic conodont taxonomy and biostratigraphy in Japan.

Materials.—Holotype: DESC-95326 from H 65.5; Paratypes: DESC-95323 from H 65.5, DESC-95324 from H 65.5, DESC-95325 from H 65.5.

Neolochriea hisayoshii sp. nov.

Figures 13-5—9

Gnathodus opimus Igo and Koike, 1965, p. 89, pl. 9, figs. 5-8 (only).

Diagnosis.—Blade is almost as long as carina, and continues onto a carina. Long and straight carina bends slightly on the anterior part of the platform and straightens on the posterior end. Carina continues to posterior end of unit, forming a long narrow row of low node-like denticle. Outer and inner sides of carina are ornamented with parapet-like row of nodes. Outer and inner surfaces of platform are smooth.

Description.—In upper view, unit is elliptical and pointed at

Figure 13. **1-4.** *Neolochriea nagatoensis* (Igo and Koike). 1: DESC-95301 from Loc. H 64, upper view, ×60, 2a, b: DESC-95300 from Loc. H 64, 2a: upper view, ×60, 2b: upper view, ×180, 3: DESC-95302 from Loc. H 64, upper view, ×60, 4: DESC-95303 from Loc. H 64, upper view, ×60. **5-9.** *Neolochriea hisayoshii* sp. nov. 5a, b: holotype, DESC-95313, from Loc. H 64.5, 5a: upper view, ×60, 5b: upper view, ×180, 6: paratype, DESC-95310 from Loc. H 64.5, upper view, ×60, 7: paratype, DESC-95312 from Loc. H 64.5, upper view, ×60, 8: paratype, DESC-95316 from Loc. H 66, upper view, ×60, 9: paratype, DESC-95311 from Loc. H 64.5, upper view, ×60. **10-13.** *Neolochriea hisaharui* sp. nov. 10: paratype, DESC-95325 from Loc. H 65.5, upper view, ×60, 11a-c: holotype, DESC-95326 from Loc. H 65.5, 11a: lateral view, ×60, 11b: upper view, ×60, 11c: upper view, ×180, 12: paratype, DESC-95324 from Loc. H 65.5, upper view, ×60, 13: paratype, DESC-95323 from Loc. H 65.5, upper view, ×60. **14-16.** *Neolochriea koikei* sp. nov. 14a,b: holotype, DESC-95334 from Loc. H 67.5, 14a: upper view, ×60, 14b: upper view, ×180, 15a, b: paratype, DESC-95335 from Loc. H 68.5, 15a: lateral view, ×60, 15b: upper view, ×60, 16: paratype, DESC-95336 from Loc. H 68.5, upper view, ×60.

the posterior end of the platform. The long blade extends onto a carina. The carina is flanked by parapet-like row of nodes in both sides. The inner row of nodes fuses to the carina at posterior part of carina. The outer row of nodes fades out in the middle part of the carina.

In lateral view, blade is high and long. Denticles of blade are low and rounded. The anterior part of the blades is slightly higher and pointed.

In aboral view, large basal cavity is present.

Remarks.—*Neolochriea hisayoshii* sp. nov. differs from *N. hisaharui* sp. nov. in having a row of nodes on both the inner and outer sides of the carina.

Igo and Koike (1965) reported *Gnathodus opimus* from the Uzura quarry of the Akiyoshi Limestone. Among the specimens which they illustrated, four specimens (Igo and Koike, 1965, pl. 9, figs. 5-8) have parapet-like nodes on both side of the carina. They are considered to be identical with the present new species.

Neolochriea hisayoshii sp. nov. is similar to *Ferganaegnathodus ferganaensis* described by Nemirovskaya and Nigmadganov (1993) from the Gaźskaya Formation (Lower Bashkirian) of Middle Asia, but the former differs from the latter in possessing a denticulate carina.

Etymology.—The specific name is dedicated to Professor Emeritus Hisayoshi Igo, Institute of Geoscience, University of Tsukuba, who has led conodont study in Japan.

Materials.—Holotype: DESC-95313 from H 64.5; Paratypes: DESC-95310 from H 64.5, DESC-95311 from H 64.5, DESC-95312 from H 64.5, DESC-95316 from H 66.

Neolochriea koikei sp. nov.

Figures 13-14—16

Diagnosis.—Blade is as long as platform or slightly longer than it, almost straight, and attaches onto the carina in a straight line and continues as a long thick carina. The carina expands laterally on the posterior end of the platform to form a transverse ridge. Outer and inner surfaces of the platform are smooth.

Description.—In upper view, the platform is elliptical and pointed at posterior end. Long blade continues as a thick carina. Carina expands into a long, elliptical flat surface that is ornamented with transverse ridges and joined with the blade in a straight line. A longitudinal sulcus or groove is absent at the anterior part of the platform.

In lateral view, the attachment part between blade and platform is slightly arched. Blade is high and platform is lower than blade. Denticles of blade are low and pointed. Under and upper side of platform is almost flat.

In aboral view, a typical gnathodid basal cavity is present.

Remarks.—*Neolochriea koikei* sp. nov. differs from *Neolochriea hisaharui* sp. nov. in having a thick and wide carina. The carina of the former species has remarkable transverse ridges and is washboard-like.

Neolochriea koikei sp. nov. closely resembles *Idiognathoides convexus* described by Ellison and Graves (1941) from the Dimple Limestone (Lower Pennsylvanian), but the latter differs from the former in having a longitudinal sulcus at the anterior of the platform. *I. pacificus* described by Savage and Barkeley (1985) from the Klawak Formation (Lower Pennsylvanian) of Alaska also resembles *N. koikei* sp. nov., but the former differ from the latter in having a short groove at the anterior of the platform. *N. koikei* sp. nov. has neither a sulcus nor groove. Considering the resemblance and stratigraphic ranges among these species, I suppose that *N. koikei* sp. nov. may evolve into these *Idiognathoides* species.

Etymology.—The specific name is dedicated to Professor Toshio Koike, Institute of Geology, Yokohama National University, for his active research on conodont biostratigraphy.

Materials.—Holotype: DESC-95334 from H 67.5; Paratypes: DESC-95335 from H 68.5, DESC-95336 from H 68.5.

Neolochriea nagatoensis (Igo and Koike, 1965)

Figures 13-1—4

Gnathodus commutatus nagatoensis Igo and Koike, 1965, p. 89, pl. 9, figs. 9, 11-12 (only); Koike, 1967, p. 297, pl. 1, fig. 17 (only).

Gnathodus nagatoensis Igo and Koike. Igo and Kobayashi, 1974, p. 421, pl. 56, figs. 14, 15.

Description.—In upper view, platform is broadly ovate and consists of a prominent, slightly bending carina. Oral surface of platform is smooth. The long blade attaches to the platform and continues as a carina. Only inner side adjacent to the carina is ornamented with a row of nodes. The nodes form a line along the carina and fuse at the posterior part of the platform.

Remarks.—*Neolochriea nagatoensis* resembles *Lochriea commutata*, but the former differs from the latter in having a row of nodes on the inner side of carina. *N. nagatoensis* also resembles *N. hisayoshii* sp. nov., but the former differs from the latter in having the nodes on only one side of the carina. Considering the resemblance of form and the appearance of these species, I suppose that *N. nagatoensis* may derive from *L. commutata* and evolve into *N. hisayoshii* sp. nov.

Materials.—DESC-95300 from H 64, DESC-95301 from H 64, DESC-95302 from H 64, DESC-95303 from H 64.

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References

Baesemann, J.F. and Lane, H.R., 1985: Taxonomy and evolution of the genus *Rhachistognathus* Dunn (Conodonta; Late Mississippian to early Middle Pennsylvanian). *Courier Forsohungsinstitut Senckenberg*, no. 74, p. 93-136, pls. 1-5.

Belka, Z., 1982: Upper Visean conodonts from Orlej in Cracow Upland: stratigraphical and paleothermal implications. *Acta Geologica Polonica*, vol. 32, nos. 1-2, p. 57-67, pls. 1, 2.

Bischoff, G., 1957: Die Conodonten-Stratigraphie des rheno-herzynischen Unterkarbons mit Berücksichtigung der Wocklumeria-Stufe und der Devon/Karbon-Grenze. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, vol. 19, p. 1-64, pls. 1-6.

Branson, E.B. and Mehl, M.G., 1941: New and little known Carboniferous conodont genera. *Journal of Paleontology*, vol. 15, no. 2, p. 97-106, pl. 19.

Brenckle, P.L., Baesemann, J.F., Lane, H.R., West, R.R., Webster, G.D., Langenheim, R.L., Brand, U., and Richards, B.C., 1997: Arrow Canyon, the Mid-Carboniferous boundary stratotype. *In*, Brenckle, P.L. and Page, W.R. *eds., PaleoForams '97 Guidebook: Post-Conferrence field trip to the Arrow Canyon Range, southern Nevada, U.S.A.* Cushman Foundation for Foraminiferal Research Supplement to Special Publication, no. 36, p. 13-32, pls. 1, 2.

Clarke, W.J., 1960: Scottish Carboniferous conodonts. *Transactions of the Edinburgh Geological Society*, vol. 18, part 1, p. 1-31, pl. 1-5.

Dunn, D.L., 1965: Late Mississippian conodonts from the Bird Spring Formation in Nevada. *Journal of Paleontology*, vol. 39, no. 6, p. 1145-1150, pl. 140.

Dunn, D.L., 1966: New Pennsylvanian platform conodonts from southwestern United States. *Journal of Paleontology*, vol. 40, no. 6, p. 1294-1303, pls. 157, 158.

Dunn, D.L., 1970: Middle Carboniferous conodonts from western United States and phylogeny of the platform group. *Journal of Paleontology*, vol. 44, no. 2, p. 312-342, pls. 61-64.

Dunn, D.L., 1971: Considerations of the *Idiognathoides-Declinognathodus-Neognathodus* complex of Middle Carboniferous conodonts. *Lethaia*, vol. 4, p. 15-19.

Ellison, S. and Graves, R.W.Jr., 1941: Lower Pennsylvanian (Dimple Limestone) conodonts of the Marathon region, Texas. *University of Missouri School of Mines and Metallurgy Bulletin*, vol. 14, no. 3, p. 1-21, pls. 1-3.

Fujimoto, M. and Sada, K., 1994: Foraminiferal biostratigraphy in the Hina Limestone, Okayama Prefecture, western Japan. *Fossils, Palaeontological Society of Japan*, no. 57, p. 6-15. (*in Japanese with English abstract*)

Grayson, R.C.Jr., 1984: Morrowan and Atokan (Pennsylvanian) conodonts from the northeastern margin of the Arbuckle Mountains, Southern Oklahoma. *In*, Sutherland, P.K. and Manger, W.L. *eds., The Atokan Series (Pennsylvanian) and its boundaries-A symposium*. Oklahoma Geological Survey Bulletin, vol. 136, p. 41-63, pls. 1-4.

Grayson, R.C.Jr., Davidson, W.T., Westergaad, E.H., Atchley, S.C., Hightower, J.H., Monaghan, P.T. and Pollard, C., 1985: Mississippian-"Pennsylvanian" (Mid-Carboniferous) boundary conodonts from the Rhoda Creek Formation: *Homoceras* equivalent in North America. *Courier Forschungsinstitut Senckenberg*, no. 74, p. 149-179, pls. 1, 2.

Grayson, R.C.Jr., Merrill, G.K. and Lambert, L.L., 1990: Carboniferous gnathodontid conodont apparatuses: evidence of dual origin for Pennsylvanian taxa. *Courier Forschungsinstitut Senckenberg*, no. 118, p. 353-396, pls. 1-4.

Haikawa, T., 1988: The basement complex and conodonts biostratigraphy of the lowest parts in Akiyoshi Limestone Group, southwest Japan. *Bulletin of the Akiyoshi-dai Museum of Natural History*, no. 23, p. 13-38, pls. 4-7. (*in Japanese with English abstract*)

Harris, R.W. and Hollingsworth, R.V., 1933: New Pennsylvanian conodonts from Oklahoma. *American Journal of Science*, vol. 25, no. 147, p. 193-204, pl. 1.

Hase, A. and Yokoyama, M., 1975: Geological age and structure of the Hina Limestone, Okayama Prefecture, southwest Japan. *Journal of Science of the Hiroshima University, Series C (Geology and Mineralogy)*, vol. 7, no. 3, p. 167-182, pls. 15-18.

Hass, W.H., 1953: Conodonts of the Barnett Formation of Texas. *U. S. Geological Survey Professional Paper*, vol. 243-F, p. 69-94, pls. 14-16.

Higgins, A.C., 1961: Some Namurian conodonts from north Staffordshire. *Geological Magazine*, vol. 98, p. 210-224, pls. 5-7.

Higgins, A.C., 1975: Conodont zonation of the Late Visean-Early Westphalian strata of northern England. *Bulletin of the Geological Survey of Great Britain*, no. 53, p. 1-99, pls. 1-18.

Higgins, A.C., 1985: Conodont of the Silesian Subsystem from Great Britain and Ireland, part 2 of the Carboniferous System. *In*, Higgins, A.C. and Austin, R.L. *eds., Stratigraphical Index of Conodonts*, p. 210-227, pls. 6.1-6.4. The British Micropalaeontological Society, Ellis Horwood Limited, Chichester.

Higgins, A.C. and Bouckaert, J., 1968: Conodont stratigraphy and palaeontology of the Namurian of Belgium. *Mémoires pour Servir à l'Explication des Cartes Géologiques et Minières de la Belgique*, no. 10, p. 1-64, pls. 1-6.

Igo, Hh., 1973: Lower Carboniferous conodonts from the Akiyoshi Limestone Group, southwest Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 92, p. 185-199, pl. 29.

Igo, Hh., 1994: Summary of Carboniferous to Triassic conodont biostratigraphy in Japan. *Bulletin of Tokyo Gakugei University, Section IV*, vol. 46, p. 99-118.

Igo, Hy. and Igo, Hh., 1979: Additional note on the Carboniferous conodont biostratigraphy of the lowest part of the Akiyoshi Limestone Group, southwestern part of Japan. *Annual Report of Institute of Geoscience, the University of Tsukuba*, no. 5, p. 47-50.

Igo, Hy. and Kobayashi, F., 1974: Carboniferous conodonts from the Itsukaichi district, Tokyo, Japan. *Transactions* *and Proceedings of the Palaeontological Society of Japan, New Series*, no. 96, p. 411-426, pl. 56.

Igo, Hy. and Koike, T., 1964: Carboniferous conodonts from the Omi Limestone, Niigata Prefecture, central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 53, p. 179-193, pls. 27, 28.

Igo, Hy. and Koike, T., 1965: Carboniferous conodonts from Yobara, Akiyoshi Limestone, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 59, p. 83-91, pls. 8, 9.

Igo, Hy. and Koike, T., 1968: Carboniferous conodonts from Kuantan, Malaya. *Geology and Palaeontology of Southeast Asia*, vol 55, p. 26-30, pl. 3. University of Tokyo Press, Tokyo.

Kanmera, K. and Nishi, H., 1983: Accreted oceanic reef complex in southwest Japan. *In*, Hashimoto, M. and Ueda, S. *eds., Accretion tectonics in the Circum-Pacific regions*. p. 195-206. Terra Scientific Publishing Company, Tokyo.

Koike, T., 1967: A Carboniferous succession of the conodont faunas from the Atetsu Limestone in southwest Japan (studies of the Asiatic conodonts, Part VI). *Tokyo Kyoiku Daigaku Science Reports, Section C (Geology, Mineralogy and Geography)*, vol. 9, no. 93, p. 279-318, pls. 1-4.

Kulagina, E.I., Rumyantseva, Z.S., Pazukhin, V.N. and Kochetova, N.N., 1992: *The Lower/Middle Carboniferous boundary at the South Urals and Central Tienshan*. 110 p., 32 pls. Nauka, Moscow. (*in Russian*)

Lane, H.R., 1967: Uppermost Mississippian and lower Pennsylvanian conodonts from the type Morrowan region, Arkansas. *Journal of Paleontology*, vol. 41, no. 4, p. 920-942, pls. 119-123.

Lane, H.R., 1995: Mid-Carboniferous Boundary Working Group. *Newsletter on Carboniferous Stratigraphy, IUGS Subcommission on Carboniferous Stratigraphy*, vol. 13, p. 3.

Lane, H.R., Baesemann, J.F., Brenckle, P.L. and West, R.R., 1985: Arrow Canyon, Nevada -A potential Mid-Carboniferous boundary stratotype. *Dixième Congrés International de Stratigraphie et de Géologie du Carbonifère*, vol. 4, p. 429-439.

Lane, H.R., Brenckle, P. and Higgins, A.C., 1994: Mid-Carboniferous Boundary Working Group decision. *Newsletter on Carboniferous Stratigraphy, IUGS Subcommission on Carboniferous Stratigraphy*, vol. 12, p. 3.

Lane, H.R. and Manger, W.L., 1985: Toward a boundary in the middle of the Carboniferous (1975-1985): ten years of progress. *Courier Forschungsinstitut Senckenberg*, no. 74, p. 1-34.

Lane, H.R. and Straka, J.J., 1974: Late Mississippian and Early Pennsylvanian conodonts, Arkansas and Oklahoma. *Geological Society of America, Special Paper*, p. 1-144, pls. 32-44.

Li, X., Shen, G., Wu, X. and Tong, Z., 1987: A proposed boundary stratotype in Jingyuan, eastern Gansu for the Upper and Lower Carboniferous of China. *In*, Wang, C. *ed., Carboniferous boundaries in China*, p. 69-88, pls. 1-4. Science Press, Beijing.

Metcalfe, I., 1980: Upper Carboniferous conodont faunas of the Panching Limestone, Pahang, west Malaysia. *Palaeontology*, vol. 23, part 2, p. 297-314, pls. 37-38.

Metcalfe, I., 1981: Conodont zonation and correlation of the Dinantian and early Namurian strata of the Craven Lowlands of northern England. *Institute of Geological Sciences, Report 80/10*, p. 1-70, pls. 1-19.

Mizuno, Y. and Ueno, K., 1995: Conodont and foraminiferal faunal changes across the Mid-Carboniferous boundary in the Hina Limestone Group, southwest Japan. *Abstracts of the 13th International Congress on Carboniferous-Permian, Kraków*, 1995, p. 102, 103. Polish Geological Institute, Warszawa.

Nemirovskaya, T.I., 1987: Konodonty nizhney chasti bashkirskogo yarusa Donbassa (Lower Bashkirian conodonts of Donets Basin). *Bulletin MOIP, Otdel Geology*, vol. 64, no. 4, p. 106-126, pls. 1, 2. (*in Russian with English abstract*)

Nemirovskaya, T.I. and Nigmadganov, I.M., 1993: Some new conodonts of the Mid-Carboniferous boundary deposits of middle Asia. *Jahrbuch der Geologischen Bundesanstalt*, vol. 136, p. 213-221, pls. 1, 2.

Nemirovskaya, T.I. and Nigmadganov, I.M., 1994: The Mid-Carboniferous Conodont Event. *Courier Forschungsinstitut Senckenberg*, no. 168, p. 319-333.

Nemirovskaya, T.I., Perret, M.F. and Meischner, D., 1994: *Lochriea ziegleri* and *Lochriea senckenbergica* - new conodont species from the latest Visean and Serpukhovian in Europe. *Courier Forschungsinstitut Senckenberg*, no. 168, p. 311-317, pls. 1, 2.

Nemirovskaya, T.I., Poletaev, V.I. and Vdovenko, M.V., 1990: The Kal'mius section, Donbass, Ukraine, U.S.S.R.: a Soviet proposal for the Mid-Carboniferous boundary stratotype. *Courier Forschungsinstitut Senckenberg*, no. 130, p. 247-272, pls. 1-5.

Nigmadganov, I.M. and Nemirovskaya, T.I., 1992: Mid-Carboniferous boundary conodonts from the Gissar Ridge, south Tienshan, middle Asia. *Courier Forschungsinstitut Senckenberg*, no. 154, p. 253-275, pls. 1-5.

Ramsbottom, W.H.C., Saunders, W.B. and Owens, B. *eds*, 1982: *Biostratigraphic Data for a Mid-Carboniferous Boundary*. 156 p. Subcommission on Carboniferous Stratigraphy, Leeds.

Rexroad, C.B., 1957: Conodonts from the Chester Series in the type area of southwestern Illinois. *Illinois Geological Survey Report Investigations*, no. 199, p. 1-43, pls. 1-4.

Rexroad, C. B., 1958: Conodonts from the Glen Dean Formation (Chester) of the Illinois Basin. *Illinois Geological Survey Report of Investigations*, no. 209, p. 1-27, pls. 1-6.

Rexroad, C.B. and Horowitz, A.S., 1990: Conodont paleoecology and multielement associations of the Beaver Bend Limestone (Chesterian) in Indiana. *Courier Forschungsinstitut Senckenberg*, no. 118, p. 493-537, pls. 1-3.

Rhodes, F.H.T., Austin, R.L. and Druce, E.C., 1969: British Avonian conodont faunas, and their value in local and intercontinental correlation. *Bulletin of the British Museum (Natural History) Geology Supplement 5*, p. 1-313, pls. 1-31.

Riley, N.J., Varker, W.J., Owens, B., Higgins, A.C. and Ramsbottom, W.H.C., 1987: Stonehead Beck, Cowling, north Yorkshire, England: a British proposal for the Mid-Carboniferous boundary stratotype. *Courier Forschungsinstitut Senckenberg*, no. 98, p. 159-177, pls. 1-

3.

Roundy, P.V., 1926 : Part II. The Micro-fauna : *In*, Roundy, P.V., Girty, G.H. and Goldman, M.I. *eds., Mississippian Formations of San Saba County, Texas. U.S. Geological Survey Professional Paper*, vol. 146, p. 5-23, pls. 1-4.

Rui, L., Wang, Z. and Zhang, L., 1987 : Luosuan-a new chronostratigraphic unit at the base of the Upper Carboniferous, with reference to the Mid-Carboniferous boundary in south China. *In*, Wang, C. *ed., Carboniferous boundaries in China*, p. 107-121, pls. 1, 2. Science Press, Beijing.

Sada, K., Hide, K. and Fujimoto, M., 1979 : Preliminary report of the stratigraphy and geologic structure of the Hina Limestone in Okayama Prefecture, Japan. *Studies in Environmental Science, Memoirs of the Faculty of Integrated Arts and Sciences 4, Hiroshima University*, vol. 4, p. 15-21. (*in Japanese with English abstract*)

Sano, H. and Kanmera, K., 1988 : Paleogeographic reconstruction of accreted oceanic rocks, Akiyoshi, southwest Japan. *Geology*, vol. 16, p. 600-603.

Savage, N.M. and Barkeley, S.J., 1985 : Early to Middle Pennsylvanian conodonts from the Klawak Formation and the Ladrones Limestone, southwestern Alaska. *Journal of Paleontology*, vol. 59, no. 6, p. 1451-1475.

Scott, H.W., 1942 : Conodont assemblages from the Heath Formation, Montana. *Journal of Paleontology*, vol. 16, no. 3, p. 293-300, pls. 37-40.

Stanley, E.A., 1958 : Some Mississippian conodonts from the high resistivity shale of the Nancy Watson no. 1 well in northeastern Mississippi. *Journal of Paleontology*, vol. 32, no. 3, p. 459-476, pls. 63-68.

Stibane, F.R., 1967 : Conodonten des Karbons aus den nordlichen Anden Sudamerikas. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, Bd. 128, p. 329-340, pls. 35-37.

Thompson, T.L., 1970 : Lower Pennsylvanian conodonts from McDonald County, Missouri. *Journal of Paleontology*, vol. 44, no. 6, p. 1041-1048, pl. 139.

Varker, W.J., Owens, B. and Riley, N.J., 1990 : Integrated biostratigraphy for the proposed Mid-Carboniferous boundary stratotype, Stonehead Beck, Cowling, north Yorkshire, England. *Courier Forschungsinstitut Senckenberg*, no. 130, p. 221-235, pls. 1, 2.

Varker, W.J. and Sevastopulo, G.D., 1985 : Conodonts of the Dinantian Subsystem from Great Britain and Ireland, part 1 of The Carboniferous System. *In*, Higgins, A.C. and Austin, R.L. *eds., Stratigraphical Index of Conodonts*, p. 167-209, pls. 5.1-5.6. The British Micropalaeontological Society, Ellis Horwood Limited, Chichester.

von Bitter, P.H. and Plint-Geberl, H.A., 1982 : Conodont biostratigraphy of the Codroy Group (Lower Carboniferous), southwestern Newfoundland, Canada. *Canadian Journal of Earth Sciences*, vol. 19, p. 193-221, pls. 1-7.

Wang, Z.H. and Higgins, A.C., 1989 : Conodont zonation of the Namurian-Lower Permian strata in south Guizhou, China. *Palaeontologia Cathayana*, no. 4, p. 261-325, pls. 1-17.

Wang, Z.H., Lane, H.R. and Manger, W.L., 1987a : Carboniferous and Early Permian conodont zonation of north and northwest China. *Courier Forshungsinstitut Senckenberg*, no. 98, p. 119-157, pls. 1-8.

Wang, Z.H., Lane, H.R. and Manger, W.L., 1987b : Conodont sequence across the Mid-Carboniferous boundary in China and its correlation with England and North America. *In*, Wang, C. *ed., Carboniferous boundaries in China*, p. 89-106, pls. 1-3. Science Press. Beijing.

Watanabe, K., 1975 : Mississippian conodonts from the Omi Limestone, Niigata Prefecture, central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 99, p. 156-171, pls. 14, 15.

Webster, G.D., 1969 : Chester through Derry conodonts and stratigraphy of northern Clark and Southern Lincoln Counties, Nevada. *University of California Publications in Geological Sciences*, vol. 79, p. 1-121, pls. 1-8.

Wirth, M. 1967 : Zur Gliederung des Höheren Paläozoikums (Givet-Namur) im Gebiet des Quinto Real (Westpyrenaen) mit Hilfe von Conodonten. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, vol. 127, p. 179-244, pls. 19-23.

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Shell microgrowth patterns of bivalves reflecting seasonal change of phytoplankton abundance

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Abstract. Seasonal patterns of shell microincrement growth in a venerid bivalve *Phacosoma japonicum* were analyzed for the three populations from Hakodate, Ariake, and Kagoshima Bays around the Japanese coasts. The northernmost Hakodate population in Hokkaido grew rapidly in a limited interval between late spring and summer. The number of microincrements within an annual increment in the specimens from this population was smallest (200-250 increments) among the three samples of populations examined, and each microincrement width was largest (0.25-0.3 mm) at the central part of an annual increment. By contrast, in the southernmost Kagoshima population in southern Kyushu, shell growth occurred slowly in a long term between early spring and fall. The specimens forming this population are characterized by having the narrowest microincrements (each 0.10-0.12 mm) and largest number of microincrements in the annual increment (300-350 increments). In this species, it has been confirmed that the growing season reflects the seasonal changes of phytoplankton abundance. The phytoplankton bloom usually occurs in spring in embayments of northern Japan and in summer in those of central and southern Japan. In Ariake Bay (central Kyushu), however, the phytoplankton becomes most abundant in winter and remains at low levels in the other seasons. The Ariake population of *P. japonicum* showed the most active growth in intervals between winter and early spring. In this sample, the microincrement width attained a maximum in the earlier portion of each annual increment, and the annual increment showed a particularly right-skewed pattern which reflects the winter phytoplankton bloom in this bay.

Key words: Bivalve, *Phacosoma japonicum*, Phytoplankton bloom, Shell microgrowth analysis

Introduction

Shell microgrowth analysis is a useful method for ecological research of extant and fossil molluscs, because microgrowth increments preserve information about environmental and physiologic conditions (Rhoads and Pannella, 1970; Kennish, 1980; Lutz and Roads, 1980; Jones, 1983). In the venerid bivalve *Phacosoma japonicum* treated in this paper, it has been confirmed that winter and spawning breaks are formed annually in the shell microgrowth pattern, and that they can be used to estimate the age of sexual maturity and shell growth rate in extant and fossil samples (Tanabe, 1988; Tanabe and Oba, 1988; Sato, 1994, 1995, 1996).

Growth and reproduction of bivalves are generally influenced by a number of environmental factors such as water temperature, salinity, and food availability. Sato (1998) suggested that monthly shell growth pattern and reproductive cycles of *P. japonicum* are strongly influenced by seasonal change of food availability, represented by phytoplankton abundance. Shell microgrowth analysis is useful to reconstruct the seasonal change of shell growth, so that it will be possible to estimate the seasonal change of phytoplankton abundance based on shell microgrowth analysis of fossil specimens.

In this study, to delineate the relationship between shell microincrement growth patterns and the seasonal change of phytoplankton abundance, seasonal patterns of shell microincrement growth in *P. japonicum* were analyzed for three populations around the Japanese coasts.

Material and methods

Seasonal changes of shell microincrement growth were examined for the samples from the subtidal sand flat of Kamiiso Coast, Hakodate Bay, southern Hokkaido (41°49′N, 140°42′E) and the intertidal sand flats of Nagahama Coast, Ariake Bay, central Kyushu (32°41′30″N, 130°33′30″E) and of Shigetomi Coast, Kagoshima Bay, southern Kyushu (31°42′30″N, 130°38′E) (Figure 1). Living individuals were collected monthly from Ariake and Kagoshima Bays during January-September, 1995, and those from Hakodate Bay were sampled on several occasions from September, 1991 to March, 1996 (Figure 1). Seasonal change of shell microgrowth patterns were analyzed for three-year-old specimens from each locality.

Shell microgrowth patterns were also examined for the samples from the other ten localities around the Japanese coasts (Figure 1). Of the ten samples, the two samples from

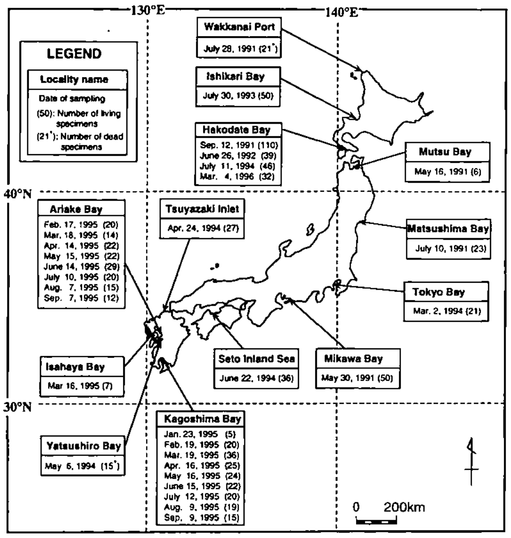


Figure 1. Locations and dates of collection for samples of *Phacosoma japonicum* treated in this paper. Number in parentheses shows the sample size.

Wakkanai Port and Yatsushiro Bay consist only of dead specimens, whereas those from the other eight localities are represented by living animals. Also, in Wakkanai Port and Ishikari and Hakodate Bays, animals from the subtidal zone were recovered from commercial port landings, and at the other localities, those from the intertidal zone were sampled manually at low tide.

To examine the shell microgrowth patterns, a single valve from each specimen was sectioned from the umbo to the ventral margin along the axis of maximum growth. The sectioned valve was polished and etched with 5% acetic acid for 10 minutes, and then an acetate peel was prepared for each specimen by pressing a sheet of acetyl cellulose film named as "Bioden R. F. A." (34 μm in thickness, Oken Shoji Co., Ltd.) on the etched surface flooded with acetone. Growth increments in each acetate peel were viewed by means of a Nikon V-16 profile projector at magnification, ×100. The maximum width of each microincrement was measured successively from the umbo to the ventral margin using a digital micrometer (accuracy$\pm$1 μm) attached to the profile projector.

Seasonal changes of shell growth and gonad development in the Hakodate, Ariake and Kagoshima samples were also

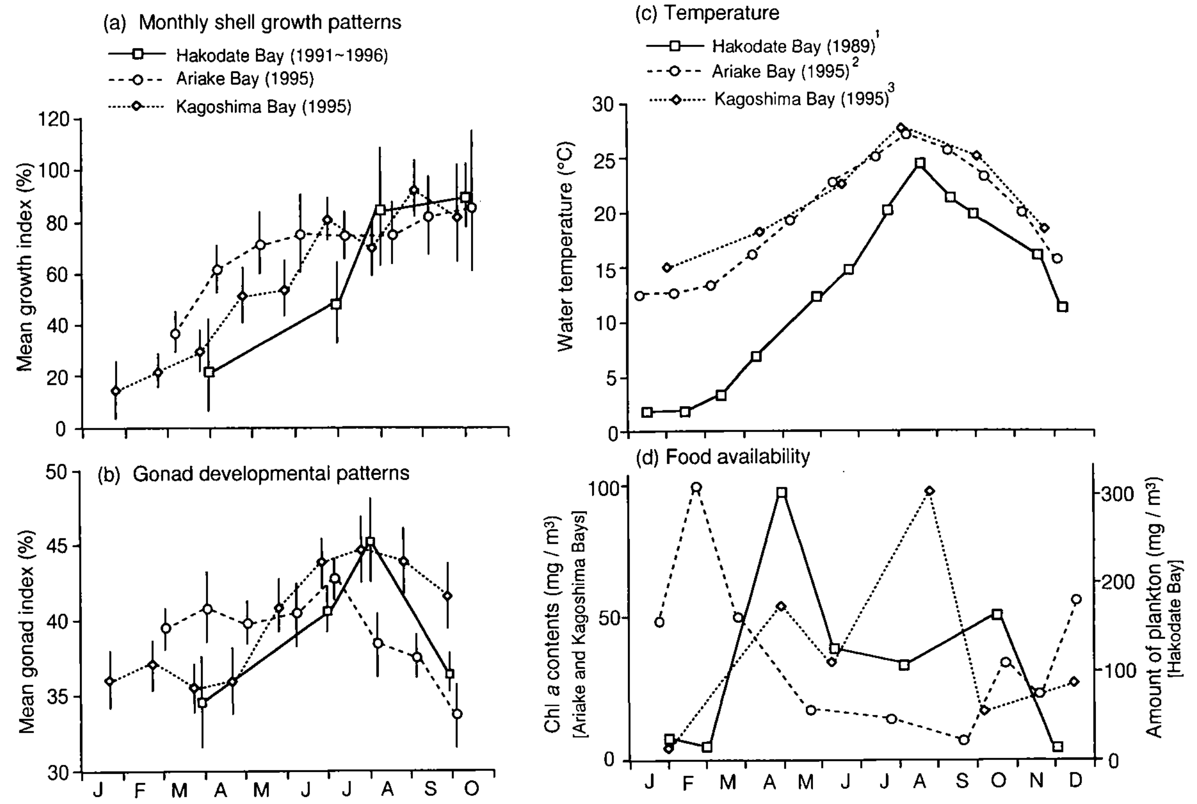


Figure 2. Seasonal changes of shell growth (a) and gonad development (b) in mature (>4 years old) specimens of *P. japonicum* from Hakodate, Ariake and Kagoshima Bays [mean value and the range of one standard deviation (vertical bar) are indicated], compared with annual variations of water temperature (c) and food availability (d) near the sampling localities. Sources of environmental data: (1) unpublished data of the Hokkaido Hakodate Fisheries Experimental Station in 1997, (2) unpublished data of the Kumamoto Prefectural Fisheries Research Station in 1997, (3) unpublished data of the Kagoshima Environmental Research and Service in 1997.

examined following the method described by Sato (1995, 1998). Gonad index [(gonad weight×100)/total soft body weight] and growth index [net growth (distance from last winter break to shell margin)/expected annual growth (distance from last winter break to expected next winter break)] were calculated in monthly collected samples. The extent of the expected annual growth for each individual was estimated using the Ford-Walford equation (Ford, 1933; Walford, 1946). The equation is expressed as

$$H_{R+1}=aH_R+b$$

where H_R is the shell height at the R th winter break (in mm), H_{R+1} is the shell height at the $R+1$ th winter break (in mm), and a and b are constants determined by a simple regression between H_R and H_{R+1} of different individuals of the same sample. Using this equation, shell height at the expected next winter break of each individual (H_{R+1}) can be estimated from shell height at the last winter break (H_R) and constants at each age class (a, b). Data of growth index and gonad index of the samples from Ariake and Kagoshima Bays were quoted from Sato (1998).

Results

Seasonal changes of growth and reproductive cycle in *P. japonicum* and some environmental factors

Figure 2 shows seasonal shell growth and gonad developmental patterns in the samples of *Phacosoma japonicum* from Hakodate, Ariake and Kagoshima Bays and the seasonal changes of some environmental factors near the sampling localities. This species exhibits distinct geographic variation in seasonal patterns of shell growth and reproductive cycles (Figure 2a, b). Shell growth and gonad development were active from February to April in the population of Ariake Bay. For example, mean gonad index of the sample from Ariake Bay had already increased at a high value (more than 40%) as early as April, although the gonad index reaches a maximum in June (Figure 2b). On the contrary, shell growth and gonad development occurred during June and July in the Hakodate Bay population and from April to August in the Kagoshima Bay population. In these samples, mean gonad index kept to low values (less than 40%) during January to April and then increased rapidly in May and June (Figure 2b).

Because Ariake Bay and Kagoshima Bay are adjacent to each other, seasonal changes of water temperature and salinity are similar between them (Figure 2c; Sato, 1998). However, they are markedly different in the seasonal abundance of phytoplankton. In Kagoshima Bay, the amount of phytoplankton increases from June to August (Figure 2d). In Ariake Bay, however, phytoplankton abundance attains a maximum from January to March. The phytoplankton bloom generally occurs in spring in embayments of northern Japan and in summer in those of central and southern Japan (Iizumi *et al*., 1990; Yamashita, 1982), so that the winter bloom in Ariake Bay is a very unique phenomenon in the Japanese coasts. Based on these data, Sato (1998) con-

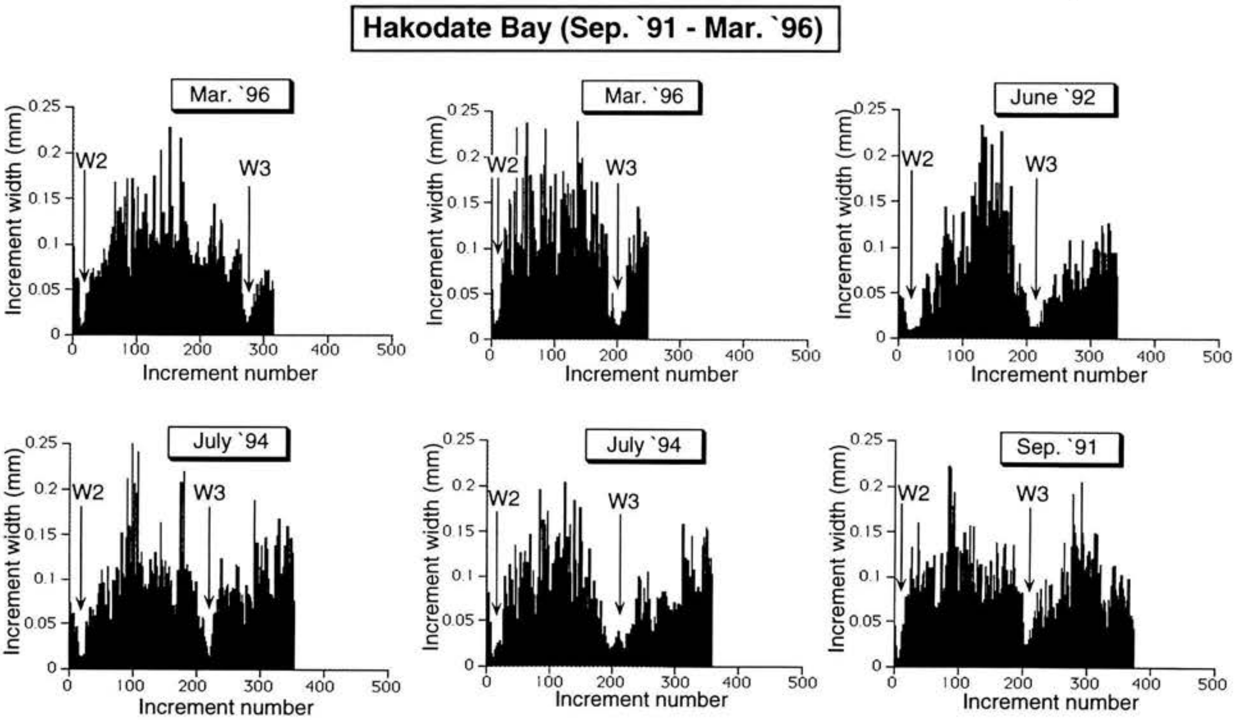


Figure 3. Shell microgrowth patterns from the 2nd winter break to shell margin in the six specimens of *P. japonicum*, each of which was collected from Hakodate Bay in March, 1996, June, 1992, July, 1994 and September, 1991 respectively. W2, W3: the 2nd and 3rd winter breaks which are fitted by eye, respectively.

cluded that growth and reproductive cycles of *P. japonicum* are primarily influenced by food availability not by water temperature.

Comparison of shell microgrowth patterns

Shell microgrowth patterns in the specimens from the three localities were examined and compared with each other. The specimens from each locality showed a similar growth pattern of microincrements. Shell microgrowth patterns in the selected three-year-old specimens from Hakodate, Ariake and Kagoshima Bays are shown in Figures 3 to 5.

The sample from Hakodate Bay

In the specimens from Hakodate Bay, a growth cessation mark represented by the discontinuity of the microincrement sequence is observed at the boundary between two annual increments (W2 and W3 in Figure 3). This cessation mark was caused by shell dissolution during the winter season (= winter break) (Tanabe, 1988), and in the specimens from this bay the winter break is clearer than in the other two bays. All of the specimens collected in March secreted fewer microincrements after the formation of the 3rd winter break than those collected in June and July. Each microincrement width rapidly increases in going from June to July and thereafter decreases in September. Thus it is suggested that the specimens in Hakodate Bay rapidly grow in a limited interval between late spring and summer, and in the other seasons they do not grow. Among the three samples examined, the number of microincrements within the 3rd annual increment is smallest (200-250 increments), and each microincrement width is largest (0.25-0.3 mm) at the central part of an annual increment.

The sample from Ariake Bay

In the specimens recovered from Ariake Bay, microincrements near the end of an annual increment are narrow and crowded, so that the winter break is usually obscure (Figure 4). Because rapid shell growth occurs between winter and early spring in this bay (Figure 2a), winter breaks appear to be formed in late fall or early winter. Comparison of the shell microgrowth patterns among monthly collected specimens also reveals that after passing the 3rd winter break, microincrement width rapidly increases in February, and then gradually decreases from April to September (Figure 4). Because microincrement width attains a maximum in February, the microincrement sequence within each annual increment shows a right-skewed pattern. In this sample, each microincrement width is narrow (0.15-0.25 mm), and the number of microincrements is considerably large in the 3rd annual increment (250-300 increments) compared with the Hakodate sample.

The sample from Kagoshima Bay

In the specimens from Kagoshima Bay, the microincrement width increased slowly after passing the 3rd winter break, and microincremental growth continued during a long interval between March and September (Figure 5). There-

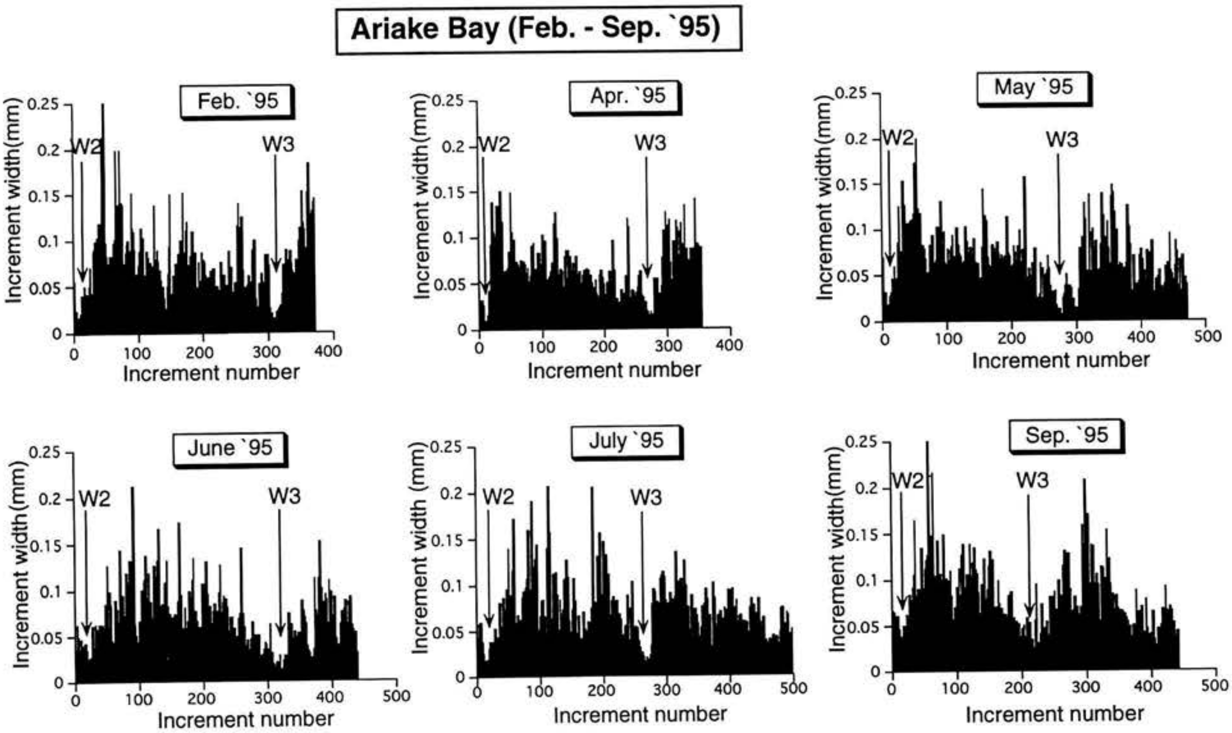


Figure 4. Shell microgrowth patterns from the 2nd winter break to shell margin in the six specimens of *P. japonicum*, each of which was collected from Ariake Bay in February, April, May, June, July and September, 1995 respectively. W2, W3 : the 2nd and 3rd winter breaks which are fitted by eye, respectively.

fore, the maximum microincrement width is smallest (0.10-0.12 mm), and the number of microincrements in the 3rd annual increment is largest (300-350 increments) among the three samples examined. In this sample, the maximum microincrement width appeared during May and June, so that each annual increment exhibited a symmetrical pattern.

Also, a clear interruption of microincrement growth appears in the central part of the 3rd annual increment (S.B. in Figure 5). This interruption proved to be the result of a spawning event (=spawning break) (Sato, 1995). Based on this break, the onset of sexual maturity in this sample can therefore be determined as two years old.

Three types of shell microgrowth patterns and their geographical range around the Japanese coasts

Comparison of the accretionary pattern of microincrements among the thirteen local samples of *Phacosoma japonicum* revealed the presence of three types; i.e. northern, southern and Ariake types (Figure 6). These three types can be distinguished on the basis of the difference in the shape of the shell microgrowth pattern in the 3rd annual increment.

The northern type is represented by the sample from Hakodate Bay. The accretionary pattern of microincrements in the 3rd annual increment has a very sharp peak at the central portion, because every microincrement widens rapidly in a limited interval between late spring and summer. Winter breaks are very clear because the ventral margin of each annual increment is partly dissolved in winter. Besides the Hakodate sample, the northern type includes all the samples from northern Japan; i.e. Wakkanai Port, Ishikari Bay (both in Hokkaido) and Mutsu Bay (northernmost Honshu). Ages of sexual maturity in those samples are at least four years, with maximum shell height of more than 6 cm (Table 1).

In the Ariake type typically represented by the sample from Ariake Bay, the accretionary pattern of microincrements in the 3rd annual increment is broad and right-skewed (Figure 6). Wide microincrements occurred during the limited interval between winter and early spring. Interestingly, this interval corresponds to the season of phytoplankton bloom occurrence (see Figure 2d). Specimens from Isahaya and Yatsushiro Bays also belong to this type. Age of sexual maturity of the Ariake-type specimens is four years, and maximum shell height of all samples in this type is more than 6 cm (Table 1).

The southern type is found in the specimens from Kagoshima Bay. The microincrement sequence in the 3rd annual increment is characterized by a symmetrical and low hillshape (Figure 6). Animals in Kagoshima Bay showed a remarkable growth in summer; the season of growth coincides with that of phytoplankton abundance. Therefore, the water temperature in growing season is much higher (20-30°C) than those of the other types (10-20°C). This kind of

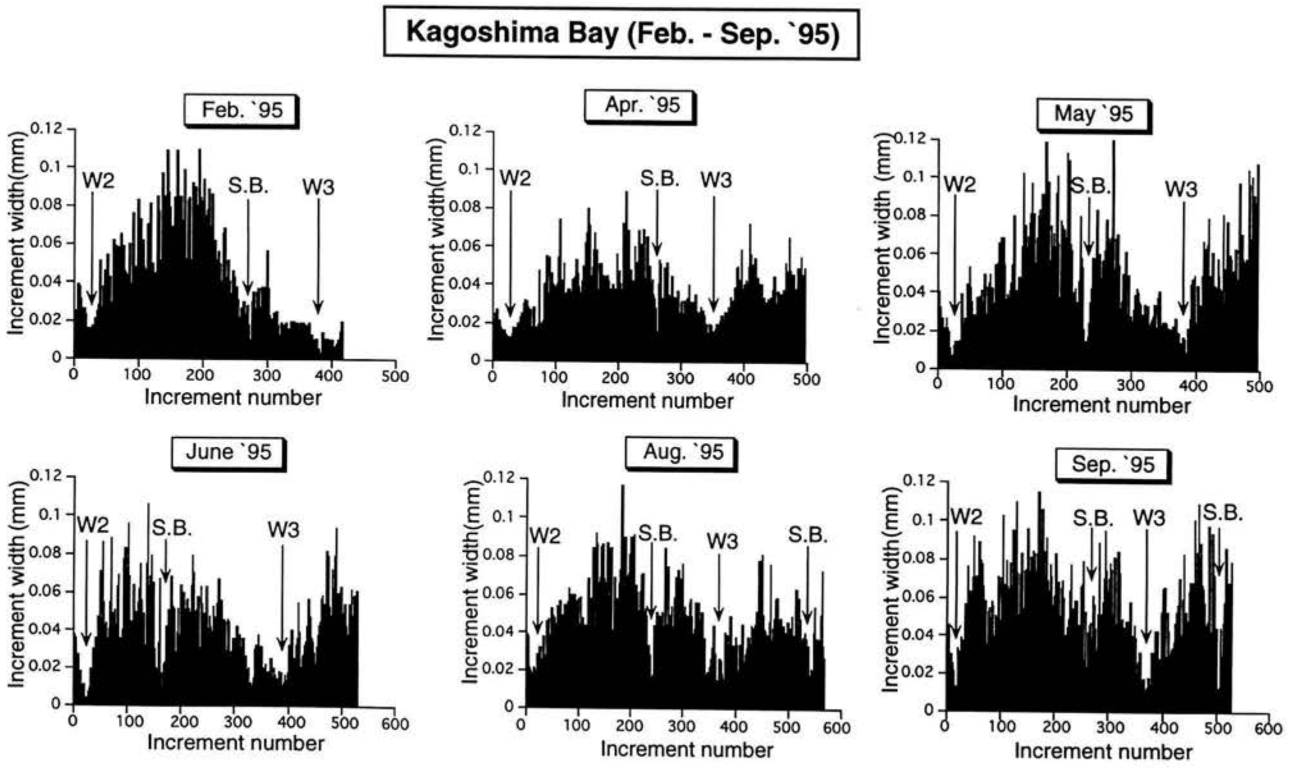


Figure 5. Shell microgrowth patterns from the 2nd winter break to shell margin in the six specimens of *P. japonicum*, each of which was collected from Kagoshima Bay in February, April, May, June, August and September, 1995 respectively. W2, W3, S.B.: the 2nd and 3rd winter breaks and spawning break which are fitted by eye, respectively.

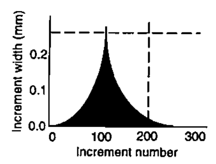
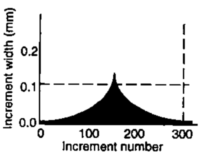
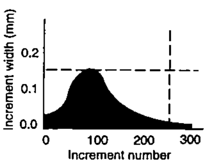
Types	Northern type	Southern type	Ariake type
localities of the populations	Wakkanai Port, Ishikari Bay, Hakodate Bay, Mutsu Bay	Matsushima Bay, Tokyo Bay, Mikawa Bay, Seto Inland Sea, Tsuyazaki Inlet, Kagoshima Bay	Ariake Bay, Isahaya Bay, Yatsushiro Bay
Maximum shell height	6.5 - 8.0 cm	4.6 - 5.8 cm	6.3 - 6.8 cm
Age of Sexual maturity	4 - 5 yrs	2 - 3 yrs	4 yrs
Growing season of this species	May - Aug.	Apr. - Sep.	Feb. - Apr.
Temperature in growing season	10 - 20 °C	20 - 30 °C	10 - 20 °C
Season of phytoplankton bloom occurs	Mar. - May	June - Aug.	Jan. - Feb.
Shape of shell microgrowth pattern in the 3rd annual increment			

Figure 6. Three shell microgrowth types recognized in the populations of *P. japonicum* around the Japanese coasts compared with the life history characteristics and environmental conditions of each type.

microincrement growth was widely recognized in the populations around the central to southern Japanese coasts including Matsushima Bay (northeastern Honshu), Tokyo and Mikawa Bays (both in central Honshu), Seto Inland Sea (Shikoku), Tsuyazaki Inlet and Kagoshima Bay (both in Kyushu). The geographical boundary between the populations showing northern-type and southern-type microincrement growth occurs between Mutsu Bay and Matsushima Bay (ca. 39°-40°N). Age of sexual maturity in the southern-type populations is at most three years, and maximum shell height of all samples in this type is less than 6 cm (Table 1). Therefore, the southern-type populations can also be clearly distinguished from the populations of the other two types by the differences in life-history traits such as age of sexual maturity and maximum shell height.

Table 1. Summaries of life history and shell microgrowth patterns of *P. japonicum* at each locality. Maximum asymptotic shell height were calculated by Gompertz equation (see Sato, 1994).

Locality	Latitude	Maximum asymptotic shell height (cm)	Age of sexual maturity (yrs)	Number of micro-increments within the 3rd annual increment	Microincrement width of the largest increments (mm)	Shape of the 3rd annual increment	Type
Wakkanai Port	45° 25' N	8.02	> 5	150 - 200	0.25 - 0.30	Symmetrical	Northern type
Ishikari Bay	43° 10' N	7.21	5	200 - 250	0.25 - 0.30	Symmetrical	
Hakodate Bay	41° 49' N	6.49	4	200 - 250	0.25 - 0.30	Symmetrical	
Mutsu Bay	40° 52' N	6.63	?	200 - 250	0.25 - 0.30	Symmetrical	
Matsushima Bay	38° 22' N	5.15	3	250 - 300	0.10 - 0.15	Symmetrical	Southern type
Tokyo Bay	35° 19' N	5.80	3	200 - 300	0.15 - 0.20	Symmetrical	
Mikawa Bay	34° 46' N	5.21	3	250 - 300	0.10 - 0.15	Symmetrical	
Seto Inland Sea	33° 58' N	4.95	3	250 - 350	0.10 - 0.15	Symmetrical	
Tsuyazaki Inlet	33° 47' N	5.37	3	250 - 300	0.15 - 0.20	Symmetrical	
Isahaya Bay	32° 52' N	6.34	4	250 - 300	0.15 - 0.25	Right skewed	Ariake type
Ariake Bay	32° 41' N	6.53	4	250 - 300	0.15 - 0.25	Right skewed	
Yatsushiro Bay	32° 37' N	6.86	?	250 - 300	0.15 - 0.25	Right skewed	
Kagoshima Bay	31° 42' N	4.61	2	300 - 350	0.10 - 0.12	Symmetrical	southern type

Discussion

This study revealed that the populations of *Phacosoma japonicum* around the Japanese coasts can be classified into the northern, southern and Ariake types based on the shell microgrowth pattern (Figure 6). The boundary between the northern- and southern-type populations of this species corresponds to the northern limit of the zoogeographic ranges of typical Japanese temperate-water species such as *Meretrix lusoria, Mactra veneriformis* and *Trapezium liratum* (Matsushima, 1984). Around the Japanese coasts facing the Pacific Ocean, these species do not live north of the Sanriku Coast (ca. 39°-40°N), where the water temperatures annually range from 8°C to 23°C (Tamura, 1966 ; Matsushima and Ohshima, 1974). *P. japonicum* is distributed in Mutsu Bay (ca. 40°N), but the shell microgrowth and life-history patterns in the northern-type populations markedly differ from those in the southern-type populations. These results suggest that the geographic boundary between 39°N and 40° N (annual range of water temperature from 8°C to 23°C) is a critical point reflected by the physiological conditions for many bivalve species living on the tidal flats.

The Ariake type included the samples from the three geographically neighboring bays in central Kyushu. Isahaya Bay is a small cove in Ariake Bay, so that seasonal change of phytoplankton abundance in this bay appears to be similar to that in the main part of Ariake Bay. In Yatsushiro Bay, phytoplankton bloom also occurred in winter (Tsuruta *et al.*, 1986). In summary, the growing season of *P. japonicum* is strongly influenced by the annual pattern of food (phytoplankton) abundance, and shell microgrowth patterns preserve well seasonal changes of phytoplankton abundance. Therefore, shell microgrowth analysis of fossil bivalves is expected to be useful in reconstructing seasonal change of phytoplankton abundance in paleoembayments.

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References cited

Ford, E., 1933 : An account of the herring investigations conducted at Plymouth during the years from 1924-1933. *Journal of the Marine Biological Association of the United Kingdom*, vol. 19, p. 305-384.

Iizumi, H., Furuya, K., Takeuchi, I., Kutsuwada, K., Tada, A. and Kawaguchi, K., 1990 : Dynamics of nutrients and chlorophyll *a* at Otsuchi Bay : analyses of the data of monthly observation. *Otsuchi Marine Research Center Report*, no. 16, p. 63-65. (*in Japanese*)

Jones, D.S., 1983 : Sclerochronology : reading the record of the molluscan shell. *American Scientist*, vol. 72, p. 384-391.

Kennish, M.J., 1980 : Shell microgrowth analysis. *Mercenaria mercenaria* as a type example for research in population dynamics. *In*, Rhoads, D.C. and Lutz, R.A. *eds., Skeletal Growth of Aquatic Organisms*, p. 255-294. Plenum Press, New York.

Lutz, R.A. and Rhoads, D.C., 1980 : Growth patterns within the molluscan shell. *In*, Rhoads, D.C. and Lutz, R.A. *eds., Skeletal Growth of Aquatic Organisms*, p. 203-254. Plenum Press, New York.

Matsushima, Y., 1984 : Shallow marine molluscan assemblages of postglacial period in the Japanese islands-Its historical and geographical changes induced by the environmental changes. *Bulletin of Kanagawa Prefectural Museum*, no. 15, p. 37-109. (*in Japanese with English abstract*)

Matsushima, Y. and Ohshima, K., 1974 : Littoral molluscan fauna of the Holocene climatic optimum (5,000-6,000 y. B.P.) in Japan. *Quaternary Research*, vol. 13, no. 3, p. 135-159. (*in Japanese with English abstract*)

Rhoads, D.C. and Pannella, G., 1970 : The use of molluscan shell growth patterns in ecology and paleoecology. *Lethaia*, vol. 3, p. 143-161.

Sato, S., 1994 : Analysis of the relationship between growth and sexual maturation in *Phacosoma japonicum* (Bivalvia : Veneridae). *Marine Biology*, vol. 118, no. 4, p. 663-672.

Sato, S., 1995 : Spawning periodicity and shell microgrowth patterns of the venerid bivalve *Phacosoma japonicum* (Reeve, 1850). *The Veliger*, vol. 38, no. 1, p. 61-72.

Sato, S., 1996 : Life history of a venerid bivalve *Phacosoma japonicum* and its evolutionary implications. 85 p., Ph. D. thesis, University of Tokyo.

Sato, S., 1998 : Genetic and environmental control of growth and reproduction of *Phacosoma japonicum* (Bivalvia : Veneridae). *The Veliger*, (in press)

Tamura, T., 1966 : *Seedlings of Shallow Marine Animals*. 331 p. Koseisha Book Company, Tokyo. (*in Japanese*)

Tanabe, K., 1988 : Age and growth rate determinations of an intertidal bivalve, *Phacosoma japonicum*, using internal shell increments. *Lethaia*, vol. 21, p. 231-241.

Tanabe, K. and Oba, T., 1988 : Latitudinal variation in shell growth patterns of *Phacosoma japonicum* (Bivalvia ; Veneridae) from the Japanese coast. *Marine Ecology Progress Series*, vol. 47, p. 75-82.

Tsuruta, A., Ueno, S., Ohgai, M. and Yamada, M., 1986 : Study on the seasonal and horizontal distributions of phytoplankton communities in Yatsushiro Sea, using a cluster analysis. *Bulletin of the Japanese Society of Scientific Fisheries*, vol. 52, no. 11, p. 1947-1955. (*in Japanese with English abstract*)

Walford, L.A., 1946 : New graphic method of describing the growth of animals. *The Biological Bulletin*, vol. 90, p. 141-147.

Yamashita, T., 1982 : Seasonal change of plankton abundance in Ariake Bay. *Research Report of Fukuoka Prefectural Ariake Fishery Experimental Station in 1982*, p. 95-101. (*in Japanese*)

Paleontological Research, vol. 1, no. 4, pp. 267-273, 3 Figs., 30 December, 1997

Phylogenetic significance of a new cheilostome bryozoan species, *Dysnoetocella* ? *voigti* from the Upper Cretaceous Izumi Group in Shikoku, Japan

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Abstract. A new anascan cheilostome bryozoan species, *Dysnoetocella* ? *voigti*, is described from the Upper Cretaceous Izumi Group in the northwestern part of Shikoku Island, Japan. The zoarium is erect and unjointed, with subcylindrical multilamellar branches. Three types of fine structure are evident in the calcareous skeletal layers from well preserved specimens. The narrow frontal shields of the zooids show ontogenetic thickening, which suggests that the species is an anascan cryptocystidean. The zoarium, consisting of many zooid columns, is reminiscent of some Paleozoic trepostomes. Although the zooid column is sometimes found in the Ascophora, it also occurs rarely in the Anasca.

Key words: Bryozoans, Cheilostome, Izumi Group, Upper Cretaceous

Introduction

The Upper Cretaceous Izumi Group is distributed as a narrow belt about 300 km long stretching from the Izumi Mountains in the Kii Peninsula to Matsuyama City in the northwestern part of Shikoku Island (Matsumoto, 1954). In the Matsuyama area, some fossil localities of the Izumi Group yielding molluscan fossils such as *Inoceramus*, *Apiotrigonia*, *Steinmannella*, etc. are distributed. All of these fossils occur from the basal part of the group and indicate a Campanian age as defined by Tashiro *et al*. (1993).

The present bryozoan materials associated with many shell (bivalve) fragments were collected from an outcrop of the Yuyama basal conglomerate Member near Kuroya-ike (an artificial pond for agricultural use) located at Takano-cho, eastern Matsuyama City (Figure 1). Some Upper Permian fusulines such as *Yabeina* and *Schwagerina* have been reported by Sada (1975) from the limestone pebbles of the conglomerate in the same locality, but we were unable to find any Paleozoic fossil remains.

The oldest calcified cheilostome reported from the Jurassic Period is morphologically simple and has an encrusting colony with uniserially budded autozooids. Rigidly erect colonies with higher states of integration are known from Late Cretaceous and Cenozoic deposits (Cheetham and Cook, 1983). Voigt (1964) established a genus *Dysnoetocella* based on the specimen from the Montian or Dano-Montian stage in Belgium and Poland. The type species, *D. aenigmatica*, has a rigidly erect, multilamellar growth habit. He considered that this genus belongs to the Anasca, but further details of its systematic position are still obscure. He also compared the type species, *Dysnoetocella aenigmatica* Voigt, with an anascan *Conopeum* ? *damicornis* Canu and Bassler which has similar growth habit and zooid morphology.

In the present article, *Dysnoetocella* ? *voigti* sp. nov. is described, and its phylogenetic significance is discussed. This is the first descriptive report of Cretaceous bryozoan from Japan. Based on thin-section observations the fine skeletal structures are described in detail, although the original fine structures have been slightly damaged by diagenetic recrystallization and replacement (see Sandberg, 1975). The body cavities are completely filled with sparry calcite cement.

Systematic paleontology

Class Gymnolaemata Allman, 1856
Order Cheilostomata Busk, 1852
Suborder Anasca Levinsen, 1909
Genus **Dysnoetocella** Voigt, 1964

Type species.—*Dysnoetocella aenigmatica* Voigt, 1964

Generic diagnosis.—Zoarium dendroid, consisting of bilamellar axial zooecia and outer cumulating zooecia enveloping the axis. Axial zooecia large, slightly convex, with an oval aperture. Cumulating zooecia small, irregular and depressed. Ovicells and avicularia not observed.

Geological age.—Late Cretaceous (Campanian) ? to

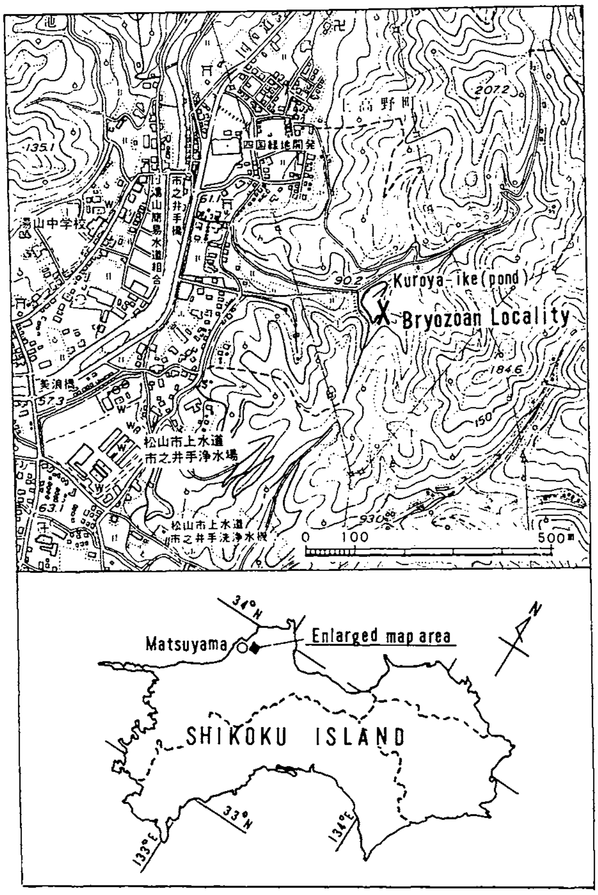


Figure 1. Locality map of bryozoan collections from the Izumi Group from "Matsuyama City" of the city planning map (scale: 1/10,000)

Early Tertiary (Montian or Dano-Montian).

Dysnoetocella? *voigti* sp. nov.

Figures 2-1—6, 3-1—10

Material.—Holotype: Reg. no. NSM-PA14018; Paratypes: Reg. nos. NSM-PA1401, NSM-PA14019, NSM-PA14020, NSM-PA14021, NSM-PA14022, NSM-PA14023, NSM-PA14024. All the specimens are stored in the Collections of National Science Museum (NSM) in Tokyo, Japan.

Description.—Zoarium erected without articulations, subcylindrical, branching dichotomously (Figures 2-1, 4), consisting of bilamellar zooecia which form a central axis and outer cumulating zooecia enveloping the axis. Each branch composed of two layers of back-to-back axial zooecia is initially flattened, and overgrown by approximately 20 zooid layers of cumulating zooecia at most, becoming subcylindrical and thick (Figures 2-2, 3). Bilamellar axial zooecia tubular, 0.34-0.49×0.14-0.20 mm in size; cryptocyst slightly convex, with a thickened superficial layer, extending one-quarter to one-third of the zooecial length from the proximal margin. Cumulating zooecia compressed, variable in size, commonly 0.44-0.54×0.26-0.32 mm; cryptocyst narrow and flat, occupying about one-third of the front, with a thickened superficial layer. Ancestrula, ovicell and avicularia are absent.

Remarks.—The colony of *Dysnoetocella*? *voigti* is large. The branches measure about 50 mm in length and 6 mm in diameter. Thin sections show well preserved internal structures. Although colonies can not be observed from frontal view because of the consolidated conglomerate, the morphological features of the calcareous frontal shield are important in taxonomic studies of cheilostomes. The zooecia, which have interzooidal communication organs in the lateral walls, demonstrate their cheilostomatous nature. Voigt (1964) considered that the genus *Dysnoetocella* belongs to the Anasca because of slight calcification of the frontal shield and the lack of an ascopore, and *Dysnoetocella*? *voigti* also lacks an ascopore. The encrusting base and ancestrula are not observed.

Occurrence and geological age.—The lowest horizon of the Yuyama conglomerate Member, which lies in the basal part of the Izumi Group. It is correlated to the Late Cretaceous Campanian age on the basis of the associated molluscan fossils (Tashiro *et al.*, 1993).

Fine structures of calcareous skeletal walls

The species produces two types of zooecia, namely, bilamellar axial and multilamellar outer zooecia. The branches are composed of 4 to 9 series of bilamellar axial zooecia initially (Figures 2-2, 3), and overgrown by multilamellar outer zooecia.

The axial zooecia, which are arranged in a brick-like pattern, are convex and slant distally upward (Figure 3-1). In longitudinal sections of the outer cumulating tissue (Figure 2-5), the multilamellar outer zooecia have a depressed box-shaped structure and differ in size. The total height of the zooecium is less than the axial one. The opecium is broad.

Dark-colored fibrous layer: —In transverse sections of the axial zooecia, dark-colored outermost skeletal layers of the basal and lateral walls are thin (about 20 μm) and evenly distributed (Figure 3-5). The fine structure of the wall is fibrous, and resembles a planar spherulitic ultrastructure which lies against the cuticle and consists of acicular calcite needles (Sandberg, 1983). However, no arrangement of the calcite crystals in wedge- or fan-shaped arrays (Sandberg, 1983) is evident, because the exterior surface of the skeleton can not be observed in thin sections. There is a possibility of significant ultrastructural changes that are not visible by light microscopy (see Sandberg, 1975).

Wavy lamellar layer: —The dark-colored outermost skeletal layers of the basal and lateral walls are overlain by wavy lamellar layers composed of 4 to 9 lamellae (Figure 3-5). Lateral tracing of each lamella is difficult. The lamellar layers are generally thicker than the dark-colored outermost skeletal layers and continuous with the frontal and transverse walls. This fine structure is considered to be a lamellar ultrastructure (Cheetham *et al.*, 1969) composed of numerous, superimposed thin calcitic layers. As Sandberg (1971) pointed out, the lamination observed appears to be large-

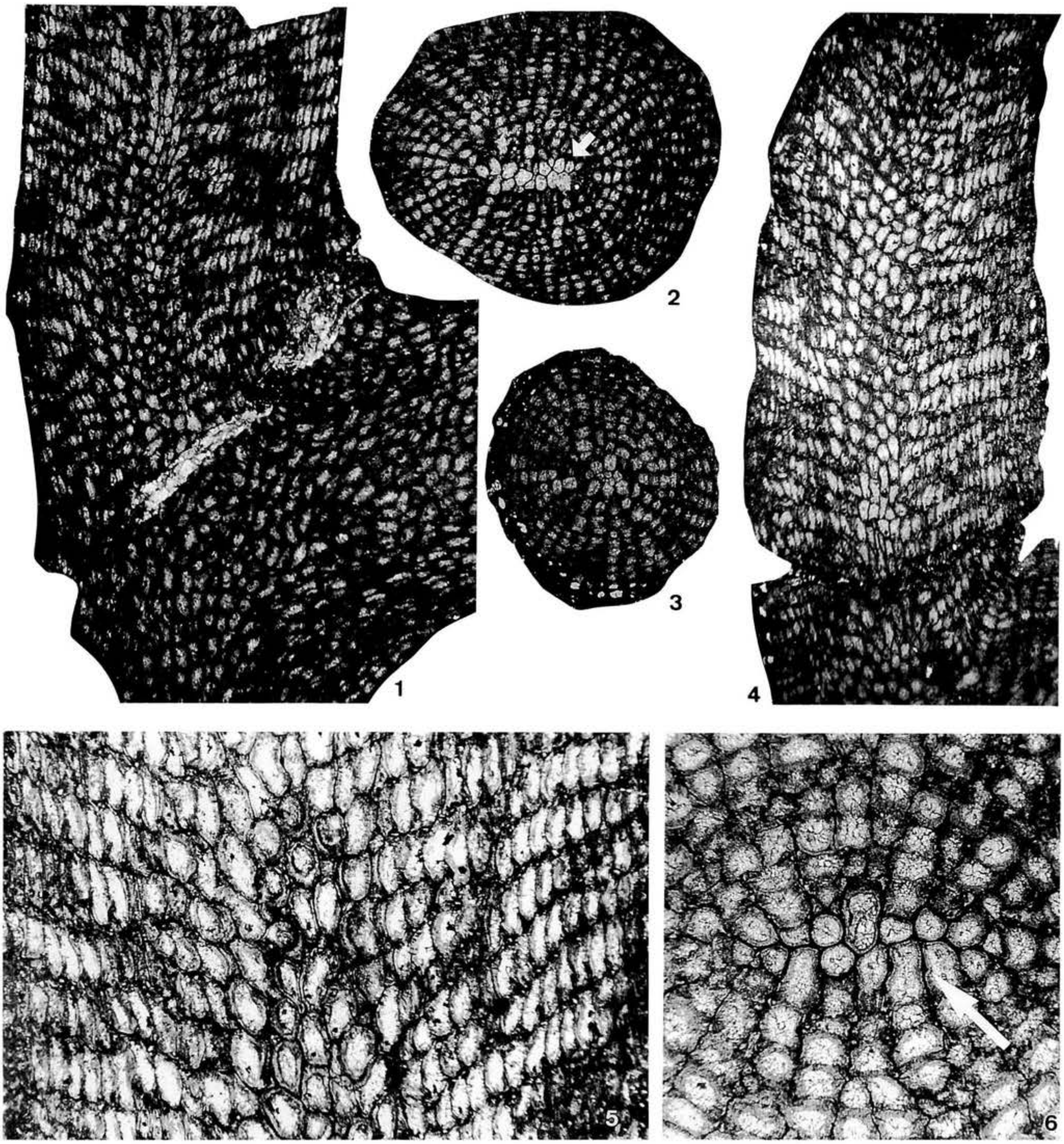
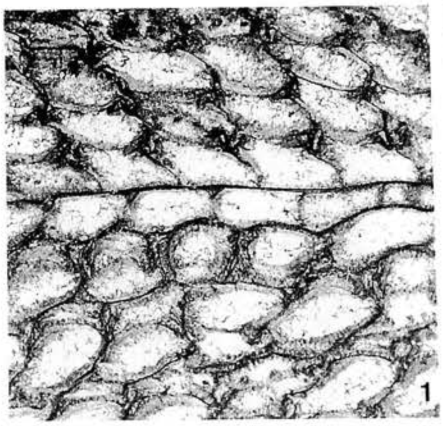


Figure 2. *Dysnoetocella*? *voigti* sp. nov. **1.** Longitudinal section of branch, ×10, NSM-PA14018. **2.** Transverse section of branch, showing bilamellar axial zooecia (arrow), ×10, NSM-PA14024. **3.** Transverse section of branch, ×10, NSM-PA14021. **4.** Longitudinal section of branch, ×10, NSM-PA14018. **5.** Axial and cumulating zooecia, distal toward top, ×20, NSM-PA14019. **6.** Transverse section of branch, showing bilamellar axial zooecia and interzooidal communication organs (arrow), ×30, NSM-PA14022.

scale lamination, each composed of finer lamellae.

Fibrous superficial layer: —The frontal shield of the cumulating zooecium, which occupies one quarter to one third of the total zooid length, is composed of two calcareous layers, the primary and superficial layers (Figure 3-4). The primary layer continuous with the lateral and transverse walls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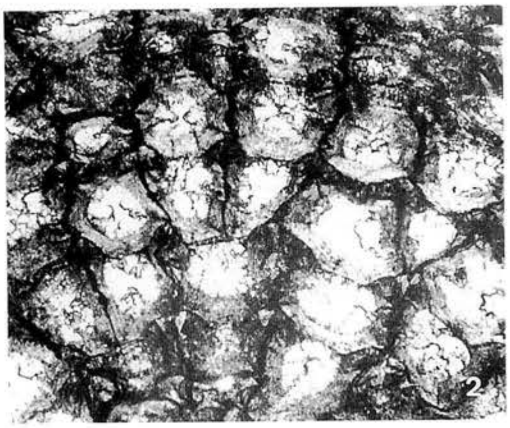
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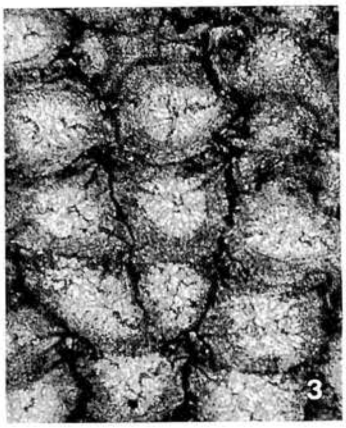
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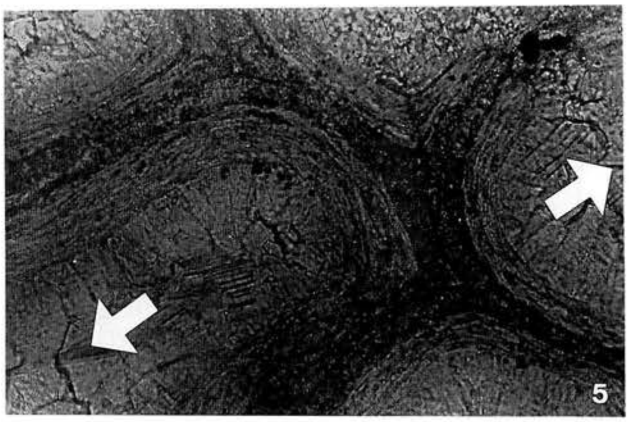
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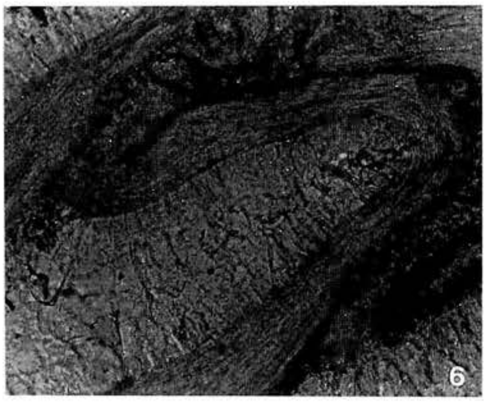
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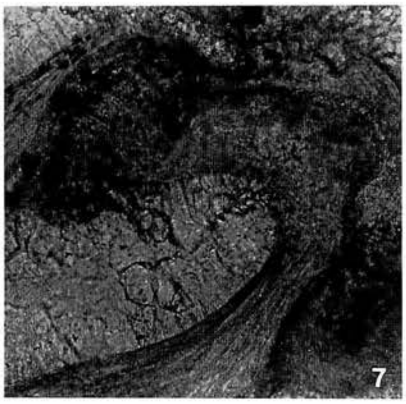
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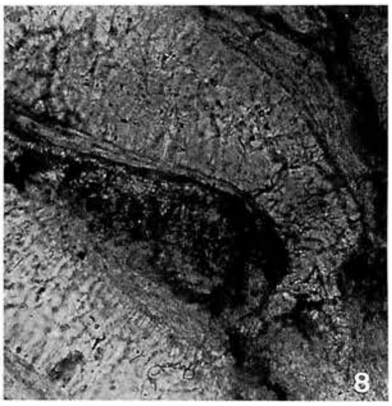
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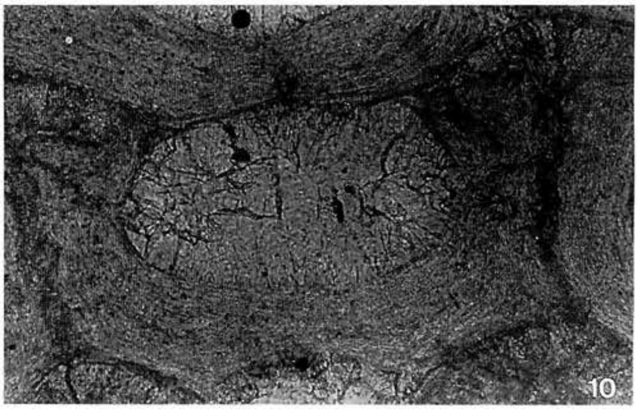
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is relatively thick, suggesting that calcareous deposition on the basal surface of the primary layer was not cut off by development of the ascus. The layer, which is smooth and laminated roughly parallel to the wall surface, has the same fine structure as the lamellar layers of the axial zooecia. There are also dark-colored thin skeletal layers between the lateral walls of adjacent zooecia (Figures 3-2, 3) like axial zooecia and between the transverse walls (Figure 3-4), but it appears that there are no dark-colored thin layers between the basal walls and the body cavities beneath, suggesting that the lateral and transverse walls are exterior and the basal walls interior.

The fibrous superficial layer that spreads over the primary layer and mural rim as a lamella, gradually thinning from the periphery to the center of the opesium, may begin exactly at the zooecial boundaries and spread distally (Figure 3-4). The fine structure of the fibrous superficial layer (Figures 3-7, 9) is somewhat similar to the conical bundles or clusters formed by acicular aragonitic crystals (see Sandberg, 1983). The calcification of the superficial layer is commonly heavy. This ontogenetic frontal thickening may occur after completion of the zooid. However, the time lag after which the superficial layer begins to develop on the upper surface of the primary layer is not known in *Dysnoetocella* ? *voigti*, as Sandberg (1971) has pointed out that "the time lag between calcification of the primary calcitic frontal and the beginning of superficial aragonite formation is quite variable among species".

In some cases, pores piercing the two frontal calcareous layers are observed near the proximal margin (Figures 3-4, 8).

Phylogenetic consideration of *Dysnoetocella*

The multilamellar zooecia are commonly as large as the axial ones in *Dysnoetocella* ? *voigti*, as in *Conopeum* ? *damicornis* Canu and Bassler from the Paleocene Midway Group in North America, which has a similar growth habit. However, the multilamellar zooecia in *Dysnoetocella aenigmatica* and *D. foliacea* Voigt are much smaller than the axial ones (Voigt, 1964, 1967). The axial zooecia are taller than the cumulating zooecia in *Dysnoetocella* ? voigti, as well as in *Dysnoetocella aenigmatica* and *D. foliacea*. In its growth form, *Dysnoetocella* ? *voigti* resembles *Heteroconopeum janieresiense* (Canu) from the Turonian age in France, but differs in its dimorphic zooecia like *D. aenigmatica* and has none of the small interopesial hollows that characterize the genera *Conopeum* and *Heteroconopeum* (Voigt, 1983).

In transverse section of axial zooecia, the lateral walls of the branch are breached to form interzooidal communication organs between adjacent axial zooecia (Figure 2-6). The lineal series of subsequently budded axial zooecia is partitioned by small interior transverse walls. The outermost skeletal layers and bounding cuticles of the lateral and basal walls are presumably continuous from zooid to zooid within a lineal series (Figure 3-1).

There are three to five dark round spots in the lateral wall of a cumulating zooecium. They are calcareous protuberances and considered to be communication organs (Figure 3-4), through which the cumulating zooids communicate with zooids at the same depth in adjacent zooid columns. A longitudinal section of cumulating tissue shows that the transverse walls separated by the dark-colored thin layers (Figure 3-4) are double, and different from those of axial zooecia, suggesting that the transverse walls are formed in a different way from the latter. Unlike axial zooecia, the calcareous lateral and basal walls of the cumulating zooecia are not continuous with those of the distal and proximal zooecia at the same depth in the colony (Figure 3-1). Therefore, the transverse walls which form a double-walled structure with the intercalated cuticle layer like lateral walls are considered to be exterior. It is thus clear that the cumulating zooid does not bud from the proximal one at the same depth in the colony.

The basal wall of cumulating zooecia is commonly thick in the distal half, and becomes thinner proximally. Some longitudinal sections show that there is a pore at the proximal end of the wall, which sometimes connects with a corresponding pore in the frontal shield of the zooecium beneath it (Figure 3-8). The superficial layer wraps the pore, but does not extend down into it. Voigt (1964) stated that in *Dysnoetocella aenigmatica* "every zooecium contains a hole in the bottom, leading into the next lower zooecium". It is therefore reasonable to infer that the cumulating zooid erupts and buds through the pore frontally. Each new daughter zooid has the same polarity as its parent. On the other hand, Voigt (1964) mentioned that cumulating zooecia increase by "budding out from the apertures" in *Dysnoetocella aenigmatica*. The cuticle layer is considered to be continuous from the parent zooid to the frontally budded daughter, but the calcareous lateral and transverse walls are not continuous in *Dysnoetocella* ? *voigti*. The daughter zooid does not use the frontal shield of the mother as a calcareous basal wall, but deposits the calcareous basal wall over the frontal shield. Although "distal" is "frontal" in frontally budded zooids, we will refer to directions in cumulating zooids as if they are axial zooids after the manner of Banta (1972).

Because thin sections show accretion of fibrous calcareous deposits on the frontal side of the frontal shield, and according to Cheetham and Cook (1983) "gymnocysts cease to be deposited relatively early in zooid life and characteristi-

Figure 3. *Dysnoetocella* ? *voigti* sp. nov. **1.** Longitudinal section, bilamellar axial zooecia, distal to left, ×30, NSM-PA14020. **2.** Transverse section, zooid column bifurcation and skeletal fine structures, ×60, NSM-PA14024. **3.** Transverse section, zooid column bifurcation and skeletal fine structures, ×60, NSM-PA14022. **4.** Longitudinal section, distal to left, showing fibrous superficial layers (arrows), ×60, NSM-PA14019. **5.** Transverse section of bilamellar axial zooecia, showing dark-colored outermost and wavy lamellar skeletal layers; arrows indicate frontal direction, ×250, NSM-PA14022. **6.** Longitudinal section, distal to left, cryptocyst, ×250, NSM-PA14019. **7.** Longitudinal section, distal to left, fibrous superficial layer, ×250, NSM-PA14019. **8.** Longitudinal section, distal to left, ×250, NSM-PA14018. **9, 10.** Transverse sections of cumulating zooecia, wavy lamellar and fibrous superficial layer, ×250, NSM-PA14022.

cally remain relatively thin", the shield may not be a gymnocyst but a cryptocyst or an umbonuloid shield. Because the primary layer of the frontal shield has no dark-colored thin layer and resembles the cryptocysts of *Labioporella calypsonis* Cook and *Membranipora grandicella* (Canu and Bassler) (see Sandberg, 1983, Fig. 116 ; Sandberg, 1973, Fig. 13) in having lamellar layers around the distal end of the cryptocyst, the frontal shields are considered to be interior cryptocysts. Although thin sections demonstrate that the walls have neither condyles, characteristic of ascophoran cryptocystideans, nor opesiules through which the parietal muscles pass, characteristic of some anascan cryptocystideans, the species is considered to be an anascan cryptocystidean because of the narrow cryptocysts and development of the primary layers of the frontal shield.

The process of frontal budding of a cryptocystidean ascophoran species, *Shizoporella unicornis floridana* Osburn, was investigated in detail by Banta (1972). He observed that frontal budding is accomplished by swelling of the hypostegal coelom, and that the cryptocystal frontal wall of the mother zooid is the basal wall of the daughter. The cumulating zooids in *Dysnoetocella* ? *voigti* are considered to have budded frontally through the uncalcified pores at the proximal end of the basal wall. In comparison with a cryptocystidean ascophoran *Schizoporella unicornis floridana* (Banta, 1972), the vertical walls of the daughter are not continuous with that of the parent, and the daughter deposits a new interior basal wall on the frontal shield of the mother.

As the frontal budding proceeds, radial zooid columns separated by an intercalated cuticle develop. Commonly in most anascan multilamellar colonies, the zooids are overgrown by subsequent zooid layers (Nishizawa, 1985) and do not produce zooid columns.

According to Cheetham and Cook (1983) and Gordon and Voigt (1996), some anascans and ascophorans known from Late Cretaceous and Cenozoic deposits exhibit a variety of growth habits, complex frontal structures and colonial integration. The cryptocystidean anascan *Dysnoetocella* ? *voigti* is a complex anascan and similar to cryptocystidean ascophorans in frontal budding and ontogenetic thickening of the frontal shield.

What is the significance of frontal budding ? As Banta (1972) has pointed out, it does not result in increasing the number of zooids, because a daughter zooid buds from the mother except for the bifurcation of the zooid column, and the mother is buried under the daughter. However, the frontal budding of erect rigid colonies of *Dysnoetocella* ? *voigti* may increase the degree of structural support. The heavy ontogenetic thickening may indicate that frontal budding does not occur as soon as the cumulating daughter zooids are completed. Rigidly erect cheilostome colonies have a tendency to inhabit relatively deep sea areas with a low rate of sedimentation, little wave action and weak current, and the number of species decreases with increased depth (see Schopf, 1969). The Yuyama conglomerate Member contains only this species and no fragments of encrusting cheilostome colonies. Thus *Dysnoetocella* ? *voigti* is considered to have lived on a calm ocean floor using gravel and shells as substrates. In *Dysnoetocella* ? *voigti* colonies, replacement of old zooids may have been preferable to rapidly increasing the number of zooids in such a stable environment after deposition of the basal conglomerate, because most of the colony fragments are thickly developed branches, and no early bilamellar branches are found.

As frontal budding proceeds, the colony forms zooid columns separated by cuticles. In the zooid column, each zooecium is broader than the one beneath it. If the width is excessive, the mother zooid gives rise to two daughters and the zooid column bifurcates.

Although the daughter zooids which bud from the axial zooid are as large as those which bud from the cumulating zooids in *Dysnoetocella* ? *voigti*, the axial zooids produce many small cumulating zooids in *Dysnoetocella aenigmatica* and *D. foliacea*. The daughter zooecia at the point of bifurcation are narrow and distorted. There is an irregularly shaped dwarfed zooecium at the point of bifurcation in some cases. The zooecium is not considered to be an avicularium because of its inconsistent size and shape. Mostly one daughter is smaller than the other. The new column appears to arise by intercalation (Figures 3-2, 3) or bifurcation (Figure 3-2). In any event, the vertical walls between two daughters have a double-walled structure, and the mode of bifurcation is entirely different from that in *Schizoporella unicornis floridana*, separated by a single vertical wall (Banta, 1972).

Banta (1972) saw that "zooids overgrown by their own frontal buds soon undergo degeneration and brown body formation" in living specimens of *Schizoporella unicornis floridana*. The parent zooid of *Dysnoetocella* ? *voigti* may have degenerated and formed brown bodies as well as *S. unicornis floridana*, though the parent zooid communicated with its daughter through the pores piercing the frontal shield. A dark and irregularly spherical spot is frequent in the zooecium. Perhaps these spots are altered brown bodies (Figure 2-5).

Summary

1. A new anascan cryptocystidean species, *Dysnoetocella* ? *voigti*, is described from the Izumi Group in the northwestern part of Shikoku Island, Japan. This is the first Cretaceous bryozoan described from Japan. The rigidly erect colony shows high states of colonial integration.

2. The zooids communicate with lateral, distal and proximal zooids through interzooidal communication organs, demonstrating their cheilostomatous nature. Frontally budded daughter zooids also communicate with their mother through pores piercing the basal wall.

3. Although there is a possibility of diagenetic alteration, three types of fine structure of the calcareous skeletal layers are recognized in thin sections; a dark-colored fibrous structure in the outermost skeletal layers, a wavy lamellar structure in the lateral, basal and transverse walls and the primary layer of the cryptocyst, and a fibrous structure in the superficial layer of the cryptocyst. These structures are similar to some microstructures described in recent and fossil specimens.

Acknowledgments

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References cited

Banta, W.C., 1972: The body wall of cheilostome Bryozoa, V. Frontal budding in *Schizoporella unicornis floridana*. *Marine Biology*, vol. 14, p. 63-71.

Canu, F. and Bassler, R.S., 1920: North American Early Tertiary Bryozoa. *U.S. National Museum, Bulletin,* vol. 106, p. 1-879, pls. 1-162.

Cheetham, A.H. and Cook, P.L., 1983: General Features of the Class Gymnolaemata. *In*, Robinson, R.A. *ed., Treatise on Invertebrate Paleontology, Part G, Bryozoa Revised*. p. 138-207, Geological Society of America and University of Kansas Press.

Cheetham, A.H., Rucker, J.B. and Carver, R.E., 1969: Wall structure and mineralogy of cheilostome bryozoan *Metrarabdotos. Journal of Paleontology*, vol. 43, p. 129-135, pl. 1.

Grodon, D.P. and Voigt, E., 1996: The kenozooidal origin of the ascophorine hypostegal coelom and associated frontal shield. *In*, Gordon, D.P., Smith, A.M. and Grant-Mackie, J.A. *eds*., *Bryozoans in Spece and Time*, p. 89-107. Nation Institute of Water and Atmospheric Research Ltd., Wellington.

Matsumoto, T., 1954: *The Cretaceous System in the Japanese Island*. 324 p., Japan Society for the Promotion of Science, Tokyo.

Nishizawa, Y., 1985: Multilaminar colonies of bryozoans from Japan. I. "Ectoproctalith" of *Antropora tincta* (Hastings). *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 137, p. 19-24.

Sada, K., 1975: On the fusulinid-bearing conglomerate in the city of Matsuyama, Shikoku. *Memorial Volume of Prof. G. Kojima, Hiroshima University*, p. 128-129. (*in Japanese*)

Sandberg, P.A., 1971: Scanning electron microscopy of cheilostome bryozoan skeletons; techniques and preliminary observations. *Micropaleontology*, vol. 17, no. 2, p. 129-151, pls. 1-4.

Sandberg, P.A., 1973: Degree of individuality in cheilostome Bryozoa: Skeletal criteria. *In*, Boardman, R.S., Cheetham, A.H. and Oliver, W.A. Jr. *eds., Animal colonies*, p. 305-315, Dowden, Hutchinson & Ross.

Sandberg, P.A.; 1975: Bryozoan diagenesis: bearing on the nature of the original skeleton of rugose corals. *Journal of Paleontology*, vol. 49, p. 587-606, pls. 1-4.

Sandberg, P.A., 1983: Ultrastructure and skeletal development in cheilostome Bryozoa. *In*, Robinson, R.A. *ed., Treatise on Invertebrate Paleontology, Part G, Bryozoa Revised*, p. 238-286. Geological Society of America and University of Kansas Press.

Schopf, T.J.M., 1969: Paleoecology of ectoprocts (Bryozoans). *Journal of Paleontology*, vol. 43, p. 234-244.

Tashiro, M., Yamazaki, K. and Yamazaki, M., 1993: On some interesting fossil assemblage beds from the Izumi Group at Kagawa Prefecture and its adjacent areas. *Research Reports of Kochi University, Natural Science*, vol. 42, p. 29-38, pls. 1, 2. (*in Japanese with English abstract*)

Voigt, E., 1964: A Bryozoan fauna of Dano-Montian age from Boryszew and Sochaczew in central Poland. *Acta Palaeontologica Polonica*, vol. 6, no. 4, p. 419-498, pls. 1-16.

Voigt, E., 1967: Oberkreide-Bryozoen aus den asiatischen Gebieten der USSR. *Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg*, vol. 36, p. 5-95, pls. 1-34.

Voigt, E., 1983: Zur Biogeographie der europäischen Oberkreide-Bryozoenfauna. *Zitteliana*, vol. 10, p. 317-347.

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Biogeography of the genus *Neptunea* (Gastropoda : Buccinidae) from the Pliocene and the lower Pleistocene of the Japan Sea borderland

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Abstract. Fourteen species of *Neptunea* are listed from the Pliocene and lower Pleistocene of the Japan Sea borderland. Among them, *Neptunea* (*Neptunea*) *eos* (Kuroda), *N.* (*N.*) *hataii* Noda, and *N.* (*Golikovia*) *nikkoensis* Nomura are extinct. These species and a part of the *N. polycostata* stock in the Japan Sea suffered extinction before the end of the early Pleistocene. However, the *N. polycostata* stock survived in the Okhotsk and Bering Seas. On the other hand, *N. intersculpta* (Sowerby) and *N.* (*Barbitonia*) *arthritica* (Bernardi) are still living in the Japan Sea. This contrast is due to the Plio-Pleistocene records on the Pacific side and eurythermal ecology of *N. intersculpta* and *N. arthritica*.

Key words : Biogeography, Japan Sea, *Neptunea*, Pleistocene, Pliocene

Introduction

The buccinid genus *Neptunea* is a group of cold-water species now living in the Northwest Pacific, Arctic and North Atlantic oceans. The genus originated in the upper Eocene of North Kyushu and invaded the Arctic and north Atlantic basins after the opening of the Bering Strait during Pliocene time (MacNeil, 1965 ; Strauch, 1972).

Recently, Amano *et al.* (1996) found that some Ancistrolepidinae (Buccinidae) which occurred in the Japan Sea borderland during the Pliocene to early Pleistocene no longer live in the Japan Sea. Instead, they survive in the Okhotsk and Bering Seas. Amano *et al.* (1996) attributed this distributional pattern to the extinction of the Japan Sea population by glaciation after the early Pleistocene. The reason why the species of Ancistrolepidinae could not reinvade the Japan Sea is their non-planktotrophic larval life, the shallow sill depth, and the higher water temperature.

Neptunea (Neptuneinae) is phylogenetically close to the Ancistrolepidinae (Goryachev, 1987). However, *Neptunea* includes many more species than the Ancistrolepidinae. Moreover, the neptuneid species have various depth ranges in contrast with the deep-water ancistrolepidines. Therefore, the genus is suited for confirming the cause of extinction observed in the Ancistrolepidinae and for examining the relationship between the depth range and the extinction event.

Up to this time, the following species and subspecies of *Neptunea* have been recorded from the Pliocene and lower Pleistocene strata of the Japan Sea borderland : *N. arthritica* (Bernardi), *N. a. asamusi* Nomura and Hatai, *N. a. hirosakiensis* Iwai, *N. eos* (Kuroda), *N.* (Sulcosipho) *hataii* Noda, *N. intersculpta* (Sowerby), *N. i. pribiloffensis* (Dall), *N. i. urataensis* Noda, *N.* aff. *intersculpta* (Sowerby), *N. iwaii* Hatai, Masuda and Suzuki, *N. lyrata* (Gmelin), *N. modesta* (Kuroda), *N. nikkoensis* Nomura, *N. rugosa* Golikov, *N. sakurai* (Ozaki), *N. soluta* (Hermann), *N. uwasoensis* Otuka, *N. vinosa* (Dall) and *N. vinosa* (Dall) var. (Hatai and Nisiyama, 1952 ; Masuda and Noda, 1976 ; Ogasawara, 1977 ; Masuda *et al.*, 1981 ; Noda *et al.*, 1983 ; Ogasawara and Naito, 1983 ; Noda *et al.*, 1984 ; Ogasawara *et al.*, 1984 ; Matsui, 1985 ; Matsuura, 1985 ; Noda and Amano, 1985 ; Ogasawara *et al.*, 1986 ; Amano *et al.*, 1989 ; Akamatsu and Suzuki, 1990, 1992 ; Nakata and Amano, 1991 ; Amano and Sato, 1995). However, some taxonomic problems exist among the above-recorded species because the fossil species were described on one or a few ill-preserved type specimens and insufficiently compared with one another.

In this paper, firstly, I revise the taxonomy of *Neptunea* by comparing the described specimens with allied species in detail. Secondly, I will discuss the historical biogeography of the group.

Subdivision of *Neptunea*

The genus *Neptunea* is subdivided into three subgenera : *Neptunea* (s.s.), *Barbitonia* and *Golikovia* (Habe and Sato, 1972 ; Tiba and Kosuge, 1988). The subgenus *Golikovia* is characterized by a smooth later stage, sculpture being confined to the early whorls, and it differs from *Neptunea* (s.s.) in having two marginal teeth on its radula. The outer lip with crenulations on its inner side distinguishes *Barbitonia*

Table 1. Taxonomic subdivision of *Neptunea* by Goryachev (1987).

Neptunea intersculpta stock
(1) *N. intersculpta* group
N. intersculpta (Sowerby)
(2) *N. contstricta* group
N. constricta (Dall), *N. varicifera* (Dall), *N. lamellosa* Golikov

Neptunea lyrata stock
(1) *N. lyrata* group
N. lyrata (Gmelin), *N. stielesi* Smith
(2) *N. beringiana* group
N. beringiana (Middendorff), *N. ventricosa* (Gmelin)
(3) *N. communis* group
N. communis (Middendorff), *N. denselirata* Broegger
(4) *N. despecta* group
N. despecta (Linnaeus)
(5) *N. antiqua* group
N. antiqua (Linnaeus), *N. contraria* (Linnaeus)

Neptunea polycostata stock
(1) *N. polycostata* group
N. polycostata Scarlato, *N. laticostata* Golikov, *N. vinosa* (Dall), *N. amianta* (Dall) (syn. *N. insularis* (Dall), *N. pribiloffensis* (Dall))
(2) *N. bulbacea* group
N. bulbacea (Bernardi), *N. rugosa* Golikov
(3) *Golikovia* group
N. smirnia (Dall), *N. fukueae* Kuroda
(4) *N. arthritica* group
N. arthritica (Bernardi), *N. cumingi* (Crosse)

from the type species of *Neptunea*.

Based on Golikov's (1963) study of shape of the penis, radula, and egg capsule, Goryachev (1987) classified the genus *Neptunea* into the following three stocks: *N. intersculpta, N. lyrata*, and *N. polycostata*. Moreover, he subdivided each stock into many groups (Table 1). From the viewpoint of hard parts, the first stock has spiral cords intercalating with secondary cords. The second one is characterized by nearly equal strong ribs while the last has smooth or sculptured whorls with an angulated shoulder. Goryachev (1987) included *Barbitonia* and *Golikovia* in the last stock.

On the other hand, Nelson (1978) considered *Barbitonia* as an independent genus of Buccinulidae, mainly based on a unique microstructure shown by Togo (1974) and the sculpture of the early whorls. Moreover, *Sulcosipho* Dall, which was included in the family Melongenidae by Goryachev (1987), was treated as a subgenus of *Neptunea* by Nelson (1978). His classification is based largely on the pattern of spiral ribs, however, this character is variable in a population. As noted earlier, all species of *Barbitonia* have similar penis morphology and radula with other neptuneids.

Material and methods

Some new specimens were collected by hand from the following localities (Figure 1).

Loc. 1. Roadside cliff about 850m east of the pass between Kitaubushi and Kitakawaguchi, Teshio Town, northwestern Hokkaido; siltstone bearing many calcareous concretions; Pliocene Yuchi Formation.

Loc. 2. River bank about 2.5 km upstream of the Soibetsu River, Kuromatsunai Town, southwestern Hokkaido; fine- to medium-grained sandstone; lower Pleistocene Setana Formation.

Loc. 3. Outcrop about 1.5 km upstream of the Hosokomata-zawa, Kami-iso Town, southwestern Hokkaido; granule-bearing fine- to medium-grained sandstone; lower Pleistocene Tomikawa Formation.

Loc. 4. River-side cliff about 800 m upstream of the Chikagawa River, Mutsu City, Aomori Prefecture; medium-grained sandstone including pumice; lower Pleistocene Hamada Formation.

Loc. 5. River bank along the Yodo River, 200 m east of Ichinowatari, Kyowa Town, Akita Prefecture; sandy siltstone; Pliocene Tentokuji Formation.

Loc. 6. Roadside cliff near the Shohei Bridge of Kamikusatsu, Yawata Town, Yamagata Prefecture; siltstone; Pliocene Kannonji Formation.

Loc. 7. River bank along the Shinano River, 250 m northeast of Unoki, Ojiya City, Niigata Prefecture; conglomerate including mudstone pebbles; Pliocene Kawaguchi Formation.

Loc. 8. Riverside cliff upstream of the Iida River, Maki Village, Niigata Prefecture; siltstone; Pliocene Higashigawa Formation.

Loc. 9. Roadside cliff near Narao, Togakushi Village, Nagano Prefecture; muddy fine-grained sandstone; Pliocene Ogikubo Formation.

Loc. 10. Riverside cliff about 400 m upstream of the Urano-sawa, Nakajo Village, Nagano Prefecture; fine-grained sandstone; Pliocene Joshita Formation.

Loc. 11. Roadside cliff near Shimo-yukawa, Nanao City, Ishikawa Prefecture; siltstone; Pliocene Sakiyama Formation.

Loc. 12. River bank of the Sai River, 1.1 km upstream of the Okuwa Bridge, Kanazawa City, Ishikawa Prefecture; fine-grained sandstone; lower Pleistocene Omma Formation.

Above specimens are housed in the Joetsu University of Education (JUE). Besides these specimens, types stored at the following institutes and museums were taxonomically reexamined: Tohoku University (IGPS), Saito Ho-on Kai Museum of Natural History (SHM), University of Tsukuba (IGUT), University Museum of the University of Tokyo (UMUT), and Kyoto University (KUGM). Moreover, private collections by Dr. Nobuomi Matsuura of Shiramine-mura Dinosaur Museum and Mr. Masayuki Shimizu of Toyama Prefectural General Education Center were also examined.

In addition to my collections and the above reexaminations, I assessed the question of geographical distribution by a critical survey of the literature (Kanehara, 1937; Iwai, 1959, 1965; Sawada, 1962; Ogasawara *et al*., 1986; Akamatsu, 1984; Akamatsu and Suzuki, 1990, 1992).

In this paper, I use Goryachev's subdivision of the stocks in *Neptunea* (s.s.) as well as Tiba and Kosuge's concept of the subgenera. The Recent specimens show a wide range of variation, especially in height of spire and number of spiral ribs on a body whorl. I considered a shell shape and the number of ribs on the penultimate whorl to be important.

Systematic notes on extinct species

Family Buccinidae Rafinesque, 1815
Subfamily Neptuneinae Troschel, 1869
Genus ***Neptunea*** Roeding, 1798
Subgenus ***Neptunea*** s.s.

Diagnosis.—Shell large, fusiform, consisting of six to eight whorls; body whorl large, occupying half to four-fifths of shell height. Surface sculptured by one or some spiral ribs and occasionally by axial rounded ribs or axial thin varices. Inner side of outer lip smooth and without any crenulations observed in *Barbitonia*. Marginal teeth on radula number three to five.

Neptunea* (*Neptunea*) *eos (Kuroda, 1931)

Figures 2-4, 5, 7—9, 11a, b, 12

Chrysodomus eos Kuroda, 1931, p. 80, pl. 10, fig. 80.
Chrysodomus uwasoensis Otuka, 1935a, p. 510, fig. 3g.
Neptunea uwasoensis (Otuka), Otuka, 1935b, p. 869-870, pl. 54, fig. 75; Amano *et al*., 1989, p. 112-113, pl. 20, fig. 26.
Neptunea cf. *uwasoensis* (Otuka), Masuda *et al*., 1981, pl. 5, fig. 15; Ogasawara and Naito, 1983, p. 52-53, pl. 8, fig. 11.
Neptunea (*Neptunea*) *uwasoensis* (Otuka), Noda *et al*., 1983, p. 7, pl. 3, figs. 9a-b.
Neptunea eos (Kuroda), Amano and Sato, 1995, fig. 5-8.

Type specimen.—Holotype, KUGM JC no. 610043 (Figure 2-11a, b).

Type locality.—Sakae, Nakajo Village, Nagano Prefecture; Joshita Formation.

Remarks.—The present species is characterized by a rather small shell (diameter of holotype = 42.5 mm), an angulated shoulder, a blunt ridge just below the suture, one primary rib intercalating with three or four interstitial ribs on the flat area above the shoulder, three or four primary ribs with one interstitial rib below the shoulder of the penultimate whorl.

These characteristics are shared with *Chrysodomus uwasoensis* Otuka (1935a) (diameter of "holotype" = 33.2 mm) from the Pliocene Sakiyama Formation in Ishikawa Prefecture. Otuka (1935a) distinguished *N. uwasoensis* from *N. eos* by lacking an angulated shoulder. However, the penultimate whorl of the holotype and some topotypes have an angulated shoulder (Figure 3-11b). As there is no difference between *N. uwasoensis* and *N. eos*, the former is a synomym of the latter.

Nelson (1978) classified *N. uwasoensis* (= *N. eos*) as a species of the subgenus *Sulcosipho*. However, the present species lacks the diagnostic features of *Sulcosipho* such as a tabulated shoulder bounded by a raised, scaly spiral cord. As an angulated shoulder is sometimes observed in species of the *N. polycostata* stock, I tentatively assign *N. eos* to this stock.

Measurements (in mm).—

Specimens	Diameter	BR1)	PAR2)	IAR3)	SSR4)
KUGM JC no. 610043 holotype	42.5	3	1	3	+
UMUT CM no. 12434	33.2	4	1	3	+

1)Number of ribs below the shoulder of penultimate whorl. 2)Number of primary ribs above the shoulder of penultimate whorl. 3)Number of secondary ribs above the shoulder of penultimate whorl. 4)Subsutural ridge.

Neptunea* (*Neptunea*) *hataii Noda, 1962

Figures 2-10a, b; 3-10

Neptunea (*Sulcosipho*) *hataii* Noda, 1962, p. 230, pl. 16, fig. 16.

Type specimen.—Holotype, IGPS no. 79055 (Figure 2-10a, b).

Type locality.—Riverside outcrop along the Higashigawa River near Nakao, Matsunoyama Town, Niigata Prefecture.

Remarks.—The present species is described on the basis of one deformed specimen. It has an angulated shoulder with a keel and a surface sculptured by numerous weak spiral threads.

Noda (1962) classified this species in the subgenus *Sulcosipho*. However, the species lacks a tabulated narrow shoulder and the raised spiral cord on it which are important characters of *Sulcosipho*. It resembles *N. rugosa* Golikov, except for having numerous spiral ribs. Therefore, I think that this species belongs to the *N. polycostata* stock.

Subgenus ***Golikovia*** Habe and Sato, 1972

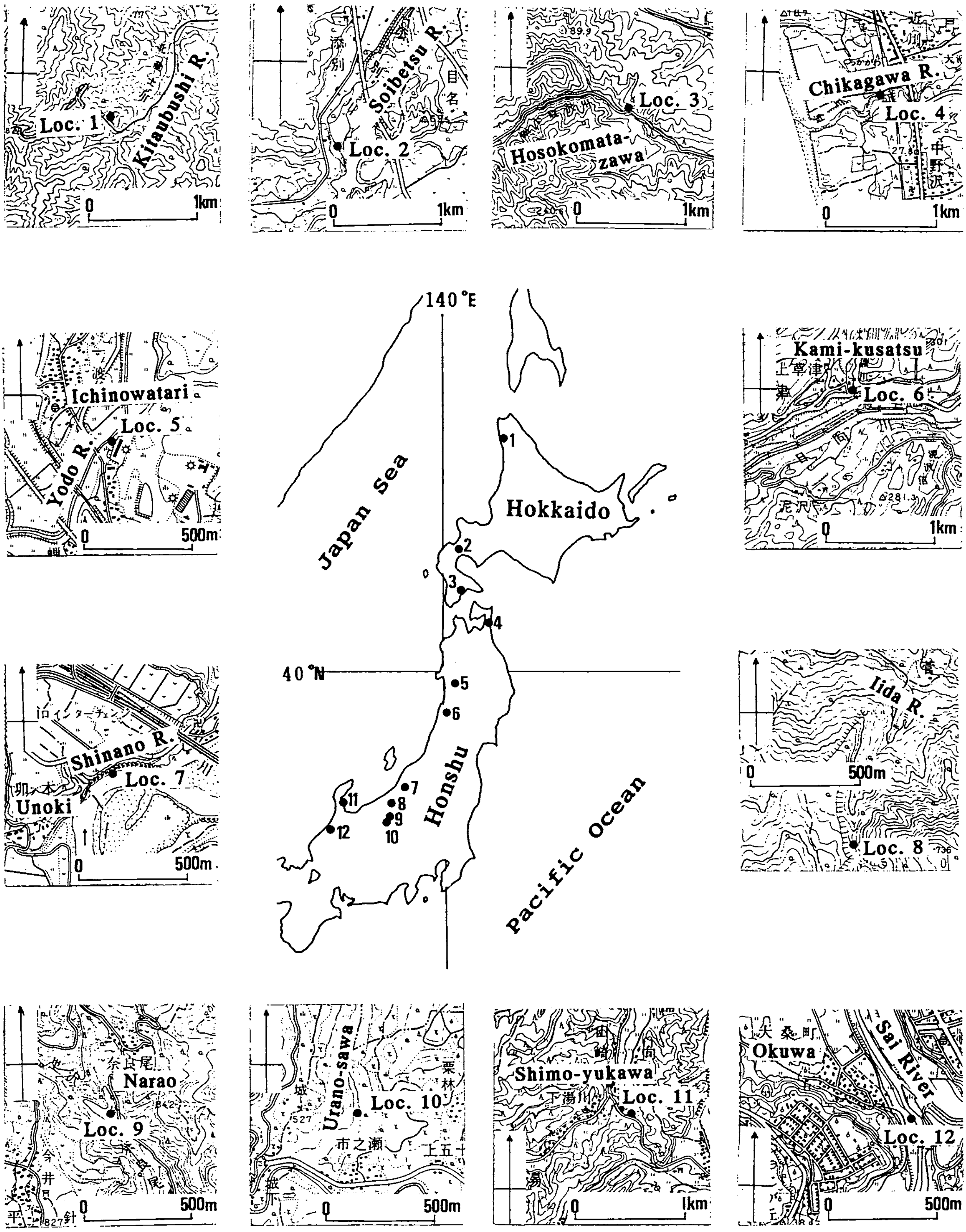
Diagnosis.—Shell small to medium in size, slender, fusiform. Shell surface sculptured by low, wide spiral ribs on early whorls, becoming obsolete on later whorls; body whorl smooth and polished. Inner side of outer lip smooth. Marginal teeth on radula number two.

Neptunea* (*Golikovia*) *nikkoensis Nomura, 1937

Figures 2-1, 2a, b, 6

Neptunea nikkoensis Nomura, 1937, p. 176-177, pl. 24, figs. 13a b; Noda, 1962, pl. 16, fig. 12; Ogasawara and Naito, 1983, p. 51-52, pl. 8, figs. 7, 13a, b; Ogasawara *et al*., 1986, pl. 29, figs. 8a b, pl. 49, figs. 18a, b; Nakata and Amano, 1991, pl. 7, figs.

Figure 1. Collecting localities of *Neptunea* (using the topographical maps of "Onoppunai", "Utasutsu", "Hakodate", "Chikagawa", "Osawa", "Koguchiseto", scale 1 : 50,000; "Ugo-Sakai", "Ojiya", "Yanagishima", "Togakushi", "Shinano-Nakajo" and "Kanazawa", scale 1 : 25,000 published by Geographical Survey Institute of Japan).


Loc. 1
Kitaubushi R.
0 1km
Soibetsu R.
Loc. 2
0 1km
Loc. 3
Hosokomata-zawa
0 1km
Chikagawa R.
Loc. 4
0 1km
Ichinowatari
Loc. 5
Yodo R.
0 500m
140°E
Japan Sea
Hokkaido
1
2
3
4
40°N
5
6
7
8
9
10
11
12
Honshu
Pacific Ocean
Kami-kusatsu
Loc. 6
0 1km
Shinano R.
Loc. 7
Unoki
0 500m
Iida R.
0 500m
Loc. 8
Narao
Loc. 9
0 500m
Urano-sawa
Loc. 10
0 500m
Shimo-yukawa
Loc. 11
0 1km
Okuwa
Sai River
Loc. 12
0 500m

8a b.

?*Neptunea arthritica hirosakiensis* Iwai, 1959, p. 50, pl. 1, figs. 17a, b; Iwai, 1965, p. 55, pl. 20, figs. 13a b.

Type specimen.—Holotype, SHM no. 12635 (Figures 2-2a, b).

Type locality.—Masuda, Yawata Town, Yamagata Prefecture.

Remarks.—The present species has a rather small, slender polished shell with a short and straight siphonal canal and an irregular suture. Early whorls are sometimes sculptured by 4-7 very weak ribs. Judging from the above characteristics, the present species can be included in the subgenus *Golikovia* as suggested by Nelson (1978).

Iwai (1959, 1965) proposed a new subspecies of *N. arthritica hirosakiensis* from the Pliocene Higashimeya Formation in Aomori Prefecture, based on one imperfect specimen. His figures show a slender shell and smooth surface lacking weak spiral ribs. I tentatively synonymize this subspecies with *N. nikkoensis*.

Comparison.—The present species is closely allied to *N.* (*G.*) *fukueae* Kira, 1959 which is now living in the Southwest Pacific-side of Japan. However, the latter differs from the former by its long and recurved siphonal canal.

N. (*G.*) *ennae* Sakurai and Tiba, 1969 is easily separated from the present one by having a more convex shell and very long siphonal canal.

Geographical distribution

The Pliocene and early Pleistocene species of *Neptunea* in the Japan Sea borderland are summarized in Table 2. Among these species, *N. iwaii* was established by Hatai, Masuda and Suzuki (1961), based on one specimen from the lower Pleistocene Hamada Formation in Aomori Prefecture. However, it is difficult to separate this species from *N. constricta* (Dall) by having low spiral ribs and five even fine spiral ribs just below the suture.

The distributional pattern of extant species in the tabulated list can be subdivided into three types (A-C types; Figure 4). The first species group (A type) does not live in the Japan Sea, but does so in the lower sublittoral to the upper bathyal zone of the Okhotsk and Bering seas, as do the Ancistrolepidinae (Golikov, 1963; Tiba and Kosuge, 1988; Table 3): *Neptunea lamellosa, N. insularis, N. vinosa* and *N. satura*. It is noteworthy that many species of the *N. polycostata* stock show this distributional pattern or suffered total extinction at the end of the early Pleistocene.

The second group of species (B type) now live in the Tatar Strait and off Primorie of Japan Sea as well as in the Okhotsk Sea (Golikov, 1963; Tiba and Kosuge, 1988): *Neptunea lyrata, N. bulbacea*, and *N. rugosa*. They live in the upper to lower sublittoral to bathyal zone (Golikov, 1963).

The third type (C type) of species are now dwellers of the Japan Sea: *Neptunea intersculpta, N. constricta*, and *N. arthritica*. They also survive on the Pacific side of Northeast Honshu and Hokkaido (Golikov, 1963; Tiba and Kosuge, 1988). Fossils of *N. intersculpta* and *N. arthritica* have been reported from the Pacific side of Northeast Honshu (see Figure 5 of Amano *et al.*, 1996).

The recent specimen of *N. sakurai* has been once illustrated from off Monbetsu, Northeast Hokkaido as *N. vinosa* by Okutani *et al.* (1988). However, as there is only one record, it is hard to determine which type this species should belong to.

Three extinct species (E type) occurred from the Pliocene fine-grained sediment of the Japan Sea borderland: *N. eos, N. hataii* and *N. nikkoensis*. These species might have lived mainly in the lower sublittoral zone.

Shaping of modern Japan Sea neptuneids

In the Pliocene, the extinct species *N. eos* and *N. nikkoensis* dominated the neptuneids of the Japan Sea borderland. In association with both species, some boreal populations of the *N. polycostata* stock and of *N. arthritica* were able to invade the Japan Sea because of cold climate and deep sill depth (Ogasawara, 1994; Tada, 1994).

Both A and E type species suffered extinction until the end of the early Pleistocene. On the other hand, C type species such as *N. arthritica* and *N. intersculpta* have been recorded from the middle Pleistocene Shibikawa and Anden formations in Akita Prefecture (Ogasawara *et al.*, 1986).

Ecologically, the C type species tolerates higher temperature of water than the stenothermal A type species (Golikov, 1963). From the stand point of sedimentology, Tada (1994) pointed out that bottom conditions started oscillating between oxic and anoxic along with glacioeustatic sea level change at 2.5 Ma. Possible causes of extinction of the A type species are warming during interglacial highstands as well as the brackish surface and euxinic bottom waters during glacial lowstands. The warm Tsushima current flowed into the Japan Sea during interglacials while the Japan Sea was enclosed during glacial periods. In the case of the A type species, the population of Okhotsk and Bering Seas survived during the deteriorated environments as did

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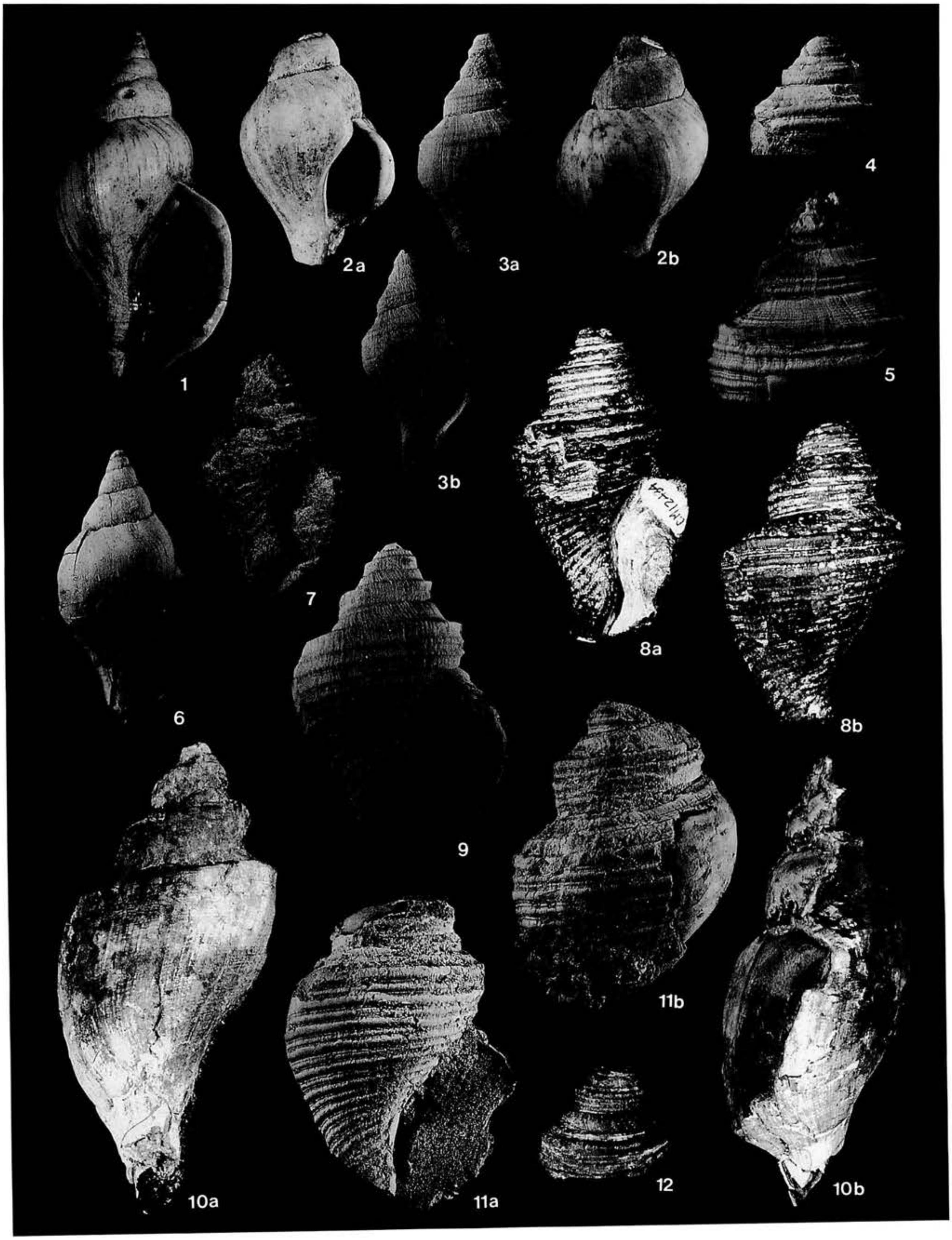
Figure 2. **1, 2, 6**: *Neptunea* (*Golikovia*) *nikkoensis Nomura*. 1; ×1, IGPS no. 97389-2, Kannonji Formation, collected by Ogasawara and Naito (1983). 2a b; ×1.5, SHM no. 12635, Kannonji Formation, Holotype. 6; ×1, JUE no. 15612, Loc. 5, Tenntokuji Formation. **3a, b**: *Neptunea* (*Neptunea*) *satura* (Martyn); ×1, JUE no. 15613, Loc. 7, Kawaguchi Formation. **4, 5, 7-9, 11, 12**: *Neptunea* (*Neptunea*) *eos* (Kuroda). 4; ×1, JUE no. 15614, Loc. 10, Joshita Formation. 5; ×1, JUE no. 15615, Loc. 11, Sakiyama Formation. 7; ×1.2, JUE no. 15266, Kuwae Formation, illustrated by Amano *et al.* (1989). 8a, b; x 1, UMUT CM no. 12434, Joshita Formation, "holotype" of *Neptunea uwasoensis* Otuka. 9; ×1, JUE no. 15616, Loc. 1, Yuchi Formation. 11a, b; ×1, KUGM JC no. 610043, Joshita Formation, Holotype. 12; ×1, UMUT CM no. 12650, Sakiyama Formation. **10a, b**: *Neptunea* (*Neptunea*) *hataii* Noda; ×0.8, IGPS no. 79055, Higashigawa Formation, Holotype described by Noda (1962) as *N.* (*Sulcosipho*) *hataii*.


1
2a
3a
2b
4
5
3b
7
8a
8b
6
9
10a
11a
11b
12
10b

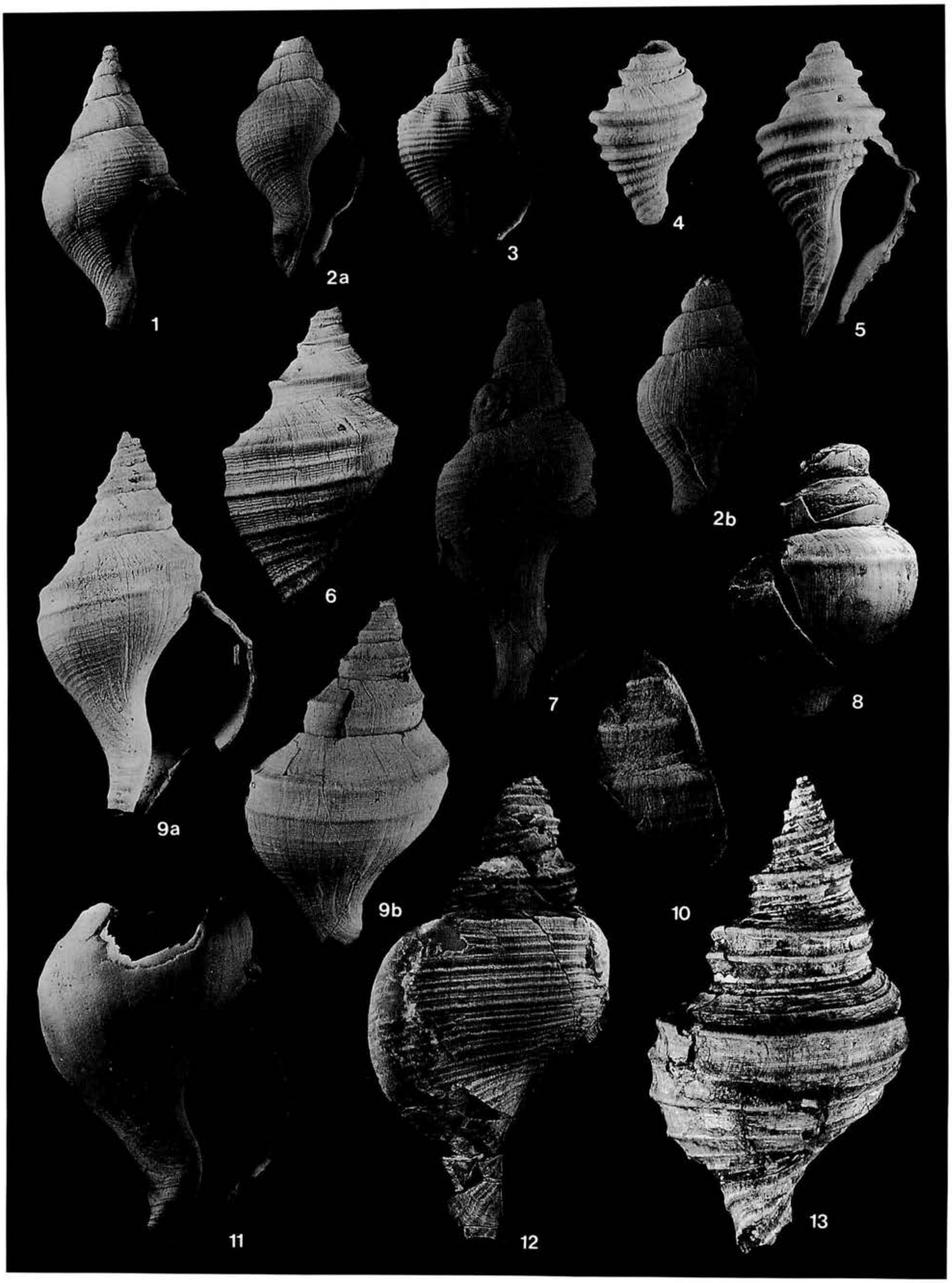

1
2a
3
4
5
6
7
2b
8
9a
9b
10
11
12
13

Table 2. Summarized list of *Neptunea* from the Pliocene and the lower Pleistocene of the Japan Sea borderland.

Genus ***Neptunea*** Roeding, 1798
Subgenus ***Neptunea*** s.s.
Neptunea intersculpta stock
N. intersculpta (Sowerby)* Poliocene: Tentokuji F.; Kannonji F.; Nagasawa F. (Figure 3-12); Yabuta F. C type**.
N. constricta (Dall)* Early Pleistocene: Hamada F., Setana F. Syn. *N. iwaii* Hatai, Masuda and Suzuki, 1961 ("holotype", Figure 3-7). C type.
N. lamellosa Golikov* Pliocene: Higashigawa F. (Loc. 8). Early Pleistocene: Hamada F. (Figure 3-9a, b). A type.
Neptunea lyrata stock
N. lyrata (Gmelin)* Pliocene: Yuchi F. (Figure 3-13). B type.
N. sakurai (Ozaki)* Early Pleistocene: Hamada F. (Figures 3-4, 5).
Neptunea polycostata stock
N. bulbacea (Bernardi)* Pliocene: Yuchi F. Early Pleistocene: Setana F. (Figure 3-11; Loc. 2). B type.
N. rugosa Golikov* Pliocene: Seguchi F. (Figure 3-8). B type.
N. insularis (Dall)* Pliocene: Mita F. (Figure 3-2a, b). Early Pleistocene: Tomikawa F. (Figure 3-1; Loc. 3). ? Syn. *N. intersculpta urataensis* Noda, 1962. A type.
N. vinosa (Dall)* Early Pleistocene: Shimonopporo F.; Tomikawa F.; Hamada F. (Figure 3-6; Loc. 4). A type.
N. satura (Martyn)* Pliocene: Kawaguchi F. (Figures 2-3a, b; Loc. 7). A type.
N. eos (Kuroda) Pliocene: Joshita F. (Figures 2-4, 11a, b; Loc. 10); Yuchi F. (Figure 2-9; Loc. 1); Kannonji F.; Kuwae F. (Figure 2-7); Mita F.; Sakiyama F. (Figures 2-5, 8a, b, 12; Loc. 11). Syn. *N. uwasoensis* (Otuka, 1935) ("holotype", UMUT CM no. 12434). E type.
N. hataii Noda Pliocene: Higashigawa F. (Figures 2-10a, b); Kannonji F. (Figure 3-11). E type.
Subgenus ***Barbitonia*** Dall, 1916
N. arthritica (Bernardi)* Pliocene: Yuchi F.; Nagasawa F.; Mita F. Early Pleistocene: Zaimokuzawa F.; Setana F.; Tomikawa F.; Daishaka F.; Omma F. (Figure 3-3; Loc. 12). C type.
Subgenus ***Golikovia*** Habe and Sato, 1972
N. nikkoensis Nomura. Pliocene: Kannonji F. (Figures 2-1, 2a, b); Tentokuji F. (Figure 2-6; Loc. 5); Kawaguchi F. (Loc. 7); Kurokura F.; Tomikura F.; Ogikubo F. (Loc. 9); ? Higashimeya F. E type.

*extant species **distributional type

Table 3. Bathymetric distribution of the extant neptuneids occurred from the Pliocene and lower Pleistocene of the Japan Sea borderland.

Species	Bathymetric range
A type	
N. lamellosa	57-550 m[1], 300-500 m[2]
N. satura	13-245 m[1]
N. insularis	230-1,000 m[1], 100-400 m[2]
N. vinosa	29-400 m[1], 30-100 m[2]
B type	
N. lyrata	16-1,724 m[1]
N. bulbacea	0.5-585 m[1]
N. rugosa	9-76 m[1]
C type	
N. intersculpta	36-895 m[1], 150-750 m[2]
N. constricta	20-468 m[1], 200-600 m[2]
N. arthritica	0-150 m[1], 0-20 m[2]

[1] Golikov (1963) [2] Tiba and Kosuge (1988)

the Ancistrolepidinae (Amano *et al.*, 1996). Because the distribution of E type species is confined to only the Japan Sea borderland, they became extinct.

There are two explanations for the distributional pattern of the B type species. First, the populations of B type species suffered extinction before the end of early Pleistocene. Later, perhaps in the Holocene, they reinvaded the cold water in the Tatar Strait and off Primorie through the northern water passages. The second explanation is a restriction of range after the middle Pleistocene. The main difference between the A and B type species is the depth at which they live. The B type species extend up to the upper sublittoral zone of the Okhotsk Sea (Golikov, 1963). Therefore, if the first hypothesis is accepted, it is easy to explain why the A type species was not able to reinvade the northern part of the Japan Sea through the shallow northern straits. Because the shallowest depth occurrence of the A type species is deeper than that of the B type species, the former

Figure 3. **1, 2**: *Neptunea* (*Neptunea*) *insularis* (Dall). 1; ×1, JUE no. 15617, Loc. 3, Tomikawa Formation. 2a, b; ×1, Mita Formation, collected by Mr. M. Shimizu. **3**: *Neptunea* (*Barbitonia*) *arthritica* (Bernardi); ×1, JUE no. 15618, Loc. 12, Omma Formation. **4, 5**: *Neptunea* (*Neptunea*) *sakurai* (Ozaki); 4, ×1.5, IGPS no. 102710-2; 5, ×1, IGPS no. 102710-1, Hamada Formation, illustrated by Hatai *et al.* (1961). **6**: *Neptunea* (*Neptunea*) *vinosa* (Dall); ×1, JUE no. 15619, Loc. 4, Hamada Formation. **7**: *Neptunea* (*Neptunea*) *constricta* (Dall); ×1, IGPS no. 93224, Hamada Formation, "holotype" of *N. iwaii* Hatai, Masuda and Suzuki, 1961. **8**: *Neptunea* (*Neptunea*) *rugosa* Golikov; ×1, JUE no. 15355, Seguchi Formation, illustrated by Nakata and Amano (1991). **9a, b**: *Neptunea* (*Neptunea*) *lamellosa* Golikov; ×1, IGPS no. 102711-2, Hamada Formation, identified as *N. vinosa* Dall var. by Hatai *et al.* (1961). **10**: *Neptunea* (*Neptunea*) *hataii* Noda; ×1, JUE no. 15620, Loc. 6, Kannonji Formation. **11**: *Neptunea* (*Neptunea*) *bulbacea* (Bernardi); ×1, JUE no. 15621, Loc. 2, Setana Formation. **12**: *Neptunea* (*Neptunea*) *intersculpta* (Sowerby); ×0.8, JUE no. 15363, Nagasawa Formation, illustrated by Nakata and Amano (1991) as "*N. intersculpta pribiloffensis* (Dall)". **13**: *Neptunea* (*Neptunea*) *lyrata* (Gmelin); ×0.8, IGUT no. 10992, Yuchi Formation, illustrated by Noda and Amano (1985).

cannot invade the Recent Japan Sea. If the second explanation is accepted, it is difficult to explain how these species could survive in the brackish surface water. *N. rugosa*, in particular, is now living at depths of 9-76 m (Golikov, 1963).

The modern neptuneid fauna around the Japan Sea borderland consists of the *N. intersculpta* stock and *Barbitonia* (Tiba and Kosuge, 1988) in contrast with the Pliocene and early Pleistocene fauna which was dominated by the *N. polycostata* stock and *Golikovia*.

The distribution of a part of the *Neptunea polycostata* stock and of the subgenus *Golikovia* is similar to that of the Ancistrolepidinae. However, the distributional patterns of the B and C types have never been recognized in the Ancistrolepidinae. The B and C type species differ from the latter in having shallower habitats or a eurythermal ecology. Amano *et al.* (1996) emphasized that a Quaternary extinction event, thermal tolerance and the bathymetric distribution of each species are important determinants of distribution of speciesin the Japan Sea. Therefore, the results of this study support those of the previous study.

Acknowledgments

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References cited

Akamatsu, M., 1984 : On the so-called Shishinai fauna from the Ishikari Hills, Hokkaido. *Annual Report of the Historical Museum of Hokkaido*, no. 12, p. 1-33. (*in Japanese with English abstract*)

Akamatsu, M. and Suzuki, A., 1990 : Pleistocene molluscan faunas in central and southwestern Hokkaido. *Journal of Faculty of Science, Hokkaido University*, vol. 22, no. 4, p. 529-552.

Akamatsu, M. and Suzuki, A., 1992 : Stratigraphy and paleoenvironment of the lower Pleistocene on the hills around the Ishikari Lowland, Hokkaido. *Annual Report of the Historical Museum of Hokkaido*, no. 20, p. 1-30. (*in Japanese with English abstract*)

Amano, K. and Kaetsu Group of Society for Earth Science Education of Niigata Prefecture, 1989 : Pliocene molluscan fauna from Asahi-mura, Iwafune-gun, Niigata Prefecture. *Bulletin of the Mizunami Fossil Museum*, no. 16, p. 109-115. (*in Japanese with English abstract*)

Amano, K. and Sato, H., 1995 : Relationship between embaymental associations and relict species. —Molluscan fauna from the Pliocene Joshita Formation in the northern part of Nagano Prefecture—. *Fossils*, no. 59, p. 1-13. (*in Japanese with English abstract*)

Amano, K., Ukita, M. and Sato, S. 1996. Taxonomy and distribution of the subfamily Ancistrolepidinae (Gastropoda : Buccinidae) from the Plio-Pleistocene of Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 182, p. 467-477.

Dall, W.H., 1916 : Prodrome of a revision of the chrysodomoid whelks of the boreal and Arctic regions. *Proceedings of the Biological Society of Washington*, vol. 29, p. 7-8

Golikov, A.N., 1963 : Gastropod genus *Neptunea* Bolten. *Fauna of the USSR, Mollusca*, vol. 5, Sect. 1, p. 1-217, pls. 1-28. (*in Russian*)

Goryachev, V.N., 1987 : To the history of the formation of *Neptunea* (Gastropoda, Buccinidae) fauna of the North Pacific. *In*, Kafanov, A. *ed., Fauna and distribution of molluscs : North Pacific and Polar Basin*, p. 57-64, Far East Science Center, Vladivostok. (*in Russian*)

Habe, T. and Sato, J., 1972 : A classification of the family Buccinidae from the North Pacific. *Proceedings of the Japan Society of Systematic Zoology*, no. 8, p. 1-8, pls. 1-2. (*in Japanese with English abstract*)

Hatai, K., Masuda, K. and Suzuki, Y., 1961 : A note on the Pliocene megafossil fauna from the Shimokita Peninsula, Aomori Prefecture, Northeast Honshu, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 30, p. 18-38, pls. 1-4.

Hatai, K. and Nisiyama, S. 1952. Check list of Japanese Tertiary marine Mollusca. *Science Reports of the Tohoku University, 2nd Series, Special Volume*, no. 3, p. 1-464.

Iwai, T., 1959 : The Pliocene deposits and molluscan fossils from the area southwest of Hirosaki City, Aomori Prefecture, Japan. *Bulletin of Educational Faculty of Hirosaki University*, no. 5, p. 39-61, pls. 1-2.

Iwai, T. 1965. The geological and paleontological studies in the marginal area of the Tsugaru basin, Aomori Prefecture, Japan. *Bulletin of Educational Faculty of Hirosaki University*, no. 15, p. 1-68, pls. 12-20.

Kanehara, K., 1937 : Pliocene shells from the Teshio Oilfield, Hokkaido. *Journal of the Geological Society of Japan*, vol. 44, no. 526, p. 703-708, pl. 22 (10).

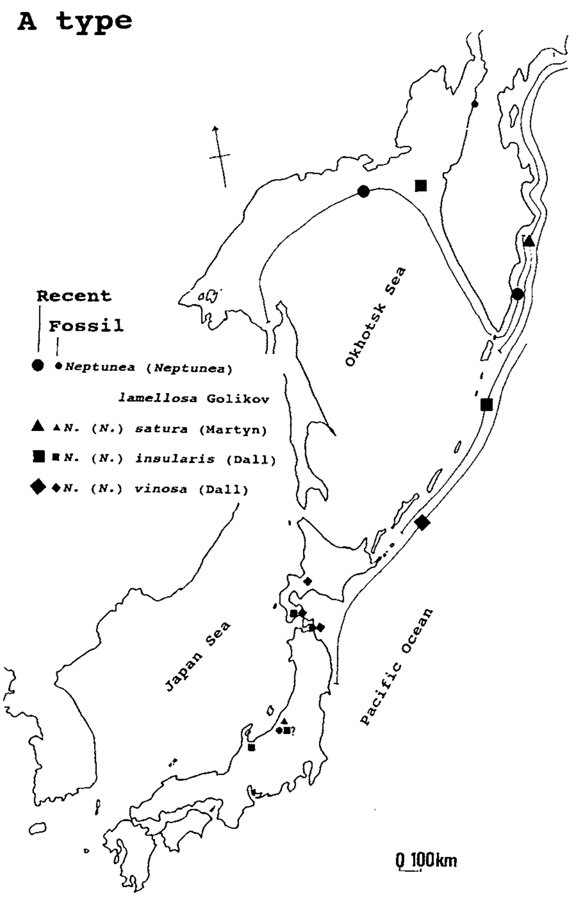
Kira, T., 1959 : *Coloured illustrations of the shells of Japan*. vol. 1. 240 p., Hoiku-sha, Osaka. (*in Japanese*)

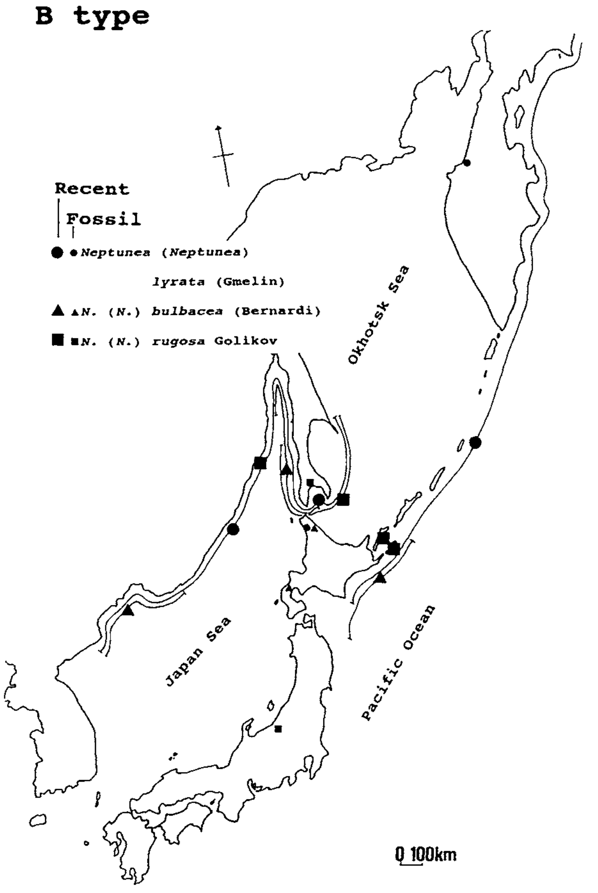
Kuroda, T., 1931 : Mollusca. *In*, Homma, F. *ed., Shinano Chubu Chishitsu-shi* (*Geology of Central Shinano*), pt. 4, p. 1-90, pls. 1-13, Kokin-shoin, Tokyo. (*in Japanese*)

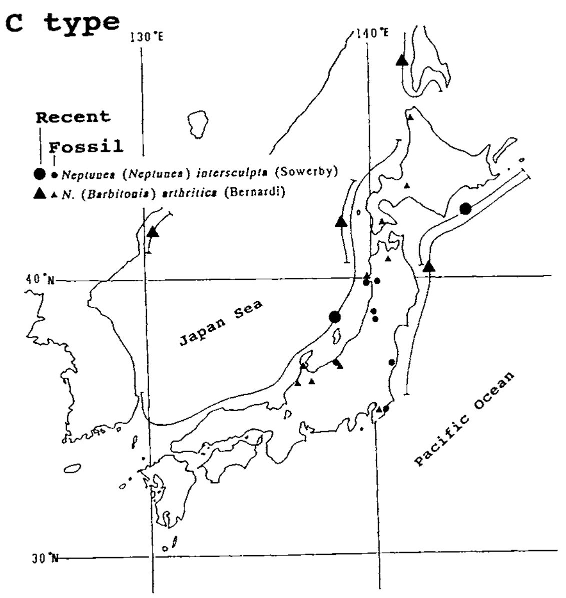
MacNeil, S.S., 1965 : Evolution and distribution of the genus *Mya* and Tertiary migration of Mollusca. *United States Geological Survey, Professional Paper*, vol. 483-G, p. 1-51, pls. 1-11.

Masuda, F., Amano, K., Katsura, Y. and Ito, M., 1981 : Shallow marine facies of Neogene and Quaternary strata at the northwest and southeast parts of Teshio Town in Hokkaido. *Human Culture and Environmental Studies in Northern Hokkaido*, vol. 2, p. 1-41, pls. 1-6. (*in*

Figure 4. Distributional pattern of *Neptunea*. (Recent geographical distribution and fossil records in Kamchatka are mainly after Golikov, 1963).


A type
Recent
Fossil
● ◆ Neptunea (Neptunea) lamellosa Golikov
▲ ▴ N. (N.) satura (Martyn)
■ ▪ N. (N.) insularis (Dall)
◆ ◆ N. (N.) vinosa (Dall)
Okhotsk Sea
Japan Sea
Pacific Ocean
0 100km


B type
Recent
Fossil
● • Neptunea (Neptunea) lyrata (Gmelin)
▲ ▴ N. (N.) bulbacea (Bernardi)
■ ▪ N. (N.) rugosa Golikov
Okhotsk Sea
Japan Sea
Pacific Ocean
0 100km


C type
130°E
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30°N
Recent
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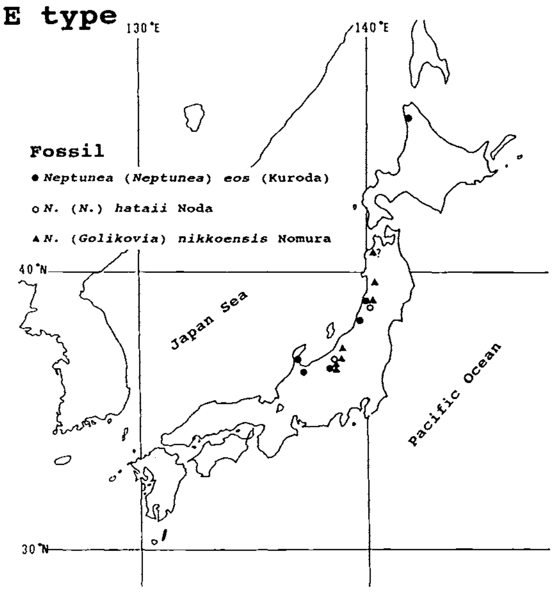
▲ ▴ N. (Barbitonia) arthritica (Bernardi)
Japan Sea
Pacific Ocean


E type
130°E
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Fossil
• Neptunea (Neptunea) eos (Kuroda)
○ N. (N.) hataii Noda
▴ N. (Golikovia) nikkoensis Nomura
Japan Sea
Pacific Ocean

Japanese with English abstract)

Masuda, K. and Noda, H., 1976: Check list and bibliography of the Tertiary and Quaternary Mollusca of Japan, 1950-1974. *Saito Ho-on Kai, Special Publication*, no. 1, p. 1-494.

Matsui, S., 1985: Recurrent molluscan associations of the Omma-Manganji fauna in the Gojome area, Northeast Honshu. Part 1. General discussions of fauna and systematic notes on gastropod and scaphopod species. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 139, p. 149-179.

Matsuura, N., 1985: Successive change of the marine molluscan faunas from the Pliocene to Holocene in Hokuriku Region, Central Japan. *Bulletin of the Mizunami Fossil Museum,* no. 12, p. 71-158, pls. 32-42. (*in Japanese with English abstract*)

Nakata, Y. and Amano, K., 1991: Pliocene molluscan associations in the Tomikura District, extended over Niigata and Nagano Prefectures, Japan. *Bulletin of the Mizunami Fossil Museum*, no. 18, p. 77-91, pls. 5-7. (*in Japanese with English abstract*)

Nelson, C.M., 1978: *Neptunea* (Gastropoda: Buccinacea) in the Neogene of the North Pacific and adjacent Bering Sea. *Veliger*, vol. 21, no. 2, p. 203-215.

Noda, H., 1962: The geology and paleontology of the environs of Matsunoyama, Niigata Prefecture, with special reference of the so-called Black Shale. *Science Reports of the Tohoku University, 2nd Series*, vol. 34, no. 3, p. 199-236, pl. 16.

Noda, H. and Amano, K., 1985: Preliminary report on the geology and paleontology of the environs of Teshio, Hokkaido. Part 6. The occurrence of the Genno-ishi and its associated marine molluscan fossils from the Pliocene "Yuchi" Formation. *Human Culture and Environmental Studies in Northern Hokkaido*, vol. 6, p. 1-12, pls. 1-5. (*in English with Japanese abstract*)

Noda, H., Amano, K. and Majima, R., 1984: Preliminary report on the geology and paleontology of the environs of Teshio, Hokkaido. Part 5. *Crenomytilus grayanus* (Dunker) from the Pliocene "Yuchi" Formation in Teshio, Hokkaido. *Human Culture and Environmental Studies in Northern Hokkaido*, vol. 5, p. 1-11, pls. 1-6.

Noda, H., Amano, K., Majima, R., Ito, M. and Kanno, S., 1983: Preliminary report on the geology and paleontology of the environs of Teshio, Hokkaido. Part 4. Molluscan fossils from the lower part of the Pliocene "Yuchi" Formation. *Human Culture and Environmental Studies in Northern Hokkaido*, vol. 4, p. 1-12. (*in Japanese*).

Nomura, S., 1937: On some Neogene fossils from along the upper course of the Nikko-gawa, Akumi-gun, Yamagata-ken, Northeast Honshu, Japan. *Saito Ho-on Kai Museum, Research Bulletin,* no. 13, p. 173-178, pl. 24.

Ogasawara, K., 1977: Paleontological analysis of Omma fauna from Toyama-Ishikawa area, Hokuriku Province, Japan. *Science Reports of the Tohoku University, 2nd Series*, vol. 47, no. 2, 43-156.

Ogasawara, K., 1994: Neogene paleogeography and marine climate of the Japanese Islands based on shallow marine molluscs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 108, nos. 3-4, p. 335-351.

Ogasawara, K., Masuda, K. and Matoba, Y., 1986: *Neogene and Quaternary Molluscs from the Akita Oil-field, Japan.* Commemorative Volume of Prof. Takayasu's Retirement, 310 p., 85 pls. (*in Japanese*)

Ogasawara, K. and Naito, K., 1983: The Omma-Manganjian molluscan fauna from Akumi-gun, Yamagata Prefecture, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 51, p. 40-61, pls. 6-8.

Ogasawara, K., Sato, H. and Ohtomo, J., 1984: Pliocene molluscan fauna from the western part of Shinjo Basin, Yamagata Prefecture, Northeast Japan. *Memoirs of the National Science Museum*, no. 17, p. 23-34, pls. 1-2. (*in Japanese with English summary*)

Okutani, K., Tagawa, M. and Horikawa, H., 1988: *Gastropods from continental shelf and slope around Japan*, 203 p. Japan Fisheries Resource Conservation Association, Tokyo. (*in Japanese and English*)

Otuka, Y., 1935a: Stratigraphy of the northeastern part of the Oti Graben, Ishikawa Prefecture. *Journal of the Geological Society of Japan*, vol. 42, no. 503, p. 483-510. (*in Japanese*)

Otuka, Y., 1935b: The Oti Graben in southern Noto Peninsula, Japan. Part 3. *Bulletin of the Earthquake Research Institute, Tokyo Imperial University*, vol. 13, pt. 4, p. 806-845, pls. 50-52.

Sakurai, K. and Tiba, R., 1969: A new species of the genus *Neptunea* from Japan. *Venus*, vol. 28, no. 2, p. 99-100.

Sawada, Y., 1962: The geology and paleontology of the Setana and Kuromatsunai areas in Southwest Hokkaido, Japan. *Memoirs of the Muroran Institute of Technology,* vol. 4, no. 1, p. 1-110, pls. 1-8.

Strauch, F., 1972: Phylogenese Adaptation und Migration einiger nordischer mariner Molluskengenera (*Neptunea, Panomya, Cyrtodaria* und *Mya*). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, vol. 531, p. 1-210, pls. 1-11. (*with English abstract*)

Tada, R., 1994: Paleoceanographic evolution of the Japan Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 108, nos. 3-4, p. 487-508.

Tiba, R. and Kosuge, S., 1988: North Pacific shells (17) Genus *Neptunea* Roeding. *Occasional Publication of the Institute of Malacology of Tokyo*, p. 1-96. (*in Japanese*)

Togo, Y., 1974: Shell structure and growth of protoconch and teleoconch in Neptunea (Gastropoda). *Journal of the Geological Society of Japan*, vol. 80, no. 8, p. 369-380, pls. 1-4. (*in Japanese with English summary*)

Paleontological Research, vol. 1, no. 4, pp. 285-290, 5 Figs., 30 December, 1997

Two permianellids (Brachiopoda) from the Middle Permian of the Southern Kitakami Mountains, Northeast Japan

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Abstract. Two species of permianellid brachiopods, *Permianella typica* He and Zhu and *Laterispina parallela* Shen, Fan, Zhang and Zhang, are described from the Middle Permian (Kubergandian) Kanokura Formation of the Southern Kitakami Mountains, Northeast Japan. This is the first description of permianellids from the Japanese Permian.

Key words: Brachiopoda, Kanokura Formation, Middle Permian, permianellid, Southern Kitakami Mountains

Introduction

Permianellids are aberrant, bilobate brachiopods belonging to the superfamily Lyttonioidea Waagen, 1883. Termier *et al.* (1974) first described a permianellid species, *Dicystoconcha lapparenti*, from the lower Murgabian (*Neoschwagerina* Zone) of Wardak, central Afghanistan as a species of lyttoniid. Afterwards, the genus *Dicystoconcha* was assigned to the family Permianellidae by He and Zhu (1979) when they established the family Permianellidae and the genus *Permianella*, with *Permianella typica* He and Zhu, 1979 from the Upper Permian Longtan Formation of Jiangxi and Sichuan Provinces, South China as the type species. Since then, several permianellid species have been described or figured from the Chihsian to Changhsingian of South China (He and Zhu, 1979; Wang *et al.*, 1982; Yang, 1984; Mou and Liu, 1989; Liang, 1990; Zhu, 1990; Wang and Jin, 1991; Shen *et al.*, 1994), the Lower and Upper Permian of Thailand (Grant, 1976; Yanagida *et al.*, 1988), the Midian of South Primorye, Far East of Russia (Likharew and Kotljar, 1978), the Dzhulfian of the Transcaucasus (Shen and Shi, 1997), the Maokouan of Northeast China (Wang and Jin, 1991) and the Middle Permian of the Southern Kitakami Mountains, Northeast Japan (Tazawa, 1987). These data indicate that permianellids are distributed in the Lower Permian (Artinskian) to Upper Permian (Changhsingian) of the eastern Tethys and surrounding regions.

Twenty permianellid specimens were collected by K. Nakamura, H. Araki and the second author (J. Tazawa) from shale and sandstone cropping out at six localities (Locs. 1-6) in the Setamai, Imo and Kamiyasse districts, Southern Kitakami Mountains, Northeast Japan (Figure 1). The fossiliferous shale and sandstone with a fusulinacean *Monodiexodina matsubaishi* (Fujimoto) are safely assigned to the lower part of the Kanokura Formation (Choi, 1970, 1973; Tazawa, 1973, 1976).

The brachiopod specimens described here are all housed in the Department of Geology, Faculty of Science, Niigata University, with the designation of NU-B for the registered number of the specimens.

Systematic descriptions

Order Productida Waagen, 1883
Suborder Strophalosiidina Waagen, 1883
Superfamily Lyttonioidea Waagen, 1883
Family Permianellidae He and Zhu, 1979

Genus *Permianella* He and Zhu, 1979

Type species.—*Permianella typica* He and Zhu, 1979, from the Upper Permian Longtan Formation of Jiangxi and Sichuan Provinces, South China (He and Zhu, 1979, p. 132, 137, pl. 1, figs. 1a, b; pl. 2, figs. 1-3; pl. 3, figs. 1-3).

Diagnosis.—Shell medium in size, elongately bilobate in outline, concavo- or plano-convex, with ventral sulcus, dorsal fold and anterior incision; incision extremely deep, attaining more than half of shell length; marginal brim well developed along lateral commissure.

Remarks.—The present genus is characterized by its elongately ovate shell with deep anterior incision and irregular marginal brim along the lateral commissure. The genus *Dicystoconcha* Termier, Termier, Lapparent and Marin, 1974 differs from *Permianella* in its smaller and wider shell, shal-

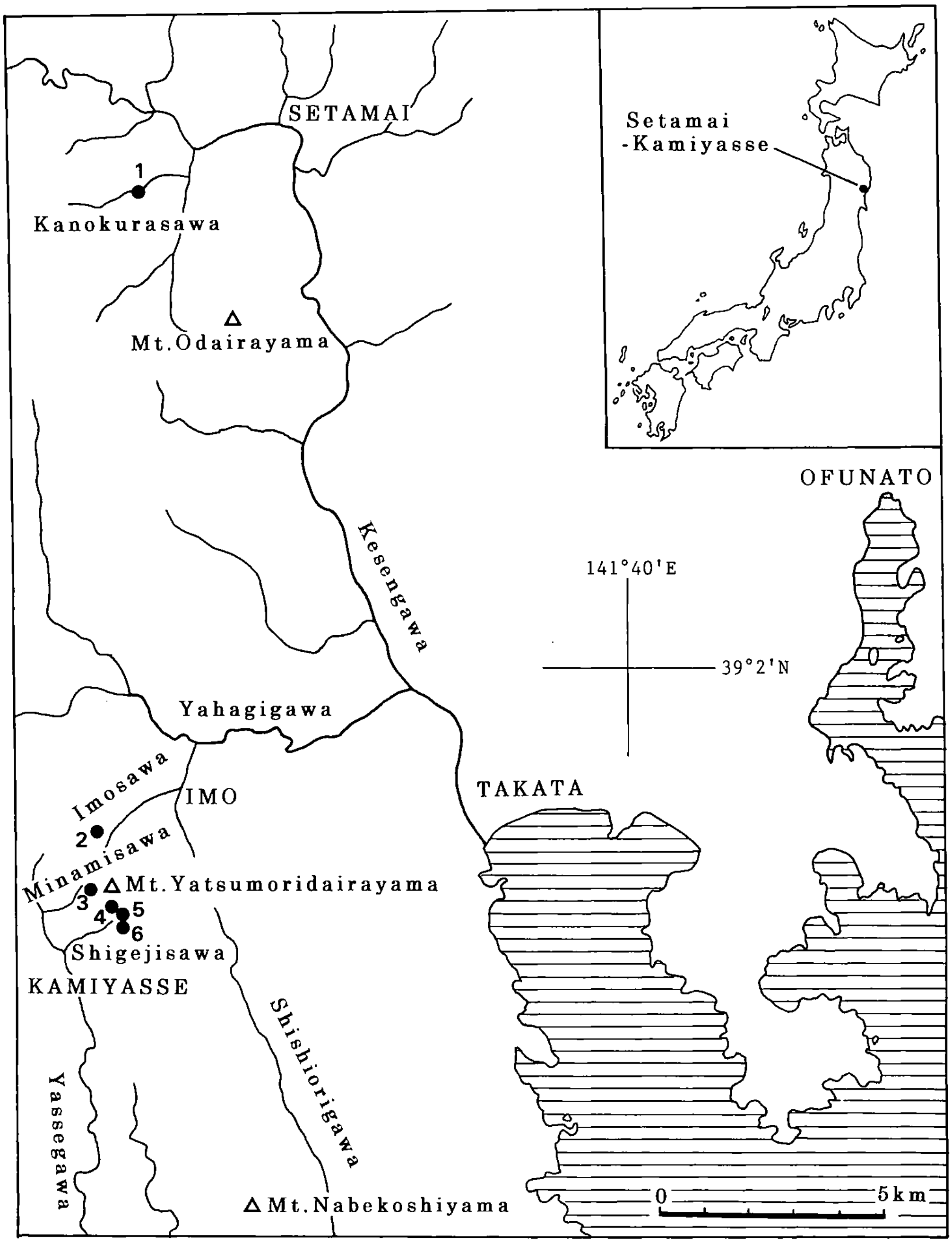

Figure 1. Map showing the fossil localities (Locs. 1-6).

lower incision, having two lateral septa on central platform and lacking lateral marginal brim. *Laterispina* Wang and Jin, 1991 also has an elongately ovate outline, deep incision and median septum on central platform, but this genus differs from *Permianella* in having a fence-shaped marginal brim (see Wang and Jin, 1991, p. 497, pl. 2, figs. 8, 9, 12).

The genera *Dipunctella*, *Tenerella* and *Paritisteges*, proposed by Liang (1990), have elongately ovate outline, deep incision and lateral marginal brim, all of the characters common with the genus *Permianella*. According to Liang's description (p. 371), these three genera differ from *Permianella* in their coiled or asymmetrical shells. However, we consider that differences of their internal structures are more important for their classification. All of the genera *Dipunctella*, *Tenerella* and *Paritisteges* have two lateral septa on the central platforms, whereas *Permianella* has a median septum on the central platform.

Species other than type species assigned to the genus.—*Permianella grunti* Shen and Shi, 1997, from the Upper Permian Dzhulfa Formation in the Dorasham II section, Transcaucasus (Shen and Shi, 1997, p. 22, pl. 1, figs. 1-7).

Occurrence.—Middle and Upper Permian ; Trans-

Figure 2. External surface of a ventral valve of *Permianella typica* He and Zhu, showing pseudopunctae of outer shell layer (NU-B63, ×8.5).

Figure 3. One section (6.95 mm anterior to the posterior margin) of *Permianella typica* He and Zhu, showing pseudopunctate outer shell layer, laminate inner shell layer, central platform and a distorted median septum (NU-B51, ×12.5).

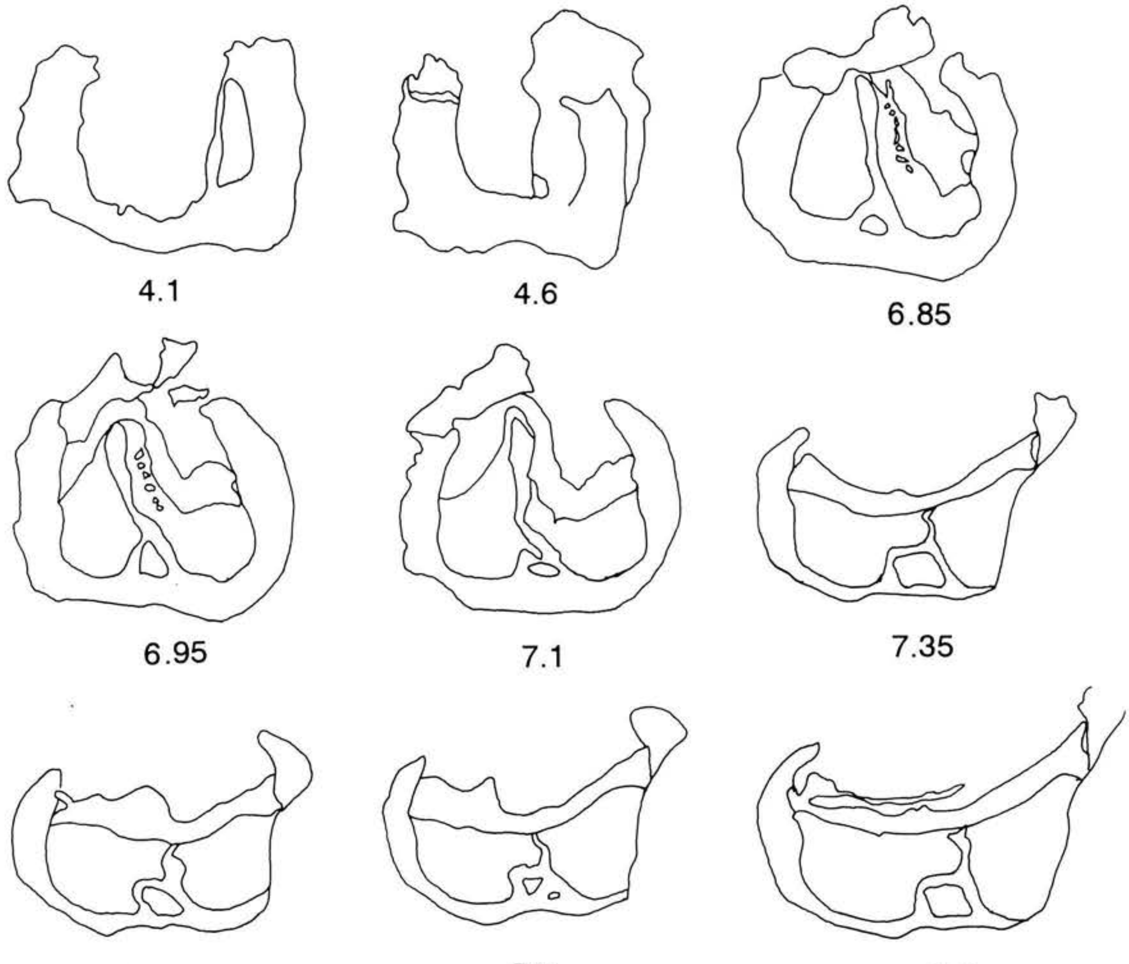

Figure 4. Serial sections of *Permianella typica* He and Zhu. The numbers indicate the distance in mm from the posterior margin (NU-B51, ×7.5).

caucasus, Thailand, South China, and Northeast Japan.

Permianella typica He and Zhu, 1979

Figures 2–4, 5-1–14

Permianella typica He and Zhu, 1979, p. 132, 137, pl. 1, figs. 1a, b; pl. 2, figs. 1-3; pl. 3, figs. 1-3; Wang and Jin, 1991, p. 496, pl. 2, figs. 1-3.
Permianella sp. He and Zhu, 1979, p. 133, 139, pl. 1, figs. 2-3.
Permianella sp. Tazawa, 1987, fig. 19-10.

Material.—Nineteen specimens: (1) two conjoined valves, NU-B51, 59; (2) a ventral valve, NU-B52; (3) external and internal moulds of three ventral valves, NU-B58, 62, 63; (4) internal moulds of ten ventral valves, NU-B53, 54, 55, 56, 61, 64, 65, 66, 68, 69; (5) external moulds of four dorsal valves, NU-B50, 57, 60, 67.

Description.—Shell large in size for genus, elongately ovate in outline, maximum width occurring near anterior margin; length 49 mm, width 17 mm in the largest specimen (NU-B64). Shell concavo-convex in anterior profile, flat to strongly curved dorsally in lateral profile. Shell having a deep anterior incision, attaining more than a half of shell length. Posterolateral sides of shell convergent posteriorly at an angle of about 30-50°. Lateral sides of shell slightly divergent or nearly parallel anteriorly. Attachment ring developed on posterior margin. Ventral sulcus originating at umbo, slightly widening anteriorly. Irregular marginal brim

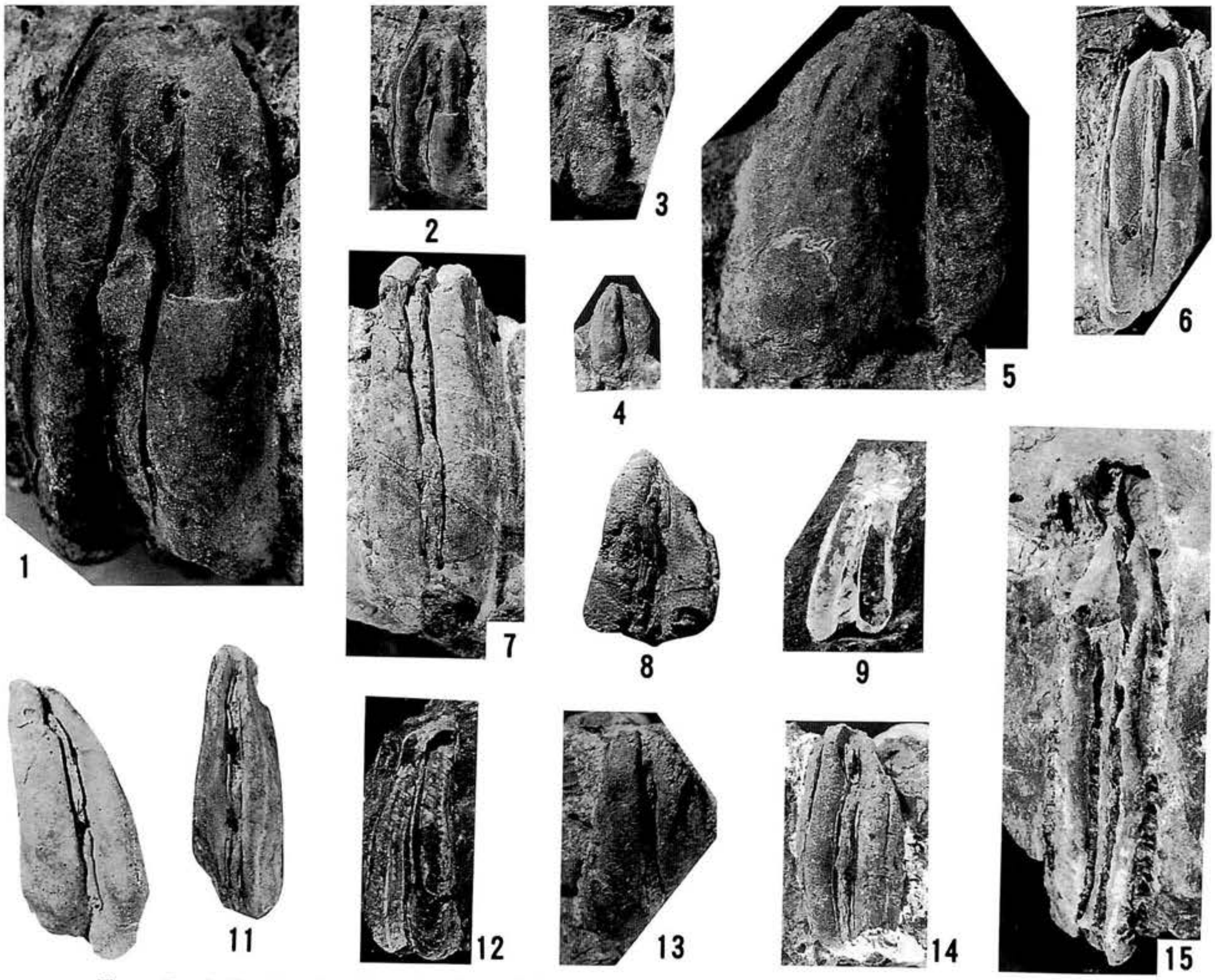

Figure 5. 1-14. *Permianella typica* He and Zhu. 1, 2: external mould of a dorsal valve with a part of ventral valve, showing marginal brim along lateral commissure and deep incision, NU-B60 (1: ×3). 3: internal mould of a ventral valve, NU-B55. 4, 5: internal mould of a ventral valve, NU-B61 (5: ×4). 6: ventral view of a shell, NU-B63. 7: internal mould of a ventral valve, NU-B64. 8: external mould of a dorsal valve, NU-B50. 9: ventral view of a shell, NU-B59. 10: internal mould of a ventral valve, NU-B65. 11: internal mould of a ventral valve, NU-B56. 12: ventral view of a shell, NU-B51. 13: internal mould of a ventral valve, NU-B58. 14: external mould of a dorsal valve, NU-B57. **15.** *Laterispina parallela* Shen, Fan, Zhang and Zhang, internal mould of a ventral valve, showing fence-shaped marginal brim along lateral commissure, NU-B70. All figures are natural size unless otherwise indicated.

observed along lateral commissure. Shell consisting of two layers, pseudopunctate outer layer and laminate inner layer (Figures 2, 3).

Ventral central platform well developed, trapezoid in transverse section. Median septum stout and slightly distorted, elevated on right side of central platform and knife-edged at anterior part, but elevated at middle part of central platform and top-thickened at posterior part (Figures 3, 4). Dorsal interior with a long brachial ridge in each lobe; brachial process not observed.

Remarks.—*Permianella typica* He and Zhu is characterized by its large size, elongately ovate outline, deep incision, irregular marginal brim and nearly parallel anterolateral sides. The present specimens quite agree with the type specimen of *P. typica* in external and internal characters except for a slightly curved lateral profile. *Permianella* sp. from the Longtan Formation of Jiangxi Province, South China (He and Zhu, 1979, p. 133, 139) has no substantial differences from *P. typica*.

Permianella grunti Shen and Shi, described and figured by Shen and Shi (1997, p. 22, pl. 1, figs. 1-7) from the Upper Permian of the Transcaucasus, is clearly distinguished from the present species by its smaller shell, inconspicuous marginal brim and very short median septum.

The Chinese species *Dipunctella stenosulcata, Tenerella usualisa, Parististeges equilateialis and Parististeges pisiformis* described by Liang (1990, p. 372, 374, 379, 380) resemble *P. typica* in their parallel lateral sides, elongately ovate outline and deep incision. However, their two lateral septa on the central platform suggest that they belong to the genus *Dicystoconcha*.

Horizon and locality.—Lower part of the Kanokura Formation; Imosawa (Loc. 2), Imo, Yahagi-cho, Rikuzentakata City, Iwate Prefecture, and Minamisawa (Loc. 3) and Shigejisawa (Locs. 4-6), Kamiyasse, Kesennuma City, Miyagi Prefecture, Northeast Japan.

Genus ***Laterispina*** Wang and Jin, 1991

Type species.—*Laterispina liaoi* Wang and Jin, 1991, from the Upper Permian Changhsing Formation of Guangxi and Sichuan Provinces, South China (Wang and Jin, p. 496, 500, pl. 2, figs. 4-12).

Diagnosis.—Shell large in size, bilobate, triangular or belt-like in outline, with ventral sulcus; anterior incision extremely deep; lateral commissure bearing fence-shaped marginal brim. Ventral interior with a median septum and a complicated central platform having internal septa. Dorsal interior with brachial processes and long brachial ridges.

Remarks.—*Laterispina* differs from *Permianella* and *Dicystoconcha* in having a complicated fence-shaped marginal brim along the lateral commissure. *Permianella* usually has an irregular wing-shaped marginal brim, but *Dicystoconcha* has a very shallow incision and no marginal brim.

Species other than type species assigned to the genus.—*Laterispina parallela* Shen, Fan, Zhang and Zhang, 1994, from the Upper Permian Changhsing Formation of Nantong, Sichuan Province, South China (Shen *et al*., 1994, p. 478, pl. 1, figs. 1-12; pl. 2, figs. 1-11, 14).

Occurrence.—Middle and Upper Permian; South China and Northeast Japan.

Laterispina parallela Shen, Fan, Zhang and Zhang, 1994

Figure 5-15

Laterispina parallela Shen, Fan, Zhang and Zhang, 1994, p. 478; pl. 1, figs. 1-12; pl. 2, figs. 1-11, 14; text-figs. 1-5.

Material.—One specimen, external and internal moulds of a ventral valve, NU-B70.

Description.—Shell large in size for genus, bilobate, very long, belt-like shape; length 55 mm, width 14 mm in the single ventral valve specimen. Shell concavo-convex in anterior profile, slightly curved dorsally in lateral profile. Anterior incision extremely deep, attaining more than two thirds of shell length. Lateral sides of shell nearly parallel. Marginal brim developed along lateral commissure and being fence-shaped. Attachment ring grasping a crinoid stem on posterior margin. Other external and internal characters unknown.

Remarks.—Although only one specimen is available for description, the fence-shaped marginal brim along the lateral commissure and parallel belt-like outline well represent the characters of *Laterispina parallela* Shen, Fan, Zhang and Zhang. It is only a minor difference between the Kitakami and the Chinese specimens that the former has a slightly curved profile.

Horizon and locality.—Lower part of the Kanokura Formation; Kanokurasawa (Loc. 1), Setamai, Sumita-cho, Kesen-gun, Iwate Prefecture, Northeast Japan.

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References cited

Choi, D.R., 1970: Permian fusulinids from Imo, southern Kitakami Mountains, N. E. Japan. *Journal of the Faculty of Science, Hokkaido University, Ser. 4*, vol. 14, no. 3, p. 327-354, pls. 9-15.

Choi, D.R., 1973: Permian fusulinids from the Setamai-Yahagi district, southern Kitakami Mountains, N. E. Japan. *Journal of the Faculty of Science, Hokkaido University, Ser. 4*, vol. 16, p. 1-132, pls. 1-20.

Grant, R.E., 1976: Permian brachiopods from southern Thailand. *Journal of Paleontology*, vol. 50, supplement to no. 3, p. 1-269, pls. 1-71.

He, X.L. and Zhu, M.L., 1979: A new form of brachiopods and its systematical classification. *Journal of China Institute of Mining and Technology*, no. 4, p. 131-140, pls. 1-3. (*in Chinese and English*)

Liang, W.P., 1990: Lengwu Formation of Permian and its brachiopod fauna in Zhejiang Province. *Geological Memoirs, People's Republic of China, Ministry of Geology and Mineral Resources, Ser. 2*, no. 10, p. 1-522, pls.

1-84, Geological Publishing House, Beijing. (*in Chinese*)

Licharew, B.K. and Kotljar, G.V., 1978 : Permian brachiopods of South Primorye. *In,* Popeko, L.I., *ed., Upper Palaeozoic of northeastern Asia*, p. 63-75, pls. 11-22, DVNTS, Vladivostok. (*in Russian*)

Mou, C.J. and Liu, C.L., 1989 : A new type of brachiopod —*Guangdongina* and its ecological environment. *Acta Palaeontologica Sinica*, vol. 28, no. 4, p. 455-462, pls. 1-3. (*in Chinese*)

Shen, S.Z., Fan, B.H., Zhang, C., and Zhang, X.P., 1994 : A new species of permianellids (Brachiopoda) : taxonomic and palaeoecologic significance. *Geobios*, no. 27, fasc. 4, p. 477-485, pls. 1, 2.

Shen, S.Z. and Shi, G.R., 1997 : *Permianella* (Brachiopoda) from the Upper Permian of Transcaucasia. *Science Reports of Niigata University, Ser. E*, no. 12, p. 19-27. pl. 1.

Tazawa, J., 1973 : Geology of the Kamiyasse area, southern Kitakami Mountains. *Journal of the Geological Society of Japan*, vol. 79, no. 10, p. 677-686. (*in Japanese*)

Tazawa, J., 1976 : The Permian of Kesennuma, Kitakami Mountains : A preliminary report. *Earth Science* (*Chikyu Kagaku*), vol. 30, no. 3, p. 175-185, pls. 1-3.

Tazawa, J., 1987, Report of the fossils from the Kamiyasse district. *Report of Cultural Assets, Kesennuma City, Miyagi Prefecture*, no. 6, p. 1-37. (*in Japanese*)

Termier, G., Termier, H., Lapparent, A.F. and Marin, P., 1974 : Monographie du Permo-Carbonifère de Wardak (Afghanistan Central). *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon, Hors Séries*, vol. 2, p. 1-167, pls. 1-38.

Waagen, W., 1883 : Salt Range fossils, 1. *Productus*-Limestone fossils. *Palaeontologia Indica, Ser. 13*, vol. 1, pt. 4, fasc. 2, p. 391-546, pls. 29-49.

Wang, G.P., Liu, Q.Z., Jin, Y.G., Hu, S.Z., Liang, W.P. and Liao, Z.T. : 1982 : Brachiopoda. *In,* Nanjing Institute of Geology and Mineral Resources, *eds., Palaeontological atlas of East China (2)*, p. 186-256, pls. 74-102, Geological Publishing House, Beijing. (*in Chinese*)

Wang, H.Y. and Jin, Y.G., 1991 : On permianellids (Brachiopoda). *Acta Palaeontologica Sinica*, vol. 30, no. 4, p. 481-501, pls. 1-3. (*in Chinese*)

Yanagida, J., Sakagami, S., Ishibashi, T., Kawabe, T., Hatta, A., Nakornsri, N., Sugiyama, T., Chonglakmani, C., Ingarat-Helmcke, R., Chongkanchanasoontorn, Y., Piyasin, S. and Wongwanich, T., 1988, *Biostratigraphic study of Paleozoic and Mesozoic Groups in central and northern Thailand : An Interim Report*. 47 p., 33 pls., Department of Geology, Faculty of Science, Kyushu University, Fukuoka.

Yang, D.L., 1984 : Brachiopoda. *In,* Yichang Institute of Geology and Mineral Resources, *eds., Biostratigraphy of the Yangtze Gorge area (3)*, p. 203-239, pls. 29-38. Geological Publishing House, Beijing. (*in Chinese*)

Zhu, T., 1990 : *The Permian coal-bearing strata and palaeobiocoenosis of Fujian*. 127 p., 47 pls., Geological Publishing House, Beijing. (*in Chinese*)

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New Planktic Foraminiferal Transfer Functions for the Kuroshio-Oyashio Current Region off Japan

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Abstract. Factor analysis of planktic foraminiferal assemblages analyzed in sediment samples from the Northwest Pacific Ocean near Japan defines five major factors including the Kuroshio, Transitional Water, Oyashio, Kuroshio Gyre Margin and Coastal Water factors which, when mapped, show distinctive distributions. These factors account for over 94% of the total variance. Each of the factors can be treated as an independent variable in a regression analysis. Equations relating factors to winter and summer sea-surface temperatures (SSTs) show a high degree of accuracy. The standard errors of estimate for the transfer function equations PFJ-125 established in this study average about ±1.75°C for estimated winter temperatures, and about ±1.17°C for summer temperatures.

Transfer functions PFJ-125 were applied to assemblages representing the last 12 K yrs. in piston core C-1 collected in the area off Joban, northeast Honshu, Japan. The lowest estimated winter SST is 4.1°C and 18.5°C for the summer SST at 10,500 yrs. B.P. whereas at 6,300 yrs. B.P. the winter highest SST is 12.8°C and 23.9°C in the summer. Based on down-core variations in estimated winter and summer SST and fluctuations of the five identified factor loadings, the C-1 core site was alternatively under the influence of the Oyashio and Kuroshio Fronts through the last 12 K yrs. Marine conditions at core site C-1 at 10,500 yrs. B.P. are comparable with those recorded in the same area for the last glacial maximum.

Key words : Latest Quaternary, paleoenvironments, planktic foraminifera, Q-mode factor analysis, transfer functions

Introduction

Planktic foraminifera (unicellular shelled protozoans) live in surface and near-surface ocean water and their distribution generally corresponds to the world's climatic zones and oceanic surface water masses (Bé and Tolderlund, 1971 ; Bradshaw, 1959). The composition of planktic foraminiferal assemblages accumulated in surface sediments on the ocean bottom reflects oceanographic conditions of the overlying surface water (Belyayeva, 1969 ; Bé, 1977).

Past variations in sea surface temperature can be estimated through quantitative analysis of fossil planktic foraminiferal assemblages in deep sea sediments. The transfer function introduced by Imbrie and Kipp (1971) is derived simply from spatial correlations between modern oceanographic data (water temperature, salinity, etc.) and census data for surface sediment collected from sea bottom assemblages of planktic foraminifera. These authors carried out factor analysis of planktic foraminiferal assemblages from surface sediments as variables, obtained statistically derived varimax assemblages which have high correlations with environmental factors, and subsequently calculated the transfer function and estimated sea surface temperatures (SSTs) by regression analysis. This method is now widely applied in Quaternary research as the technique provides calibrated quantitative estimates of several parameters of past oceanic environments including surface temperatures (see for example CLIMAP, 1976 ; Moore *et al.*, 1980, and others).

This method has been used by many investigators to obtain the transfer function for planktic foraminiferal assemblages in the north and equatorial Atlantic (Gardner and Hays, 1976 ; Kipp, 1976 ; Prell *et al.*, 1976 ; Dowsett and Poore, 1990 and others). These latter functions, however, have inherent geographic limits in their applicability because they are entirely based upon biotic and oceanographic parameters defined for a given geographically confined oceanic region. In order to interpret paleoenvironmental changes as accurately as possible, it is necessary to select a transfer function specific to the region in question. This method was applied to planktic foraminifers in the western Pacific Ocean by Thompson (1981), Oda *et al.* (1983) and Takayanagi *et al.* (1987).

In the northwestern Pacific Ocean near Japan, there are two dominant surface currents, the north flowing Kuroshio and the south-flowing Oyashio. Surface sediments used by Thompson (1981) to derive the transfer function FP-12E were mainly collected in the Kuroshio Region, with only a few samples from the Oyashio Region near Japan. The Oda *et al.* (1983) and Takayanagi *et al.* (1987) studies lacked samples from the Kuroshio Region. Therefore, the transfer function equations derived by their authors are not efficient enough to apply to cores from areas near Japan under the influence of the Oyashio and Kuroshio Currents.

In this study, we have attempted to formulate new multiple regression equations applicable to the Kuroshio to Oyashio regions and derive transfer functions to estimate sea-surface temperature (SST) in the piston core KT81-19, C-1 taken along the Joban coast off Northeast Honshu, Japan (Figure 1).

Hydrographic conditions of the Northwest Pacific Ocean near Japan

The Japanese Islands extend in an arc from northwest to southeast along the northwestern margin of the Pacific Ocean. The surface ocean off Japan can be generally subdivided into three regions which correspond to distinctive surface flow patterns and physical properties (Kawai, 1972) including the Kuroshio Area, the Oyashio Area and the Perturbed (Transitional) Area (Figure 1). The hydrography in each area is summarized as follows.

The Kuroshio Current represents one of the major western boundary currents in the world ocean and flows toward the northeast along the coast of Japan. The so-called Kuroshio extension, which runs eastward away from Japan into the Pacific, is distinguished from the Kuroshio Current proper which runs along the coast. The Kuroshio area of influence extends from seas off southwest Japan to approximately Lat. 35°N, where the northern boundary is determined by the Kuroshio Front and the Kuroshio Extension.

Two stable flow patterns are known for the Kuroshio Current (Taft, 1972; Nitani, 1975). One runs parallel to the Japanese Islands and bathes the upper portion of the continental slope. Another is called the meander, which leaves the continental slope off the Enshu Gulf (Enshu-nada, Lat. 33°N). The meander surrounds the Cold Water Mass resulting from upwelling of cold water (Nan'niti, 1958, 1960), leading to sea surface temperatures some 4 to 5°C lower than mean surrounding values (Fujimori, 1964). Although many investigators have suggested that the meander must be treated within the context of the Pacific circulation as a whole (Shoji, 1972), there are not enough data at this time to fully analyze the meander and associated occurrence of the Cold Water Mass.

The Oyashio Current is the second most important surface current near Japan; it flows southward along the southeast coast of Hokkaido and is characterized by low temperature and low salinity (Kawai, 1972). The Oyashio area of influence is located north of approximately Lat. 41°N. The southern boundary of this area is demarcated by the Oyashio-Kuroshio Front which lies approximately at Lat. 38°N as a weak easterly flow of the Oyashio, and also a southward intrusion of the Oyashio, termed the first Oyashio Intrusion.

The so-called Perturbed Area is located between approximately Lat. 38°N to 41°N between the Oyashio and Kuroshio Fronts and the axis of the Kuroshio Extension, where steep temperature and salinity gradients prevail. Numerous eddies exist in the Perturbed Area forming an area of a complicated surface character (Kawai, 1972).

Finally, a warm surface current flows from the Sea of Japan into the northwest Pacific through the Tsugaru Strait (the so-called Tsugaru Current) and affects the surface water from the Tsugaru Strait to off Kinkazan Island (Kawai, 1972; Moriyasu, 1972) at approximately Lat. 38°N. The Tsugaru Warm Current has its origin in the Tsushima Current, a warm current which flows northward into the Sea of Japan through the Tsushima Strait.

Sea surface temperature (SST) data used in this report are based on the Marine Environmental Atlas compiled by the Japan Oceanographic Data Center (1978) (Figure 2). In the Kuroshio Area, SST ranges from 20°C to 30°C in the summer, and 7.5°C to 20°C in the winter. In the Oyashio Area, SST ranges from 14°C to 22°C in the summer, and −2.5°C to 10°C in the winter. In the Perturbed Area, SST ranges from 18°C to 22°C in the summer, and 5°C to 10°C in the winter.

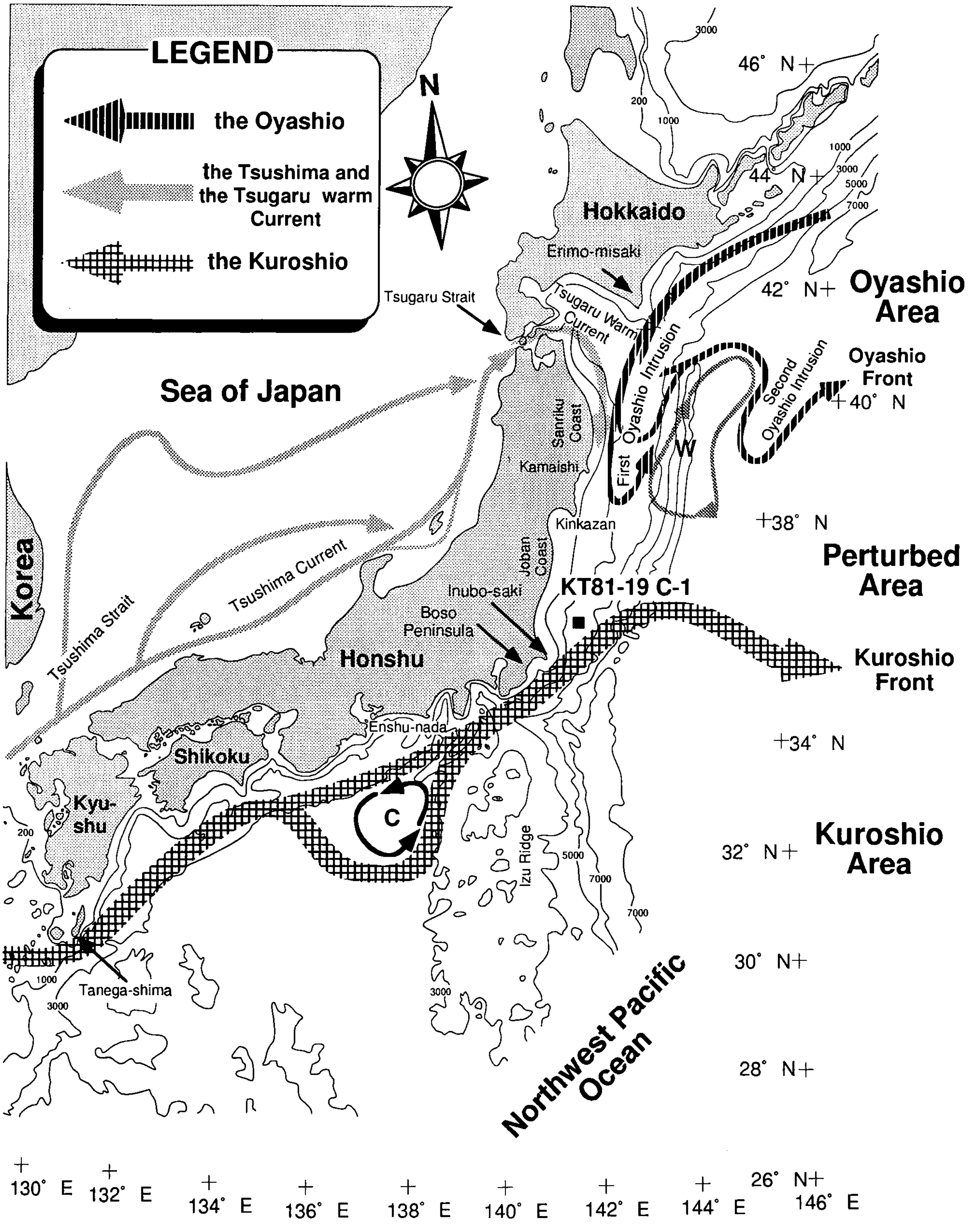
Formulation of Transfer Functions

(1) Samples

Surface sediment assemblages of planktic foraminifera analyzed for this study include those collected off northeast Honshu (Takayanagi and Oda, 1983) and from off southeast Japan (Oda and Takemoto, 1992). Generally, sediment samples from water depth greater than 3,500 m contain foraminiferal assemblages displaying evidence of dissolution; samples yielding foraminifers severely influenced by dissolution were removed from analysis. In the end, 81 surface sediment samples containing modern surface populations were selected from the area off Hokkaido to the area off Tanega-shima, encompassing some 12° of latitude between Lat. 30°N to 42°N (Figure 3, Table 1).

Samples were washed on a 63 μm opening sieve with tap water; sediment residues on the screen were then dried.

Figure 1. Map showing major current systems, the generalized distribution of surface water masses in seas adjacent to the Japanese Islands and a piston core KT81-19, C-1 used in this study.
C: areas dominated by cold water masses during the meandering of the Kuroshio Current, W: areas dominated by warm water masses within the so-called Perturbed Area between the Kuroshio and Oyashio Currents. (Modified after Masuzawa, 1957 and Kawai, 1972).


LEGEND
the Oyashio
the Tsushima and the Tsugaru warm Current
the Kuroshio
N
Sea of Japan
Korea
Hokkaido
Honshu
Shikoku
Kyu-shu
Erimo-misaki
Tsugaru Strait
Tsugaru Warm Current
Sanriku Coast
Kamaishi
Kinkazan
Joban Coast
Inubo-saki
Boso Peninsula
KT81-19 C-1
Tsushima Current
Tsushima Strait
Enshu-nada
C
W
Izu Ridge
Tanega-shima
First Oyashio Intrusion
Second Oyashio Intrusion
Oyashio Area
Oyashio Front
Perturbed Area
Kuroshio Front
Kuroshio Area
Northwest Pacific Ocean
46° N
44° N
42° N
40° N
38° N
34° N
32° N
30° N
28° N
26° N
130° E
132° E
134° E
136° E
138° E
140° E
142° E
144° E
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200
1000
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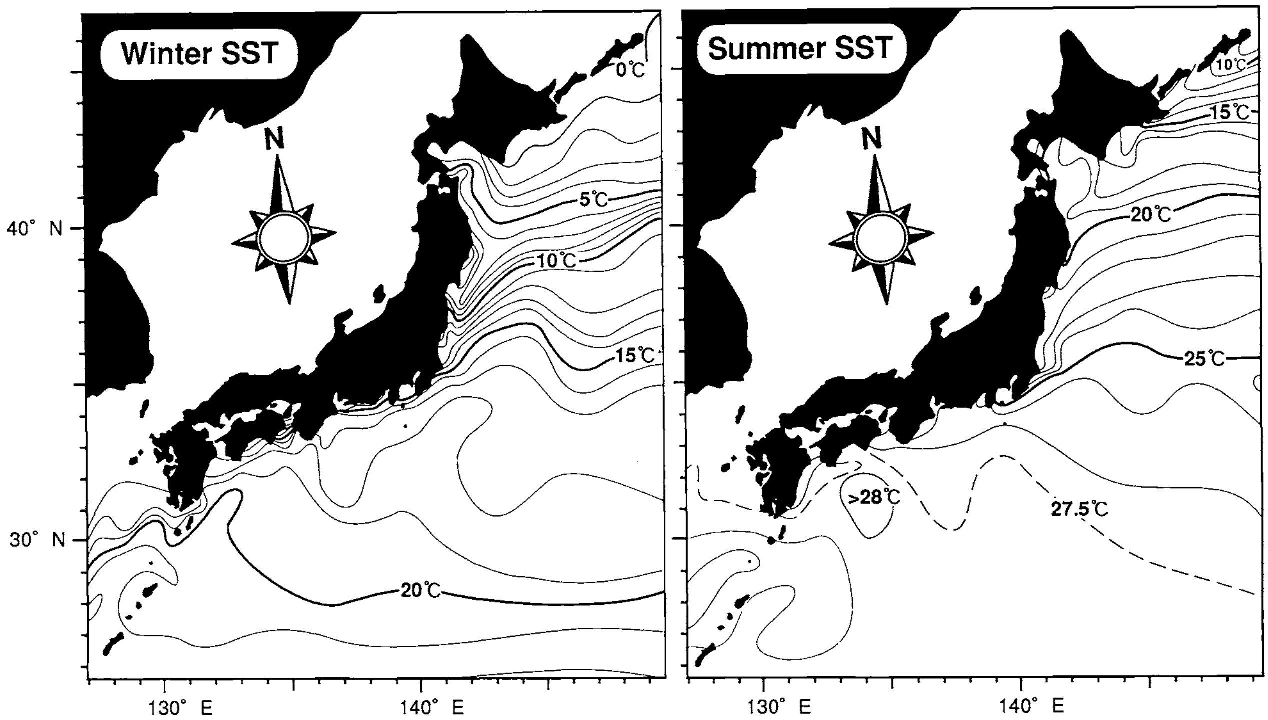


Figure 2. Map illustrating modern winter and summer surface water temperatures in the northwest Pacific Ocean ; temperature values taken from the Marine Environmental Atlas (1978)

Residues were subsequently split with a micro-splitter to yield more than 200 foraminiferal specimens. Each sample aliquot was then sieved through a 125 μm opening screen and all planktic foraminiferal specimens picked from the coarser fraction and identified to species to compile a faunal census. On average, 377 specimens were identified and counted in each sample.

(2) Factor Analysis

Thirty-seven species and 16 genera of planktic foraminifera were recognized in the 81 surface sediment samples analyzed. Twenty-four species assigned to nine genera were selected for Q-mode factor analysis on the basis of their high frequencies (Table 2). Species listed in Table 3 make only a small contribution to the analysis because of their very low frequencies or limited geographic occurrences. The most frequently occurring species (Table 2), on average, account for 98% of the total planktic foraminifera in any given sample.

We recalculated the percentage frequency of each taxon among the 24 most frequent species. We next employed Q-mode factor analysis using the faunal similarities cosine-theta of the 81 surface sediment samples analyzed, following procedures detailed by Imbrie and Kipp (1971). The specific program we utilized is described by Klovan and Imbrie (1971). Computer FUJITSU M1800 of the Computer Center of Kyushu University was used to carry out calculations. The calculated eigenvalues indicate that the first five factors account for more than 94% of the total variance among the samples analyzed (Table 4).

Figures 4-8 illustrate the distribution of the varimax factor loadings (Table 5) when are classified into six categories, e.g. 0.000, 0.138, 0.572 four times and 1.000 as maximum of absolute values. The distribution of each varimax factor loadings is interpreted and correlated with key oceanographic parameters.

The first varimax factor explains 49.44% of the total variance. The first varimax assemblage is dominated by *Globigerinita glutinata* (Egger) and *Globigerina bulloides* d'Orbigny, accompanied by *Neogloboquadrina dutertrei* (d'Orbigny) and *Globigerinoides ruber* (d'Orbigny). The varimax factor loadings show high values in almost all stations south of Lat. 35°N (Figure 4). In contrast, varimax factor loadings display low values in stations north of Lat. 35°N, and especially north of Lat. 38°N. Thus, the distribution of the varimax factor loadings clearly demonstrates that the first factor reflects the relative importance and influence of the Kuroshio water mass on the distribution of planktic foraminifera in the sample analyzed.

Bradshaw (1959) reported that *Globigerinita glutinata* is most abundant in tropical regions but also ranges into subarctic waters. *Globigerina bulloides* has been reported from subarctic cold water to tropical regions (Bradshaw, 1959 ; Tolderlund and Bé, 1971 ; Bé, 1977 ; Reynolds and Thunell, 1985), is reported to feed on phytoplankton, and its production has been shown to rapidly increase in areas of upwelling and phytoplankton blooms in both the Pacific and Atlantic Oceans (Tolderlund and Bé, 1971 ; Thunell and Reynolds, 1984 ; Reynolds and Thunell, 1985). Moreover, *Gnt. glutinata* mainly feeds on diatoms (Hemleben *et al.*,

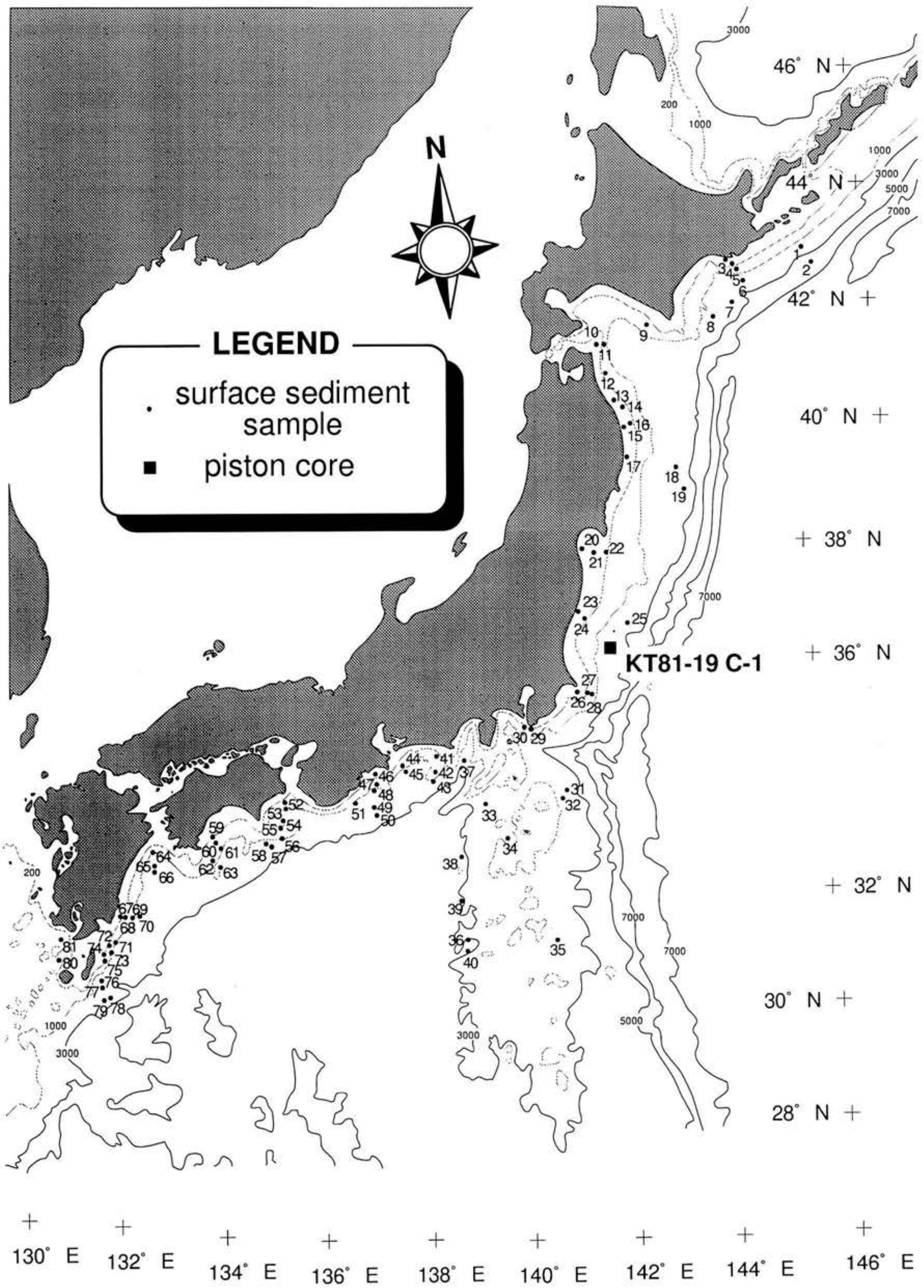


Figure 3. Map illustrating the location sites of the 81 surface sediment sample used in this study and a piston core (KT81-19, C-1) analyzed here.

Table 1. Locations and water depths of surface sediment samples used in study.

	cruise No.	latitude	longitude	depth (m)
1	GH76-2	42°56′	146°20.7′	2,488
2	GH76-2	42°37.9′	146°33.8′	3,383
3	KT78-8	42°53.6′	144°41.5′	53
4	KT78-8	42°45′	144°48.3′	152
5	KT78-8	42°37.7′	144°54.8′	883
6	KT78-8	42°32.1′	144°59.4′	1,530
7	GH76-2	42°06′	144°46.2′	2,195
8	GH76-2	41°56.1′	144°11.1′	1,405
9	KT69-18	41°46.1′	142°39.4′	902
10	KT67-10	41°30′	141°31.9′	70
11	KT67-10	41°30.3′	141°38.8′	598
12	KT69-18	47°59.2′	141°28.8′	300
13	KT69-18	40°41.3′	141°47.5′	100
14	GH76-3-II	40°29.8′	141°57.8′	120
15	GH76-3-II	39°57.0′	142°02.7′	110
16	GH76-3-II	40°01.5′	142°10.8′	150
17	KT70-11	39°22.4′	142°03.2′	120
18	KT70-11	39°15.2′	143°02.9′	1,965
19	KH94-3	38°53.52′	143°22.11′	2,353
20	KT65	37°59′	141°03.3′	38
21	KT65	37°56.5′	141′29.34′	130
22	KT65	37°58.4′	141°42′	185
23	KT75-7	36°49.5′	140°54.3′	30
24	KT75-7	36°40.7′	141°07.5′	160
25	KT95-10	36°40.07′	141°59.94′	2,516
26	KT70-11	35°34.8′	141°02.9′	100
27	KT70-11	35°31.8′	141°13.6′	388
28	KT70-11	35°31.5′	141°14.5′	642
29	GH75-3	34°54′	140°01′	190
30	GH75-3	34°57.5′	139°39.7′	595
31	GH80-4	33°51.9′	140°36.3′	2,160
32	KT86-10	33°40.4′	140°30′	1,693
33	KT86-10	33°37.2′	139°08.6′	1,868
34	KT86-10	33°08.1′	139°24′	1,294
35	GH79-4	30°59.7′	141°04.8′	2,915
36	GH79-4	31°15.3′	138°17.6′	3,680
37	KH74-3	34°20.6′	138°37′	1,423
38	KT92-17	32°40.1′	138°27.3′	3,256
39	KT92-17	31°55.5′	138°25.1′	3,313
40	KT92-17	31°05.7′	138°39.9′	3,335
41	KT85-6	34°26.7′	138°00.1′	495
42	KT85-6	34°10.6′	138°00.0′	938
43	KT85-6	34°01.8′	137°58.1′	1,406
44	KT85-6	34°15.6′	137°16.5′	587
45	KT85-6	34°10.0′	137°21.1′	1,249
46	GH82-2	34°13.3′	136°37.8′	100
47	GH82-2	34°04.7′	136°43.5′	670
48	GH82-2	33°58′	136°41′	1,500
49	GDP-8	33°36.5′	136°44.5′	2,078
50	GDP-8	33°22′	136°50.8′	2,375
51	GH82-2	33°44.2′	136°10.2′	1,217
52	KT81-15	34°30.3′	134°48.2′	720
53	KT81-15	33°26.7′	134°48.1′	1,135
54	GH82-1	33°17.8′	134°41.2′	1,110
55	GH82-1	33°09.9′	134°38′	750
56	GH82-1	32°56.5′	134°39′	1,000
57	GH82-1	32°50.4′	134°17.2′	1,500
58	GH82-1	32°49.9′	134°26.6′	1,700
59	KH72-2	32°57.5′	133°21.4′	202
60	KH72-2	32°50.5′	133°26′	475
61	KH72-2	32°43.8′	133°30.4′	808
62	GH83	32°35.3′	133°38.5′	900
63	GH83	32°22.6′	133°47.3′	1,200
64	GH83-2	32°34.4′	132°17.43′	900
65	GH83-2	32°26.49′	132°17.51′	1,482
66	GH83-2	32°21.97′	132°17.60′	1,589
67	GH83-2	31°32.49′	131°32.42′	124
68	GH83-2	31°32.7′	131°41.6′	375
69	GH83-2	31°32.66′	131°50.52′	930
70	GH83-2	31°33.31′	131°55.28′	1,125
71	GH84-3	30°58.22′	131°29.49′	970
72	GH84-3	30°52′	131°22.26′	676
73	GH84-3	30°43.9′	131°24.94′	1,185
74	GH84-3	30°42.61′	131°19.12′	196
75	GH84-3	30°37.95′	131°17.71′	254
76	GH84-3	30°19.18′	131°11.29′	1,520
77	GH84-3	30°11.17′	131°13.87′	1,750
78	GH84-3	30°02.36′	131°30.95′	2,710
79	GH84-3	30°01.48′	131°25.87′	2,309
80	G6K8	31°00.1′	130°24.6′	310
81	G9K15	30°39.9′	130°24.9′	375

1989 ; Ottens, 1992), and its production is also triggered by upwelling and high phytoplankton productivity bloom, as in the case of *Gna. bulloides* (Thunell and Reynolds, 1984 ; Reynolds and Thunell, 1985 ; Sautter and Sancetta, 1992). Thus, it is generally assumed that the distribution of *Gnt. glutinata* and *Gna. bulloides* depends largely on food supply, and that they can tolerate wide ranges in sea surface temperature. *Nqd. dutertrei* and *Gds. ruber*, subordinate species of the characteristic Kuroshio assemblage, are typical warm-water species, widely distributed in tropical and subtropical regions (Tolderlund and Bé, 1971 ; Bé, 1977). Thus, the composition of the Kuroshio assemblages represents an indicator of relatively warm water accompanied and influenced by seasonal phytoplankton blooms.

The second varimax factor explains 21.67% of the total variance. The second varimax assemblage is characterized by an extraordinarily high contribution of *Neogloboquadrina incompta* (Cifelli) and a subordinate contribution of *Globigerina quinqueloba* Natland. The second factor clearly reflects an association with the Transitional Water between the Oyashio and Kuroshio fronts. The varimax factor loadings show high values in areas extending from the Tsugaru Strait to off Inubo-saki along the Sanriku coast, and in seas off Enshu-nada, northeast Honshu (Figure 5). The former reflects the relative importance of the Tsugaru Warm Current whereas the latter correlates with the area where the Kuroshio meanders, forming the Cold Water Mass. These

Table 2. Planktic foraminiferal species used for factor analysis including their average percentage abundance, standard deviation and maximum abundance (%).

No.	Species	Average	Standard deviation	Maximum occurrence
1	*Globigerina bulloides* d'Orbigny	15.25	9.33	35.67
2	*Gna. falconensis* Blow	3.96	3.73	14.60
3	*Gna. quinqueloba* Natland	6.91	10.25	53.54
4	*Gna. rubescens* Hofker	0.87	1.02	4.09
5	*Globigerinella aequilateralis* (Brady)	0.49	0.62	2.48
6	*Gnl. calida* (Parker)	0.46	1.02	7.70
7	*Globigerinita glutinata* (Egger)	13.67	11.39	38.35
8	*Gnt. iota* Parker	0.93	1.57	7.49
9	*Globigerinoides conglobatus* (Brady)	0.38	0.65	3.74
10	*Gds. ruber* (d'Orbigny)	6.57	4.70	16.26
11	*Gds. sacculifer* (Brady)	1.41	1.75	9.85
12	*Gds. tenellus* Parker	1.00	1.10	5.31
13	*Globorotalia inflata* (d'Orbigny)	5.50	5.35	26.58
14	*Grt. menardii* (Parker, Jones and Brady)	0.39	0.72	3.49
15	*Grt. scitula* (Brady)	0.14	0.29	1.57
16	*Grt. truncatulinoides* (d'Orbigny)	0.41	0.69	3.90
17	*Grt. tumida* (Brady)	0.18	0.55	4.41
18	*Neogloboquadrina dutertrei* (d'Orbigny)	9.99	7.25	34.23
19	*Nqd. incompta* (Cifelli)	13.77	18.33	80.21
20	*Nqd. pachyderma* (Ehrenberg) (D*)	0.37	0.94	4.55
21	*Nqd. pachyderma* (Ehrenberg) (S**)	12.59	27.22	98.68
22	*Orbulina universa* (d'Orbigny)	0.22	0.60	4.95
23	*Pulleniatina obliquiloculata* (Parker and Jones)	4.38	5.36	32.35
24	*Turborotalita humilis* (Brady)	0.17	0.33	1.79

Table 3. Planktic foraminiferal species identified but not used in formulating transfer function Eq. PFJ-125 along with their maximum occurrence (%).

No.	Species	Maximum occurrence
1	*Beella digitata* (Brady)	1.18
2	*Candeina nitida* d'Orbigny	0.07
3	*Globigerinella adamsi* (Banner and Blow)	0.21
4	*Globorotalia bermudezi* Rögl and Bolli	0.93
5	*Grt. hirsuta* (d'Orbigny)	0.93
6	*Globoquadrina conglomerata* (Schwager)	0.77
7	*Hastigerina pelagica* (d'Orbigny)	0.26
8	*Hastigerinopsis riedeli* (Rögl and Bolli)	0.23
9	*Sphaeroidinella dehiscens* (Parker and Jones)	0.47
10	*Tenuitella fleisheri* Li	1.77
11	*Turborotalita anfracta* (Parker)	2.71
12	*Tbt guaymasensis* Matoba and Oda	3.56
13	*Tbt. parkerae* (Brönnimann and Resig)	0.61

particular varimax factor loadings are barely detectable at stations west of Long. 134°E off southeast Japan, where the paths of the Kuroshio do not differ, irrespective of its meandering (Taft, 1972). Therefore, the second varimax factor is an excellent indicator of the Transitional Water, or more specifically, the Tsugaru Warm Current, the Cold Water Mass, or both.

Nqd. incompta is an established indicator of the Tsugaru Warm Current (Oda *et al.*, 1983). In addition, high frequencies of *Nqd. incompta* are also present off Enshu-nada

Table 4. Varimax factor score matrix showing the contribution of planktic foraminiferal species to each factor.

	1st factor	2nd factor	3rd factor	4th factor	5th factor
Gna. bulloides	0.569	0.066	0.038	0.108	0.060
Gna falconensis	0.166	0.023	−0.010	−0.002	−0.128
Gna. quinqueloba	0.057	0.308	−0.010	−0.009	0.869
Gna. rubescens	0.040	−0.007	0.000	0.003	0.042
Gnl. aequlateralis	0.019	−0.004	0.000	0.016	−0.013
Gnl. calida	0.024	−0.006	0.001	−0.004	0.015
Gnt. glutinata	0.701	−0.028	0.021	−0.495	−0.065
Gnt. iota	0.039	0.024	−0.006	−0.038	−0.110
Gds. conglobatus	0.010	−0.008	0.001	0.040	−0.002
Gds. ruber	0.239	0.014	−0.010	0.156	−0.018
Gds. sacculifer	0.042	−0.021	0.003	0.109	−0.014
Gds. tenellus	0.045	−0.002	0.002	−0.009	0.034
Grt. inflata	0.099	0.157	−0.013	0.226	−0.384
Grt. menardii	0.012	−0.001	0.000	0.018	−0.027
Grt. scitula	0.003	0.005	−0.001	0.004	−0.013
Grt. truncatulinoides	0.006	0.014	−0.002	0.021	−0.019
Grt. tumida	0.004	0.005	−0.002	0.009	−0.011
Nqd. dutertrei	0.244	−0.012	0.018	0.718	0.082
Nqd. incompta	−0.045	0.929	−0.047	−0.013	−0.222
Nqd. pachyderma (D)	−0.004	0.007	0.022	0.017	−0.008
Nqd. pachyderma (S)	−0.038	0.049	0.997	−0.009	−0.011
Orb. unversa	0.010	−0.001	0.000	0.003	0.001
Pul. obliquiloculata	0.130	−0.084	0.014	0.367	−0.013
Tbt. humilis	0.008	0.002	−0.001	−0.008	−0.009
variance	49.443	21.668	13.166	6.091	3.837
cumulative var.	49.443	71.111	84.277	90.367	94.204

Table 5. The varimax factor loading matrix and communalities for the 81 surface sediment samples from the northwest Pacific Ocean off Japan.

	1st factor	2nd factor	3rd factor	4th factor	5th factor	communality
1	−0.038	0.050	0.997	−0.007	−0.014	0.999
2	0.006	0.092	0.994	0.008	0.019	0.998
3	0.051	0.197	0.968	−0.034	0.133	0.997
4	0.025	0.099	0.991	0.004	0.049	0.995
5	−0.008	0.070	0.997	−0.007	−0.008	0.999
6	−0.027	0.050	0.998	−0.007	−0.010	0.999
7	−0.025	0.054	0.998	−0.006	0.000	0.999
8	0.059	0.072	0.990	0.006	0.020	0.989
9	−0.003	0.711	0.689	0.031	0.009	0.982
10	−0.011	0.955	−0.004	0.009	−0.149	0.935
11	−0.004	0.961	0.095	−0.001	−0.100	0.942
12	0.038	0.961	0.189	−0.002	−0.042	0.963
13	0.009	0.954	0.130	−0.003	0.235	0.983
14	0.096	0.918	0.292	0.015	0.235	0.993
15	0.077	0.943	0.133	−0.001	0.279	0.990
16	0.047	0.893	0.421	0.007	0.096	0.986
17	0.063	0.915	0.263	−0.019	0.275	0.987
18	0.047	0.358	0.899	0.172	−0.117	0.981
19	0.045	0.211	0.970	0.070	−0.066	0.997
20	0.165	0.661	0.080	−0.007	0.693	0.952
21	0.105	0.957	0.093	0.052	0.033	0.940
22	0.112	0.962	0.168	0.095	0.037	0.976
23	0.262	0.564	0.067	0.053	0.728	0.923
24	0.273	0.808	0.130	0.408	−0.189	0.946

Table 5 continue

	1st factor	2nd factor	3rd factor	4th factor	5th factor	communality
25	0.420	0.534	0.180	0.579	−0.106	0.840
26	0.518	0.216	0.016	0.695	0.331	0.907
27	0.782	0.334	0.077	0.368	0.174	0.895
28	0.648	0.722	0.132	0.042	−0.131	0.978
29	0.808	0.321	0.017	0.407	0.031	0.924
30	0.831	0.283	0.021	0.319	0.138	0.891
31	0.877	0.208	0.011	−0.028	−0.203	0.854
32	0.923	0.049	0.024	−0.030	−0.041	0.858
33	0.643	0.535	−0.011	0.115	−0.343	0.831
34	0.953	0.106	0.029	−0.117	−0.124	0.949
35	0.686	0.531	−0.003	0.199	−0.286	0.873
36	0.243	0.793	−0.030	0.368	−0.346	0.944
37	0.551	0.733	−0.009	0.248	−0.223	0.952
38	0.751	0.516	0.007	0.283	−0.232	0.965
39	0.608	0.574	−0.007	0.432	−0.280	0.964
40	0.911	0.279	0.013	−0.097	−0.211	0.962
41	0.625	0.422	0.000	0.498	−0.171	0.845
42	0.693	0.580	−0.001	0.215	−0.149	0.886
43	0.597	0.687	−0.005	0.259	−0.186	0.930
44	0.507	0.750	−0.028	0.022	−0.331	0.930
45	0.681	0.572	−0.009	0.184	−0.280	0.902
46	0.773	0.253	0.023	0.444	0.318	0.960
47	0.951	0.134	0.036	0.164	0.140	0.970
48	0.947	0.248	0.025	0.144	−0.064	0.984
49	0.874	0.176	0.034	0.326	−0.048	0.905
50	0.926	0.186	0.028	0.036	−0.138	0.914
51	0.736	0.569	0.004	0.271	−0.201	0.978
52	0.941	0.254	0.028	0.033	0.190	0.987
53	0.933	0.227	0.030	0.161	0.139	0.969
54	0.938	0.135	0.035	0.170	0.224	0.978
55	0.966	0.128	0.031	−0.127	0.147	0.988
56	0.960	0.149	0.035	0.154	−0.042	0.970
57	0.855	0.343	0.022	0.205	−0.144	0.912
58	0.958	0.176	0.033	−0.093	−0.054	0.961
59	0.870	0.178	0.029	0.359	0.166	0.946
60	0.949	0.183	0.028	0.063	0.102	0.949
61	0.912	0.062	0.042	0.329	0.066	0.949
62	0.963	0.056	0.029	−0.129	0.023	0.948
63	0.955	0.147	0.026	0.189	−0.059	0.974
64	0.961	0.085	0.039	−0.031	0.038	0.935
65	0.945	0.116	0.038	0.205	−0.041	0.952
66	0.946	0.042	0.044	0.111	0.010	0.911
67	0.865	0.166	0.030	0.167	0.420	0.980
68	0.910	0.106	0.037	0.150	0.195	0.902
69	0.990	0.026	0.036	−0.079	−0.004	0.988
70	0.966	0.011	0.033	−0.101	−0.024	0.945
71	0.971	0.014	0.042	0.155	0.004	0.968
72	0.818	−0.010	0.030	0.420	−0.010	0.847
73	0.977	0.027	0.036	0.083	0.047	0.965
74	0.496	−0.032	0.023	0.757	−0.009	0.820
75	0.394	−0.044	0.020	0.755	−0.033	0.728
76	0.957	0.013	0.034	−0.134	−0.034	0.936
77	0.966	0.005	0.033	−0.093	−0.024	0.944
78	0.886	−0.017	0.034	0.309	−0.039	0.883
79	0.927	0.000	0.035	0.234	−0.068	0.920
80	0.943	0.079	0.033	0.136	0.179	0.948
81	0.968	0.030	0.035	0.150	0.036	0.962

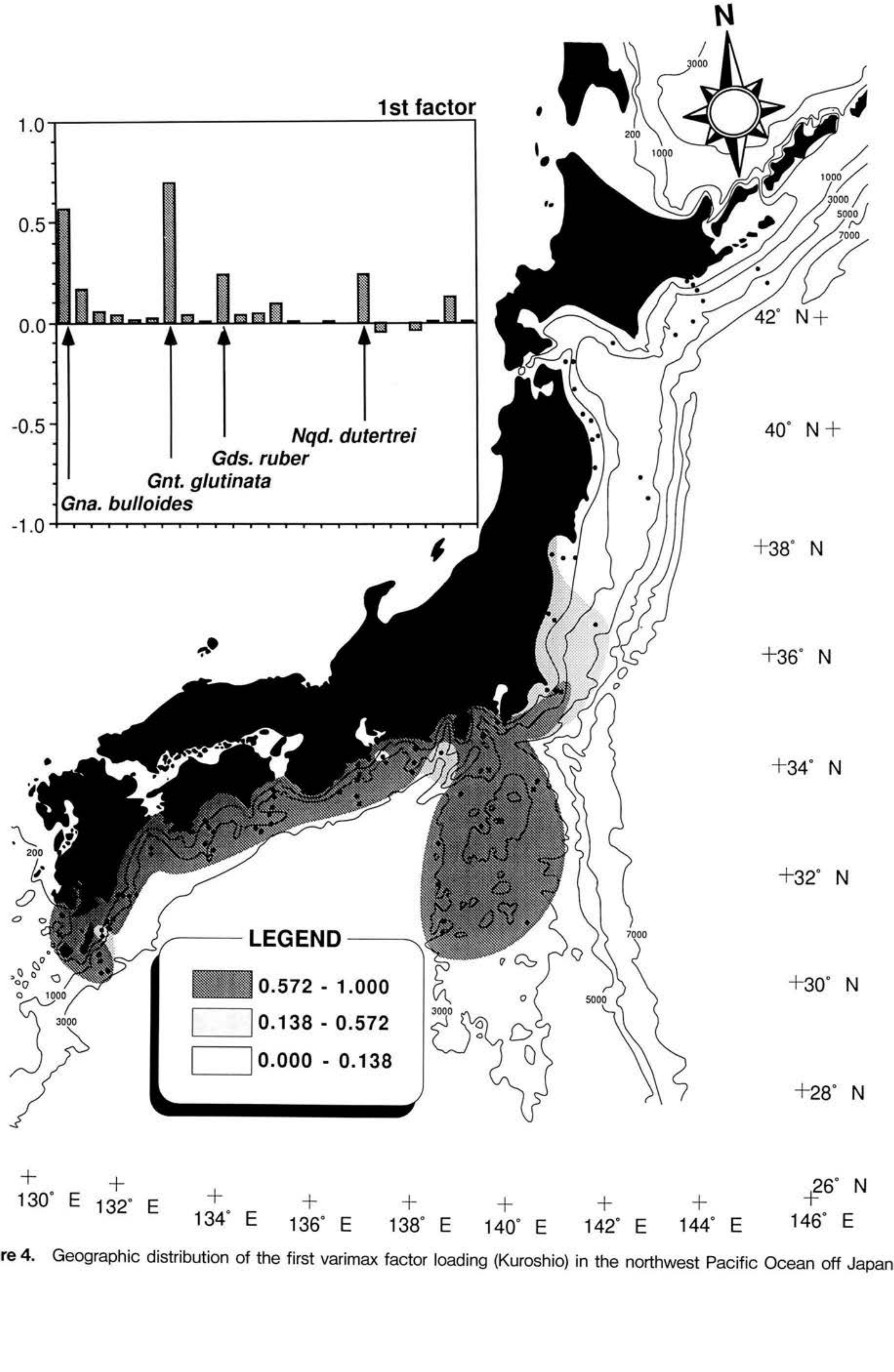


Figure 4. Geographic distribution of the first varimax factor loading (Kuroshio) in the northwest Pacific Ocean off Japan.

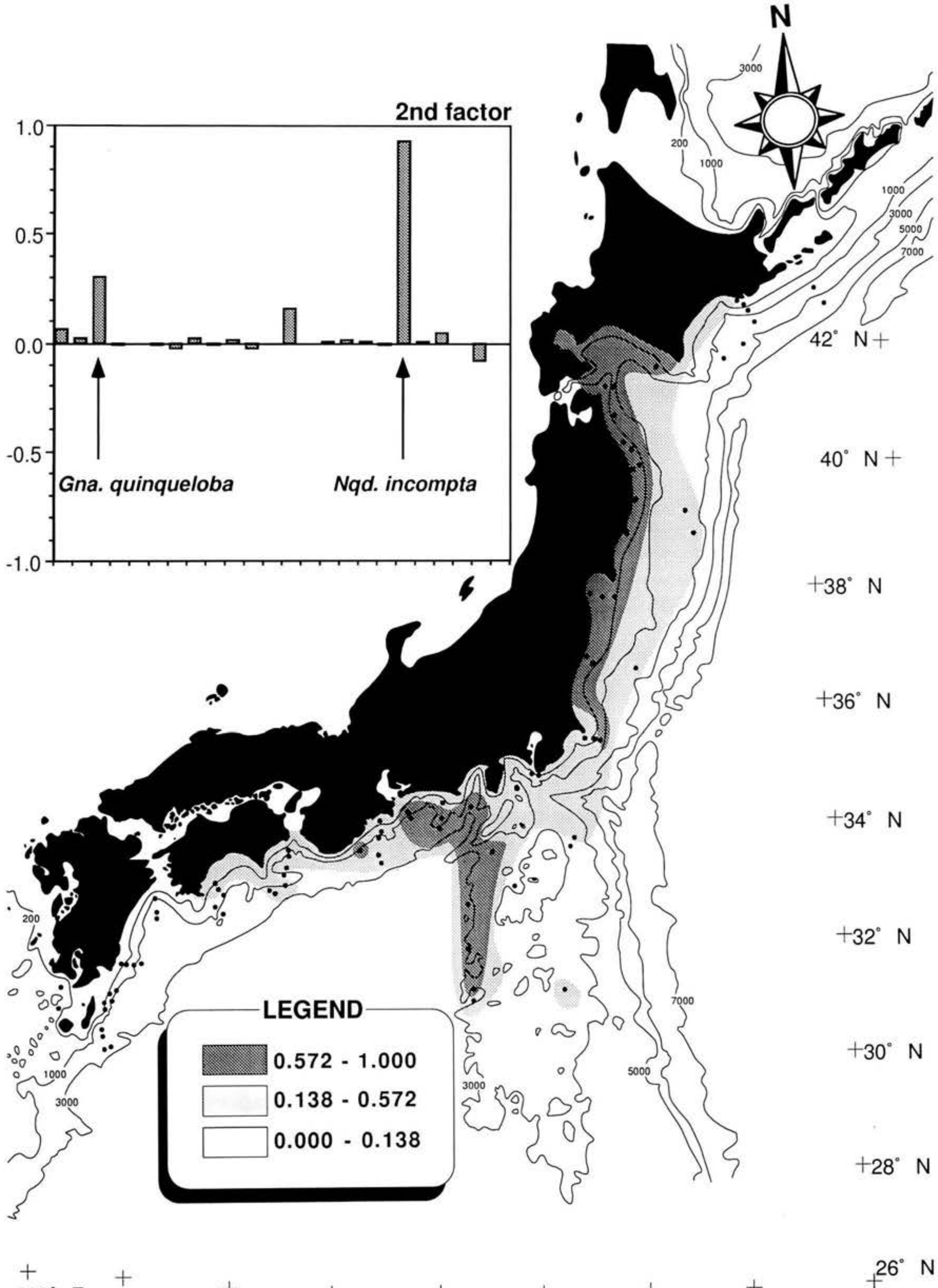


Figure 5. Geographic distribution of the second varimax factor loading (Transitional) in the northwest Pacific Ocean off Japan.

where the Cold Water Mass frequently occurs. Since the southern limit of the Tsugaru Warm Current is at approximately Lat. 38°N, near Kinkazan Island and the northern limit of the Cold Water Mass is at approximately Lat. 34°N off Enshu-nada these two water masses are geographically isolated from each other. The former is characterized by the occurrence of the sinistral form of *Neogloboquadrina pachyderma* (Ehrenberg) (given as *Nqd. pachyderma* (S)), whereas this species is not present in the latter water mass. Consequently, we conclude that there are two possible influences on the assemblage, the Tsugaru Warm Current and the Cold Water Mass, with a possible distinction based upon the occurrence of *Nqd. pachyderma* (S).

The third varimax factor explains 13.17% of the total variance. The third varimax assemblage is represented by only one species, *Nqd. pachyderma* (S). Figure 6 shows the varimax factor loadings which are apparently high to the north of the Oyashio Front as might be anticipated. Thus, the third factor reflects an association with the cold Oyashio Current.

Nqd. pachyderma (S) is the dominant species of cold water (Reynolds and Thunell, 1985; Sautter and Thunell, 1989) in polar and subpolar regions (Bradshaw, 1959; Bé, 1977; Tolderlund and Bé, 1971). This species has also been regarded as a typical indicator species of the Oyashio Current near Japan (Takayanagi and Oda, 1983; Oda *et al.*, 1983; Chinzei *et al.*, 1987).

The fourth varimax factor explains 6.09% of the total variance. The fourth varimax assemblage is composed of such tropical species as *Nqd. dutertrei* and *Pulleniatina obliquiloculata* (Parker and Jones). Figure 7 shows the varimax factor loadings which have high values at stations off the Joban coast (Lat. 36°40′N), off Inubo-saki (Lat. 35°35′ N), and around Tanega-shima Island (Lat. 30°60′N), and have middle values at stations off the Pacific coast of southeast Japan. Stations north of Lat. 37°N show very little influence of the fourth varimax factor except for one station where warm core eddies frequently occur. Accordingly, the fourth varimax factor suggests an association with the Kuroshio Gyre Margin.

The fifth varimax factor explains 3.84% of the total variance. The fifth varimax assemblage is again represented by only one taxon, *Gna. quinqueloba*. The varimax factor loading shows high values along the Joban coast in the Perturbed Region (Figure 8), while low values are recognized in the coastal area from off southeast Kyushu to off southeast Shikoku. The distribution of the fifth factor loadings suggests the degree to which particular oceanic regions can be influenced by coastal influences, for instance, increasing mixing with low-salinity waters.

Gna. quinqueloba is abundant in coastal areas including shelf areas off Japan and shows a propensity for low-salinity areas (Wang *et al.*, 1988; Takayanagi and Oda, 1983). Thus, the distribution of the fifth varimax factor loadings expresses the influence of Coastal Water.

(3) Regression Analysis

Multiple regression analysis was used to verify the relationship between the planktic foraminiferal data set and oceanographic data within the study area, and subsequently used to formulate multiple regression equations. The oceanographic data set includes average surface water temperatures for both the summer and the winter taken from the Marine Environmental Atlas (the Japan Oceanographic Data Center, 1978). The planktic foraminiferal data set includes the five varimax assemblages identified in 81 surface samples. The program ANALYST was used to carry out the multiple regression analysis using the FACOM operation system of the Computer Center of Kyushu University.

The following two transfer functions, termed Equation PFJ-125, yield surface water temperatures (SST) for the winter and the summer:

SST in the winter is given by

(1) $Tw = 5.49x_1 - 4.65x_2 - 10.93x_3 + 2.59x_4 - 4.81x_5 + 13.71$,
R^2(contribution) = 0.92, standard error = 1.75°C.

SST in the summer is given by

(2) $Ts = 4.16x_1 - 2.28x_2 - 6.50x_3 + 1.23x_4 - 3.41x_5 + 23.74$,
R^2(contribution) = 0.92, standard error = 1.17°C.

Note that x_1 to x_5 indicate the proportions of the varimax loadings.

To ascertain the reliability of the equation in estimating sea surface temperature, we applied calculated values derived for each of the foraminiferal samples analyzed and compared the estimated values with observed SST values (Figure 9). The standard error of estimated winter SST is about 8.92% of the present SST range (0.7∼20.3°C) and about 8.96% of the present summer SST range (15.0∼28.1°C). Standard ANOVA F-statistics are shown in Table 6. For each equation, the correlation coefficient squared is greater than 0.9, and the standard error is less than 9.0% of the total range. Thus, these equations yield SST values of apparent accuracy and precision.

Estimated Variations in Downcore Surface Temperature Value

Piston core KT81-19 C-1 (243 cm in length), obtained from the sea bottom beneath the Perturbed Region north of the Kuroshio Front (water depth of 1,545 m; Lat. 36°15.9′N, Long. 141°1.8′E) off the Joban coast of Northeast Honshu, Japan (Figure 1), was selected to test the reliability of equations in estimating paleo-SST. The bottom of this core was estimated by Chinzei *et al.* (1987) to be younger than 12,000 yrs. B.P. based on radiocarbon dating of two horizons and five tephra key beds. Oda and Takemoto (1992) studied planktic foraminiferal assemblages from 41 sediment samples taken at 5 cm sampling intervals through core KT81-19 C-1, with a time resolution of 163-383 yrs. The method of sample preparation and treatment was identical to that applied to surface sediment samples analyzed for this study.

Down-core fluctuations in winter and summer SSTs calculated by the equations discussed above span the last 12 Kyrs, where the first through fifth factor loadings represent the proportions of the first five varimax assemblages (Figure 10). Communalities of all the samples are higher than 0.7 and average 0.92 (Table 7).

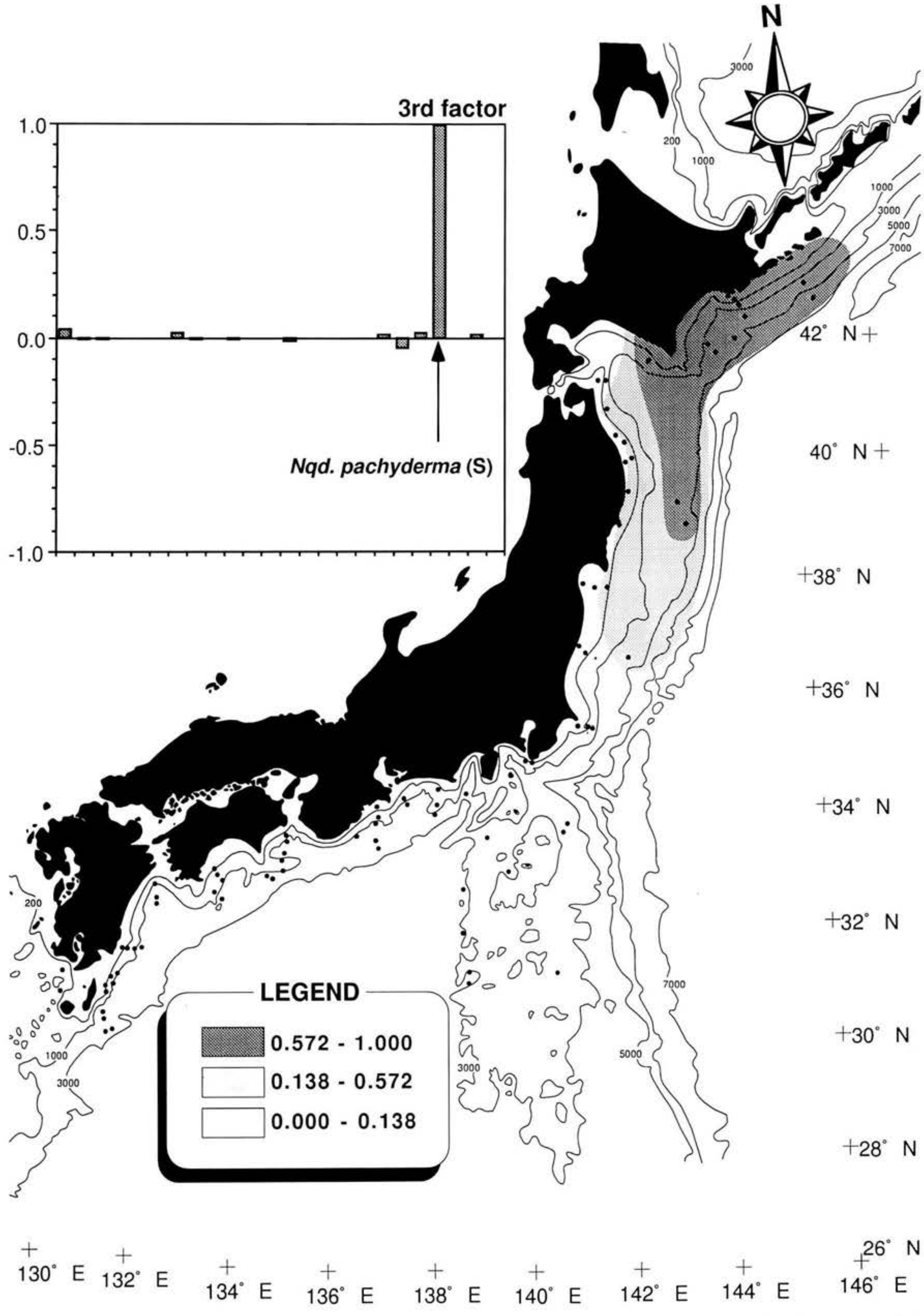


Figure 6. Geographic distribution of the third varimax factor loading (Oyashio) in the northwest Pacific Ocean off Japan.

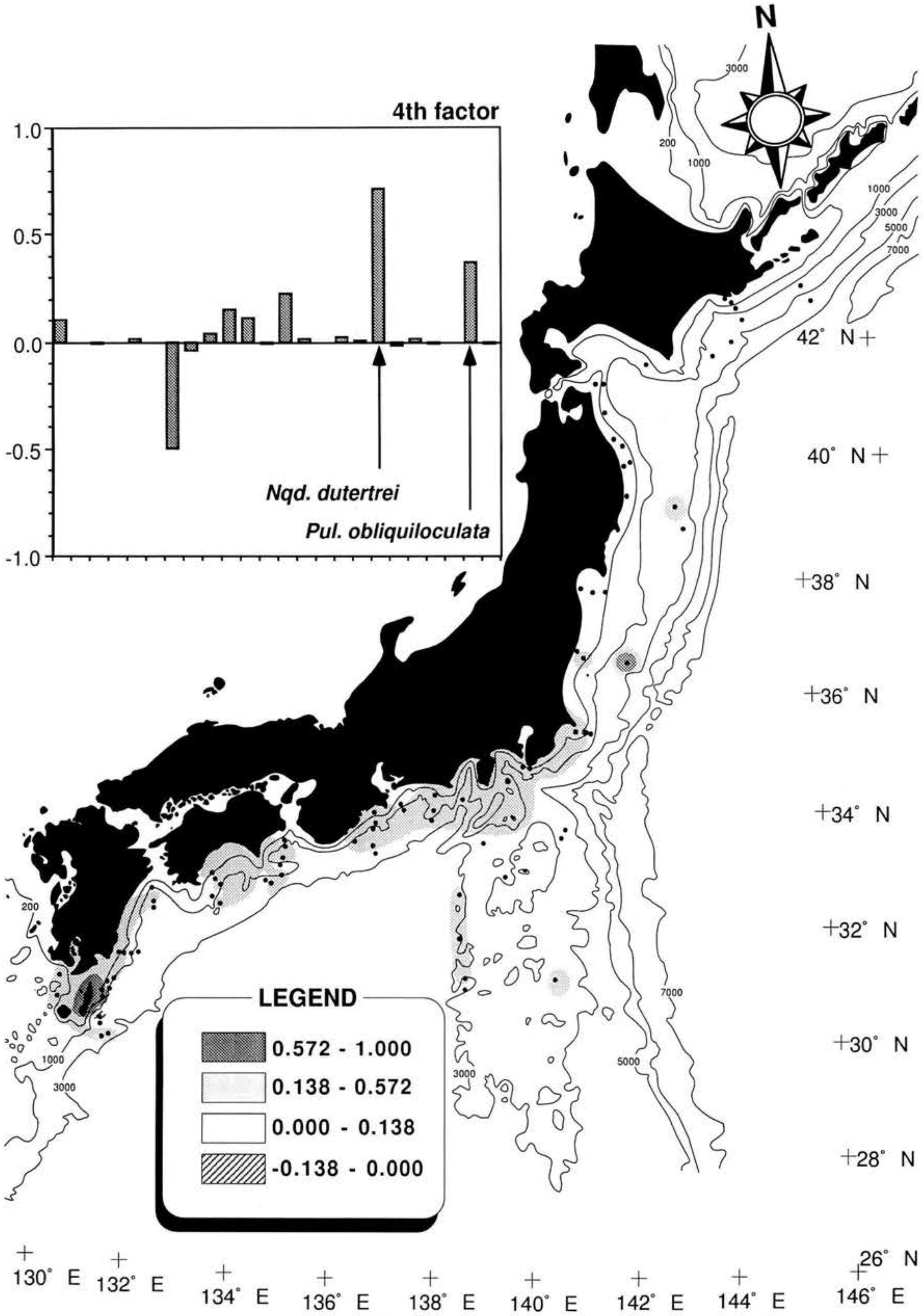


Figure 7. Geographic distribution of the fourth varimax factor loading (Kuroshio Gyre Margin) in the northwest Pacific Ocean off Japan.

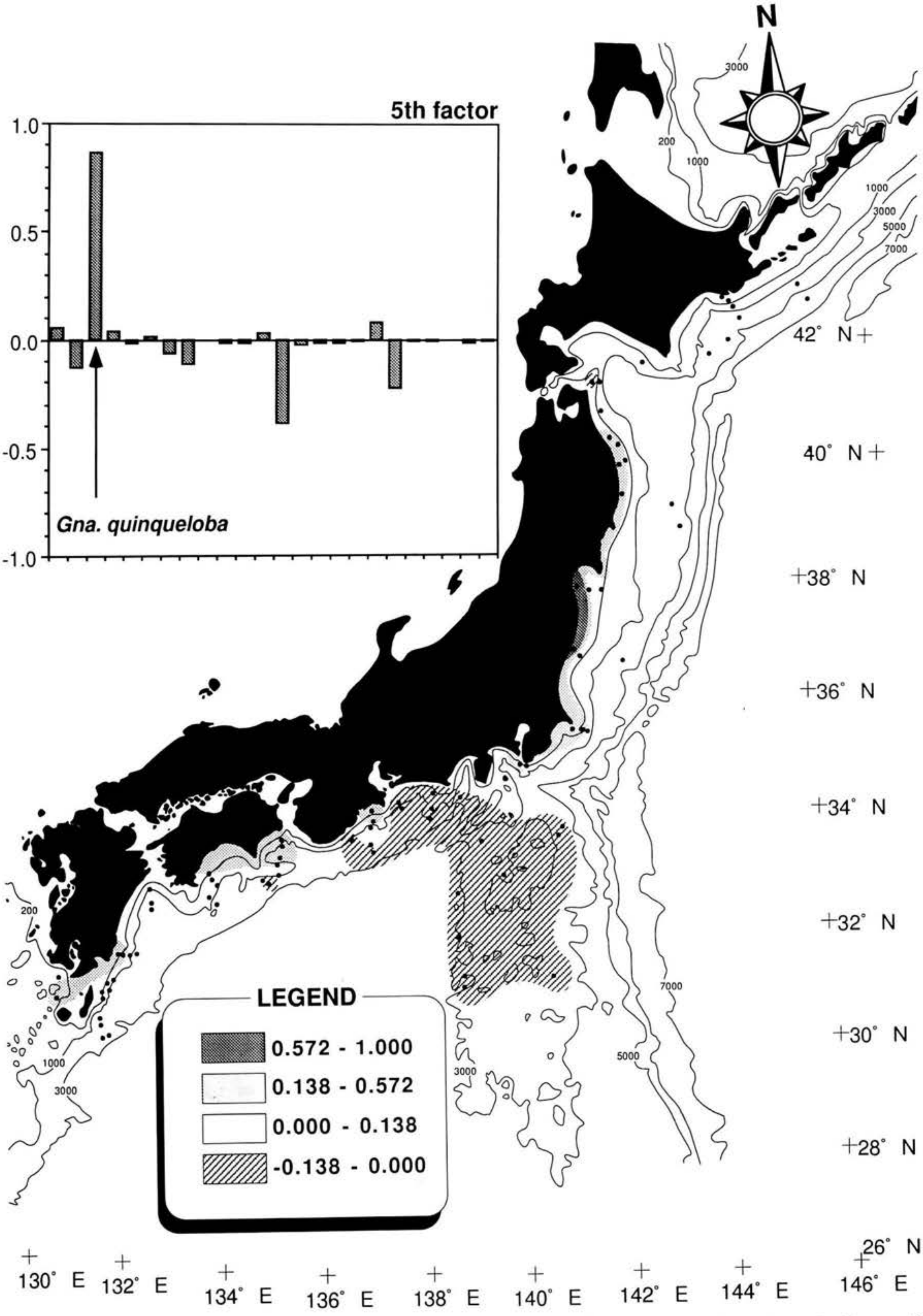


Figure 8. Geographic distribution of the fifth varimax factor loading (Coastal Water) in the northwest Pacific Ocean off Japan.

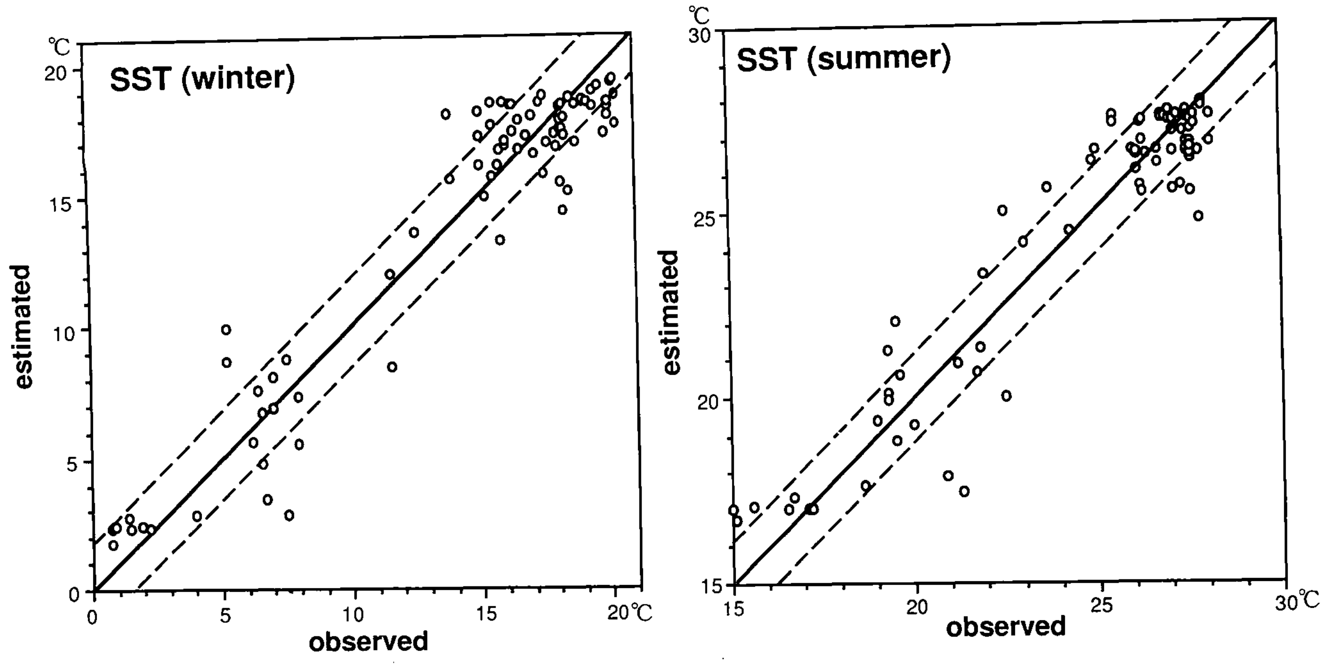


Figure 9. Comparison of observed winter and summer sea surface temperatures (SST) in the northwest Pacific Ocean off Japan and estimated SST derived through application of the paleontological transfer functions PFJ-125, Tw and Ts. Broken lines denote the limit of standard errors.

Table 6. ANOVA F-statistics for equations Ts and Tw.

	Standard error	sum of square	degree of freedom	unibiased variance	F-value
Ts	1.17				
regression		1,126.82	5	225.36	163
residual		103.40	75	1.38	
total		1,230.22	80	15.38	
Tw	1.75				
regression		2,749.76	5	549.95	180
residual		229.31	75	3.06	
total		2,979.07	80	37.24	

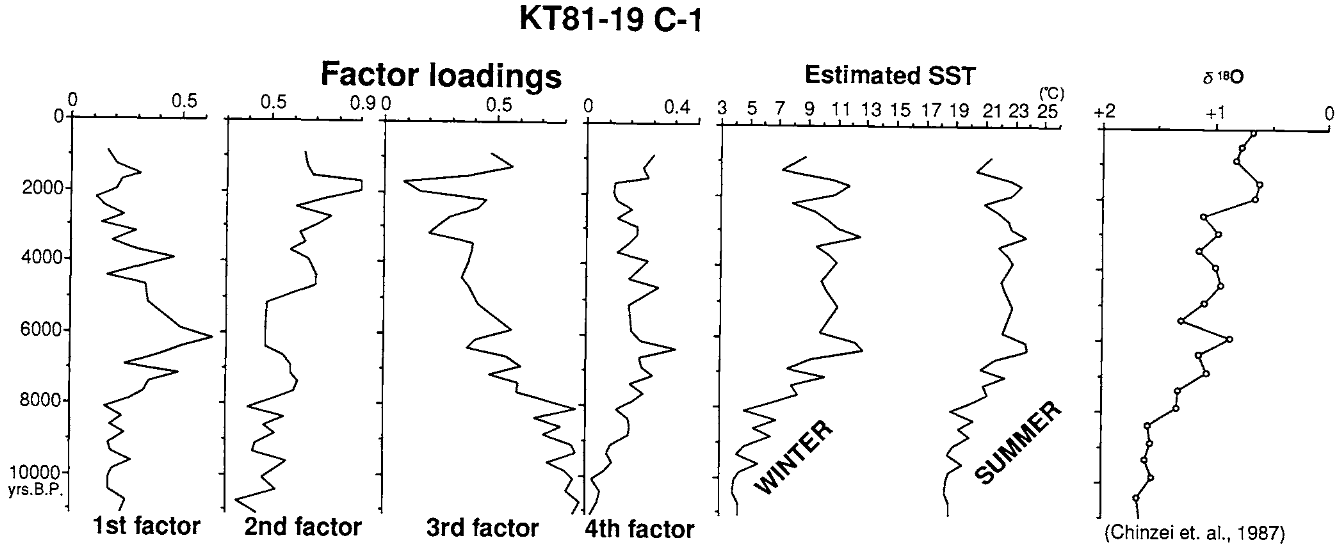
Estimated sea surface temperatures (SST) down core KT81-19 C-1 indicate the coldest period at approximately 10,500 yrs. B.P. (about 3.9°C in the winter and 18.5°C in the summer). After 10,000 yrs B.P., there are indications of a slight warming of SST with a radical increase in SST at 8,000 yrs. B.P. (about 6.9°C in the winter and 20.3°C in the summer.). This latter warming trend displays a peak at 6,300 yrs. B.P. (12.8°C in the winter and 23.9°C in the summer.). After 6,000 yrs. B.P., the SST decreased gradually, with a warming peak again at 3,100 yrs B.P. (about 12.6°C in the winter and 23.8°C in the summer). After 3,000 yrs. B.P., two cooling peaks centered at about 2,200 yrs. B.P. and 1,300 yrs. B.P. can be recognized (7.9°C and 7.2°C in the winter, 20.9°C and 20.4°C in the summer, respectively), with a final warming peak centered at about 1,800 yrs. B.P. (11.8°C in the winter and 23.4°C in the summer).

The coldest estimated winter and summer SSTs (c.a. 10,500 yrs. B.P.) in this core are similar to values of the modern ocean off cape Erimo (Erimo-misaki), southern Hokkaido. It is noteworthy that the difference in winter SST at 10,500 yrs.B.P. and that for the modern winter in this area is about 8°C.

Discussion

The validity of the computed SST values downcore to 11,000 yrs. B.P. for core KT81-19 C-1 can be examined by comparing the distribution of each of the varimax factor loadings (Figure 10).

The most significant fluctuations in factor loadings include the distinctive dominance of the third (Oyashio) factor between 11,000 and 8,000 yrs B.P., the decline of the Oyashio factor after 8,000 yrs B.P., a peak of the first (Kuroshio) factor at 6,300 yrs B.P., and an increase of the second (Transitional



(Chinzei et. al., 1987)

Figure 10. Estimated winter and summer sea surface temperatures (°C) down core KT 81-19, C-1 as analyzed using the paleontological transfer functions PFJ-125, with the first four varimax factor loadings ; δ^{18}O curve based on analyses of the planktic foraminifera *Grt. inflata* (from Chinzei *et al.*, 1987).

Water) factor after 5,000 yrs B.P. These fluctuations are thought to express northward and/or southward shifts of the Kuroshio Front in the region off Japan.

The Oyashio factor dominated during 11,000-8,000 yrs. B. P. Estimated SST values are low during the latter period, with the lowest SST about 3.9°C in the winter and 18.5°C in the summer at 10,500 yrs B.P. These estimates of the winter and summer temperatures are close to those values for the modern Oyashio water off Erimo-misaki, southern Hokkaido, which is situated 5° north of the C-1 core site. Thus, we conclude that the Oyashio Front was near the C-1 core site during this period.

Although the Oyashio factor decreased rapidly after 8,000 yrs B.P. the Kuroshio factor began to increase and peaks at 6,300 yrs. B.P. The increase in amplitude of the estimated SST is about 8.2°C in winter and 5.2°C in summer between 8,000-6,000 yrs. B.P. At 6,300 yrs. B.P., corresponding to the peak in the Kuroshio factor, the estimated winter and summer SST reached their maxima of 12.8°C and 23.9°C, respectively, representing an especially distinctive winter maximum. These estimations of the winter and summer temperatures are close to the modern SST values of the Kuroshio frontal zone off Point Inubo (Inubo-saki, Lat. 35°70′N). Furthermore, an increase of the fourth Kuroshio Gyre margin factor preceded the increase in Kuroshio factor, showing a peak at 6,400 yrs. B.P. Thus, we assume that the increase in the Kuroshio Gyre margin factor indicates a northward shift of the Kuroshio Front.

Thus, the decreasing values of the Kuroshio factor indicates a southward shift of the Kuroshio Front after 6,300 yrs. B.P. Almost simultaneously, there is a general increase in the proportion of the Transitional Water factor after 5,000 yrs. B.P. We assume that the core C-1 site region was influenced by the Transitional Water, especially, the Tsugaru Warm Current at that time. Influence of the Tsugaru Warm Current has continued to the present in this area, although our estimated SST values indicate short warm peaks at 3,100, 2,200, 1,800 and 1,200 yrs B.P. These latter events are thought to reflect the influence of the Oyashio Factor because of varimax factor loadings.

Chinzei *et al.* (1987) analyzed oxygen isotopes in the planktic foraminifer *Grt. inflata* in piston core C-1. The resulting oxygen isotope records display a trend of heavier values downcore and a sharp shift toward the heaviest value of δ^{18}O in the basal part of the core. This same record indicates an episode of cooling around 10,500 yrs. B.P. and a warm trend around 7,000-6,000 yrs. B.P. which peaked at 6,300 yrs. B.P. The results of this study generally agree with those of Chinzei *et al.* (1987). In particular, both studies recognize an episode of cooling at about 10,500 yrs. B.P., followed by a warming trend, and a warm maximum at 6,300 yrs. B.P. Chinzei *et al.* (1987) also suggested that the cooling episode recorded at 10,500 yrs. B.P. was likely correlated with the Younger Dryas cool period. These same authors also concluded that the water temperature maximum at 6,300 yrs. B.P. likely reflected the arrival of the Kuroshio Front at the C-1 core site.

The earliest cool episode in core C-1, which corresponds to the horizon of heaviest values of δ^{18}O in the lowest part of this core, indicates a cooling of surface water in the Perturbed Area by about 8°C (both winter and summer), with SST values close to those of the modern Oyashio water off Erimo-misaki, southern Hokkaido. The difference between the estimated winter SST at 10,500 yrs. B.P., an averaged modern winter sea surface temperature at this site, and the composition of the planktic foraminiferal assemblage are collectively viewed as evidence of the southward penetration of the Oyashio Current. Marine conditions during this latter cooling episode recorded in core C-1 are comparable to those of the last glacial maximum, based upon the southward penetration of the Oyashio Current off Japan at 18,000 yrs. B.P. and average modern February sea surface tempera-

Table 7. Varimax factor loading matrix for core C-1.

yrs.B.P.	1st factor	2nd factor	3rd factor	4th factor	5th factor	communality
88	0.165	0.645	0.467	0.303	−0.325	0.860
1270	0.207	0.658	0.564	0.255	−0.191	0.900
1557	0.313	0.679	0.354	0.280	−0.330	0.870
1719	0.231	0.897	0.082	0.129	−0.318	0.980
1966	0.205	0.895	0.156	0.120	−0.315	0.980
2212	0.114	0.732	0.450	0.141	−0.320	0.870
2458	0.149	0.608	0.414	0.202	−0.372	0.740
2704	0.240	0.765	0.289	0.142	−0.366	0.880
2951	0.136	0.706	0.243	0.226	−0.400	0.790
3197	0.296	0.624	0.198	0.226	−0.368	0.700
3443	0.189	0.648	0.393	0.188	−0.348	0.770
3689	0.286	0.586	0.386	0.139	−0.353	0.720
3936	0.463	0.661	0.376	0.275	−0.248	0.930
4428	0.160	0.699	0.343	0.191	−0.377	0.810
4675	0.336	0.701	0.375	0.327	−0.246	0.910
5167	0.346	0.481	0.418	0.192	−0.369	0.700
5906	0.496	0.473	0.567	0.208	−0.256	0.900
6152	0.637	0.473	0.404	0.250	−0.218	0.900
6399	0.501	0.475	0.366	0.401	−0.310	0.870
6645	0.396	0.556	0.541	0.243	−0.256	0.880
6892	0.246	0.591	0.607	0.253	−0.276	0.920
7139	0.489	0.592	0.471	0.301	−0.190	0.940
7386	0.357	0.621	0.596	0.199	−0.221	0.960
7632	0.333	0.600	0.588	0.259	−0.277	0.960
7879	0.273	0.505	0.722	0.211	−0.232	0.950
8126	0.156	0.400	0.855	0.138	−0.190	0.970
8373	0.237	0.560	0.669	0.195	−0.275	0.930
8619	0.181	0.473	0.790	0.197	−0.203	0.960
8866	0.248	0.516	0.712	0.192	−0.233	0.930
9113	0.172	0.434	0.835	0.112	−0.203	0.970
9360	0.186	0.424	0.858	0.099	−0.119	0.970
9606	0.276	0.575	0.730	0.123	−0.163	0.980
9853	0.192	0.517	0.807	0.082	−0.124	0.980
10100	0.176	0.461	0.841	0.033	−0.117	0.970
10433	0.175	0.524	0.814	0.066	−0.087	0.980
10767	0.253	0.347	0.873	0.055	−0.049	0.950
11100	0.229	0.442	0.842	0.027	−0.100	0.970

tures as indicated by Moore *et al.* (1980) and Thompson (1981). Thus, the 10,500 yrs. B.P. cooling episode represents a dramatic event in the northwest Pacific on the same scale as the Last Glacial Maximum when the steepest gradient was developed between subarctic and subtropical waters off northeast Honshu, Japan.

Summary

(1) Planktic foraminifera were quantitatively analyzed in eighty-one surface sediment samples collected at deep sea stations off Japan in the northwestern Pacific Ocean. Two hundred or more specimens were identified and counted in each sample and census data used for Q-mode principal components factor analysis. Species selected include 24 taxa belonging to 9 genera. The calculated eigenvalues indicate that the first to fifth factors, which account for more than 94% of the total variance, correspond to a Kuroshio factor, a Transitional Water factor, an Oyashio factor, a Kuroshio Gyre Margin factor and a Coastal Water factor, respectively.

(2) The varimax factor loadings of the first five factors were used as explanatory variables; modern winter and summer surface temperatures (SSTs) values. Each equation derived by this analysis shares multiple correlation coefficients greater than 0.9, and standard errors of less than 9.0% of the total range. Transfer functions, which we term Equation PFJ-125, were derived from regression analysis of planktic foraminiferal assemblages to observed SST values. The transfer functions have a standard error of 1.75°C in estimating winter SST and 1.17°C in estimating summer SST.

(3) Application of transfer functions PFJ-125 to planktic foraminiferal assemblages in piston core C-1 representing the last 12 K yrs in the Perturbed Area off Joban, northeast

Honshu (Lat. 36°15.9′N, Long. 141°31.8′E), discloses a cool episode at 10,500 yrs. B.P. with a winter SST of about 3.9°C and a summer SST of about 18.5°C. A warm peak occurred at 6,300 yrs. B.P. with a winter SST of about 12.8°C and summer SST of 23.9°C. The difference in SST values between winter 10,500 yrs. B.P. and average modern winter at the C-1 core site is about 8°C, essentially equivalent to values of modern Oyashio Current water off Erimo-misaki, southern Hokkaido, or about five degrees of latitude north of the core C-1 site. Thus, marine conditions 10,500 yrs. B.P at core site C-1 off Honshu, Japan were comparable to those established for the last glacial maximum in this area and provide evidence of a southward shift of the Kuroshio and Oyashio Fronts.

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References

Bé, A.W.H., 1977: An ecological, zoogeographic and taxonomic review of recent planktonic foraminifera. *Oceanic Micropaleontology*, vol. 1, p. 1-100.

Bé, A.W.H. and Tolderlund, D.S., 1971: Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans. *In,* Funnel, B.M. and Riedel, W.R., *eds., The micropalaeontology of the oceans*, p. 105-149. Cambridge University Press, Cambridge.

Beleyayeva, N.V, 1969: Planktonic foraminifera in sediments of the world's oceans. *Voprosy Mikropaleontologii*, vol. 12, p. 168-172. (*in Russian*)

Bradshaw, J.S., 1959: Ecology of living planktic foraminifera in the North and Equatorial Pacific Ocean. *Contributions from the Cushman Foundation for Foraminiferal Research*, vol. 10, part 2, p. 25-64.

Chinzei, K., Fujioka, K., Kitazato, H., Koizumi, I., Oba, T., Oda, M., Okada, H., Sakai, T. and Tanimura, Y., 1987: Postglacial environmental change of the Pacific Ocean off the coasts of Central Japan. *Marine Micropaleontology*, vol. 11, p. 273-291

CLIMAP Project Members, 1976: The surface of the Ice-Age. *Science*, vol. 191, no. 4232, p. 1131-1137.

Dowsett, H.J. and Poore, R.Z., 1990: A new planktic foraminifer transfer function for estimating Pliocene-Holocene paleoceanographic conditions in the North Atlantic. *Marine Micropaleontology*, vol. 16, p. 1-23.

Fujimori, T., 1964: Preliminary report on the oceanographic anomaly in the early half of 1963 in the water adjacent to Kanto district. *Bulletin Tokai Regional Fisheries Research Laboratory*, vol. 38, p. 77-98.

Gardner, J.V. and Hays, J.D. 1976: Responses of SST and circulation to Global Climatic Change during the past 200,000 years in the Eastern Equatorial Atlantic Ocean. *Geological Society of America, Memoir*, vol. 145, p. 221-246.

Hemleben, C., Spindler, M. and Anderson, O.R., 1989: *Modern Planktonic Foraminifera*, 363 p. Springer-Verlag, New York.

Imbrie, J. and Kipp, N.G., 1971: A new micropaleontological method for quantitative paleoclimatology; Application to a Late Pleistocene Caribbean core. *In*, Turekian, K. K., *ed., The Late Cenozoic Glacial Ages*, p. 71-181, Yale University Press. New Haven.

Japan Oceanographical Data Center, 1978: *Marine Environmental Atlas*, 157 p. Tokyo.

Kawai, H., 1972: Hydrography of the Kuroshio Extension. *In*, Stommel, H. and Yoshida, K., *eds., Kuroshio and its physical aspects*, p. 235-352. University of Tokyo Press.

Kipp, N.G., 1976: New transfer function for estimating past sea-surface conditions from sea-bed distribution of planktonic foraminiferal assemblages in the North Atlantic. *Geological Society of America*, *Memoir*, vol. 145, p. 3-41.

Klovan, J.E. and Imbrie, J., 1971: An algorithm and FORTRAN-IV Program for large-scale Q-Mode factor analysis and calculation of factor scores. *Mathematical Geology*, vol. 3, no. 1, p. 61-77.

Masuzawa, J., 1957: On the fluctuation of the Kuroshio east of Honshu and its forecast. *Proceeding of the symposium on the oceanographic forecast near Japan*, Sendai, March, 1957, p. 25-38. (*in Japanese*)

Moore, T.C., Burckle, J.H., Geitzenauer, K., Luz, B., Molina-Cruz, A., Robertson, J.H., Sachs, H., Sancetta, C., Thiede, J., Thompson, P. and Wenkam, C., 1980: The reconstruction of sea surface temperatures in the Pacific Ocean of 18,000 B.P. *Marine Micropaleontology*, vol. 5, p. 215-247.

Moriyasu, S., 1972: The Tsushima Current. *In*, Stommel, H. and Yoshida, K., *eds., Kuroshio and its physical aspects*, p. 353-369. University of Tokyo Press.

Nan'niti, T., 1958: A theory of the mechanism of the generation of the Cold Water Region in the offing of Enshunada. *Papers in meteorology and geophysics*, vol. 8, no. 4, p. 317-331.

Nan'niti, T. 1960: Long-period fluctuations in the Kuroshio. *Papers in meteorology and geophysics*, vol. 11, nos. 2-4, p. 339-347.

Nitani, H., 1975: Variation of the Kuroshio, south of Japan. *Journal of Oceanographic Society of Japan*, vol. 31, p. 154-173.

Oda, M., Ishizaki K., and Takayanagi Y., 1983: Analysis of planktic foraminifera in the marine surface sediments of east of Honshu. *Special Project Research*, "*The Ocean Characteristics and their Changes*", *News Letter*, vol. 11, p. 3-9. (*in Japanese*)

Oda, M. and Takemoto, A., 1992: Planktonic foraminifera and paleoceanography in the domain of the Kuroshio current around Japan during the last 20,000 years. *The Quaternary Research*. vol. 31, no. 5, p. 341-357. (*in Japanese with English abstract*)

Ottens, J.J., 1992: April and August Northeast Atlantic surface water masses reflected in planktic foraminifera. *Netherlands Journal of Sea Research*. vol. 28, no. 4, p. 261-283.

Prell, W.L., Gardner, J.V., Be, A.W.H. and Hays, J.D., 1976: Equatorial Atlantic and Caribbean foraminiferal assemblages, temperatures, and circulation; Interglacial and glacial comparisons. *Geological Society of America, Memoir*, vol. 145, p. 247-266.

Reynolds, L.A. and Thunell, R.C., 1985: Seasonal succession of planktic foraminifera in the subpolar North Pacific. *Journal of Foraminiferal Research*, vol. 15, no. 4, p. 282-301.

Sautter, L.R. and Sancetta, C., 1992: Seasonal associations of phytoplankton and planktic foraminifera in an upwelling region and their contribution to the seafloor. *Marine Micropaleontology*, vol. 18, p. 263-278.

Sautter, L.R. and Thunell, R.C., 1989: Seasonal succession of planktonic foraminifera: results from a four-year time-series sediment trap experiment in the Northeast Pacific. *Journal of Foraminiferal Research*, vol. 19, no. 4, p. 253-267.

Shoji, D., 1972: Time variation of the Kuroshio, South of Japan. *In*, Stommel, H. and Yoshida, K., *eds., Kuroshio and its physical aspects*, p. 217-234. University of Tokyo Press.

Taft, B., 1972: Characteristics of the flow of the Kuroshio, south of Japan. *In*, Stommel, H. and Yoshida, K., *eds., Kuroshio and its physical aspects*, p. 165-216. University of Tokyo Press.

Takayanagi, Y. and Oda, M., 1983: Distribution of planktic foraminifera in the surface marine sediments of east of Honshu. *Marine Sciences Monthly*, vol. 15, no. 3, p. 138-144. (*in Japanese*)

Takayanagi, Y., Saito, T., Okada, H., Ishizaki, K., Oda, M., Hasegawa, H., Okada, H., and Manickam, S., 1987: Mid-Quaternary paleoceanographic trend in near-shore waters of the Northwest Pacific. *Science Reports, Tohoku University, Sendai, Second Series* (*Geology*), vol. 57, no. 2, p. 105-137.

Thompson, P.R., 1981: Planktonic foraminifer in the western North Pacific during the past 150,000 years; comparison of modern and fossil assemblages. *Palaeogeography, Palaeoclimatology, Palaeocecology*, vol. 35, p. 241-279.

Thunell, R.C., and Reynolds, L.A., 1984: Sedimentation of planktic foraminifera: Seasonal changes in species flux in the Panama Basin. *Micropaleontology*, vol. 30, p. 241-260.

Tolderlund, D.S. and Be, A.W.H., 1971: Seasonal distribution of planktic foraminifera in the western North Atlantic. *Micropaleontology*, vol. 17, no. 3, p. 297-329.

Wang, P., Zhang, J., Zhao. Q., Bian, Y., Zheng, L., Cheng, X., and Chen, R., 1988: *Foraminifera and Ostracoda in bottom sediments of the East China Sea*, 438 p. Ocean Press, Beijing. (*in Chinese with English abstract*)

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The first record of an amphicyonid (Mammalia: Carnivora) from Japan, and its implication for amphicyonid paleobiogeography

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Abstract. A mammalian tooth from the lower Middle Miocene Korematsu Formation (ca. 16.3-15.6 Ma) within the Bihoku Group in Shobara City, Hiroshima Prefecture, southwestern Japan, is described and identified as a right upper first molar of the amphicyonid carnivore *Ysengrinia* sp. This is the first amphicyonid to be described from Far East Asia and it provides additional evidence for the carnivoran faunal connections between Europe-Asia-North America during the Early and early Middle Miocene.

Key words: Amphicyonidae, Japan, Miocene, paleobiogeography, *Ysengrinia*

Introduction

Amphicyonidae (sensu Hunt, 1972) is an extinct carnivoran family within the Arctoidea Flower, and is thought to be the closest relative of the ursids (e.g., Wyss and Flynn, 1993) or the sister group to other arctoid carnivorans (e.g., Tedford *et al.*, 1994). Amphicyonids are now known from the latest Eocene to early Late Miocene (ca. 40-8 Ma) of Europe, Africa, Asia, and North America (Hunt, 1996). Although there have been a few reports of amphicyonids from Central and Southeast Asia (e.g., Colbert, 1939; Yan *et al.*, 1983; Ginsburg *et al.*, 1992), no amphicyonid has yet been known from Far East Asia.

In the present report, I provide the description of an amphicyonid tooth referable to the genus *Ysengrinia* Ginsburg, 1965, from the lower Middle Miocene Korematsu Formation within the Bihoku Group in Shobara City, Hiroshima Prefecture, southwestern Japan. This is the first record of an amphicyonid from Far East Asia and is the youngest record of this genus. The specimen was collected by Messrs. Takanobu Yamaoka and Masami Sugihara on the New Year's Day of 1996 and has been deposited at the Hiwa Museum of Natural History (**HMN**), Hiwa Town, Hiba-gun, Hiroshima Prefecture, Japan.

The following institutional acronyms are also used in this report: **AMNH**, Department of Vertebrate Peleontology, American Museum of Natural History, New York, U.S.A.; **MNHN**, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France; **UNSM**, Division of Vertebrate Paleontology, University of Nebraska State Museum, Nebraska, U.S.A.

Systematic paleontology

Order Carnivora Bowdich, 1821
Family Amphichyonidae (Trouessart, 1885) Hunt, 1972
Genus ***Ysengrinia*** Ginsburg, 1965

Ysengrinia sp.

Figure 1

Material.—HMN-F00002, right upper first molar, lacking all the roots at the base.

Locality.—A small valley, so-called "Kaisekidani" (=Shellstone Valley), located about 2.1 km east of the Bingo-Shobara Station of the Japan Railroad (JR), and about 2.3 km northeast of the Shobara Interchange of the Chugoku Expressway, Miyauchi Town, Shobara City, Hiroshima Prefecture, southwestern Japan, 34°51′31″ North latitude, and 133°02′22″ East longitude.

Formation and Age.—The specimen was found in a gray, somewhat indurated, medium-grained marine sandstone, at the "Ka2 Horizon" of Okamoto *et al.* (1990) in the lower part of the Korematsu Formation (Ueda, 1986) of the Bihoku Group. Although the upper part of the Korematsu Formation and the overlying lower part of the Itabashi Formation correspond to the NN 4 Zone (18.4-15.6 Ma: Young *et al.*, 1994) of the calcareous nannofossil zonation (Okamoto, 1992), occurrence of the bivalve genus *Hataiarca* in association with many tropical and subtropical species of molluscs and crustaceans from the entire Korematsu Formation including the "Ka2 Horizon" (e.g., Okamoto *et al.*, 1990; Karasawa, 1993) suggests an equivalency of the Korematsu Formation in whole with Neogene first climatic optimum (see

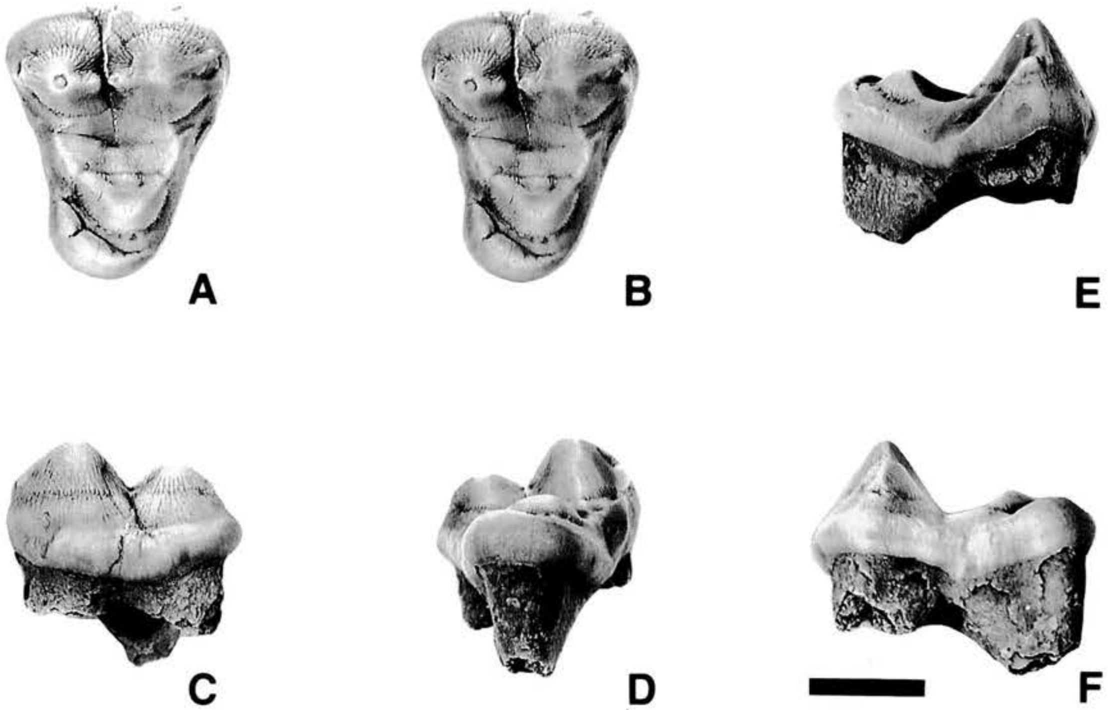

Figure 1. *Ysengrinia* sp., HMN-F00002, right M^1. A-B, occlusal view (stereograph); C, buccal view; D, lingual view; E, anterior view; F, posterior view. Scale bar equals 1 cm.

also Noda and Takahashi, 1986; Itoigawa, 1988; Ogasawara and Noda, 1996). Therefore, the best current estimate of the geologic age for the Korematsu Formation is early Middle Miocene, approximately 16.3-15.6 Ma.

Description.—The tooth is very large and consists of three principal cusps: anterobuccally located paracone, posterobuccally located metacone, and lingually located protocone. The paracone is a prominent cusp and is larger and higher than the metacone. Although smaller than the paracone, the metacone is also prominent. The two cusps are bordered buccally by a very weak bulge at the base of the crown. The enamel surface of the paracone and metacone is vertically wrinkled. A small parastyle is present beside the paracone at the anterobuccal corner of the crown. The protocone is almost like a low V-shaped ridge descending to the paraconule and metaconule, at the base of the paracone and metacone respectively around the depressed protocone basin. There is a well-developed cingulum at the posterolingual portion of the protocone, but no cingulum at anterior and posterobuccal borders of the crown, giving the form of a "pear-shaped" outline of the crown in occlusal view. This tooth has three roots corresponding to the three principal cusps, although they are broken off at each base. The anterobuccal root (for the paracone) and the posterobuccal one (for the metacone) are both round in cross section, and the medial one (for the protocone) is buccolingually elliptical and approximately twice larger in diameter than the other two at the base.

Comparisons

HMN-F00002 is characterized by its very large size, the "pear-shaped" outline in occlusal view, with well developed posterolingual cingulum, and very large paracone relative to the metacone. All these characters correspond to the characteristics of M^{1}s of Oligo-Miocene *Ysengrinia* species known from western Europe (Ginsburg, 1965; Savage and Russel, 1983; Viranta, 1996) and North America (Hunt, 1972; Tedford *et al*., 1987). Some other Miocene amphicyonids such as *Amphicyon* Lartet and *Pseudocyon* Lartet also have large M^{1}s, but they are almost equilaterally triangular in shape with cingula developed both anteriorly and posteriorly, and the paracone and metacone are almost equal in size

Table 1. Measurements of HMN-F0002 in mm.

Mesiodistal diameter of the crown	21.6
Buccolingual diameter of the crown	26.2
Height of the crown at the buccal side	12.3
Mesiodistal diameter of the anterobuccal root at the base	8.6
Buccolingual diameter of the anterobuccal root at the base	9.3
Mesiodistal diameter of the posterobuccal root at the base	7.8
Buccolingual diameter of the posterobuccal root at the base	8.3
Mesiodistal diameter of the lingual root at the base	8.8
Buccolingual diameter of the lingual root at the base	13.4

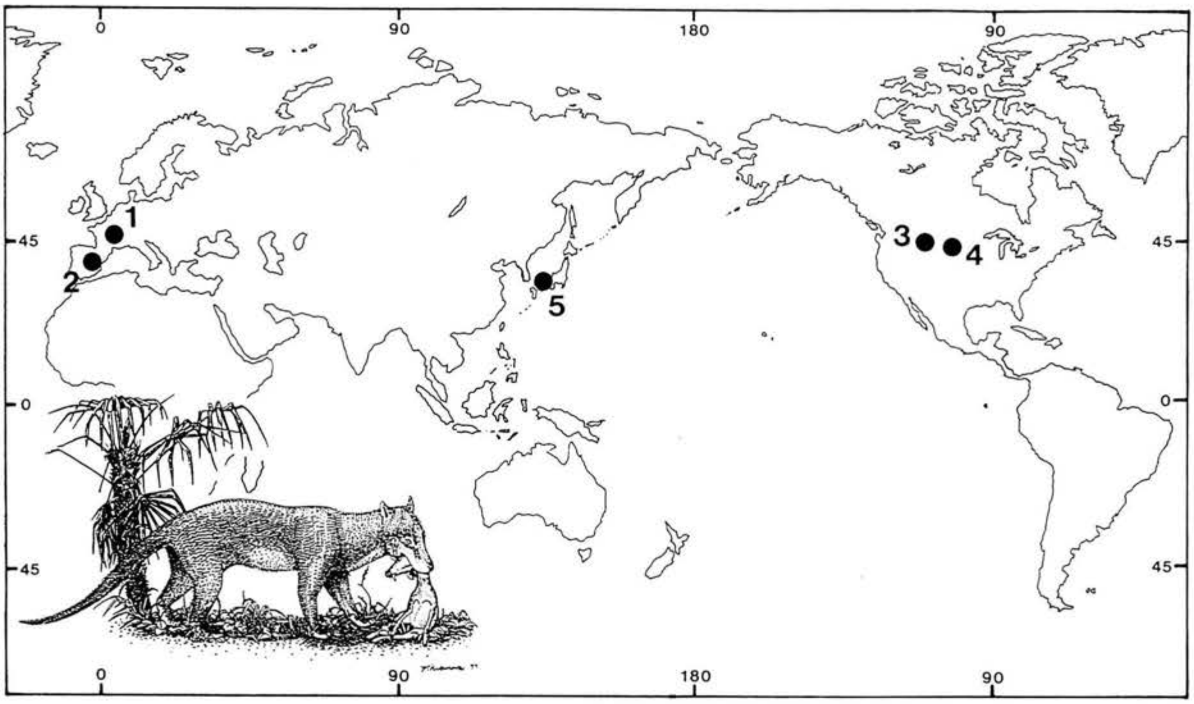

Figure 2. Distribution of *Ysengrinia*. 1, *Y. tolosana*, Late Oligocene ; *Y. gerandiana*, early Early Miocene ; *Y. depereti*, late Early Miocene, France. 2, *Y. valentiana*, late Early Miocene, Spain. 3, *Y.* sp., Early Miocene, Wyoming, U.S.A. 4, *Y.* sp., Early Miocene, Nebraska, U.S.A. 5, *Y.* sp., early Middle Miocene, Japan. Illustration is a generalized life restoration of an amphicyonid.

(Viranta, 1996). Likewise, HMN-F00002 cannot be referred to the M^1s of small pre-Miocene amphicyonids nor to the other Miocene amphicyonids that have "triangular" upper first molars.

The genus *Ysengrinia* was established by Ginsburg (1965) on the basis of the dental morphology of *"Pseudocyon" gerandianus* Viret, 1929, and four species have been recognized so far within the genus (Viranta, 1996). The upper first molars are known in *Y. gerandiana* (Viret, 1929) from the early Early Miocene (European Neogene Mammal Faunal Zone MN 2 of Steiniger *et al*., 1996, ca. 22.8-20.0 Ma) of France and *Y. valentiana* Belinchón and Morales, 1989, from the late Early Miocene (MN 4, ca. 18.0-17.0 Ma) of Spain. As can be seen from the illustrations of Viret (1929) and Kuss (1965) and from the descriptions of Belinchón and Morales (1989) and Viranta (1996), *Y. gerandiana* and *Y. valentiana* have large M^1 with a prominent paracone which is larger than the metacone, with a posterolingually projected cingulum, and without anterior and posterobuccal cingula. These characters produce a "pear-shaped" outline in occlusal view that is almost identical to that of HMN-F00002.

As for the North American record of *Ysengrinia*, Hunt (1972) referred two M^1s and some postcranial bones from the Early Miocene (now known from the late Late Arikareean to Early Hemingfordian of the North American Land Mammal Age, ca. 21-18 Ma ; Tedford *et al*., 1987) of Nebraska and Wyoming as a species of (?)*Ysengrinia*, since there remained some doubts regarding the status of *Ysengrinia* at that time (Hunt, 1972 : p. 31). It is, however, clear that the structure and proportion of the two M^1s (Hunt, 1972 : Fig. 10) all agree with the emended diagnoses for the M^1s of *Ysengrinia* species by Viranta (1996). Therefore, I believe that *Ysengrinia* without a question mark is warranted for the teeth described by Hunt (1972). The American *Ysengrinia* M^1s also resemble HMN-F00002 in their size and proportion, but the development of buccal and lingual cingula in the former is slightly stronger than in the latter.

Since the inter- and intra-specific variations of M^1s in the species of *Ysengrinia* are presently not well understood (see also Hunt, 1972 ; Viranta, 1996), a species-level definition based upon the morphologies of M^1s seems not to be feasible. Thus, I refer herein HMN-F00002 only to *Ysengrinia* species indeterminate until more diagnostic material is obtained.

Paleobiogeography

Ysengrinia had previously been known only from western Europe and North America during the Late Oligocene and Early Miocene (Hunt, 1972 ; Savage and Russel, 1983). HMN-F00002 from the early Middle Miocene (ca. 16.3-15.6 Ma) of Japan is, therefore, not only the first record of *Ysengrinia* from Asia but also the youngest record of this genus (Figure 2).

Judging from their oldest stratigraphic record and geographic distribution of their closest relatives, i.e., *Brachycyon* from France (Hunt, 1972) or *Pseudocyonopsis* from western Europe (Ginsburg, 1966 ; Springhorn, 1977), *Ysengrinia* is thought to have originated in western Europe during the Late Oligocene and might have spread out rapidly from Europe into North America across the Asian Continent during the Early Miocene (Hunt, 1996). The biogeographic range extension of *Ysengrinia* into Far East Asia is, therefore, consistent with the scenario originally proposed by Hunt (1972). In addition, since only one carnivoran genus (i.e., the Miocene large-sized amphicyonid *Amphicyon*) was previously known in Europe, Asia, and North America during the Early to early Middle Miocene (Savage, 1967 ; Savage and Russel, 1983), HMN-F00002 provides new evidence that *Ysengrinia* is also one of the key elements for recognizing carnivoran faunal connections between Europe, Asia, and North America during that time. Such large amphicyonids as *Ysengrinia* and *Amphicyon* might have been the topmost predators in the terrestrial ecosystem throughout the Northern Hemisphere during the Early and early Middle Miocene.

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References

Belinchón, M. and Morales, J., 1989 : Los carnívoros del Mioceno inferior de Bunnol (Valencia, Espana). *Revista Española de Paleontología*, vol. 4, p. 3-8.

Colbert, E.H., 1939 : Carnivora of the Tung Gur Formation of Mongolia. *Bulletin of the American Museum of Natural History*, vol. 76, p. 47-81.

Ginsburg, L., 1965 : L' *"Amphicyon" ambiguus* des phosphorites du Quercy. *Bulletin du Muséum National d'Histoire Naturelle*, vol. 37, p. 724-730.

Ginsburg, L., 1966 : Les Amphicyons des Phosphorites du Quercy. *Annales de Paléontologie*, vol. 52, p. 23-44.

Ginsburg, L., van Minh, L., Kieu, Q., and van Thuan, D., 1992 : Premiéres découvertes de vertébrés continentaux dans le Néogène du Nord du Vietnam. *Comptes Rendus de l'Académie des Sciences, Paris, Série II*, vol. 313, p. 627-630.

Hunt, R.M. Jr., 1972 : Miocene amphicyonids (Mammalia, Carnivora) from the Agate Spring Quarries, Sioux County, Nebraska. *American Museum Novitates*, no. 2506, p. 1-39.

Hunt, R.M. Jr., 1996 : Biogeography of the Order Carnivora. *In*, Gittleman, J.L. *ed.*, *Carnivore Behavior, Ecology and Evolution*, vol. 2, p. 485-541. Chapman and Hall, London.

Itoigawa, J., 1988 : The Miocene Kadonosawa Fauna of Japan. *Saito Ho-on Kai Special Publication* (*Prof. Tamio Kotaka Commemorative Volume*), p. 397-403.

Karasawa, H., 1993 : Cenozoic decapod Crustacea from southwest Japan. *Bulletin of the Mizunami Fossil Museum*, no. 20, p. 1-92.

Kuss, S.E., 1965 : Revision der europäischen Amphicyoninae (Canidae, Carnivora, Mammalia). *Sitzungsberichte der Heidelberger Akademie der Wissenschaften*, vol. 1, p. 1-169.

Noda, H. and Takahashi, H., 1986 : Distribution of *Anadara* (*Hataiarca*) *kakehataensis* and characteristics of the associated molluscan fauna in the early Middle Miocene of Japan. *Monograph of the Mizunami Fossil Museum*, no. 6, p. 49-58. (*in Japanese with English abstract*)

Ogasawara, K. and Noda, H., 1996 : Miocene *Hataiarca* (Mollusca, Bivalvia) invasion event in the Japanese Islands from a viewpoint of Indo-Pacific connection. *In*, Noda, H. and Sashida, K. *eds.*, *Professor Hisayoshi Igo Commemorative Volume on Geology and Paleontology of Japan and Southeast Asia*, p. 133-139. Gakujyutsu Tosho Insatsu Co. Ltd., Tokyo.

Okamoto, K., 1992 : Vertical sequence of molluscan assemblages from the Miocene Bihoku Group in Shobara City, southwest Japan. *Bulletin of the Mizunami Fossil Museum*, no. 19, p. 319-328. (*in Japanese with English abstract*)

Okamoto, K., Katsuhara, M., Ueno, Y. and Sumiyoshi, O., 1990 : Molluscan assemblages from the Miocene Bihoku Group in the Kaisekidani area, Miyauchi-cho, Shobara City, southwest Japan. *Bulletin of the Mizunami Fossil Museum*, no. 17, p. 35-49. (*in Japanese with English abstract*)

Savage, D.E. and Russell, D.E., 1983 : *Mammalian Paleofaunas of the World*, 432 p. Addison-Wesley Publishing Co., London.

Savage, R.J.G., 1967 : Early Miocene mammal faunas of the Tethyan region. *In*, Adams, C.G. and Ager, D.V. *eds.*, *Aspects of Tethyan Biogeography*, p. 247-282. Systematics Association Publication, London.

Springhorn, R., 1977 : Revision der Alttertiären Europäischen Amphicyonidae (Carnivora, Mammalia). *Palaeontographica Abteilung A*, bd. 158, p. 26-113.

Steininger, F.F., Berggren, W.A., Kent, D.V., Bernor, R.L., Sen, S., and Agusti, J., 1996 : Circum-Mediterranean Neogene (Miocene and Pliocene) marine-continental chronologic correlations of European mammal units. *In*, Bernor, R.L., Fahlbusch, V. and Mittmann, H.-W. *eds.*, *The Evolution of Western Eurasian Neogene Mammal Faunas*, p. 7-46. Columbia University Press, New York.

Tedford, R.H., Barnes, L.G. and Ray, C.E., 1994 : The Early Miocene littoral ursoid carnivoran *Kolponomos* : Systematics and mode of life. *Proceedings of the San Diego Society of Natural History*, no. 29, p. 11-32.

Tedford, R.H., Galusha, T., Skinner, M.F., Taylor, B.E., Fields, R.W., Macdonald, J.R., Rensberger, J.M., Webb, D. and Whistler, D.P., 1987 : Faunal succession and biochronology of the Arikareean through Hemphillian interval (Late Oligocene through earliest Pliocene epochs) in North America. *In*, Woodburne, M.O. *ed*., *Cenozoic Mammals of North America*, p. 153-210. University of California Press, Berkeley and Los Angeles.

Ueda, T., 1986: The Miocene Bihoku Group and its molluscan assemblages in the Shobara district, Hiroshima Prefecture, west Japan. *Chikyu-Kagaku*, vol. 40, p. 437-448. (*in Japanese with English abstract*)

Viranta, S., 1996: European Miocene Amphicyonidae: Taxonomy, systematics and ecology. *Acta Zoologica Fenica*, vol. 204, p. 1-61.

Viret, J., 1929: Les faunes de Mammifères de l'Oligocène supérieur de la Limagne Bourbonnaise. *Annales de l' Université de Lyon, Nouvelle Série*, fasc. 47, p. 1-328.

Wyss, A.R. and Flynn, J.J., 1993: A phylogenetic analysis and definition of the Carnivora. *In*, Szalay, F.S., Novacek, M.J. and McKenna, M.C., *eds*., *Mammal Phylogeny*, p. 32-52. Springer-Verlag, New York.

Yan, D., Qiu, Z. and Men, Z., 1983: Miocene stratigraphy and mammals of Shanwang, Shandong. *Vertebrata PalAsiatica*, vol. 17, p. 210-222 (*in Chinese with English summary*)

Young, J.R., Flores, J-A. and Wei, W., 1994: A summary chart of Neogene nannofossil magnetobiostratigraphy. *Journal of Nannoplankton Research*, vol. 16, no. 1, p. 21-27.

Paleontological Research, vol. 1, no. 4, pp. 316-317, 30 December, 1997

A note on the Jinomori horse, *Equus nipponicus* Shikama and Onuki (Mammalia, Equidae), and some other equine remains from Japan.

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Abstract. The species *Equus nipponicus* Shikama and Onuki is a true horse, possibly even a domestic animal, not an Asiatic wild ass. It has been dated to 1,530±60 years B.P.

Key words : *Equus*, Japan, late Pleistocene-Holocene

Shikama and Onuki (1962) described a new species of horse, *Equus nipponicus*, from allegedly late Pleistocene beds of Jinomori, Iwate Prefecture, and from two other localities in northern Honshu, Japan. They believed *Equus nipponicus* to differ in dental morphology and small size both from the true horse (*E. caballus* L., including *E. przewalskii* Polj.) and from the Asiatic wild ass (*E. hemionus* Pallas). *Equus nipponicus* has since been referred to as a subspecies of the Asiatic ass (Kahlke, 1975 ; Kamei, 1981 ; Kuzmina, 1989), probably because of its small size.

By the courtesy of Prof. Kei Mori, Institute of Geology and Paleontology, Tohoku University, Sendai, I was allowed to borrow and to date the type material of *E. nipponicus* from Jinomori. The sample (collection No. 66164) consists of the right and left, somewhat worn upper and lower teeth, probably of a single male individual. The teeth are clearly not those of an Asiatic ass, but of a true or caballoid horse (Shikama and Onuki, 1962, plates 14-15), as shown by the U-shaped entoflexid and lingually directed metaconid and metastylid. Dr. Högne Jugner and his team at the Dating Laboratory of the University of Helsinki kindly did a radiometric dating of a piece of the jaw, which gave an age of 1,530±60 years B.P. (Hela-155). The late age and the morphology of the specimens indicate that they probably belong to a domestic horse (*E. caballus*), which may also explain their small size.

In addition to the finds from Iwate and Miyagi Prefectures described by Shikama and Onuki (1962), fossil/subfossil horses have been found from several other localities in Japan, i.e. from Keisei and Kuroi (Shikama, 1938, citing Tokunaga, 1934), from Tsukinoki (Shikama, 1938), from Kotari (Kamei, 1981, citing Naora, 1942), and from Shioda (Kamei and Taruno, 1973, Kamei, 1981), all on Honshu. The latter was referred to as an Asiatic ass. The oldest find, an isolated tooth from Tsukinoki, is said to be mid-Pleistocene in age ; the youngest find is from Kyushu and Neolithic in age (Shikama, 1938, citing Hasebe, 1925). Aside from our work only the Shioda find has been radiometrically dated, its age being determined as, 28,400±1,800 B.P. (Kamei and Taruno, 1973).

The radiometric ages of the known Japanese fossil/subfossil horses would be very interesting, as they could throw light on the first appearance and survival of the horse in Japan. Horses are poor migrants across water (Sondaar, 1977), thus they probably arrived in Japan over land from the Asiatic continent during a period of low sea level. In the late Pleistocene, between 35,000 B.P. or earlier and 18,000 B.P., the sea level is believed to have dropped 130 m (Manabe, 1977, citing Nakagawa, 1967). Possible routes of distribution were via Korea from northeastern China or via Sakhalin from southeastern Russia ; moderately sized true horses lived in both areas. If wild horses survived in Japan in the Neolithic, domestication may have happened in situ, the Japanese domestic horse still showing molecular similarity with the Mongolian domestic horse and the until recently extant wild Przewalski's horse (Ishida *et al*., 1995, fig. 2).

References

Ishida, N., Oyunsuren, T., Mashima, S., Mukoyama, H. and Saitou, N., 1995 : Mitochondrial DNA sequences of various species of the genus *Equus* with special reference to the phylogenetic relationship between Przewalskii's wild horse and domestic horse. *Journal of Molecular Evolution*, vol. 41, p. 180-188.

Kahlke, H.-D., 1975 : Die Südgrenze des spätpleistozänen Europäisch-Sibirischen Faunenblocks in Ost-Asien. *Quartärpaläontologie*, vol. 1, p. 243-253.

Kamei, T., 1981 : Faunal succession of Pleistocene mammals in the Japanese islands : an aspect. *Quartärpaläontologie*, vol. 4, p. 165-194.

Kamei, T. and Taruno, H., 1973 : Note on the occurrence of the latest Pleistocene mammals from Lake Nojiri (Part I). *Memoirs of the Faculty of Sciences, Kyoto University, Ser. Geology and Mineralogy*, vol. 39, p. 99-122.

Kuzmina, I.E., 1989 : Sravnitelnaya morfo-ekologicheskaya kharakteristika loshadei severnoi Evrazii v antropogene. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*, vol. 198, p. 83-102. (*in Russian*)

Manabe, K., 1977 : Reversed magnetozone in the late Pleistocene sediments from the Pacific coast of Odaka, northeast Japan. *Quaternary Research*, vol. 7, p. 372-379.

Shikama, T., 1938 : On some Japanese fossil equids. *Journal of the Geological Society of Japan*, vol. 45, p. 430-436.

Shikama, T. and Onuki, Y., 1962 : Equid fossils from Iwate and Miyagi Prefectures. *Science Reports of the Tohoku University, Geology*, vol. 34, p. 187-197.

Sondaar, P.Y., 1977 : Insularity and its effect on mammal evolution. *In*, Hecht, M.K., Goody, P.C. and Hecht, B.M. *eds., Major Patterns in Vertebrate Evolution*, p. 671-707. Plenum Press, New York.

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Ager, D.V., 1963 : *Principles of Paleoecology*, 371 p. McGraw-Hill Co., New York.

Barron, J.A., 1983 : Latest Oligocene through early Middle Miocene diatom biostratigraphy of the eastern tropical Pacific. *Marine Micropaleontology,* vol. 7, p. 487-515.

Barron, J.A., 1989 : Lower Miocene to Quaternary diatom biostratigraphy of Leg 57, off northeastern Japan, Deep Sea Drilling Project. *In*, Scientific Party, *Initial Reports of the Deep Sea Drilling Project*, vols. 56 and 57, p. 641-685. U.S. Govt. Printing Office, Washington, D.C.

Burckle, L.H., 1978 : Marine diatoms. *In*, Haq, B.U. and Boersma, A. *eds., Introduction to Marine Micropaleontology*, p. 245-266. Elsevier, New York.

Fenner, J. and Mikkelsen, N., 1990 : Eocene-Oligocene diatoms in the western Indian Ocean : Taxonomy, stratigraphy, and paleoecology. *In,* Duncan, R.A., Backman, J., Peterson, L.C., *et al., Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 115, p. 433-463. College Station, TX (Ocean Drilling Program).

Koizumi, I., 1972 : Marine diatom flora of the Pliocene Tatsunokuchi Formation in Fukushima Prefecture. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series,* no. 86, p. 340-359.

Kuramoto, S., 1996 : Geophysical investigation for methane hydrates and the significance of BSR. *Journal of the Geological Society of Japan,* vol. 11, p. 951-958. (*in Japanese with English abstract*)

Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on December 20, the JSP Standing Committee enacted the following changes to its membership.

New members elected ;

Kazuhiko Masuda, Katsuyuki Miyoshi, Makoto Miyawaki,
Masahiro Matsumoto, Kazuhiro Koyasu, Hideaki Yamauchi,
Xuedong Xu, Haruhiko Arisaka, Naoko Takenaka,
Tsutomu Ihara, Hiroto Kimura, Leigh Van Valen,
Francisco J. Vega.

Subscribing member elected ;
Thomas Jellinek.

Resigned members ;
Jun Nakano, Mohammad Mohiudd Mia.

Deceased member ;
Akio Suzuki.

Errata : Read September 20 for March 8, in JPS Standing Committee Actions, p. 236, vol. 1, no. 3.

行事予定

◎1998年年会・総会は1998年1月30日（金）～2月1日（日）に，神奈川県立生命の星・地球博物館で開催します。シンポジウムとして1月30日に「復元の科学」（世話人：小泉　格，濱田隆士，松島義章，大野照文）が予定されています。

◎第148回例会は1998年6月27日（土）～6月28日（日）に，北海道大学で開催が予定されています。一般講演の申し込み締切は5月10日です。

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