

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).**Material and methods*****Neptunea intersculpta* stock**(1) *N. intersculpta* group*N. intersculpta* (Sowerby)(2) *N. constricta* 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.

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 synonym 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	BR ¹⁾	PAR ²⁾	IAR ³⁾	SSR ⁴⁾
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

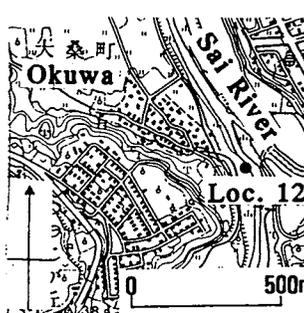
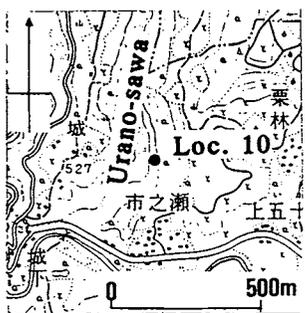
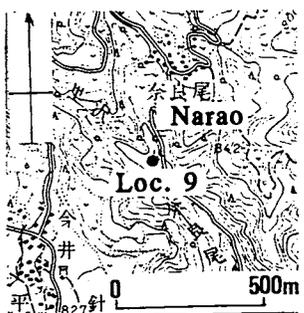
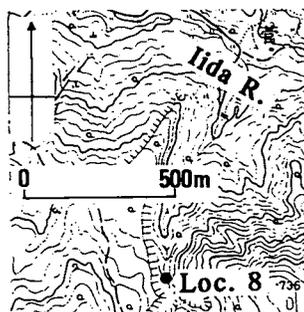
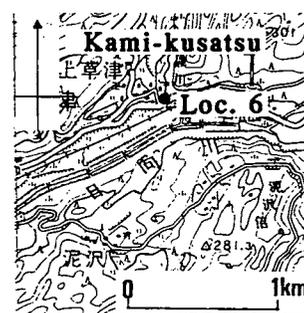
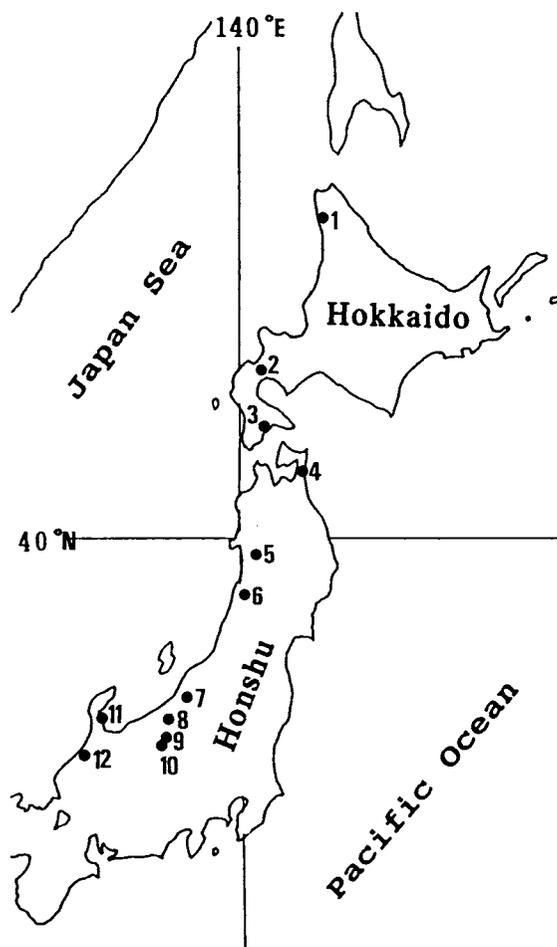
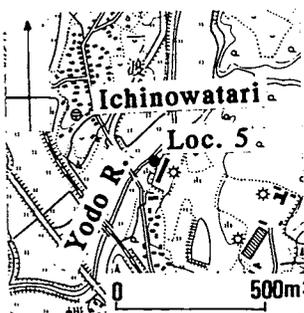
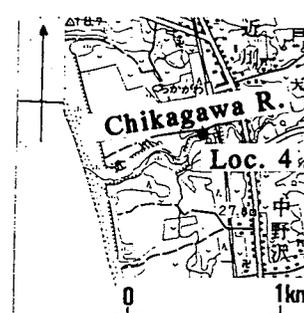
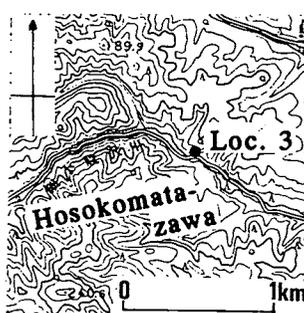
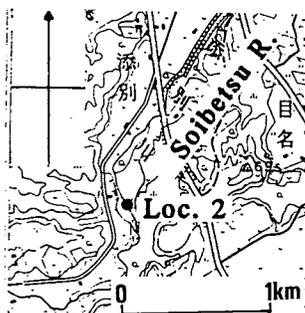
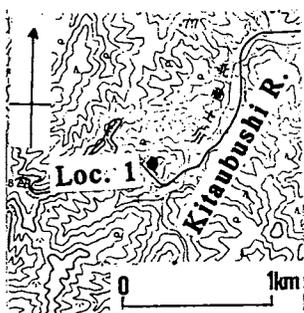
Diagnosis.—Shell small to medium in size, slender, fusiform. Shell surface sculptured by low, wide spiral ribs on early whorls, becoming obsolete on later whorls; body whorl smooth and polished. Inner side of outer lip smooth. Marginal teeth on radula number two.

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", "Koguchisetu", scale 1: 50,000; "Ugo-Sakai", "Ojiya", "Yanagishima", "Togakushi", "Shinano-Nakajo" and "Kanazawa", scale 1: 25,000 published by Geographical Survey Institute of Japan).



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.

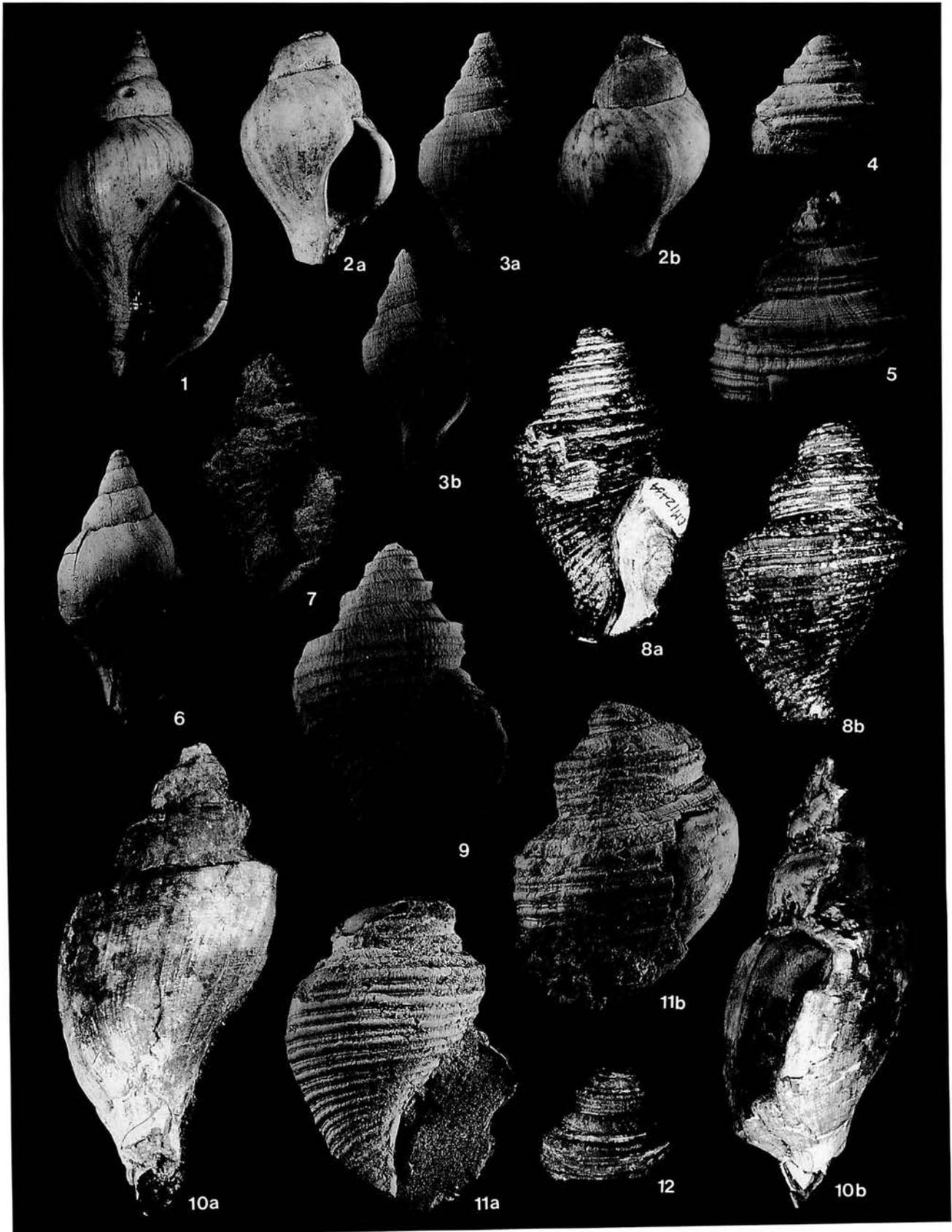
Shaping of modern Japan Sea neptuneids

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

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



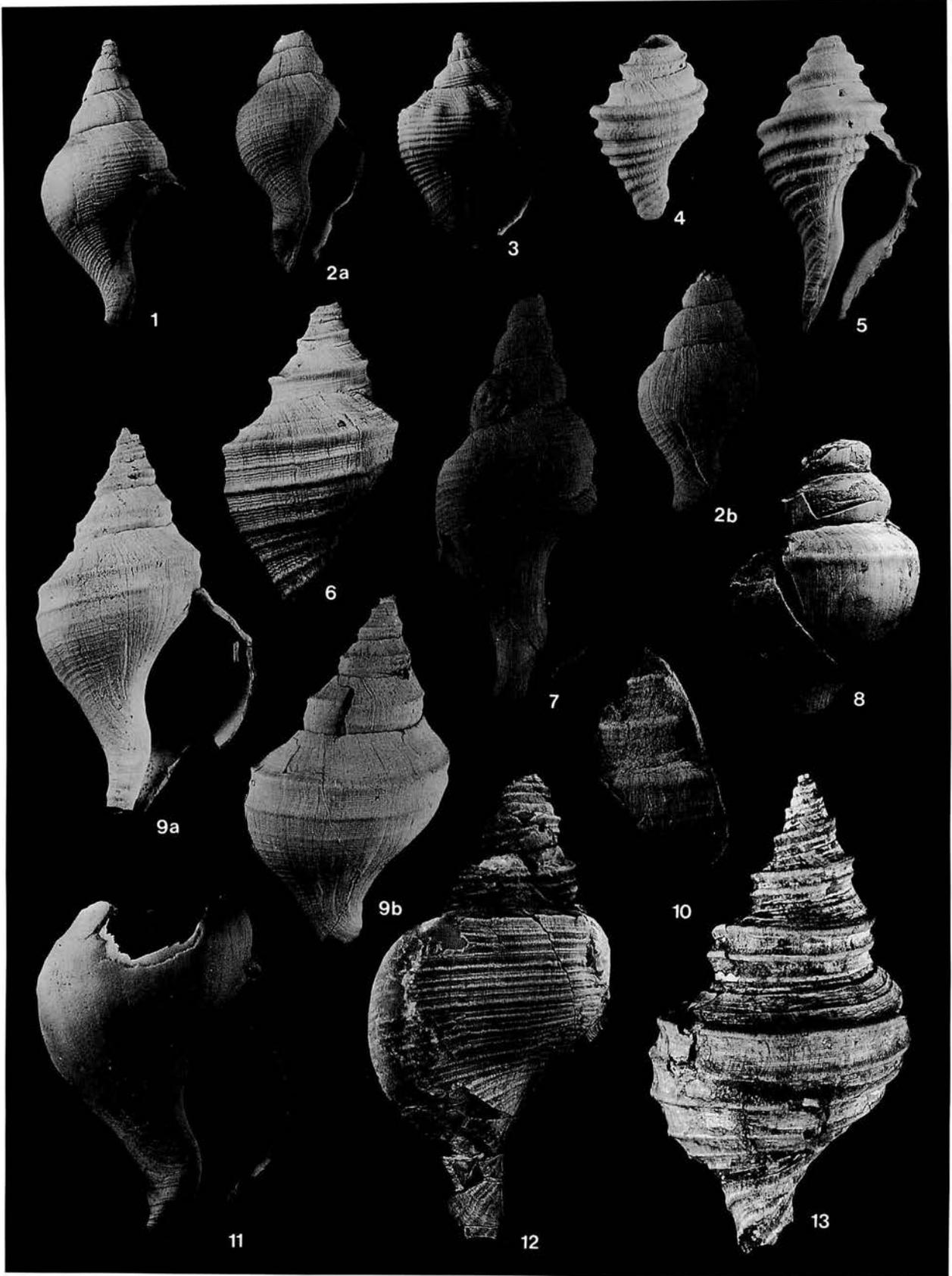


Table 2. Summarized list of *Neptunea* from the Pliocene and the lower Pleistocene of the Japan Sea borderland.

Genus *Neptunea* Roeding, 1798

Subgenus *Neptunea* s.s.

***Neptunea intersculpta* stock**

N. intersculpta (Sowerby)* Pliocene: 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: Shimonoporo 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	
<i>N. lamellosa</i>	57-550 m ¹⁾ , 300-500 m ²⁾
<i>N. satura</i>	13-245 m ¹⁾
<i>N. insularis</i>	230-1,000 m ¹⁾ , 100-400 m ²⁾
<i>N. vinosa</i>	29-400 m ¹⁾ , 30-100 m ²⁾
B type	
<i>N. lyrata</i>	16-1,724 m ¹⁾
<i>N. bulbacea</i>	0.5-585 m ¹⁾
<i>N. rugosa</i>	9-76 m ¹⁾
C type	
<i>N. intersculpta</i>	36-895 m ¹⁾ , 150-750 m ²⁾
<i>N. constricta</i>	20-468 m ¹⁾ , 200-600 m ²⁾
<i>N. arthritica</i>	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; $\times 1$, JUE no. 15617, Loc. 3, Tomikawa Formation. 2a, b; $\times 1$, Mita Formation, collected by Mr. M. Shimizu. 3: *Neptunea (Barbitonia) arthritica* (Bernardi); $\times 1$, JUE no. 15618, Loc. 12, Omma Formation. 4, 5: *Neptunea (Neptunea) sakurai* (Ozaki); 4, $\times 1.5$, IGPS no. 102710-2; 5, $\times 1$, IGPS no. 102710-1, Hamada Formation, illustrated by Hatai *et al.* (1961). 6: *Neptunea (Neptunea) vinosa* (Dall); $\times 1$, JUE no. 15619, Loc. 4, Hamada Formation. 7: *Neptunea (Neptunea) constricta* (Dall); $\times 1$, IGPS no. 93224, Hamada Formation, "holotype" of *N. iwaii* Hatai, Masuda and Suzuki, 1961. 8: *Neptunea (Neptunea) rugosa* Golikov; $\times 1$, JUE no. 15355, Seguchi Formation, illustrated by Nakata and Amano (1991). 9a, b: *Neptunea (Neptunea) lamellosa* Golikov; $\times 1$, IGPS no. 102711-2, Hamada Formation, identified as *N. vinosa* Dall var. by Hatai *et al.* (1961). 10: *Neptunea (Neptunea) hataii* Noda; $\times 1$, JUE no. 15620, Loc. 6, Kannonji Formation. 11: *Neptunea (Neptunea) bulbacea* (Bernardi); $\times 1$, JUE no. 15621, Loc. 2, Setana Formation. 12: *Neptunea (Neptunea) intersculpta* (Sowerby); $\times 0.8$, JUE no. 15363, Nagasawa Formation, illustrated by Nakata and Amano (1991) as "*N. intersculpta pribiloffensis* (Dall)". 13: *Neptunea (Neptunea) lyrata* (Gmelin); $\times 0.8$, 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 species in the Japan Sea. Therefore, the results of this study support those of the previous study.

Acknowledgments

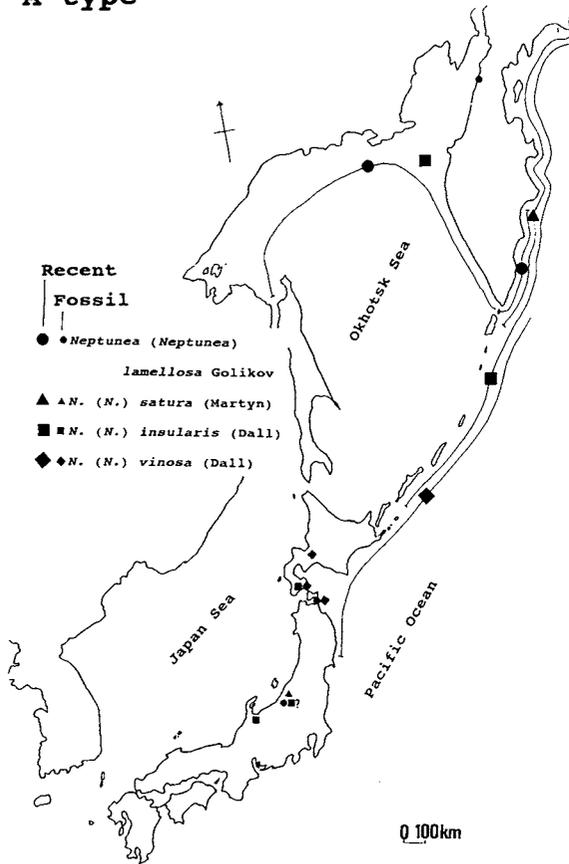
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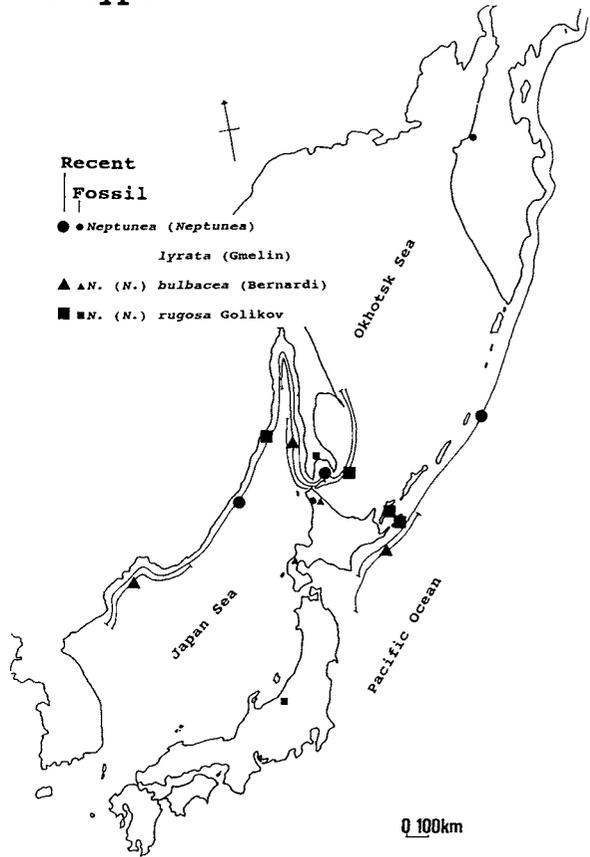
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Figure 4. Distributional pattern of *Neptunea*. (Recent geographical distribution and fossil records in Kamchatka are mainly after Golikov, 1963).

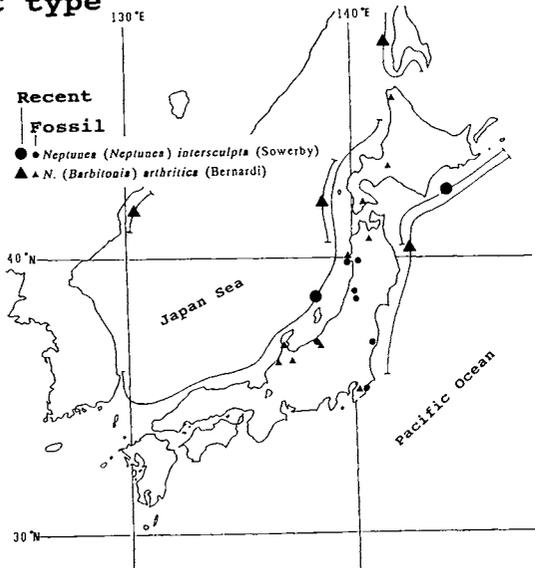
A type



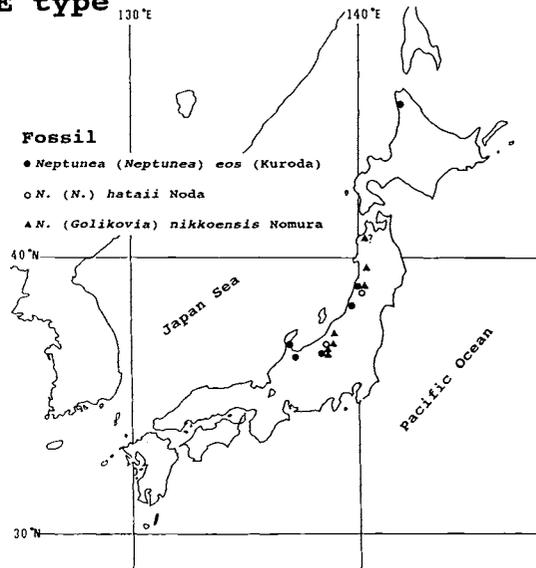
B type



C type



E type



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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 Lytonioidea 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 lytoniid. 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 fos-

siferous 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 Lytonioidea 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-

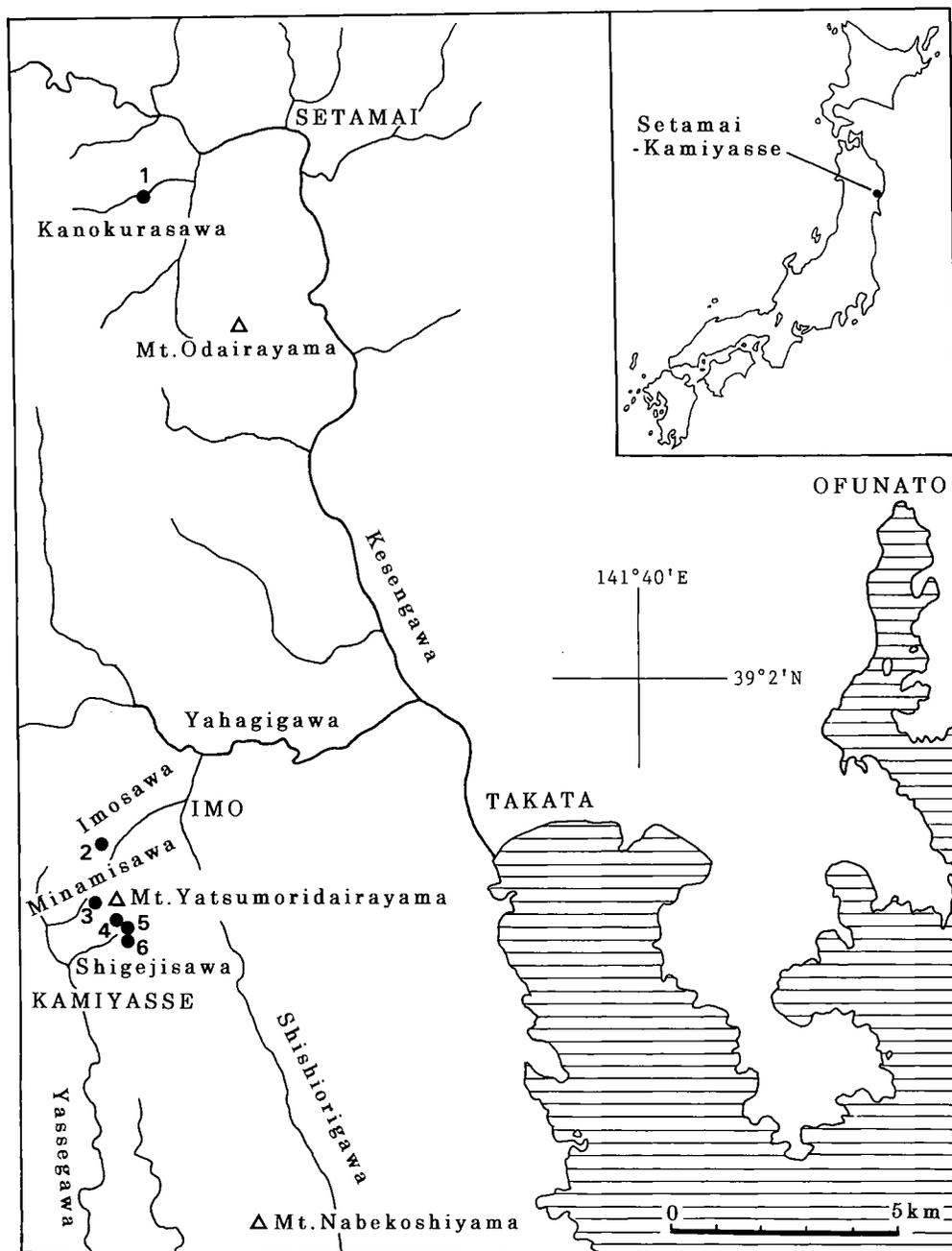


Figure 1. Map showing the fossil localities (Locs. 1-6).

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-

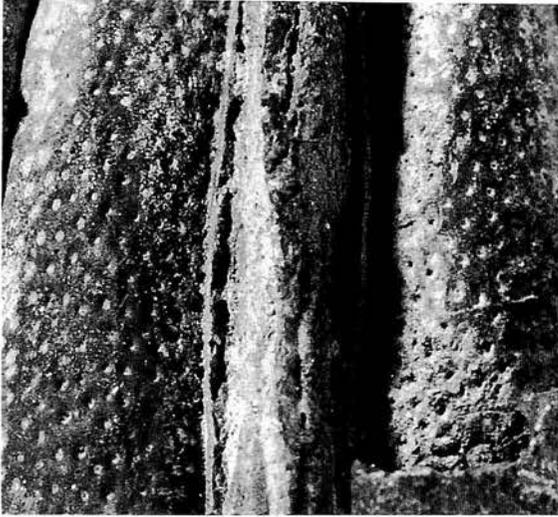


Figure 2. External surface of a ventral valve of *Permianella typica* He and Zhu, showing pseudopunctae of outer shell layer (NU-B63, $\times 8.5$).

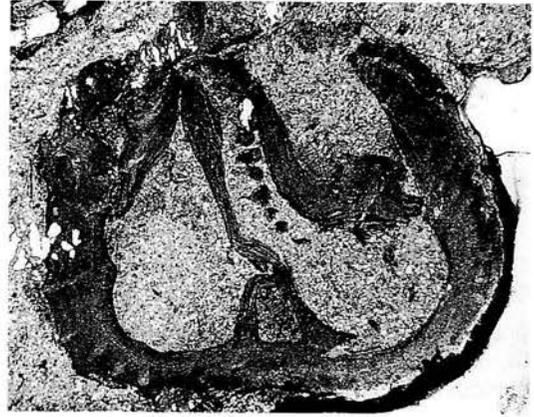


Figure 3. One section (6.95 mm anterior to the posterior margin) of *Permianella typica* He and Zhu, showing pseudopunctate outer shell layer, laminate inner shell layer, central platform and a distorted median septum (NU-B51, $\times 12.5$).

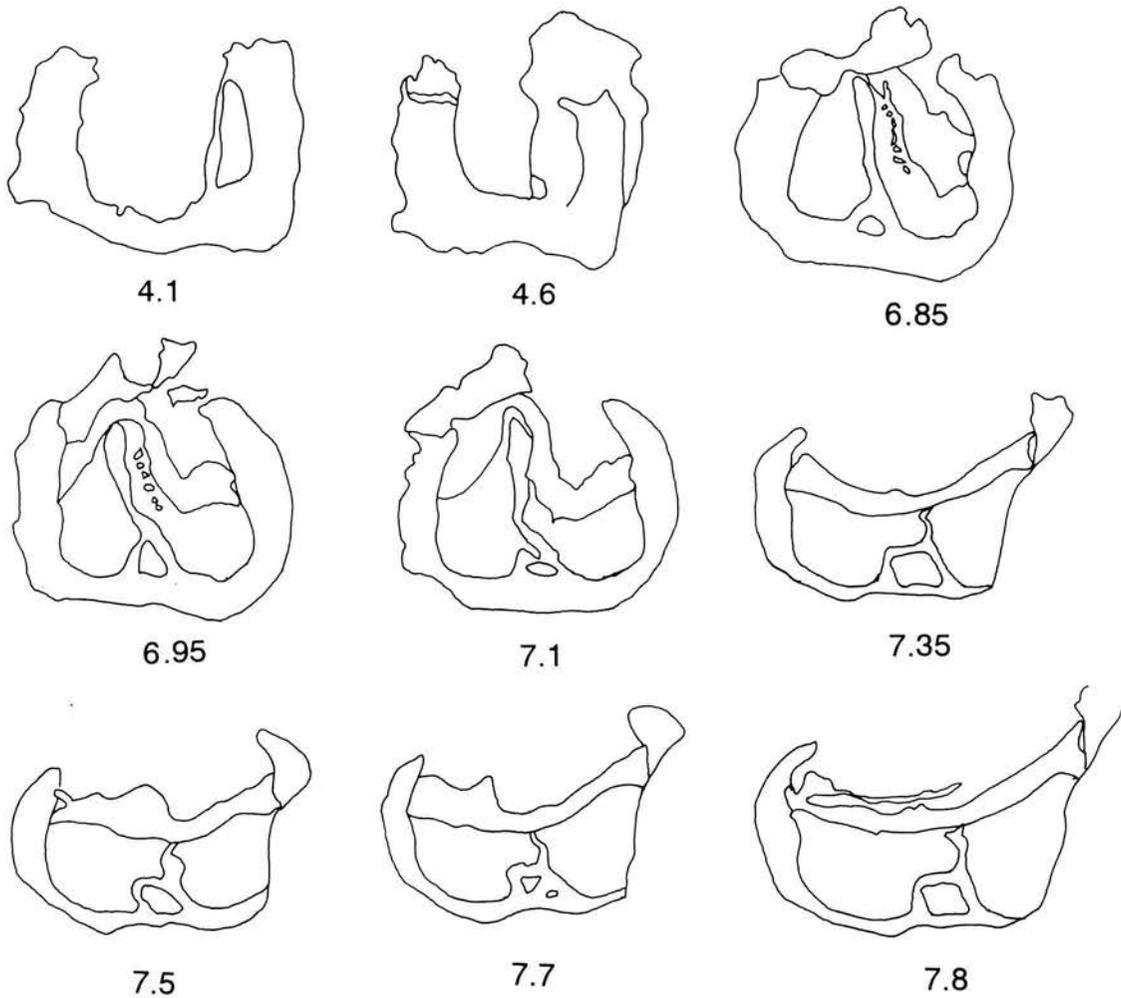


Figure 4. Serial sections of *Permianella typica* He and Zhu. The numbers indicate the distance in mm from the posterior margin (NU-B51, $\times 7.5$).

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

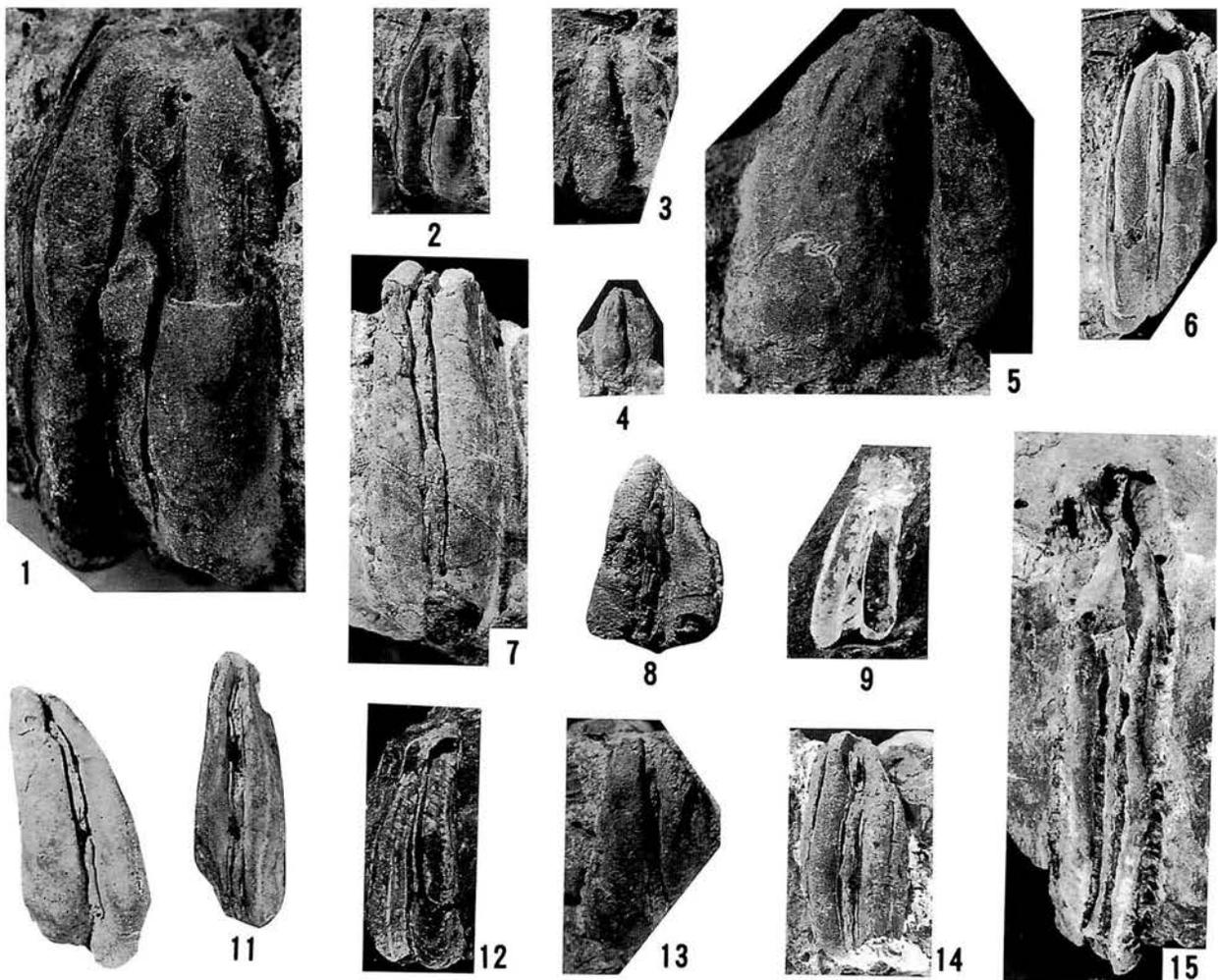


Figure 5. 1-14. *Permianella typica* He and Zhu. 1, 2: external mould of a dorsal valve with a part of ventral valve, showing marginal brim along lateral commissure and deep incision, NU-B60 (1: $\times 3$). 3: internal mould of a ventral valve, NU-B55. 4, 5: internal mould of a ventral valve, NU-B61 (5: $\times 4$). 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, Kesenuma 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, Kesenuma, Iwate Prefecture, Northeast Japan.

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