Deep-sea Fauna of the Sea of Japan, edited by T. Fujita, National Museum of Nature and Science Monographs, No. 44, pp. 75–148, 2014

A Review of Bathyal Rissoidae in the Sea of Japan and Adjacent Waters (Gastropoda: Rissooidea)

Kazunori Hasegawa

Department of Zoology, National Museum of Nature and Science,
4–1–1 Amakubo, Tsukuba-shi, Ibaraki, 305–0005 Japan
Email: hasegawa@kahaku.go.jp

Abstract: Rissoid gastropods collected during the sampling program, "Research on Deep-sea Fauna of the Sea of Japan", carried out by the Department of Zoology, National Museum of Nature and Science, in 2009–2013, from bathyal depths (deeper than 200 m), were studied taxonomically, and classified into eight species, including five that are new: *Frigidoalvania tanseimaruae* n. sp., *Punctulum soyomaruae* n. sp., *P. tanshumaruae* n. sp., *Alvania nihonkaiensis* n. sp. and *A. yamatoensis* n. sp. Voucher material of previous records at the bathyal depths in the Sea of Japan were also examined, resulting in the recognition of three additional species. Distributions of these species in areas other than the Sea of Japan were also mapped, based on material deposited in the National Museum of Nature and Science, and one additional new species from off the Pacific coast of north-eastern Honshu is described, *Punctulum sanrikuense* n. sp., which is closely related to, and probably represents a counterpart of *P. soyomaruae* n. sp. in the Sea of Japan. Distributions and speciations of these species are briefly discussed with regard to the geological history of the Sea of Japan.

Key words: Rissoidae, bathyal, Sea of Japan, taxonomy, new species.

Introduction

The Rissoidae is a family of small to minute gastropods that are abundant in seas throughout the world from intertidal to bathyal and abyssal depths. Because of their size and considerable convergence in shell characters, they have proved to be very difficult to classify, both at species and supraspecific levels (Ponder, 1985). Although shallow-water species of this and similar-looking families are relatively well surveyed in some areas, such as the northern Atlantic and Mediterranean (*e.g.*, Nordsieck, 1972), Australasia (*e.g.*, Laseron, 1956; Ponder, 1967), southwestern South America (Ponder and Worsfold, 1994) and the Antarctic ocean (*e.g.*, Ponder, 1983), no comprehensive studies have been carried out in the Indo-West Pacific, which is known to have the richest biodiversity of all world oceans. Furthermore, there have been only a few studies that treat deep-water species outside the Northeast Atlantic (Warén, 1973, 1974; Bouchet and Warén, 1993; Gofas, 2007) and the Antarctic and Sub-Antarctic (Ponder, 1983). Although more than 120 rissoid species have been recorded in Japanese waters (Higo *et al.*, 1999), only three had been reported from bathyal depths (*i.e.*, deeper than 200 m) by the end of the last century. Several additional species have been recorded in the last few decades from Japanese and adjacent waters (Table 1), especially in Russian waters, though most of them were described based on only a few specimens and some were unnamed. In the Sea of Japan, eight species in total have been recorded at bathyal depths to date (Appendix).

The Sea of Japan is a semi-closed marginal sea of the northwestern Pacific surrounded by a

Table 1. A review of previous records of bathyal rissoids (recorded at depths of >200 m) in the Japanese and adjacent waters. *See remarks of the respective species for discussion on the identification. Abbreviations: *A.*, *Alvania*; *F.*, *Frididoalvania*; JS, Sea of Japan; *M.*, *Mohrensternia*; OS, Okhotsk Sea; *P.*, *Punctulum*.

Species		Regions	Depths (m)	Sources
A. asura (Yokoyama, 1926)	= *F. asura* (Yokoyama, 1926)*	off Tajima, Hyogo, JS	300–400	Ito (1967)
A. asura (Yokoyama, 1926)	= *F. asura* (Yokoyama, 1926)*	off Sado and Awashima Is., JS	200–300	Ito (1985: pl. 2, figs. 1-1–2)
A. asura (Yokoyama, 1926)	= *F. asura* (Yokoyama, 1926)*	off Noto Peninsula, JS	100–264	Ito *el al.* (1986: pl. 4, fig. 4)
M. derjugini Golikov & Licharev, 1985	= *F. asura* (Yokoyama, 1926)*	off southern Sakhalin, OS	128–424	Golikov & Scarlato (1985: fig. 2)
F. sp.	= *F. asura* (Yokoyama, 1926)*	Sagami Bay, NW Pacific	725–730	Hasegawa (2006: fig. 4A)
F. sp.	= *F. asura* (Yokoyama, 1926)*	off Sanriku, NW Pacific	249–1470	Hasegawa (2009: figs. 67–69)
A. sitta (Yokoyama, 1926)	= *F. sitta* (Yokoyama, 1926)*	off Noto Peninsula, JS	200–204	Ito *et al.* (1986: pl. 4, fig. 5)
A. ferruginea A. Adams, 1860	= *F. sitta* (Yokoyama, 1926)*	off Primorsky Krai, northern JS	8–250	Golikov *et al.* (2001b)
F. janmayeni (Friele, 1878)	= *F. sitta* (Yokoyama, 1926)*	off Primorsky Krai, JS, and OS	8–890	Golikov *et al.* (2001b)
F. flavida Golikov & Sirenko, 1998	(valid; generic position uncertain)	Kurile Is., NW Pacific	500	Golikov & Sirenko (1998: fig. 3C)
Microstelma flava Okutani, 1964	= *P. flavum* (Okutani, 1964)*	Sagami Bay, NW Pacific	550	Okutani (1964)
A. flava (Okutani, 1964)	= *P. flavum* (Okutani, 1964)*	Suruga and Tosa Bays, NW Pacific	742–776	Hasegawa (2001)
P. flava (Okutani, 1964)	= *P. flavum* (Okutani, 1964)*	off Sanriku, NW Pacific	480–481	Hasegawa (2009: fig. 65)
P. ochotense Golikov & Sirenko, 1998	= *P. flavum* (Okutani, 1964)*	OS	500	Golikov & Sirenko (1998: 3E)
P. delicatum Golikov & Sirenko, 1998	= *P. flavum* (Okutani, 1964)*	OS	500	Golikov & Sirenko (1998: 3D)
P. reticulatum Golikov, 1986	(valid)*	off Primorsky Krai, northern JS	240–880	Golikov (1986: fig. 4); Golikov *et al.* (2001b)
P. sp.	= *A. akibai* (Yokoyama, 1926)*	off Primorye, northern JS	373–494	Golikov *et al.* (2001b)
A. cf. *awa* Chinzei, 1959	= *A. awa* Chinzei, 1959*	off Sado and Awashima Is., JS	200–300	Ito (1985: pl. 2, fig. 2)
A. sp.		Tosa Bay, NW Pacific	753–1001	Hasegawa (2001: pl. 2, figs. F–G)
A. sp. 1	= *A.* sp. *fide* Hasegawa (2001)	off Nansei Is., NW Pacific	955–1533	Hasegawa (2005)
A. sp. 2		off Nansei Is., NW Pacific	991–955	Hasegawa (2005: fig. 5I)
A. sp.		off Sanriku, NW Pacific	213–249	Hasegawa (2009: fig. 66)
A. sp. A		Sagami Bay, NW Pacific	1190	Hasegawa & Okutani (2011: fig. 16)
A. sp. B		Sagami Bay, NW Pacific	690	Hasegawa & Okutani (2011: fig. 17)
Pseudosetia sp. A		Sagami Bay, NW Pacific	681–1104	Hasegawa & Okutani (2011: fig. 14)
Pseudosetia sp. B		Sagami Bay, NW Pacific	490	Hasegawa & Okutani (2011: fig. 15)
Pusillina (*Haurakia*) sp.		off Nansei Is., NW Pacific	523–528	Hasegawa (2005: fig. 5H)
Benthonellania sp.		off Nansei Is., NW Pacific	391–404	Hasegawa (2005: fig. 5J)
Benthonella sp.		off Nansei Is., NW Pacific	955–1533	Hasegawa (2005: figs. K, L)

part of the Japanese Archipelago (Honshu and Hokkaido), eastern Korea, Russia and Sakhalin. It is separated from adjacent seas by narrow straits, which are all shallower than 150 m (Fig. 51) and function as geographical barriers. This geographical isolation has resulted in the formation of an independent bathyal circulation system, and a uniform endemic water body below *ca.* 300 m in the Sea of Japan that is characterized by low temperature and rich dissolved oxygen content. Together with its peculiar geological history, as described in more detail in the discussion part, the Sea of Japan can provide a good model to examine genetic separation and speciation of deep-sea animals (Kojima *et al.*, 2001).

The molluscan fauna of the continental shelf and bathyal zone in the Sea of Japan has been surveyed to some extent since the middle of the 19th century. In 1859, HMS *Acteon* carried out dredging for the first time at several places on the continental shelf in the Sea of Japan, with the most productive station located off Mino Sima [= Mishima Island, Yamaguchi Prefecture, the western Sea of Japan] at a depth of 63 fathoms [= 115 m], where 183 molluscs were recorded in total including 163 new species (Tsuchida and Hori, 1996). Those new species were described in a series of short papers by the English conchologist Arthur Adams, but the descriptions were inadequate in detail, and accompanied by neither measurements nor illustrations. Furthermore, a type was not designated for each taxon, and the voucher material (possible syntypes) is scattered through many institutions or even lost (Ponder and Keyzer, 1992), making it difficult to clarify the identifications of many nominal taxa. In 1906, the USS *Albatross* visited Japan to survey fisheries resources, and carried out bottom trawls at 74 stations in the Sea of Japan alone, in a depth range of 44–846 m. At least 18 new molluscan species, mostly buccinids and turrids (*s.l.*), were described from the Sea of Japan based on the material (*e.g.*, Dall, 1919; Bartch, 1941), but most other groups remain unstudied to date. During the years 1923–1930, a project entitled "Survey of the continental shelf bordering Japan" was carried out by the Imperial Fisheries Experimental Station using the S/S *Soyo-Maru*, and 184 stations were set in the Sea of Japan down to a depth of 406 m (Horikoshi *et al.*, 1982). This was the first comprehensive deep-sea survey by a Japanese institute, but except for a few groups (*e.g.*, cephalaspideans: Habe, 1954) most of the material was unfortunately scattered and lost before it could be studied in detail. The first comprehensive faunal reports on the molluscs of the continental shelf and upper bathyal zone was published as a series of papers by K. Ito (Ito, 1985, 1989, 1990; Ito *et al.*, 1986), based mainly on material collected during ecological and resource surveys focusing on the queen crab, *Chionoecetes opilio*, down to a depth of *ca.* 300 m, reflecting the vertical distribution of the crab. Ito illustrated most of the recovered species, but small to minute species were mostly left unidentified to the species level, or rather tentatively identified by putting "cf." before species name. More recently, Tsuchida and Hayashi (1994) published a brief report on lower-sublittoral and bathyal molluscs collected from the western area of the Sea of Japan, and recorded 38 molluscs, including 26 gastropods from the bathyal zone, in a depth range of 255–1233 m, but it contains few minute species, probably due to the sampling method. There are no other published records on bathyal molluscs, especially those from deeper than 1000 m, except for commercially important buccinids (*e.g.*, Kato, 1979). Apart from these records from the Japanese coasts, some bathyal molluscs have been recorded by Russian authors from northern part of the Sea of Japan, such as in Peter the Great Bay and off Primorsky Krai (*e.g.*, Golikov and Sirenko, 1998). Although most of these species were recorded only as names or sometimes rough line drawings, a part of the voucher material was subsequently illustrated in color photographs by Kantor and Sysoev (2006), making it possible to reconsider their identifications.

The Department of Zoology of the National Museum of Nature and Science has been carry-

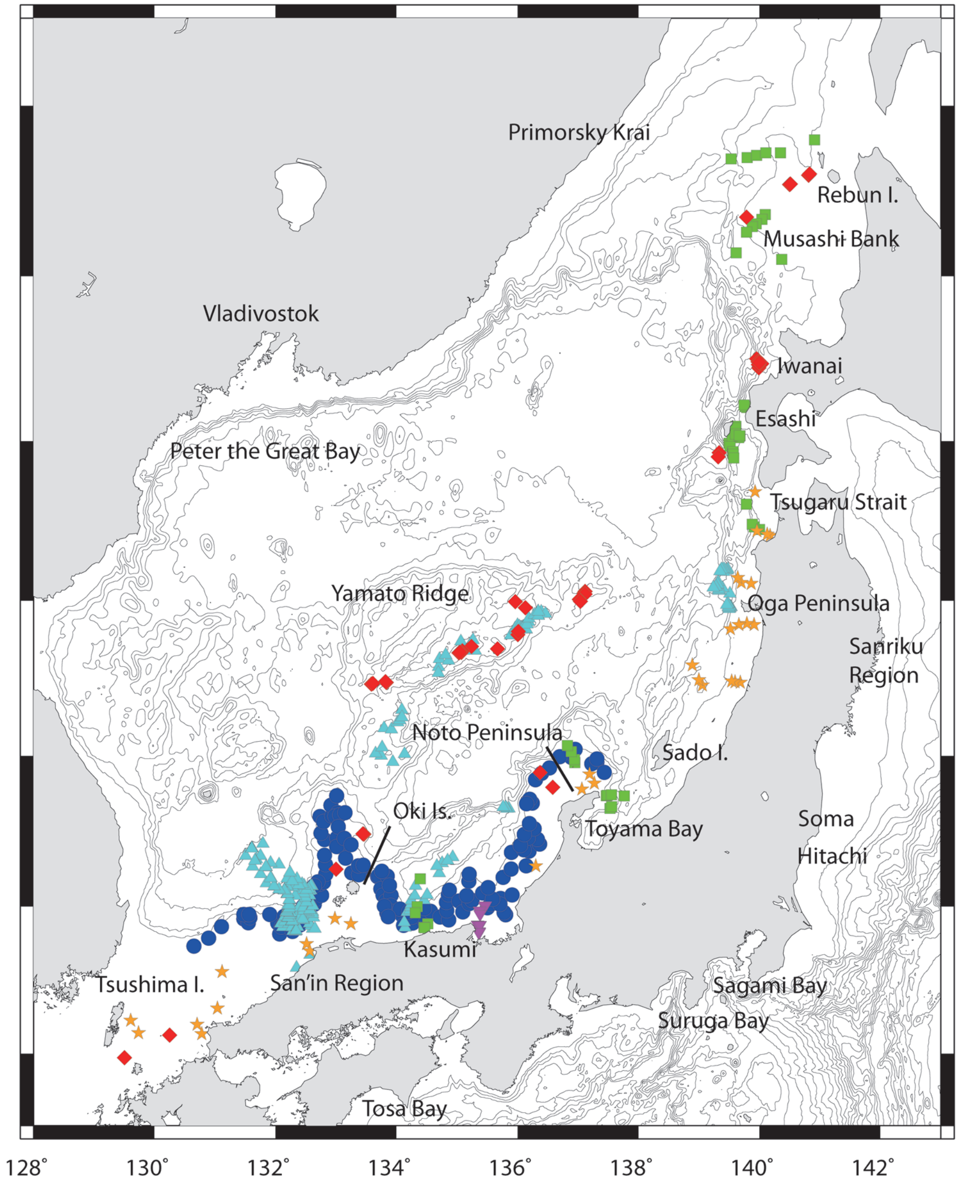


Fig. 1. A map showing all the sampling stations in the present project, with major place names that are mentioned in the text. Circles, the T/S *Tanshu-maru* (otter trawls; 132 stations); triangles, the T/S *Tanshu-maru* (large dredges; 249 stations); asterisks, the R/V *Mizuho-maru* (dredges; 31 stations); squares, the R/V *Tansei-maru* (beam-trawls and dredges; 53 stations); rhombuses, the R/V *Soyo-maru* (benthos nets, traps and dredges; 44 stations).

ing out a deep-sea sampling program since 1993, and it focused on the Sea of Japan during its fifth period in 2009–2013, under the title "Research on Deep-sea Fauna of the Sea of Japan", in cooperation with the Japan Sea Regional Research Institute of the National Fisheries Agency (NFA). Several research vessels were used, as described in the material and methods section, and trawling and dredging were carried out at more than 500 stations (Fig. 1). A large number of gastropod specimens were obtained, and are currently being studied taxonomically by the present author. In the present paper, rissoid gastropods that occurred at bathyal depths (deeper than 200 m) are treated in detail. In order to clarify the geographical distributions of these species, additional material obtained from off the Pacific coasts during other projects and independent cruises was also examined. Species that did not occur in the Sea of Japan are not treated, with the sole exception of a species that is exclusively distributed off the Sanriku region on the Pacific coast of northeastern Honshu, because it is considered to be closely related to a species in the Sea of Japan.

Materials and Methods

The main body of the material examined in the present study was collected during the sampling program, "Research on Deep-sea Fauna of the Sea of Japan", carried out by the Department of Zoology, National Museum of Nature and Science, in 2009–2013. The following research and training vessels and gears were used at 509 stations in total, in a depth range of 53–2381 m (Fig. 1): the T/V *Tanshu-maru* of Kasumi High School, Hyogo Prefecture (Pref.), with large dredges (Hirose *et al.*, 2006), and otter trawls; the R/V *Tansei-maru* of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), with 3 m ORE-type beam trawls and 1 m biological dredges; the R/V *Mizuho-maru* of the Fisheries Research Agency (FRA), with 1 m biological dredges, and the R/V *Soyo-maru* of the FRA, with larger beam trawls (benthos nets) and crab cages. More than 660 rissoid specimens in 118 lots, including juveniles and empty shells, were obtained from the Sea of Japan in the bathyal zone (deeper than 200 m), at 72 positive stations within a range of 200–1894 m (Table 2), and they were identified to the species level. Additional rissoid material collected from other areas in the Japanese waters during other sampling programs and research expeditions, and preserved in the National Museum of Nature and Science, was also examined for comparison (Table 3).

Type and voucher materials of previous studies were examined at the Zoological Institute, Russian Academy of Science, Sankt-Petersburg, at the Ryotsu Kyodo Hakubutsukan [Ryotsu Folk Museum], Sado, Niigata, and the University Museum, the University of Tokyo. Part of the unsorted material collected from the Sea of Japan by the R/V *Vityaz* of the Institute of Oceanology, Russian Academy of Science, Moscow, was also examined.

Specimens were primarily examined and classified into superficially distinguishable provisional groups under stereomicroscopes, and selected representative specimens were photographed with a digital camera, Nikon D300, attached to either a stereomicroscope, Leica M420, or ordinary interchangeable lenses such as MicroNikkor 60 mm and reversely attached Nikkor 20 mm with or without several extension rings. Generally at least 10 shots of gradually changing focus were taken and combined with the aid of the focus stacking software CombineZP. All the combined images were processed with Adobe Photoshop. Measurements of shells were made on the digital images, and the number of protoconch whorls was counted following Warén (1974: fig. 2) based either on digital images or sketches.

For preparation of radula, at least two examples of each species and phenotype were dissected under a stereomicroscope. After examination of gross external anatomy, such as the head-foot parts and mantle organs, including external parts of the reproductive system, the buccal mass was removed and dissolved in 10-times diluted bleach, Kitchen Haiter, Kao Co., according to the method described by Hasegawa (1995). It is noticeable that all the larger examples of all species, with the sole exception of *Alvania yamatonensis* n. sp., turned out to be female, and most of the smaller mature specimens were male, suggesting a general tendency to sexual dimor-

Table 2. Positive stations of R/V *Tansei-maru* (KT), R/V *Mizuho-maru* (MZ), R/V *Soyo-maru* (SO) and T/S *Tanshu-maru* (TS) cruises in the Sea of Japan. Abbreviations: BN, benthos net; BT, ORE-type 3 m beam trawl; BT', 2 m beam trawl; DG, 1 m biological dredge; BZ, large dredge.

St. no.	Date	Gear	Position in	Position out	Depth (m)	Bottom Temp (℃)	Region
KT-10-08 Es2	26/05/2010	BT	42°05.07′N, 139°36.40′E	42°03.13′N, 139°36.76′E	670–671	NA	Off Esahi
KT-10-08 Es3	26/05/2010	BT	42°03.89′N, 139°40.79′E	42°01.71′N, 139°39.68′E	839–821	NA	Off Esahi
KT-10-08 R2	23/05/2010	BT	45°27.25′N, 140°20.90′E	45°26.15′N, 140°21.94′E	402–393	NA	Off Reibun Island
KT-10-08 R3	23/05/2010	BT	45°27.21′N, 140°06.48′E	45°26.09′N, 140°08.45′E	615–594	NA	Off Reibun Island
KT-10-08 T1	21/05/2010	BT	40°53.90′N, 140°00.04′E	40°53.28′N, 139°58.62′E	350–315	NA	Off Tsugaru Strait
KT-10-08 T2	21/05/2010	BT	40°55.81′N, 139°54.84′E	40°53.96′N, 139°53.88′E	679–715	NA	Off Tsugaru Strait
KT-10-08 T3	21/05/2010	BT	40°57.96′N, 139°53.01′E	40°58.86′N, 139°52.87′E	851–839	NA	Off Tsugaru Strait
KT-11-9 E1	29/05/2011	BT	41°52.01′N, 139°33.90′E	41°52.94′N, 139°34.33′E	220–247	NA	Off Esashi
KT-11-9 E2	29/05/2011	BT	41°50.26′N, 139°34.03′E	41°48.70′N, 139°34.18′E	388–538	NA	Off Esashi
KT-11-9 E3	29/05/2011	BT	41°47.46′N, 139°34.49′E	41°48.96′N, 139°34.88′E	563–635	NA	Off Esashi
KT-11-9 E4	29/05/2011	BT	42°03.91′N, 139°40.11′E	42°03.38′N, 139°39.98′E	787–854	NA	E off Okushiri Island
KT-11-9 K2	03/06/2011	BT	35°46.11′N, 134°30.94′E	35°46.57′N, 134°32.09′E	203–205	NA	Off Kasumi
KT-11-9 K3	02/06/2011	BT	35°54.85′N, 134°18.60′E	35°55.17′N, 134°20.08′E	370–411	NA	Off Kasumi
KT-11-9 K4	02/06/2011	BT	35°59.92′N, 134°20.58′E	35°59.61′N, 134°18.82′E	603–613	NA	Off Kasumi
KT-11-9 K5	02/06/2011	BT	36°22.25′N, 134°23.61′E	36°20.18′N, 134°22.84′E	1277–1290	NA	Off Kasumi
KT-11-9 M2	28/05/2011	BT	44°40.48′N, 140°02.38′E	44°39.53′N, 140°02.83′E	198–206	NA	Musashi Bank
KT-11-9 M3	28/05/2011	BT	44°37.21′N, 139°56.68′E	44°36.29′N, 139°57.82′E	407–413	NA	Musashi Bank
KT-11-9 M6	28/05/2011	BT	44°16.68′N, 139°36.85′E	44°14.25′N, 139°37.25′E	1421–1465	NA	Musashi Bank
KT-11-9 N3	01/06/2011	BT	38°03.25′N, 136°53.39′E	38°03.82′N, 136°55.13′E	402–414	NA	N off Noto Peninsula
KT-11-9 N4	01/06/2011	BT	38°08.04′N, 136°49.64′E	38°09.00′N, 136°51.20′E	603–622	NA	N off Noto Peninsula
KT-11-9 T2	31/05/2011	BT	37°28.77′N, 137°29.07′E	37°29.53′N, 137°28.63′E	207–258	NA	Toyama Bay
KT-11-9 T3	31/05/2011	BT	37°29.18′N, 137°33.25′E	37°29.35′N, 137°31.96′E	383–460	NA	Toyama Bay
KT-11-9 T4	01/06/2011	BT	37°19.80′N, 137°33.38′E	37°20.02′N, 137°34.20′E	561–583	NA	Toyama Bay
KT-11-9 T5	01/06/2011	BT	37°18.45′N, 137°31.77′E	37°18.66′N, 137°32.85′E	790–808	NA	Toyama Bay
KT-11-9 T6	01/06/2011	BT	37°28.29′N, 137°45.89′E	37°26.70′N, 137°44.59′E	1410–1564	NA	Toyama Bay
MZ10–03	19/09/2010	BT′	38°58.09′N, 139°32.51′E	38°58.35′N, 139°32.70′E	182–185	4.34	Off Sakata
SO07-C2-B	21/07/2007	BN	39°54.60′N, 136°07.80′E	39°56.90′N, 136°07.00′E	1360–1341	NA	N of Yamato Bank
SO07-C4-B1	25/07/2007	BN	43°00.40′N, 139°57.20′E	43°00.70′N, 140°00.40′E	1607–1369	NA	Off Iwanai
SO07-C4-B2	25/07/2007	BN	42°53.70′N, 139°59.40′E	42°54.20′N, 140°02.00′E	843–760	NA	Off Iwanai
SO08-C3-B	25/07/2008	BN	38°56.40′N, 133°36.50′E	38°58.60′N, 133°35.60′E	1768–1696	NA	Yamato Bank
SO08-D3-1	30/07/2008	DG	36°57.90′N, 133°27.60′E	36°58.20′N, 133°26.80′E	368–NA	NA	Sanban-se, Oki Islands
SO08-D3-2	30/07/2008	DG	36°58.20′N, 133°26.70′E	36°58.10′N, 133°26.90′E	369–NA	NA	Sanban-se, Oki Islands
TS09-BZ200	29/06/2009	BZ	35°01.31′N, 132°02.85′E	35°01.44′N, 132°21.60′E	200–200	NA	W off Oki Islands
TS09-BZ250	26/06/2009	BZ	35°44.53′N, 132°16.58′E	35°44.43′N, 132°16.25′E	250–251	NA	W off Oki Islands
TS09-OW08	24/08/2009	BZ	35°57.96′N, 132°13.50′E	35°58.17′N, 132°13.53′	897–908	0.36	W off Oki Islands
TS09-OW09	24/08/2009	BZ	35°58.93′N, 132°12.28′E	35°59.06′N, 132°12.83′E	997–1001	0.35	W off Oki Islands
TS09-OW11	24/08/2009	BZ	36°05.30′N, 132°13.78′E	36°05.48′N, 132°14.31′E	1204–1204	0.31	W off Oki Islands
TS09-OW28	26/08/2009	BZ	36°12.59′N, 132°34.97′E	36°12.16′N, 132°34.89′E	601–598	0.39	W off Oki Islands
TS09-OW29	26/08/2009	BZ	36°12.48′N, 132°33.60′E	36°12.50′N, 132°33.52′E	697–702	0.38	W off Oki Islands
TS09-OW30	26/08/2009	BZ	36°08.72′N, 132°33.77′E	36°08.48′N, 132°33.44′E	796–796	0.45	W off Oki Islands
TS09-OW30	26/08/2009	BZ	36°08.72′N, 132°33.77′E	36°08.48′N, 132°33.44′E	796–796	0.45	W off Oki Islands
TS09-OW30	26/08/2009	BZ	36°08.72′N, 132°33.77′E	36°08.48′N, 132°33.44′E	796–796	0.45	W off Oki Islands
TS09-OW31	26/08/2009	BZ	36°07.19′N, 132°29.53′E	36°07.00′N, 132°29.60′E	888–900	0.36	W off Oki Islands
TS09-OW33	25/08/2009	BZ	36°13.58′N, 132°26.30′E	36°13.19′N, 132°26.53′E	1090–1082	0.31	W off Oki Islands
TS09-OW34	25/08/2009	BZ	36°08.64′N, 132°19.53′E	36°08.85′N, 132°20.01′E	1200–1190	0.30	W off Oki Islands
TS09-OW37	25/08/2009	BZ	36°22.52′N, 132°11.64′E	36°22.97′N, 132°11.79′E	1500–1497	0.28	W off Oki Islands
TS09-OW38	26/08/2009	BZ	36°16.25′N, 132°36.27′E	36°15.76′N, 132°36.12′E	600–604	0.40	W off Oki Islands
TS09-OW39	26/08/2009	BZ	36°16.45′N, 132°35.15′E	36°16.08′N, 132°35.02′E	702–704	0.36	W off Oki Islands
TS09-OW40	28/08/2009	BZ	36°14.40′N, 132°32.72′E	36°13.70′N, 132°32.44′E	795–800	0.42	W off Oki Islands
TS09-OW41	28/08/2009	BZ	36°13.40′N, 132°30.78′E	36°13.66′N, 132°31.25′E	885–870	0.35	W off Oki Islands
TS09-OW43	27/08/2009	BZ	36°18.10′N, 132°26.43′E	36°17.72′N, 132°26.15′E	1097–1090	0.32	W off Oki Islands
TS09-OW47	27/08/2009	BZ	36°27.23′N, 132°14.29′E	36°27.71′N, 132°14.61′E	1504–1497	0.28	W off Oki Islands
TS09-ZY18	29/6/2009	BZ	35°43.23′N, 132°16.32′E	35°43.10′N, 132°16.49′E	237–235	0.32	W off Oki Islands
TS09-ZY33	29/06/2009	BZ	35°51.96′N, 132°09.33′E	35°52.25′N, 132°01.30′E	445–460	NA	W off Oki Islands
TS10-AK07	09/09/2010	BZ	39°55.70′N, 139°30.48′E	39°55.17′N, 139°30.51′E	793–823	0.30	Oga Peninsula
TS10-AK10	06/09/2010	BZ	39°55.35′N, 139°29.15′E	39°54.83′N, 139°29.00′E	1104–1102	0.32	Oga Peninsula
TS10-AK15	07/09/2010	BZ	40°07.57′N, 139°21.11′E	40°07.21′N, 139°21.50′E	1598–1567	0.26	Oga Peninsula
TS10-AK24	11/09/2010	BZ	40°22.93′N, 139°27.93′E	40°22.46′N, 139°27.94′E	1703–1695	0.26	Oga Peninsula
TS10-T55	01/09/2010	BZ	39°04.45′N, 134°41.45′E	39°04.29′N, 134°40.90′E	316–328	1.77	Central Yamato Bank
TS12-D01	26/08/2008	BZ	36°05.08′N, 134°27.29′E	36°04.85′N, 134°26.72′E	870–874	NA	Off Kasumi
TS12-D02	26/08/2008	BZ	36°09.33′N, 134°30.42′E	36°09.03′N, 134°29.85′E	1027–1028	NA	Off Kasumi
TS12-D04	28/08/2008	BZ	36°26.78′N, 134°42.36′E	36°26.53′N, 134°41.85′E	1304–1304	NA	Off Kasumi
TS12-HY06	27/08/2008	BZ	36°01.80′N, 134°14.68′E	36°01.91′N, 134°14.04′E	701–699	NA	Off Kasumi
TS12-HY10	28/08/2008	BZ	36°32.55′N, 134°40.03′E	36°33.03′N, 134°39.96′E	1397–1399	NA	Off Kasumi

Table 2. (continued)

St. no.	Date	Gear	Position in	Position out	Depth (m)	Bottom Temp (°C)	Region
TS12-OW01	24/08/2008	BZ	35°40.45′N, 132°20.39′E	35°40.77′N, 132°20.94′E	200–201	NA	W off Oki Islands
TS12-OW02	24/08/2008	BZ	35°48.08′N, 132°16.40′E	35°48.25′N, 132°17.08′E	301–301	NA	W off Oki Islands
TS12-OW04	24/08/2008	BZ	35°53.15′N, 132°13.68′E	35°53.27′N, 132°14.32′E	500–500	NA	W off Oki Islands
TS12-OW06	24/08/2008	BZ	35°55.10′N, 132°12.05′E	35°55.17′N, 132°12.71′E	704–700	NA	W off Oki Islands
TS12-OW14	29/08/2008	BZ	36°13.66′N, 132°03.60′E	36°13.17′N, 132°03.40′E	1493–1497	NA	W off Oki Islands
TS12-OW16	25/08/2008	BZ	36°22.76′N, 131°55.14′E	36°22.36′N, 131°54.99′E	1694–1695	NA	W off Oki Islands
TS12-OW18	25/08/2008	BZ	36°36.78′N, 131°39.53′E	36°37.05′N, 131°39.84′E	1894–1892	NA	W off Oki Islands
TS13-S13	27/08/2013	BZ	38°26.12′N, 134°01.16′E	38°25.98′N, 134°00.56′E	1600–1500	0.25	Yamato Bank

Table 3. Additoinal stations from off the Pacific coasts of Japan that are cited in the present paper. Abbreviations: D, dredge; OT, otter trawl; BT, beam trawl; CC, crab cage.

St. no	Date	Gear	Position in	Position out	Depth (m)	Region
WA05-DE250D	19/11/2005	D	38°04.60′N, 141°55.30′E	38°04.20′N, 141°55.20′E	249–249	NE Japan
WA05-FG250D	14/11/2005	D	37°19.90′N, 141°37.70′E	37°02.00′N, 141°37.40′E	255–253	NE Japan
WA06-DE280D	23/11/2006	D	38°42.90′N, 141°58.30′E	38°43.10′N, 141°58.40′E	284–285	NE Japan
WA06-H480	13/11/2006	OT	36°32.10′N, 141°06.00′E	36°32.70′N, 141°06.90′E	481–480	NE Japan
WA06-H1500D	15/11/2006	D	36°36.50′N, 141°36.20′E	36°36.70′N, 141°36.10′E	1470–1450	NE Japan
WA07–D310	18/10/2007	OT	38°53.50′N, 142°02.80′E	38°55.00′N, 142°03.30′E	303–307	NE Japan
KH-01-2 KC-0	18/09/2001	BT	42°10.79′N, 144°11.04′E	42°11.14′N, 144°11.61′E	1134–1219	NE Japan
KH-01-2 TD-2	25/09/2001	BT	39°31.50′N, 142°32.82′E	39°32.03′N, 142°33.57′E	1002–1069	NE Japan
KH-01-2 XR-2-1	15/09/2001	BT	42°27.52′N, 144°14.47′E	42°26.85′N, 144°12.98′E	965–981	NE Japan
KH-01-2 XR-2-2	15/09/2001	BT	42°27.44′N, 144°14.14′E	42°27.00′N, 144°13.44′E	973–982	NE Japan
KH-02-3 TB-3	14/09/2002	BT	32°25.95′N, 133°43.80′E	32°52.10′N, 133°41.51′E	1042–1045	Tosa Bay
KH-69-2-13	02/05/1969	BT	39°39.00′N, 142°20.70′E	39°40.00′N, 142°20.40′E	620–640	NE Japan
KH-69-2-3	29/04/1969	BT	36°44.50′N, 141°28.60′E	36°45.80′N, 141°30.30′E	615–620	NE Japan
KT-99-18 BT-3	16/12/1999	BT	32°26.50′N, 132°14.60′E	32°27.30′N, 132°16.50′E	1291–1298	Tosa Bay
KT-99-18 BT-4	16/12/1999	BT	32°23.40′N, 132°15.10′E	32°25.20′N, 132°17.20′E	1501–1516	Tosa Bay
KT-99-18 BT-6	20/12/1999	BT	33°38.20′N, 136°30.40′E	33°38.20′N, 136°34.60′E	2072–2075	Tosa Bay
KT-99-18 BT-8	20/12/1999	BT	33°50.00′N, 136°36.90′E	33°50.00′N, 136°33.90′E	2035–2043	Tosa Bay
KT-99-18 BT-9	20/12/1999	BT	33°50.00′N, 136°32.60′E	33°50.00′N, 136°28.90′E	1947–2023	Tosa Bay
KT-00-8 BT-2	25/06/2000	BT	33°07.00′N, 133°42.10′E	33°05.40′N, 133°41.60′E	742–776	Tosa Bay
KT-07-29 H-2	08/11/2007	BT	40°00.00′N, 143°31.37′E	41°00.76′N, 143°30.25′E	2055–2032	NE Japan
KT-07-29 K-1	07/11/2007	BT	42°34.99′N, 144°48.02′E	42°34.68′N, 144°49.91′E	1028–1075	NE Japan
KT-07-29 M-1	05/11/2007	BT	39°17.86′N, 142°28.40′E	39°16.80′N, 142°27.37′E	1039–1041	NE Japan
KT-07-29 M-2	05/11/2007	BT	39°16.20′N, 142°41.07′E	39°18.62′N, 142°43.73′E	1528–1603	NE Japan
KT-08-27 K-2	23/10/2008	BT	38°26.25′N, 143°02.13′E	38°24.90′N, 143°01.40′E	1906–1853	NE Japan
KT-08-27 S-2	20/10/2008	BT	41°03.05′N, 143°21.65′E	41°02.67′N, 143°23.26′E	2022–2027	NE Japan
KT-12-8 A-1	26/7/2012	BT	40°57.96′N, 141°45.30′E	40°57.69′N, 141°46.24′E	498–459	NE Japan
S13	27/11/1960	DG	35°05.40′N, 139°18.70′E		550	Sagami Bay
SH-BT93-1	27/10/1993	BT	35°01.10′N, 138°41.70′E	34°59.70′N, 138°42.00′E	870–950	Suruga Bay
SH-DG93-11	21/11/1993	DG	34°56.70′N, 138°41.30′E	34°55.50′N, 138°41.30′E	760–820	Suruga Bay
SO07-C5-B	29/07/2007	BT	44°32.00′N, 143°57.10′E	44°32.50′N, 143°56.90′E	177–176	Okhotsk Sea
SO07-C7	5–6/8/2007	CC	39°36.70′N, 142°33.30′E	39°35.90′N, 142°34.00′E	894–935	NE Japan
SO07-C7-B	05/08/2007	BT	39°40.60′N, 142°35.20′E	39°39.80′N, 142°33.70′E	818–815	NE Japan
SO07-K1	06/08/2007	BT	38°35.40′N, 143°04.50′E	38°34.00′N, 143°06.90′E	2137–2183	NE Japan
TS96-K2	20/04/1996	OT	38°02.60′N, 142°04.90′E	38°02.10′N, 142°41.10′E	1455–1451	NE Japan
RK-01-4	21/02/2001	D	35°08.80′N, 139°30.90′E	35°08.70′N, 139°30.90′E	730–725	Sagami Bay

phism in size in this group. This phenomenon makes it possible to examine the radula of both sexes in each species/phenotype with the fewest trials. Cusp formulae of the radulae are expressed following Ponder (1985: 10). Shells for SEM examination were only lightly sonicated in 70% ethanol or distilled water, without any chemical treatment in order to keep the periostracum intact, and mounted on stubs. Radulae, opercula and juvenile or immature shells with an intact protoconch were coated with gold/palladium alloy, and observed at relatively high acceleration voltage (higher than 5 kv) with a scanning electron microscope, JEOL JSM-6380LV, whereas whole shell specimens, including holotypes, were examined without coating at low acceleration voltages (5 kV or less).

Unless otherwise stated, all the voucher material is preserved in the National Museum of Nature and Science, Tsukuba, with registry numbers given here.

Distribution maps were prepared using GMT, with bathymetry data from Satellite Geodesy, Scripps Institution of Oceanography, University of California at San Diego. Depth contours are drawn at an interval of 500 m.

Institutional abbreviations. IORAN – Institute of Oceanology, Russian Academy of Science, Moscow; NHMUK – Natural History Museum, United Kingdom; NMV – Museum Victoria, Australia; NSMT – Department of Zoology, National Museum of Nature and Science, Tsukuba; NSM – Department of Paleontology, National Museum of Nature and Science, Tsukuba; RFM – Ryotsu Kyodo Hakubutsukan [= Ryotsu Folk Museum], Sado, Niigata; UMUT – University Museum, the University of Tokyo; ZISP – Zoological Institute, Russian Academy of Science, Saint-Petersburg.

Abbreviations used in shell descriptions and measurements. AL – aperural length; d – dried lived-collected specimen (attached to the number of specimens in parentheses); e – dead-collected empty shell (attached to the number of specimens in parentheses), SL – shell length; SW – shell width.

Taxonomy

Family Rissoidae Gray, 1847

Genus ***Frigidoalvania*** Warén, 1974: 125

Type species. *Rissoa janmayeni* Friele, 1878, by original designation.

Remarks. *Frigidoalvania* was separated from the allied genus *Alvania* based on conchological characters, such as a thick, smooth, brownish periostracum and widely spaced distinct teleoconch sculpture (Warén, 1974). The generic distinction was subsequently confirmed by Ponder (1985) on the basis of reproductive anatomy. In the present study, radulae of two species that can be reasonably assigned to this genus in shell morphology were examined, and they were shown to share similar characters to those in the type species, *F. janmayeni* as illustrated by Ponder (1985: fig. 103C). Shared characters include the simple outer marginal teeth, with complete absence of cusps on the inner margin, and distinctly finer and more numerous cusps on the central and lateral teeth, in comparison to the type species of *Alvania* (*A. cimex* Linnaeus, 1758: Ponder, 1985, fig. 86E) and other species here assigned to *Alvania* and *Punctulum*. Furthermore, shells of the species in this genus commonly have a considerably thickened outer apertural lip with a sharp edge, whereas the species here assigned to *Alvania* and *Punctulum* generally have a simple aperture. Accordingly, at least in the northwestern Pacific, *Frigidoalvania* can be clearly distinguished morphologically from other *Alvania*-like species.

Species of *Frigidoalvania* are widely distributed in arctic and subarctic seas, especially in the northern Atlantic. In the Eurasian arctic seas, three Atlantic species have been recorded (Golikov *et al.*, 2001a): *F. janmayeni* (Friele, 1878) (eastward to Chukchi Sea), *F. cruenta* (Odhner, 1915) (eastward to Chukchi Sea) and *F. scrobiculata* (Möller, 1842) (eastward to East Siberian Sea). The last one, *Rissoa scrobiculata*, was assigned by Warén (1974) to the genus *Alvania*, and this view is supported here based on the overall shell characters.

In the northwestern Pacific and adjacent areas, two species of *Frigidoalvania* have been recorded in the Sea of Japan (Hasegawa, 2000; *F. asura* and *F. sitta*), with one additional unidentified species from the Pacific coast of northern Honshu (Hasegawa, 1999), which is shown in the present study to be a phenotype of *F. asura*. In addition, two species of this genus have been recorded in Russian waters (Golikov *et al.*, 2001b): *F. janmayeni* and *F. flavida* Golikov and Sirenko, 1998. Records of *F. janmayeni* in the northwestern Pacific (Okhotsk Sea) were based on the specimens preserved in the ZISP, and examination of the voucher specimens (Fig. 3L) revealed that they were actually indistinguishable from *Mohrensternia coronata* (= *F. asura* in this study) that was described from the same area. *Frigidoalvania flavida* was originally described from off Paramushir Island, in the western Okhotsk Sea, at a depth of 500 m (Golikov and Sirenko, 1998: 101–102, fig. 3C, 15C, J). Although the holotype of this taxon (ZISP 54239; Fig. 48I–K) has been considerably damaged by crystallization in alcohol, preventing precise examination, it seems to show closer resemblance to certain species of the genus *Punctulum*, especially *P. reticulatum*, by its rather depressed shell with rougher periostracum, and simple aperture. It is thus provisionally removed from this genus. On the other hand, the species assigned by Russian authors to the genus *Mohrensternia* Stoliczka, 1885 (*M. derjugini* and *M. coronata*) are apparently members of *Frigidoalvania*, and they are regarded as junior synonyms of *F. asura*, in the present study. *Mohrensternia* was originally erected for Miocene species occurring in the semi-marine to brackish-water deposits of central and eastern Europe (type species: *Rissoa angulata* Eichwald, 1830, by subsequent designation of Nevill, 1885: 105) (Anistratenko, 2005). Although some species of *Mohrensternia* do show a superficial resemblance to *Frigidoalvania* species in teleoconch features, they differ considerably from the latter in having a distinctly inflated protoconch, and Ponder (1985) suggested the possibility that *Mohrensternia* may be a hydrobiid.

In summary, three species of *Frigidoalvania* are currently recognized in the northwestern Pacific, including one new species as described below.

Frigidoalvania asura (Yokoyama, 1926)
[Japanese name: Ashura-tsubo]
(Figs. 2–3, 4A–F, 5, 6A–D, 7–9, 48A; Table 4)

Rissoa (*Apicularia*?) *asura* Yokoyama, 1926: 273, pl. 33, fig. 15 [type locality: Sawane Formation, Sado Island, Pliocene].

Rissoa (*Persephona*) *asura* — Hatai and Nisiyama, 1952: 241.

Alvania asura — Makiyama, 1958: pl. 45, fig. 15; Ito, 1967: 50 [off Tajima, Hygo Pref.; *ca.* 300–400 m]; Ito, 1985: 26, pl. 2, figs. 1-1–2 [Awashima Island, 200–250 m; Suizu, Sado Island; 200–300 m; Akadama, Sado Island, 200–250 m]; Ito *et al.*, 1986: 8–9, pl. 4, fig. 4 [off Ishikawa Pref., 100–264 m]; Ogasawara *et al.* (eds.), 1986: pl. 70, fig. 3a–b [Anden formation, Oga Peninsula, Akita Pref., Pleistocene]; Ito, 1999: 18 [off Kasumi, Hyogo Pref., 350–400 m].

Mohrensternia derjugini Golikov and Licharev in Golikov and Scarlato, 1985: 387, fig. 2 [type locality: eastern coast of southern Sakhalin, 47°34.0′N, 143°37.5′E, 187 m, mud]. **New synonym**.

Mohrensternia coronata Golikov, 1986: 86, fig. 1 [type locality: off western coast of Kamchatka, Okhotsk Sea, 53°17′N, 154°47′E, 140 m].

Putilla paudinoides [sic; = *paludinoides*] (Yokoyama) — Ogasawara *et al.* (eds.), 1986: pl. 70, fig. 5a–b [Anden formation, Oga Peninsula, Akita Pref., Pleistocene] [*non Rissoa* (*Cingula*) *paludinoides* Yokoyama, 1927].

Turboella coronata — Golikov and Sirenko, 1998: 101, fig. 3B [off Paramushir Island, Okhotsk Sea, 50°39.2′N, 155°37.4′E, 500 m].

Frigidoalvania janmayeni — Golikov *et al.*, 2001b: 158 (name only, in part; voucher specimens examined) [*non Rissoa janmayeni* Friele, 1878]

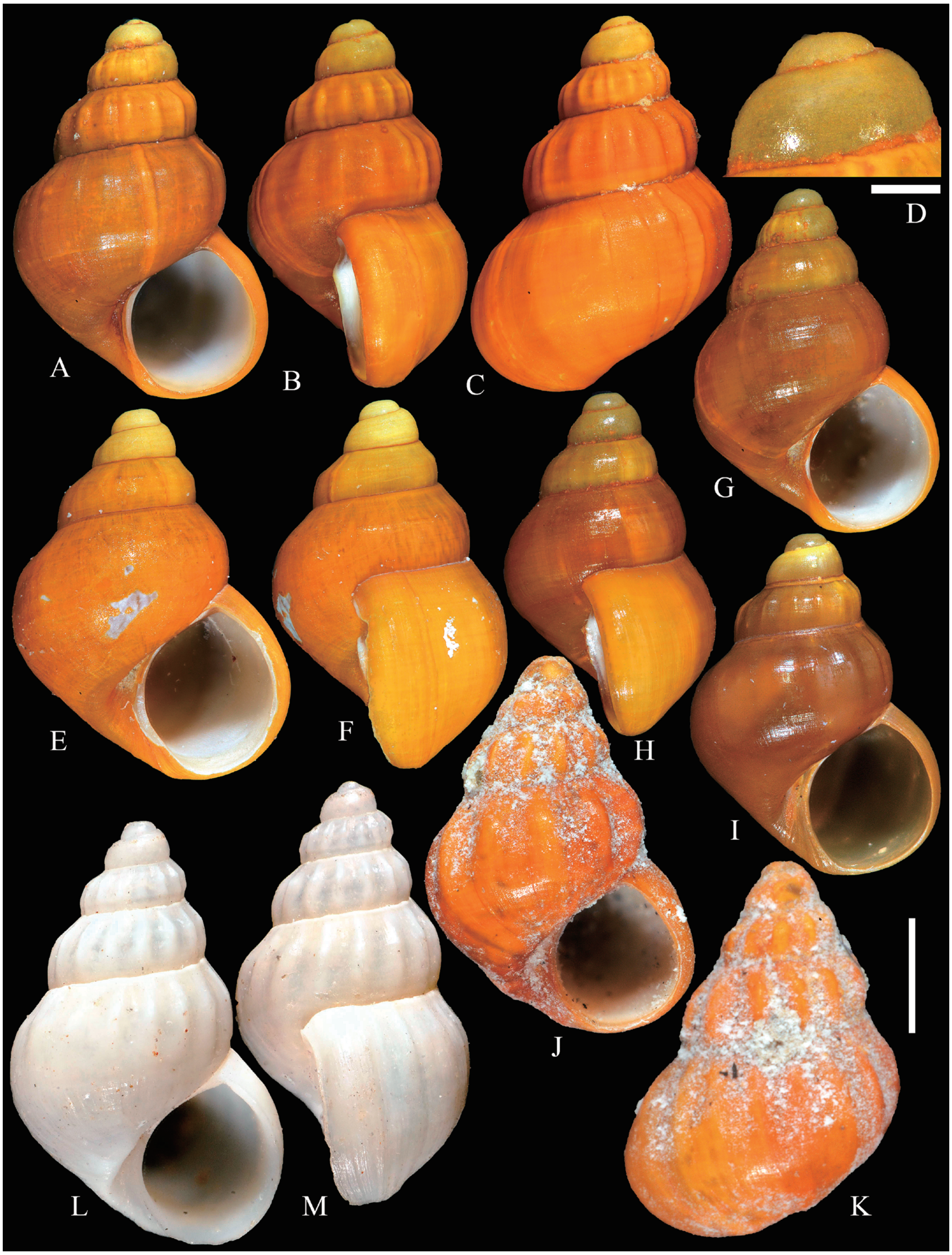


Fig. 2. Shells of *Frigidoalvania asura* from the Sea of Japan. A–D, NSMT-Mo 102085, off Esashi, 670–671 m; E–F, NSMT-Mo 95830, off Oki Islands, 598–601 m; G–H, NSMT-Mo 102115, off Noto Peninsula, 603–613 m; I, NSMT-Mo 95831, off Oki Islands, 796 m; J–K, ZISP 36615, Peter the Great Bay, 100 m; L–M, figured syntype of *Rissoa* (*Apicularia*?) *asura*, UMUT CM 23129, Pliocene fossil, Sawane Formation, Sado Island. All at the same scale (scale bar = 1 mm), except D (scale bar = 200 μm).

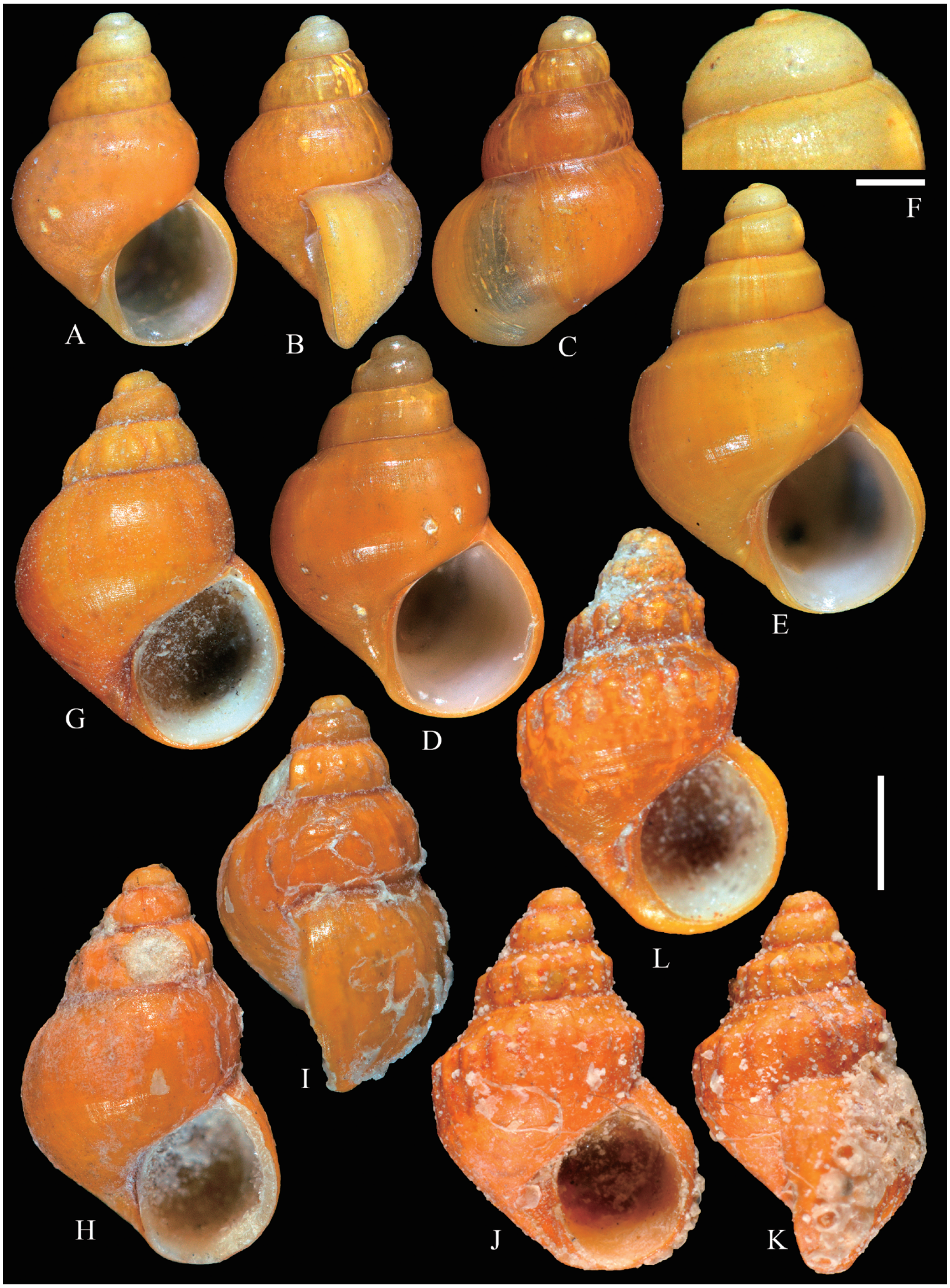


Fig. 3. Shells of *Frigidoalvania asura* from the Pacific Ocean and Okhotsk Sea. A–C, NSNT-Mo 93603, off Soma, 253–255 m; D, NSMT-Mo 93629, off Hitachi, 480–481 m; E–F, NSMT-Mo 93630, off Hitachi, 1450–1470 m; G, ZISP 42759, off Kunashir Island, 148 m; H–I, holotype of *Mohrensternia derjugini*, ZISP 33507/1, Okhotsk Sea, 187 m; J–K, holotype of *Mohrensternia coronata*, ZISP 42518/1, Okhotsk Sea, 500 m; L, ZISP 36703, Okhotsk Sea, 146 m (voucher of "*Frigidoalvania janmayeni*" *fide* Golikov *et al.*, 2001b). All at the same scale (scale bar = 1 mm), except F (scale bar = 200 μm).

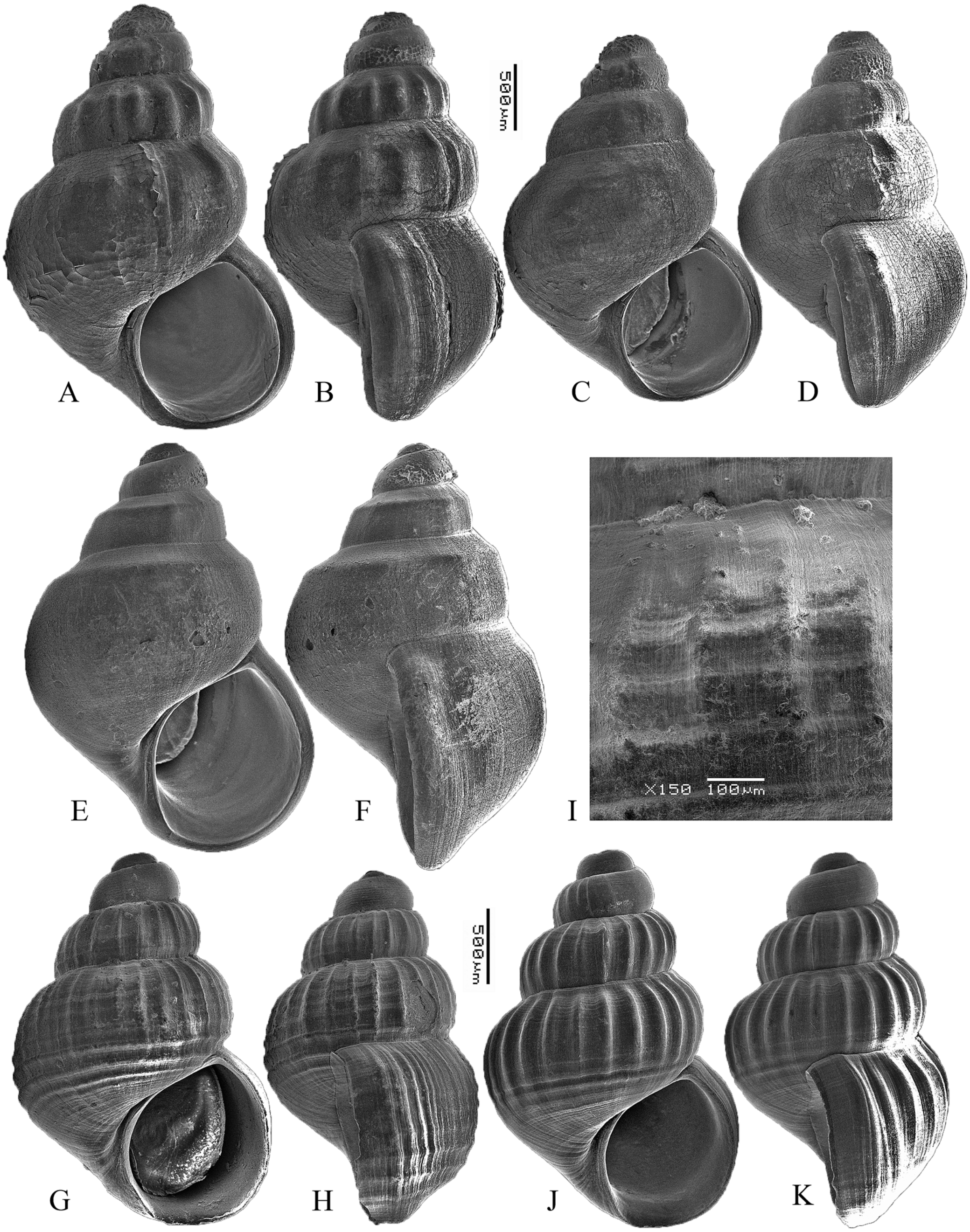


Fig. 4. Scanning electron micrographs (SEM) of shells of *Frigidoalvania* spp. A–F, *F. asura*; A–B, NSMT-Mo 102085, off Esashi, 670–671 m; C–D, NSMT-Mo 102115, off Noto Peninsula, 603–622 m; E–F, NSMT-Mo 93629, off Hitachi (Pacific), 480–481 m. G–K, *F. tanseimaruae* n. sp.; G–I, holotype, NSMT-Mo 102215, off Iwanai, 843–760 m (I, enlarged adapical part of the last whorl); J–K, paratype, NSMT-Mo 102187, off Oki Islands, 897–908 m. A–F and G–K at the same scale, respectively, except I.

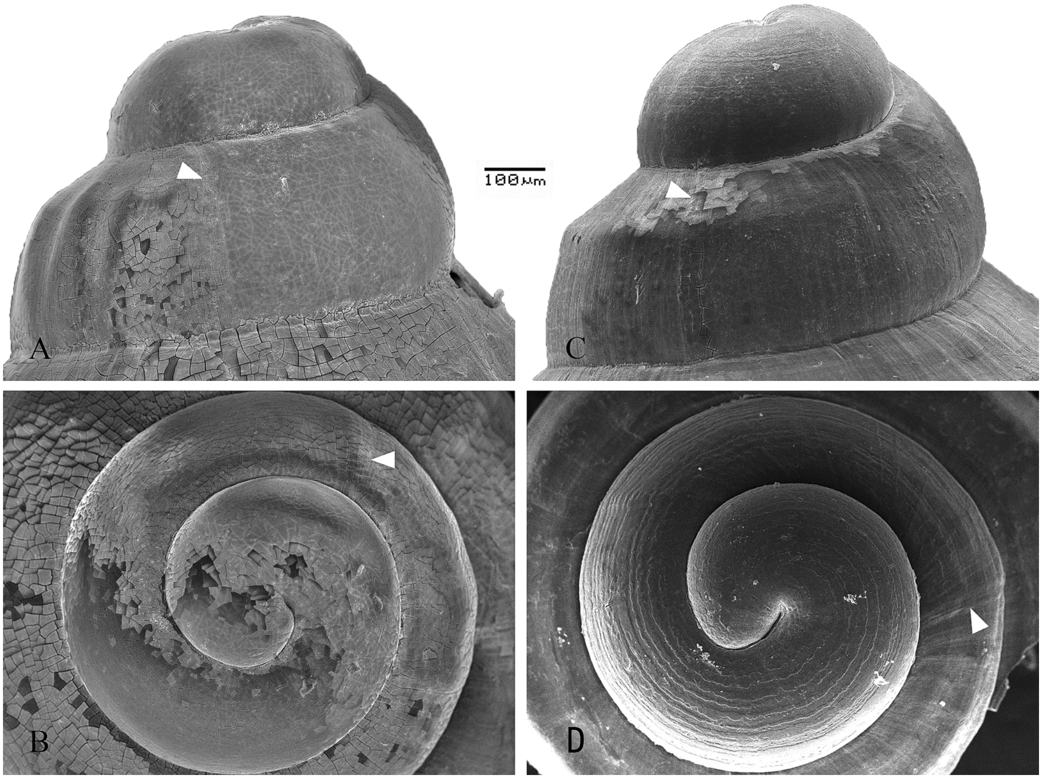


Fig. 5. SEM of protoconchs of *Frigidoalvania asura*. A–B, NSMT-Mo 102112, Toyama Bay, 383–443 m; C–D, NSMT-Mo 93629, off Hitachi (Pacific), 480–481 m. All at the same scale. Arrowheads indicate demarcation between protoconch and teleoconch.

Frigidoalvania sp. — Hasegawa, 2006: 241–242, fig. 4A [Sagami Bay, 725–730 m]; Hasegawa, 2009: 256, figs. 67–69 [off northeastern Honshu, 250–1500 m].

Type material. *Rissoa* (*Apicularia*?) *asura* Yokoyama, 1926, 3 syntypes, UMUT CM 23129 (Fig. 2L–M: originally figured syntype). *Mohrensternia derjugini* Golikov and Licharev in Golikov and Scarlato, 1985, holotype, ZISP 33507/1 (Fig. 3H–I) and several additional specimens from the type locality ZISP 33618/5. *Mohrensternia coronata* Golikov, 1986, holotype, ZISP 42518/1 (Fig. 3J–K).

Material examined (Sea of Japan). NSMT-Mo 95828, TS09-ZY18, 235–237 m (5+2e); NSMT-Mo 95829, TS09-BZ200, 200 m (2); NSMT-Mo 95830, TS-09-OW28, 598–601 m (7: Fig. 2E–F); NSMT-Mo 95831, TS09-OW30, 796 m (2+1e: Fig. 2I); NSMT-Mo 95832, TS-09-OW38, 600–604 m (2); NSMT-Mo 102108, TS09-OW39, 702–704 m (1e); NSMT-Mo 95833, TS09-OW40, 795–800 m (1); NSMT-Mo 102109, TS09-OW41, 870–885 m (3e); NSMT-Mo 102118, TS12-D01, 870–874 m (1+1e); NSMT-Mo 102119, TS12-OW01, 200–201 m (4+1e); NSMT-Mo 102120, TS12-OW02, 301 m (3e); NSMT-Mo 102121, TS12-OW06, 700–704 m (1); NSMT-Mo 102084, SO07-C4-B2, 760–843 m (60+14e); NSMT-Mo 102085, KT-10-08 Es2, 670–671 m (10+1d: Figs. 2A–D, 4A–F); NSMT-Mo 102086, KT-10-08 Es3, 821–839 m (2); NSMT-Mo 102087, KT-10-08 T1, 315–350 m (40+1e and 2 radula preparations on SEM stub: Fig. 6C–D, radulae; Fig. 49A, operculum); NSMT-Mo 102088, KT-10-8 T2, 679–715 m (2); NSMT-Mo 102089, KT-10-8 T3, 851–839 m (7+2e); NSMT-Mo 102110, KT-11-9 E3, 563–635 m (1);

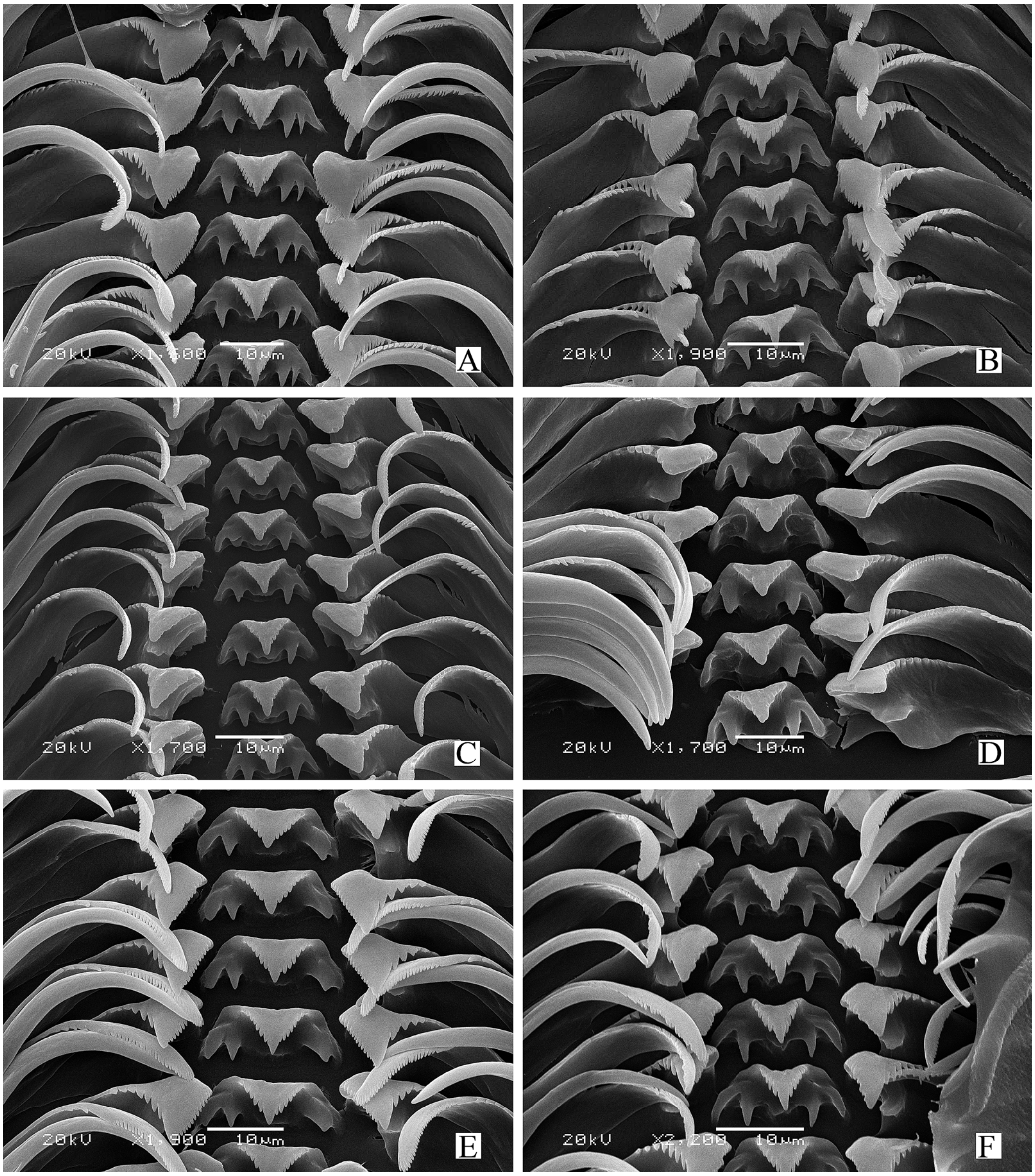


Fig. 6. SEM of radulae of *Frigidoalvania* spp. A–D, *F. asura*; A–B, NSMT-Mo 102104, off Sanriku (Pacific), 1002–1069 m; C–D, NSMT-Mo 102087, off Tsugaru, 315–350 m. E–F, *F. tanseimaruae* n. sp., paratypes, NSMT-Mo 102182, off Iwanai, 843–760 m. Images in the right column (A, C, E), females; those in the left column (B, D, F), males.

NSMT-Mo 102111, KT-11-9 E4, 787–854 m (1+1e); NSMT-Mo 102112, KT-11-9 T3, 383–460 m (28+7e and 2 specimens mounted on SEM stub: protoconchs examined by SEM); NSMT-Mo 102113, KT-11-9 T4, 561–583 m (3); NSMT-Mo 102114, KT-11-9 T5, 790–808 m (5+1e); NSMT-Mo 102117, KT-11-9 N3, 402–414 m (1e); NSMT-Mo 102115, KT-11-9 N4, 603–622 m (20+1d+8e: Figs. 2G–H, 4C–D); NSMT-Mo 102116, KT-11-9 K4, 603–613 m (4+3e); NSMT-Mo 102122, MZ10–03, 182–185 m (2e); NSMT-Mo, non-registered, several lots from Toyama Bay, Sado Island, and Kasumi, with no detailed data; RFM no. 340, off Kasumi, lacking coordi-

Table 4. Measurements of *Frigidoalvania asura.* *: shell dissolved for radula preparation; **: holotype of *Mohrensternia coronata*; ***: holotype of *Mohrensternia derjugini.*

Category	Register no.	Station	Locality	Depth (m)	SL	SW	SL/W	AL	Figures
Syntype	UMUT CM 23129		Sado I., Pliocene		4.26	2.72	1.57	1.75	2L–M
Sea of Japan	NSMT-Mo 95830	TS09-OW28	Off Oki Is.	601–598	3.21	2.44	1.32	1.55	2E–F
	NSMT-Mo 95831	TS09-OW30	Off Oki Is.	796–796	2.99	2.18	1.37	1.36	I
	NSMT-Mo 102084	SO07-C4-B2	Off Iwanai	843–800	3.38	2.25	1.50	1.41	
	NSMT-Mo 102115	KT-11-9 N4	Off Noto Peninsula	617–604	3.02	2.13	1.42	1.29	2G–H
	NSMT-Mo 102085	KT-10-8 Es2	Off Esashi	670–671	3.31	2.24	1.48	1.34	2A–D
	NSMT-Mo 102087	KT-10-8 T1	Off Tsugaru	350–315	3.13	2.20	1.42	1.42	
	NSMT-Mo 102087*	KT-10-8 T1	Off Tsugaru	350–315	3.37+α	2.45	—	1.57	6C
	NSMT-Mo 102087*	KT-10-8 T1	Off Tsugaru	350–315	2.61+α	2.12	—	1.35	6D
Mean (n = 6)					3.17	2.24	1.42	1.40	
Pacific	NSMT-Mo92603	WA05-FG250G	Off Soma	255–253	2.93	1.97	1.49	1.29	
	NSMT-Mo92603	WA05-FG250G	Off Soma	255–253	2.96	1.95	1.52	1.30	3A–C
	NSMT-Mo 93629	WA06-H480	Off Hitachi	481–480	3.38	2.42	1.40	1.60	
	NSMT-Mo 93629	WA06-H480	Off Hitachi	481–480	3.37	2.39	1.41	1.56	3D
	NSMT-Mo 93630	WA06-H1500	Off Hitachi	1470–1450	3.79	2.55	1.49	1.65	3E–F
	NSMT-Mo 102104*	KH-01-2 TD-2	Off Sanriku	1002–1069	2.97	1.97	1.51	1.42	6A
	NSMT-Mo 102104*	KH-01-2 TD-2	Off Sanriku		3.26	2.42	1.35	1.54	6B
Mean (n = 7)					3.24	2.24	1.45	1.48	
Other areas	ZISP 42759		Off Kunashiri I.	148	3.37	2.41	1.40	1.54	3G
	ZISP 33507/1**		S off Sakhalin	187	3.54	2.34	1.51	1.55	3H–I
	ZISP 42518/1***		W off Kamchatka	140	3.38	2.37	1.43	1.47	3J–K
	ZISP 36703		W off Kamchatka	146	3.57	2.42	1.48	1.58	3L
	ZISP 36615		Peter the Great Bay	100	3.37	2.38	1.42	1.34	2J–K

nate data, 350–400 m; IORAN, non-registered, *Vityaz* st. 6665, N off Noto Peninsula, 37°54.8′N, 136°13.0′E–37°59.8′N, 136°11.2′E, 940 m; ZISP 33623, off SW Sakhalin, N Sea of Japan, 202–222 m, 49°14.8′N, 141°09.7′E, 100 m (3); ZISP 33625, Peter the Great Bay, 42°18.8′N, 131°09.5′E, 247 m (6); ZISP 36609, Peter the Great Bay, 42°15.4′N, 130°44.6′E, 140 m (1); ZISP 36610, Peter the Great Bay, 42°28.0′N, 131°40.5′E, 125 m (6); ZISP 36611, Peter the Great Bay, 42°25.7′N, 132°36.8′E, 157–140 m (1); ZISP 36612, Peter the Great Bay, 42°33.0′N, 132°51.0′E, 133 m (2); ZISP 36613, Peter the Great Bay, 42°35.3′N, 132°51.1′E, 110 m (4); ZISP 36614, Peter the Great Bay, 42°35.7′N, 133°06.2′E, 143 m (1); ZISP 36615, Peter the Great Bay, 42°38′N, 132°43.2′E, 100 m (2).

Additional material examined (other areas). Pacific coast of NE Japan: NSMT-Mo 92602, WA05–DE250D, 249 m (2+1e); NSNT-Mo 93603, WA05–FG250D, 253–255 m (14+12e: Fig. 3A–C); NSMT-Mo 93628, WA06-DE280D, 284–285 m (5+3e); NSMT-Mo 93629, WA06-H480, 480–481 m (16+1d+7e: Figs. 3D, 4E–F); NSMT-Mo 93630, WA06-H1500D, 1450–1470 m (2+1e: Fig. 3E–F); NSMT-Mo 93631, WA07-D310, 303–307 m (1); NSMT-Mo 95303, TS96-K2, 1451–1455 m (2); NSMT-Mo 102106, KH-69-2-3, 615–620 m (2+4e); NSMT-Mo 102105, KH-69-2-13, 620–640 m (14+12e); NSMT-Mo 102104, KH-01-2 TD-2, 1002–1069 m (37 and 2 radula preparations on SEM stub: Fig. 6A–B, radulae); NSNT-Mo 102103, KT-07-29 M-1, 1039–1041 m (3); NSMT-Mo 102102, SO07-C7-B, 815–818 m (>50+4e and 2 specimens on SEM stub: protoconchs examined by SEM); IORAN, non-registered, R/V *Vityaz* st. 6669, off Sanriku, 39°58.8′N, 142°19.7′E, 425 m (1); ZISP 42759, off Shikotan Island, 43°41.4′N, 147°02.8′E, 148 m (5); ZISP 42760, off Shikotan Island, 43°53.0′N, 146°53.5′E, 50 m (1). Sagami Bay: R02 [725 m] (2e). Okhotsk Sea: SO07-C5-B, 176–177 m (3); ZISP 36703, off Kamchatka Peninsula, 53°20′N, 154°52.5′E, 146 m (19: Fig. 3L); ZISP 33627, off SE Sakhalin, 45°58.4′N,

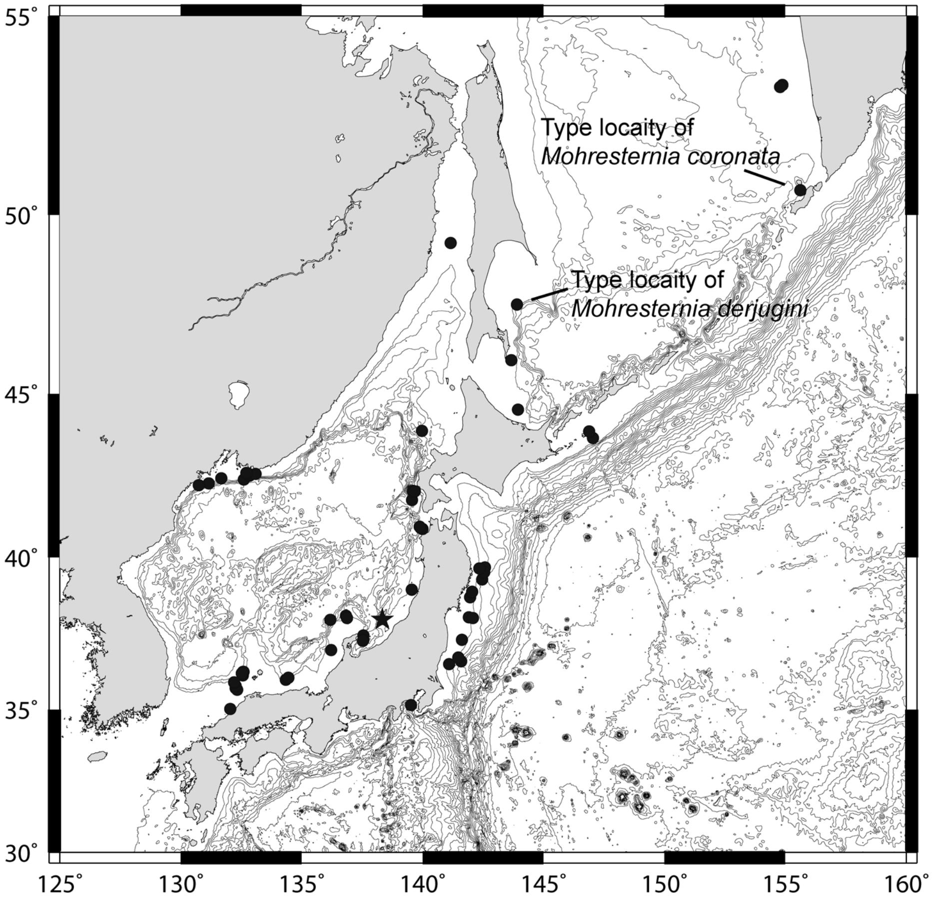


Fig. 7. Geographical distribution of *Frigidoalvania asura*, based on the material examined. Asterisk: type locality (Pliocene fossil).

143°40.3′E, 142 m (1); ZISP 33511, R/V *Toporok*, st. 58, off SE Sakhalin, 47°13.8′N, 143°37.5′E, 52–187 m; ZISP 42758, off SE Sakhalin, 47°33.0′N, 143°54.2′E, 144 m (14) ; ZISP 36703, off Kamchatka Peninsula, 53°20′N, 154°52.5′E, 146 m (19) [probably the same lot as ZISP 30763].

Distribution. Widely distributed in the northwestern Pacific, from the eastern part of the Okhotsk Sea, west off Kamchatka Peninsula, to the western part of the Sea of Japan, and to Sagami Bay along the Pacific coast (Figs. 7, 9), within the depth range of 182–885 m in the Sea of Japan with the mode around 700 m, and 177–1460 m in the Pacific (Fig. 8).

Diagnosis (based mainly on specimens from Sea of Japan). Shell (Figs. 2–3, 4A–F, 5) small, 3.17 mm SL (mean of 6 specimens from Sea of Japan; Table 4), thick and solid for size, conical in shape, with firmly attached thick and brownish periostracum. Protoconch dome-shaped, consisting of 1.0 whorl, smooth and glossy, sometimes with slightly winding irregular spiral cords that fluctuate in thickness (Fig. 5C–D). End of protoconch only slightly thickened, and not very clearly demarcated. Teleoconch of *ca.* 3.0 convex whorls, with weakly to rather strongly angulate shoulder and constricted suture. Surface smooth and glossy, sometimes with faint irregular spiral striae, and regularly spaced thick axial ribs that gradually attenuate on last whorl toward outer lip. Aperture oval to almost evenly rounded, weakly angled at both anterior and posterior ends. Inner lip moderate in thickness, attached to parietal wall at upper portion;

outer lip orthocline, with prominent apertural varix behind lip. Umbilical chink narrow to moderate. Operculum (Fig. 49A) thin, chitinous, paucispiral, oval to leaf-shaped, with convex outer ridge. Head-foot unpigmented, lacking pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe or projections. Radula (Figs. 6A–D) taenioglossate; small for size of shell (114 μm in width for 2.5 mm SW). Central teeth of cusp formula 6–8+1+6–8, with narrowly elongate median cusp and triangular cutting edge; usually one but sometimes two pair(s) of well-developed basal denticles; U-shaped basal extension rather indistinct and irregular in shape. Lateral teeth of cusp formula >15+1+9–11, with triangular primary cusp; inner cusps very fine and numerous, outer cusps apparently larger and less crowed than inner cusps. Inner marginal teeth sickle-shaped, rather broad; distal end rapidly sharpening and curved, with small and sharp cusps on outer edge. Outer marginal teeth distinctly more elongate in shape than inner marginal teeth, lacking cusps on both inner and outer edges.

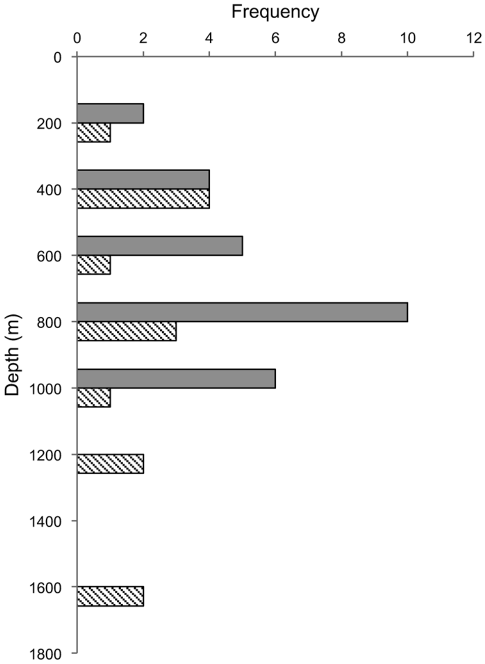


Fig. 8. Vertical distribution of *Frigidoalvania asura* in the Sea of Japan (grey bars) and off the Pacific coast of Honshu (crosshatched bars). Number of sampling stations within 100 m of depth.

Variations. Sea of Japan: this species is highly variable in the Sea of Japan, in mature size, general shape and sculpture. In the southwestern area (off Oki Islands and in Toyama Bay), axial ribs are often very weak or absent, but rather thick and widely spaced if present. The umbilicus is rather widely perforate. In the northeastern area (off Hokkaido), axial ribs become more prominent and slightly more crowded, often with more apparent spiral striae on the spire whorls. The

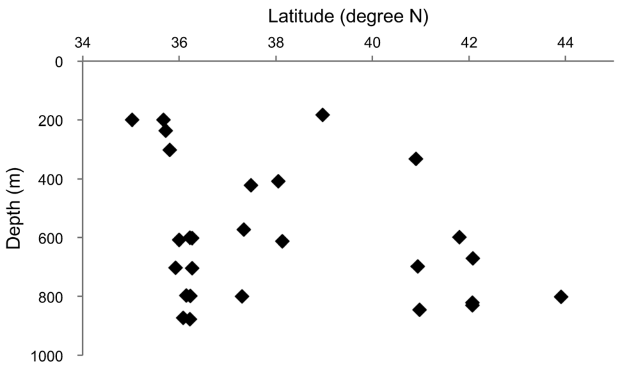


Fig. 9. Relationship between the depth and latitude in the distribution of *Frigidoalvania asura* in the Sea of Japan (excluding Russian territorial waters).

umbilicus is usually very narrow. In the northern area (Peter the Great Bay), the shell is also variable in shape and sculpture, and the axial ribs sometimes develop significantly (Fig. 2J–K). Pacific coast of northern Japan: the shell is rather uniform in shape, and completely lacks axial sculpture. There is a tendency for specimens from shallower depths to have a smaller and more elongate shell with an indistinct angulation at the shoulder (Fig. 3A–C), and those from deeper waters to have a larger shell with stronger angulation (Fig. 3E). The umbilical chink is usually narrow. This phenotype has been reported as *Frigidoalvania* sp. by Hasegawa (2006, 2009). There are slight differences in radular characters between populations in the Sea of Japan and the Pacific. Cusps on the central and lateral teeth are more sharply pointed in the latter, although they were compared only in a limited number of specimens. Okhotsk Sea (based mainly on the specimens preserved in ZISP): in the western area (off the east coast of Sakhalin), most specimens are more conical in shape, and lack shoulder angulation. Axial ribs on the last whorl are always absent, but thick and widely spaced axial ribs are sometime present on the upper whorls, including the penultimate whorl. *Mohrensternia derjugini* corresponds to this phenotype. In the eastern area (off the southern tip of the Kamchatka Peninsula), the shell is rather uniform in shape and characterized by a rather deeply constricted suture, strong angulation at the shoulder and thick axial ribs, which are usually present even on the last whorl, and that form nodes at the shoulder. *Mohrensternia coronata* corresponds to this phenotype. Pliocene Japan: the shell is larger than specimens in any Recent populations, with strong axial ribs that persist on the last whorl, and angulation at the shoulder.

Remarks. This species is rather distinctly characterized by a thick and smooth shell covered by a thick and glossy brownish periostracum, with large and smooth protoconch, and considerably thickened aperture. It was originally described based on Pliocene fossils from Sado Island in the Sea of Japan, and its Recent representatives have repeatedly been recorded in the southern part of the Sea of Japan at bathyal depths (Ito, 1967, 1985; Ito *et al.*, 1986). In the present study, it became clear that even in the same population *F. asura* exhibits a wide range of variation in conchological characters such as size, shape and sculpture. Sometimes specimens superficially look very different from the typical form, but they are connected by intermediate forms. Several nominal taxa in adjacent waters are thus regarded as phenotypes or geographical variations of this morphospecies, as shown in the synonymy. Furthermore, specimens from northern localities, *e.g.*, the Okhotsk Sea and northwestern Bering Sea, show a resemblance to their probable North Atlantic counterpart *F. janmayeni*, and they have sometimes been confused with the latter (*e.g.*, Golikov *et al.*, 2001b) as mentioned in the remarks for the genus. However, the distribution of *F. janmayeni* seems to be restricted to the arctic seas east to East Siberian Sea, and no specimens that are positively identifiable to *F. janmayeni* could be found in the ZISP collection from the Okhotsk Sea by the present author.

Regarding the vertical distribution of *F. asura*, it is similar in the Sea of Japan (182–854 m) and off the Pacific coast of northern Honshu (249–1470 m), based on the material examined in the present study. The upper limits in both areas are slightly deeper than the shallowest part of the Tsugaru Strait (140 m at the deepest). It is noticeable that the upper limits of the vertical distribution of this species are much shallower in northern parts of the Sea of Japan (near Peter the Great Bay and off Primorsky Krai: 100 m) and Okhotsk Sea (50 m), based on the material preserved in ZISP. These limits are comparable to the depth of the Soya Strait (*ca.* 70 m at deepest), which separates both areas. The relationships between the vertical distributions of the species in adjacent areas and depths of the partitions (straits) may reflect discontinuous gene flow between the areas due to the fluctuation of sea level after the Last Glacial Maximum (see discussion), resulting in partial genetic isolation and thus the emergence of geographic forms.

Frigidoalvania tanseimaruae **n. sp.**
[New Japanese name: Kizami-ashura-tsubo]
(Figs. 4G–K, 6E–F, 10–13, 49B; Table 5)

Type material. Holotype, NSMT-Mo 102215, SO07-C4-B2, 843–760 m (type locality) (Figs. 4G–I, 10A–D, 11A–C). Paratypes, NSMT-Mo 102182, from the type locality (11+2e and 4 specimens mounted on SEM stub: Fig. 11D–E, protoconchs; Figs. 6E–F, radulae; Fig. 49B, operculum); NSMT-Mo 102187, TS09-OW08, 897–908 m (1d: Fig. 4J–K).

Type locality. Off Iwanai, southwestern Hokkaido, 43°53.7′N, 139°59.4′E–43°54.2′N, 140°02.0′E, 843–760 m.

Additional material examined (Sea of Japan). NSMT-Mo 102181, KT-11-9 N4, 603–622 m (1+2e: Fig. 10E); NSMT-Mo 102180, KT-11-9 T5, 790–808 m (1); NSMT-Mo 102183, SO07-C2-B, 1341–1360 m (8: Fig. 10 L–M); NSMT-Mo 102188, SO08-D3-2, 369 m (1e); NSMT-Mo 102192, TS09-OW09, 997–1001 m (1e); NSMT-Mo 95827, TS09-OW28, 598–601 m, (1: Fig. 10F–G); NSMT-Mo 102191, TS09-OW30, 796 m (1e); NSMT-Mo 102186, TS09-OW31, 888–900 m (1+1e: Fig. 10J–K); NSMT-Mo 102189, TS09-OW33, 1082–1090 m (2e); NSMT-Mo 102190, TS09-OW34, 1190–1200 m (2e); NSMT-Mo 95845, TS09-OW41, 870–885 m (3); NSMT-Mo 102193, TS09-OW43, 1090–1097 m (1e); NSMT-Mo 102184, TS12-D02, 1027–1028 m (6); NSMT-Mo 102185, TS12-HY06, 699–701 m (3); IORAN, non-registered, R/V *Vityaz* st. 6649, Peter the Great Bay, 42°37.4′N, 134°19.2′E–42°37.8′N, 134°18.5′E, 1186–1130 m (3); IORAN, non-registered, R/V *Vityaz* st. 6665, N off Noto Peninsula, 37°54.8′N, 136°13.0′E–37°59.8′N, 136°11.2′E, 940 m (1).

Distribution. From off southwestern Hokkaido to off Oki Islands, and Peter the Great Bay, in a depth range of 369–1360 m with the clear mode around 1000 m (Figs. 12–13). Probably endemic to the Sea of Japan.

Diagnosis (based mainly on holotype). Shell (Figs. 4G–K, 10–11) small, 2.53 mm SL (mean of 13 specimens; Table 5), moderately thick and solid for size, conical in shape, with thick, glossy, light brown periostracum. Protoconch dome-shaped, consisting of 1.0–1.1 whorls, with rather distinct, irregularly winding spiral ribs that fluctuate in thickness. End of protoconch slightly thickened, and rather clearly demarcated from teleoconch. Teleoconch of *ca.* 2.7 distinctly convex whorls, with deeply constricted suture. Surface glossy, always with characteristic axial and spiral sculpture. Axial sculpture consisting of inconspicuous microscopic growth lines and straight, thick axial ribs that appear at initial part of teleoconch and usually persist to last whorl, becoming weaker abapically and disappearing below periphery on last whorl. Spiral sculpture variable, consisting of indistinct spiral striae and strong spiral ribs; spiral ribs becoming most distinct around periphery on last whorl, usually forming 2–3 distinct spiral cords with groove-like interspaces just below periphery; axial ribs sometimes present (including holotype) but often becoming weaker or completely absent on adapical part of last whorl and spire whorls. Aperture oval to almost round, very weakly angled at posterior end. Inner lip moderate in thickness, attached to parietal wall in upper portion; outer lip orthocline to slightly prosocline, with prominent apertural varix behind lip. Umbilical chink usually narrow but sometimes moderately broader. Operculum (Fig. 49B) thin, chitinous, paucispiral, oval, with moderately convex inner and outer ridges. Head-foot unpigmented, lacking pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe or projections. Radula (Figs. 6E–F) rather small for size of shell

Fig. 10. Shells of *Frigidoalvania tanseimaruae* n. sp. A–D, holotype, NSMT-Mo 102215, off Iwanai, 843–760 m; E, NSMT-Mo 102181, off Noto Peninsula, 603–622 m; F–G, NSMT-Mo 95827, off Oki Islands, 598–601 m; H–I, paratype, NSMT-Mo 102187, off Oki Islands, 897–908 m; J–K, NSMT-Mo 102186, off Oki Islands, 888–900 m; L–M, NSMT-Mo 102183, Yamato Bank, 1341–1360 m. All at the same scale (scale bar = 1 mm), except D (scale bar = 200 μm).

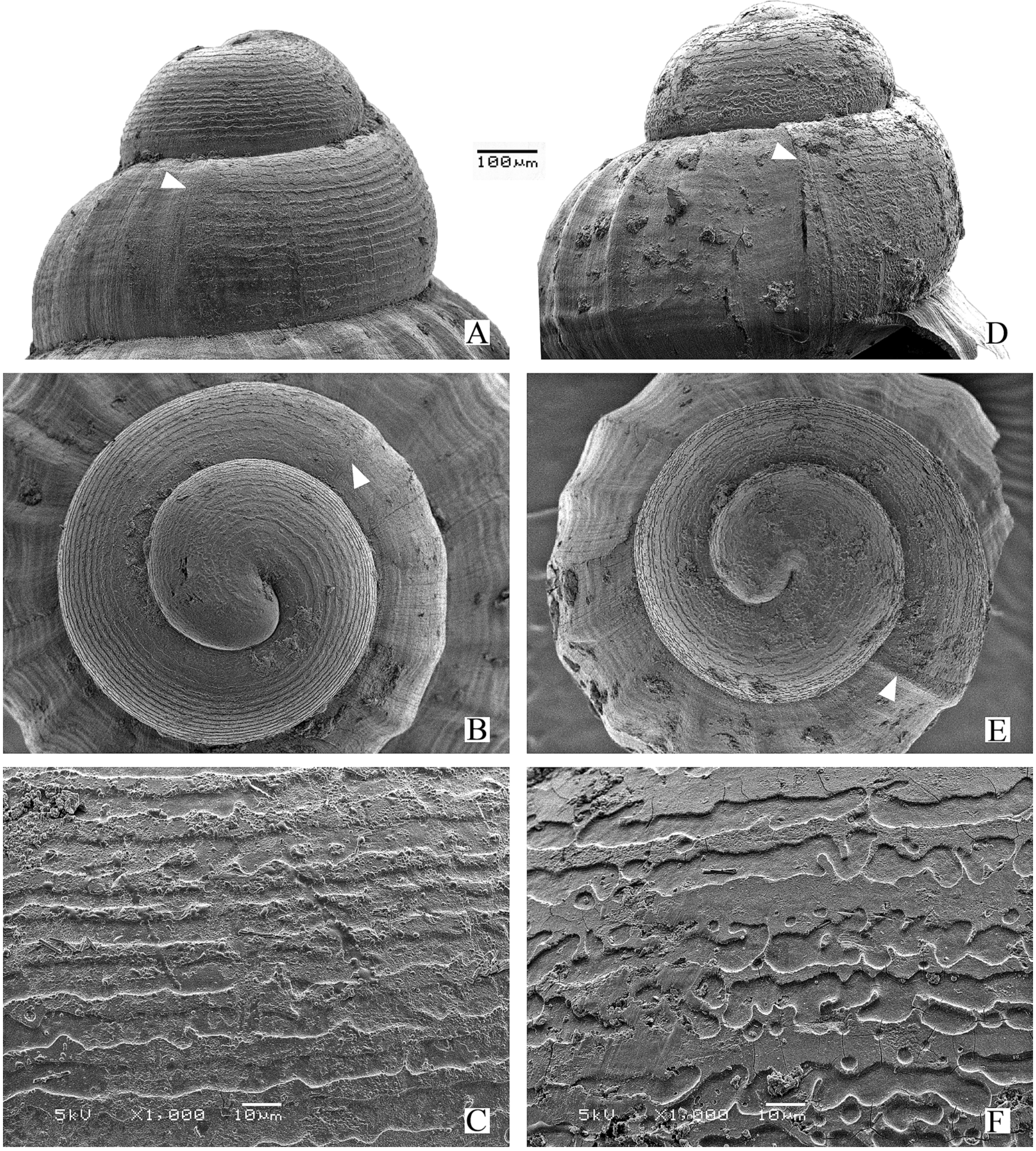


Fig. 11. SEM of protoconchs of *Frigidoalvania tanseimaruae* n. sp. A–C, holotype, NSMT-Mo 102215, off Iwanai, 843–760 m; D–F, paratype from the type locality, NSMT-Mo 102182 (C, F, enlarged lateral views of the first protoconch whorl of A, D, respectively). A–B and D–E, at the same scale; C and D at the same scale. Arrowheads indicate demarcation between protoconch and teleoconch.

(103 μm in width for 1.9 mm SW). Central teeth of cusp formula 5–6+1+5–6, with narrowly elongate median cusp and triangular cutting edge; one pair of well-developed basal denticles present; U-shaped basal extension indistinct and irregular. Lateral teeth of cusp formula >15+1+6–7, with triangular primary cusp; inner cusps very fine and numerous, outer cusps apparently larger and less crowded. Inner marginal teeth sickle-shaped; distal end rapidly sharpening and curved, with small and sharp cusps on outer edge. Outer marginal teeth distinctly more elongate, lacking cusps on both inner and outer edges.

Table 5. Measurements of *Frigidoalvania tanseimaruae* n. sp. *: shell dissolved for radula preparation.

Type status	Register no.	Station	Locality	Depth (m)	SL	SW	SL/ SW	AL	Figures
Holotype	NSMT-Mo 102215	SO07-C4-B2	Off Iwanai	843–800	2.49	1.74	1.43	1.11	
Paratype	NSMT-Mo 102182	SO07-C4-B2	Off Iwanai	843–800	2.39	1.73	1.38	1.08	
Paratype	NSMT-Mo 102187	TS09-OW08	Off Oki Is.	897–908	2.60	1.76	1.48	1.08	10H–I
	NSMT-Mo 102180	KT-11-9 T5	Toyama Bay	794–790	2.81	1.92	1.46	1.17	
	NSMT-Mo 102181	KT-11-9 N4	Off Noto Peninsula	617–604	2.26	1.59	1.42	0.96	10E
	NSMT-Mo 95827	TS09-OW28	Off Oki Is.	601–598	2.65	1.74	1.52	1.09	10F–G
	NSMT-Mo 102186	TS09-OW31	Off Oki Is.	888–900	2.91	2.06	1.41	1.29	10J–K
	NSMT-Mo 102190	TS09-OW34	Off Oki Is.	1200–1190	2.31	1.59	1.45	1.00	
	NSMT-Mo 102183	SO07-C2-B	Yamato Bank	1341–1360	2.39	1.78	1.34	1.14	10L–M
	NSMT-Mo 102183	SO07-C2-B	Yamato Bank	1341–1360	2.25	1.60	1.41	1.09	
	NSMT-Mo 102183	SO07-C2-B	Yamato Bank	1341–1360	2.68	1.88	1.43	1.21	
	NSMT-Mo 102182*	SO07-C4-B2	Off Iwanai	843–800	2.73	1.88	1.45	1.25	6E
	NSMT-Mo 102182*	SO07-C4-B2	Off Iwanai	843–800	2.43	1.63	1.49	1.07	6F
Mean (n = 13)					2.53	1.76	1.44	1.12	

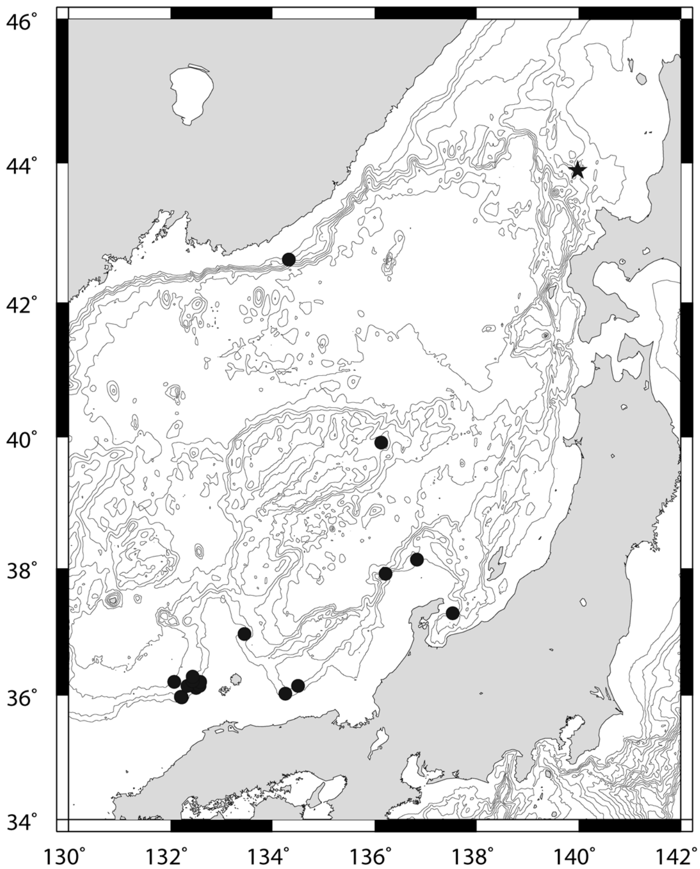


Fig. 12. Distribution of *Frigidoalvania tanseimaruae* n. sp. Asterisk: type locality.

Variations. Protoconch microsculpture usually consists of rather regularly spaced fluctuating spiral ribs (Fig. 11A–C), but the ribs sometimes become more irregular, and interconnect to adjacent ribs (Fig. 11D–F). Teleoconch whorls are usually well inflated, with deep to extremely deep sutures. Sculpture of the teleoconch is variable; strong axial ribs are always present on spire whorls, and they usually continue to the last whorl, but the thickness of the ribs varies from very thin (Fig. 10 L–M) to extremely thick (Fig. 10H–I). Strength of spiral cords is also variable, from rather strong (Fig. 10A–C) to weak (Fig. 10F–G), but the spiral cords are always apparent around the periphery below the suture.

Etymology. Named after the R/V *Tansei-maru II*, which was retired from official service in January 2013, as recognition of her significant contribution to marine science for more than 30 years.

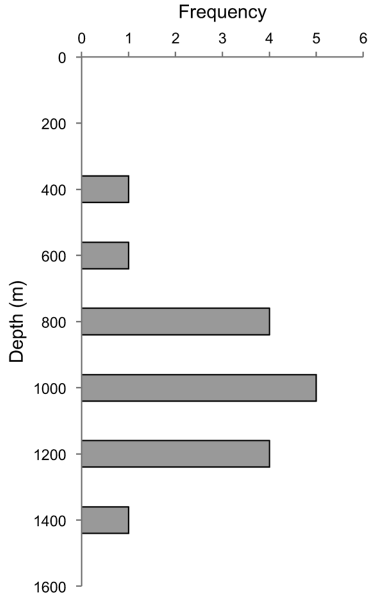


Fig. 13. Vertical distribution of *Frigidoalvania tanseimaruae* n. sp. Number of sampling stations within 100 m of depth.

Remarks. This new species differs considerably from most others in the genus, including the type species, in having a smaller and more lightly built shell with a relatively thin and yellowish periostracum and coarser sculpture. Nevertheless it can be assigned to this genus by the significant similarities in protoconch microsculpture and radula morphology to *F. asura*. A glossy periostracum may also be a synapomorphic character of the genus (Bouchet and Warén, 1993). Furthermore, this new species closely resembles *F. thalassae* Bouchet and Warén, 1993, which was described from the Bay of Biscay, northeastern Atlantic, at a depth of 885 m. *F. thalassae* shows similar variations in conchological characters to the present species; the holotype (Bouchet and Warén, 1993: figs. 1522–1523) possesses well inflated whorls with weaker spiral cords, like the specimen shown in Figs. 4J–K and 10H–I in the present species, and a specimen of *F. thalassae* from MONACO Exp st 66 (Bouchet and Warén, 1993: fig. 1524) resembles the holotype of the present species. However, *F. thalassae* differs from the present new species in possessing spiral grooves, not spiral cords, and in having a different microsculpture on the protoconch.

This new species superficially resembles several species of the genus *Punctulum*, especially *P. flavum*, in the general appearance of the teleoconch, but it is easily distinguished from the latter by its more elongate shell and somewhat glossy periostracum, and the distinctive microsculpture of the protoconch. The adapical margin of the outer lip is weakly but always expanded, and this is also an important character to distinguish this species.

Frigidoalvania sitta (Yokoyama, 1926)
[Japanese name: Makisuji-ashura-tsubo]
(Fig. 14)

Rissoa (*Alvania*) *sitta* Yokoyama, 1926: 274, pl. 33, fig. 13 [type locality: Sawane Formation, Sado Island, Pliocene].
Alvania (*Taramella*) *sitta* — Hatai and Nisiyama, 1952: 242.
Alvania (Nishiyama) sitta — Makiyama, 1958: pl. 45, fig. 13 [reproduction of the original plate].
Alvania sitta — Ito *et al.*, 1986: 9, pl. 4, fig. 5 [off Noto Penisula, Ishikawa Pref.; 200–204 m] (Fig. 14K).
Frigidoalvania sitta — Hasegawa, 2000: 149, pl. 74, fig. Rissoidae-9 [syntype of *Rissoa* (*Alvania*) *sitta*].
Alvania ferruginea — Golikov *et al.*, 2001b: 158; Kantor and Sysoev, 2006: 67, pl. 33, fig. B (*non Alvania ferruginea* A.

Fig. 14. Shells of *Frigidoalvania sitta*. A–B, figured syntype of *Rissoa* (*Alvania*) *sitta*, UMUT CM 23133, Pliocene fossil, Sawane Formation, Sado Island; C–D, RFM no. 346, off Kasumi, 175 m; E–F, ZISP 42529, Peter the Great Bay, 120 m; G, ZISP 36760, off Cape Povorotniy, 67 m; H–I, ZISP 28639, Peter the Great Bay, 74 m; J, ZISP 33510, off SE Sakhalin, 144 m; K, "*Alvania* cf. *sitta*" *fide* Ito *et al.* (1986: 9, pl. 4, fig. 5), reproduced with permission. All at the same scale (scale bar = 1 mm).

Adams, 1861).

Type material. *Rissoa* (*Alvania*) *sitta* Yokoyama, 1926, 3 syntypes, UMUT CM 23132 (5 syntypes; labeled as "figured syntype", but none of them agree with the original figure); 1 syntype, UMUT CM 23133 (1 syntype; agree well with the original figure) (Fig. 14A–B).

Material examined. No specimens that were identifiable as this taxon were found in the material obtained during the present project.

Additional material examined. The Sea of Japan: RFM no. 346, off Kasumi, Hyogo Pref., Sea of Japan, 175 m; ZISP 28639, Peter the Great Bay, 42°37.2′N, 131°38.7′E, 74 m (22: Fig. 14H–I); ZISP 28635, Peter the Great Bay, 42°38.3′N, 132°51.1′E, 88 m (2); ZISPN 42529, off Tjuleniy Island, Peter the Great Bay, 120 m (7: Fig. 14E–F); ZISP 36760, WNW off Cape Povorotniy, 67 m (5: Fig. 14G); ZISP 36766, R/V *Tamango*, st 54/1, Peter the Great Bay, 42°28.8′N, 131°36.6′E, *ca.* 120 m (1); ZISP 36769, R/V *Tamango*, st 81, Peter the Great Bay, 42°38.5′N, 132°19.5′E, 90 m (13); ZISP, 3 additional lots with coordinate data from Peter the Great Bay. Okhotsk Sea: ZISP 33510, R/V *Toporok*, st. 67, off SE Sakhalin, 47°33,0′N, 143°54.2′E, 144 m (5: Fig. 14J); ZISP 36762, SW Sakhalin, 44°54.5′N, 144°24.3′E, 146–150 m (1); ZISP 36764, SW Sakhalin, 45°32.8′N, 142°37.5′E, 95 m (19). [Specimens preserved in ZISP were all identified as "*Alvania ferruginea*", except for ZISP 33510, which was registered as "*Mohrensternia derjugini*"].

Distribution. Off Kasumi, Hyogo Pref., and northwards in the Sea of Japan, Okhotsk Sea, at depths of 8–204 m.

Remarks. *Frigidoalvania sitta* was originally described based on Pliocene fossils from the same deposit in Sado Island as *F. asura* (Fig. 14A–B). A Recent specimen that agrees well with this fossil taxon was reported by Ito *et al.* (1986) from the Sea of Japan at a bathyal depth (200–204 m) with a clear photograph (Fig. 14K). Although the voucher material of this record was not located in the Ito Collection now deposited in the RFM, other specimens that were collected from off Kasumi, Hyogo Pref. at a depth of 175 m and identified as this taxon were found in the collection and are illustrated herein (Figs. 14C, D). These specimens differ from the one illustrated by Ito *et al.* (1986) in their pure white coloration (dark brown in the reported specimen) and more inflated whorls with thicker axial ribs. Both forms are otherwise very similar, however, especially in possessing a thick and glossy periostracum and strong spiral cords that are crossed by thick but rather obscure axial ribs. These characters also agree well with the diagnosis of the genus *Frigidoalvania*. Accordingly, all of these Recent specimens are identified here as this fossil taxon.

Russian authors recorded a similar form from the northern part of the Sea of Japan and Okhotsk Sea as "*Alvania ferruginea* A. Adams, 1861" (Golikov *et al.*, 2001b). Although Golikov *et al.* (2001b) did not provide any illustrations, one of the voucher specimens was subsequently illustrated by Kantor and Sysoev (2006: pl. 33, fig. B). Possible syntypes of *A. ferruginea* are preserved in the NHMUK (reg. no. 1874.5.18.7) and NMV (F31420), and examination of digital images of both specimens revealed that this taxon is conspecific with the one previously known as *Merelina tokyoensis* (Pilsbry, 1904), a sublittoral species that is distributed in temperate Japanese waters, and apparently different from the present deep-water form (Hasegawa, in preparation). Voucher specimens of "*A. ferruginea*" of Russian authors are preserved in the ZISP. Examination of the specimens proved that they actually represent a mixture of several species, and the majority of them from the Sea of Japan and Okhotsk Sea, including the one illustrated by Kantor and Sysoev (2006) (Fig. 14H–I: from Peter the Great Bay at a depth of 74 m), are conspecific with the present taxon.

This species closely resembles *F. asura* in having relatively large and thick shell with a thick and often reddish brown periostracum, and is only distinguished by the presence of remarkably thick spiral cords. Although Hasegawa (2000) noted the possibility that *F. sitta* is a phenotype of *F. asura*, the former is regarded here as a valid taxon, because of the absence of intermediate forms among the material examined. Furthermore, this species is mainly distributed on the continental slope, and only rarely found in upper margin of the bathyal zone, in contrast to *F. asura*, which exclusively inhabits the bathyal zone at least in the Sea of Japan.

Among the members of the genus in other areas, *F. pelagica* (Stimpson, 1851) and *F. cruenta* (Odhner, 1915) should be compared with this species. *F. pelagica* is known to be distributed in the northwestern Atlantic from the Gulf of St. Lawrence to Casco Bay (Warén, 1974), and is strikingly similar to the reddish brown form of *F. sitta*, not only in coloration but also in sculpture. The two species can only be distinguished by small differences in the morphology of the aperture (outer lip is more protruding at the suture in the former species), and by their broad geographical isolation. *F. cruenta* was originally described from Svalbard Island in the Barents Sea, and has been recorded as far east as the Chukchi Sea (Golikov *et al.*, 2001a), although it was subsequently excluded from Chukchi Sea in a more detailed list of this area (Sirenko, 2009). Some smaller specimens of *F. sitta* from Okhotsk Sea (Fig. 14J) closely resemble *F. cruenta* in possessing fewer and stronger spiral cords with very weak axial ribs, but *F. cruenta* is said to lack axial ribs (Warén, 1974). Considering these similarities, more detailed comparison with these Atlantic species will apparently be necessary to determine the precise identity of the present material.

Genus ***Punctulum*** Jeffreys, 1884: 122

Type species. *Rissoa wyvillethomsoni* Friele, 1877, subsequent designation by Ponder (1985: 44).

Remarks. This taxon was originally introduced as a section of *Rissoa* by Jeffreyes (1884) to include three Atlantic species, but it had been overlooked by subsequent authors until Ponder (1985: 44) redefined it, by designating *R. wyvillethomsoni* as the type species. He regarded it as a subgenus of *Alvania* Risso, 1826, based mainly on differences in conchological and anatomical features that separate it from most of the species in *Alvania*. Among the conchological features, Ponder (1985) considered the large and completely smooth protoconch to be an important distinguishing character of this genus, and included *Alvania porcupinae* Gofas and Warén, 1982, which possesses very different teleoconch features from the type species but a similarly smooth protoconch (Gofas and Warén, 1982: figs. 23, 30–31), in the newly defined subgenus. However, Bouchet and Warén (1993: 652) did not recognize any subgenera in the genus *Alvania*, because of the high morphological diversity of the genus (*s.l.*) and the absence of integrated anatomical information, and this view was adopted by most subsequent European authors (*e.g.*, Rolán, 2005; Gofas, 2007). On the other hand, Russian authors regarded *Punctulum* as a full genus with slightly different concept, and included several northwestern Pacific species in the genus, such as *P. reticulatum*, *P. delicatum* and *P. ochotense* (Golikov, 1986; Golikov and Sirenko, 1998). Hasegawa (2009) followed this view, and transferred *Microstelma flava* Okutani, 1964 to *Punctulum*. These species generally show very similar teleoconch features to the type species, such as a rather depressed conical shell with a perforate umbilicus and no varix behind the outer lip. However, these species differ from the type species of the genus in possessing a spirally sculptured protoconch, not a smooth one. These conchological characters are also shared by some additional Japanese species, as treated below. They also commonly have an unpigmented head-foot without pigmented eyes, in contrast to the species tentatively assigned to the genus *Alvania* in the present paper, which have distinct black eyes. It has been proven that the genus *Alvania* as defined by Ponder (1985) comprises various polyphyletic groups, and as the species having a depressed and clearly umbilicate shell in the northeastern Pacific seem to form a clade based on a preliminary molecular phylogenetic analysis (Kano, personal communication), they are only provisionally placed together in the genus *Punctulum*.

Punctulum flavum (Okutani, 1964)
[Japanese name: Watazoko-tsubo]
(Figs. 15–25, 49C; Table 6)

Microstelma flava Okutani, 1964: 389–390, pl. 6, fig. 5; The Committee for Celebrating Dr Okutani's Retirement from Tokyo University of Fisheries, 1996: 73, pl. 2, fig. 12 (holotype) [type locality: R/V *Soyo-maru*, St. 59, 35°05.35′N, 139°18.65′E, Sagami Bay, 550 m].

Punctulum delicatum Golikov and Sirenko, 1998: 101–102, figs. 3C, 15C, J [type locality: Okhotsk Sea coast of Paramushir Island, Kurile Islands, 50°39.2′N, 155°37.4′E, 500 m].

Punctulum ochotense Golikov and Sirenko, 1998: 102, figs. 3E, 15D, K [type locality: Okhotsk Sea coast of Paramushir Island, Kurile Islands, 50°39.2′N, 155°37.4′E, 500 m]; Kantor and Sysoev, 2006: 75, pl. 36, figs. F–G. **New synonym.**

Alvania (*Alvania*) *flava* — Hasegawa, 2000: 149, pl. 74, fig. Rissoidae-6 [Suruga Bay, 870–950 m; illustrated specimen: NSMT-Mo 102129].

Alvania flava – Hasegawa, 2001: 134 [Tosa Bay,742–776 m].

Punctulum flava [*sic*; = *fluvum*] — Hasegawa, 2009: 255–256, fig. 65; Hasegawa and Okutani, 2011: 113, fig. 18 (holotype).

Type material. *Microstelma flava* Okutani, 1964, holotype, UMUT RM 8817 (slightly damaged by Byne's disease; Fig. 15A–C); paratype, NSMT-Mo 69584, from the type locality (1e: Figs. 18D, 19A). *Punctulum delicatum* Golikov and Sirenko, 1998, holotype, ZISP 54202/1 (damaged by crystallization in preservative; Fig. 16P–Q); *Punctulum ochotense* Golikov and Sirenko, 1998, holotype, ZISP 54204/1 (damaged by crystallization in preservative; Fig. 16N–O).

Material examined (Sea of Japan) (lots with an asterisk correspond to the "deep-water form"): NSMT-Mo 102098, KT-10-8 R3, 594–615 m (3+1e: Fig. 16J–K); NSMT-Mo 102099, KT-10-8 Es2, 670–671 m (4); NSMT-Mo KT-10-8 T3, 839–851 m (1e); NSMT-Mo 102160, KT-11-9 E1, 220–247 m (1e); NSMT-Mo 102161, KT-11-9 E2, 388–538 m (1e); NSMT-Mo 102151, KT-11-9 E3, 563–635 m (1); NSMT-Mo 102156, KT-11-9 E4, 787–854 m (1d: Figs. 16A–D, 18G–H); NSMT-Mo 102152, KT-11-9 K4, 603–613 m (5: Fig. 16 L–M); NSMT-Mo 102164*, KT-11-9 K5, 1277–1290 m (1+2e); NSMT-Mo 102165*, KT-11-9 M6, 1421–1465 m (28); NSMT-Mo 102149, KT-11-9 N4, 603–622 m (8); NSMT-Mo 102145, KT-11-9 T3, 383–460 m (1); NSMT-Mo 102150, KT-11-9 T4, 561–583 m (3+1e); NSMT-Mo 102155, KT-11-9 T5, 790–808 m (1+3e); NSMT-Mo 102167*, KT-11-9 T6, 1410–1564 m (6); NSMT-Mo 102100*, SO07-C2-B, 1341–1360 m (11+1d: Figs. 17A–C, D–F, 18I–K); NSMT-Mo 102091*, SO07-C4-B1, 1369–1607 m (5: Figs. 17G, L–M); NSMT-Mo 102090, SO07-C4-B2, 760–843 m (15: Fig. 16G–H); NSMT-Mo 102101*, SO08-C3-B, 1696–1768 m (27+1d+4e: Figs. 17N–P, 18 L–M); NSMT-Mo 102153, SO08-D3-1, 368 m (1); NSMT-Mo 102162, SO08-D3-2, 369 m (1e); NSMT-Mo 102158, TS09-BZ250, 250–251 m (1e); NSMT-Mo 95840, TS09-OW08, 897–

Fig. 15. Shells of *Punctulum flavum* from the Pacific Ocean. A–C, holotype of *Microstelma flava*, UMUT RM 8817, Sagami Bay, 550 m; D–F, NSMT-Mo 102129, Suruga Bay, 870–950 m; G–H, NSMT-Mo 90226, Tosa Bay, 742–776 m; I, NSMT-Mo 102124, Hyuga-nada, 1501–1516 m; J, NSMT-Mo 102125, Kumano-nada, 2072–2075 m; K, M, NSMT-Mo 102132, off Sanriku, 2137–2183 m (2 examples); L, NSMT-Mo 102138, off Sanriku, 1039–1041 m; N–O, NSMT-Mo 102137, off Sanriku, 1002–1069 m. All at the same scale (scale bar = 1 mm).

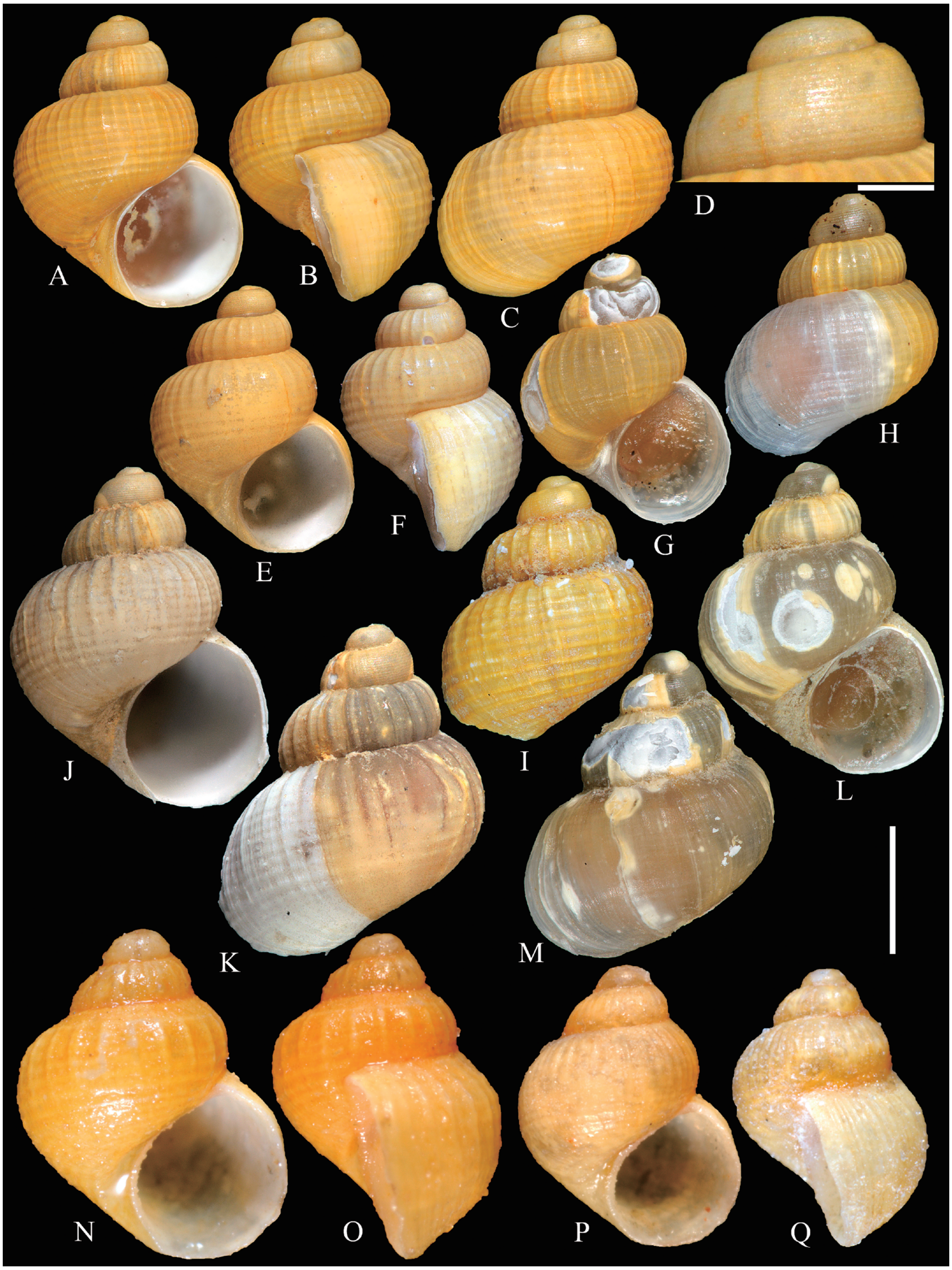


Fig. 16. Shells of *Punctulum flavum* from the Sea of Japan and Okhotsk Sea ("shallow-water form"). A–D, NSMT-Mo 102156, off Esashi, 787–854 m; E–F, NSMT-Mo 102146, off Oki Islands, 301 m; G–H, NSMT-Mo 102090, off Iwanai, 760–843 m; I, NSMT-Mo 102157, off Oki Islands, 235–237 m; J–K, NSMT-Mo 102098, off Rebun Island, 594–615 m; L–M, NSMT-Mo 102152, off Kasumi, 603–613 m; N–O, holotype of *Punctulum ochotense*, ZISP 54204/1, Okhotsk Sea, 500 m; P–Q, holotype of *Punctulum delicatum*, ZISP 54202/1, Okhotsk Sea, 500 m; All at the same scale (scale bar = 1 mm), except for D (scale bar = 200 μm).

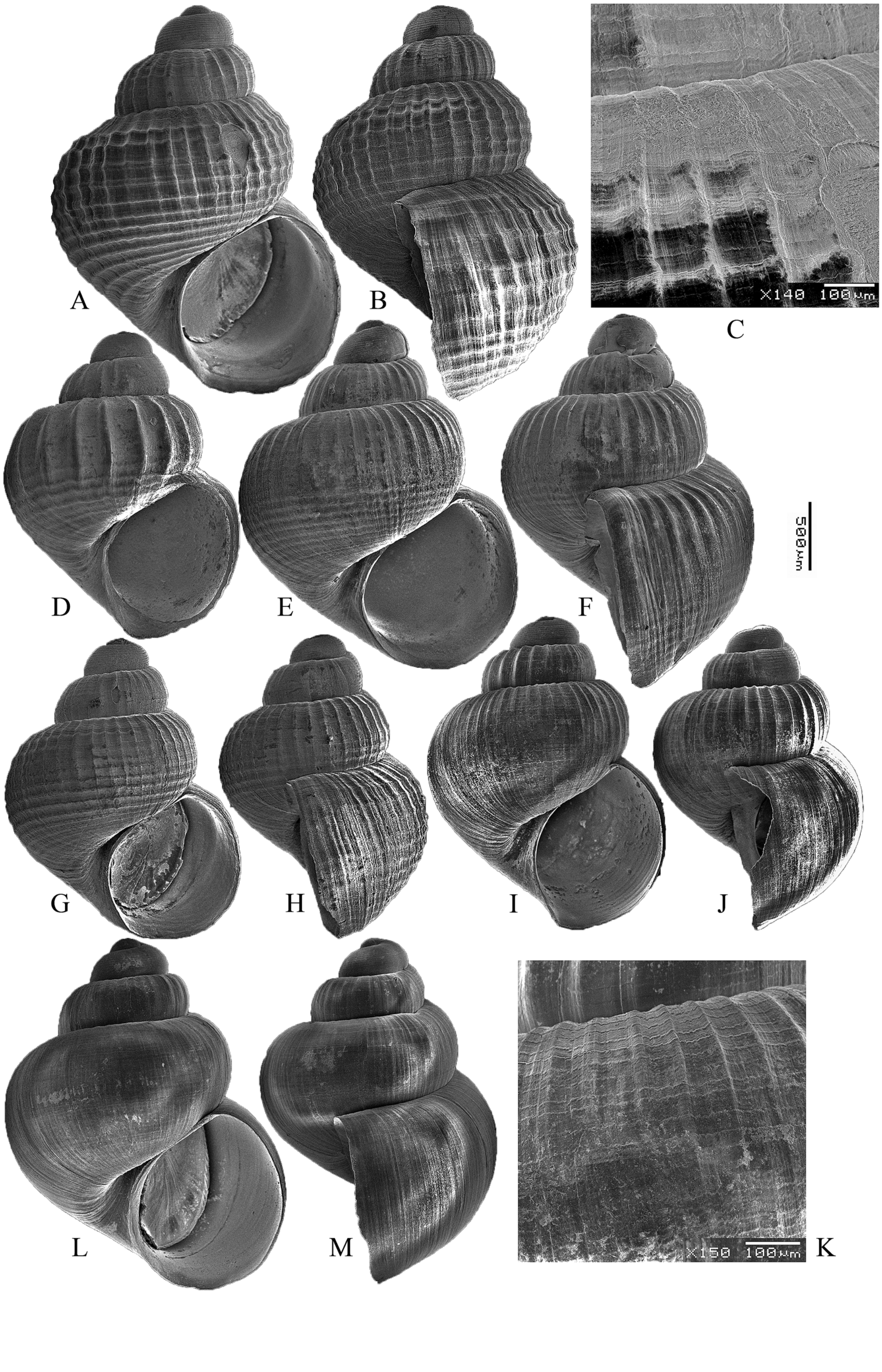
Fig. 17. Shells of *Punctulum flavum* from the Sea of Japan ("deep-water form"). A–C, D–F, NSMT-Mo 102100, Yamato Bank, 1341–1360 m (2 examples); G, L–M, NSMT-Mo 102091, off Iwanai, 1369–1607 m (2 examples); H–I, NSMT-Mo 95837, off Oki Islands, 888–900 m; J–K, NSMT-Mo 95844, off Oki Islands, 1497–1500 m; N–P, NSMT-Mo 102101, Yamato Bank, 1696–1768 m. All at the same scale (scale bar = 1 mm), except C and P (scale bars = 200 μm).

908 m (1); NSMT-Mo 102170*, TS09-OW11, 1204 m (2e); NSMT-Mo 95835, TS09-OW28, 598–601 m (6+2d: Fig. 20A–B, protoconch); NSMT-Mo 95836, TS09-OW29, 697–702 m (2); NSMT-Mo 95837*, TS09-OW31, 888–900 m (3+2e: Fig. 17H–I); NSMT-Mo 95843*, TS09-OW33, 1082–1090 m (3); NSMT-Mo 95844*, TS09-OW37, 1497–1500 m (15 and 3 radula preparations on SEM stub: Fig. 17J–K, shell; Fig. 22E, radula; Fig. 20C–E, protoconch; Fig. 49C, operculum); NSMT-Mo 95838, TS09-OW38, 600–604 m (4 and 2 specimens mounted on SEM stub: Fig. 21C–D, radulae); NSMT-Mo 95839, TS09-OW39, 702–704 m (1+1e); NSMT-Mo 95846*, TS09-OW43, 1090–1097 m (3); NSMT-Mo 95847*, TS09-OW47, 1497–1504 m (9); NSMT-Mo 102157, TS09-ZY18, 235–237 m (1e: Fig. 16I); NSMT-Mo 95834, TS09-ZY33, 445–460 m (1); NSMT-Mo 102092, TS10-AK7, 793–823 m (1); NSMT-Mo 102093*, TS10-AK10, 1102–1104 m (1); NSMT-Mo 102094*, TS10-AK15, 1567–1598 m (1); NSMT-Mo 102095*, TS10-AK24, 1695–1703 m (1); NSMT-Mo 102163*, TS12-D04, 1304 m (1); NSMT-Mo 102166*, TS12-HY10, 1397–1399 m (1); NSMT-Mo 102148, TS12-OW01, 200–201 m (1); NSMT-Mo 102146, TS12-OW02, 301 m (1: Fig. 16E–F); NSMT-Mo 102147, TS12-OW04, 500 m (1); NSMT-Mo 102154, TS12-OW06, 700–704 m (1); NSMT-Mo 102171*, TS12-OW14, 1493–1497 m (1e); NSMT-Mo 102172*, TS12-OW16, 1694–1695 m (1e); NSMT-Mo 102173*, TS12-OW18, 1892–1894 m (1e); NSMT-Mo 102168*, TS13-S13, 1500–1600 m (4); IORAN, non-registered, R/V *Vityaz* st. 6649, Peter the Great Bay, 42°37.4′N, 134°19.2′E–42°37.8′N, 134°18.5′E, 1186–1130 m (3).

Additional material examined. Pacific coast of NE Japan: NSMT-Mo 102141, KH-69-2-3, 615–620 m (6+2e); NSMT-Mo 102142, KH-69-2-13, 620–640 m (18+4e); NSMT-Mo102133, KH-01-2 KC-0, 1134–1219 m (4d); NSMT-Mo 102137, KH-01-2 TD-2, 1002–1069 m (*ca.* 70+1d: Figs. 15N–O, 18A–C); NSMT-Mo 102139, KH-01-2 XR-2-1, 965–981 m (1); NSMT-Mo 102140, KH-01-2 XR-2-2, 973–982 m (4); NSMT-Mo 102131, KT-07-29 H-2, 2032–2055 m (5); NSMT-Mo 102134, KT-07-29 K-1, 1028–1075 m (5); NSMT-Mo 102138, KT-07-29 M-1, 1039–1041 m (*ca.* 40: Fig. 15L); NSMT-Mo 102135, KT-07-29 M-2, 1528–1603 m (10); NSMT-Mo 102136, KT-08-27 S-2, 2022–2027 m (3); NSMT-Mo 102143, SO07-C7, 894–935 m (>100+9e and 2 radula preparations on SEM stub: Fig. 22A–B, radulae; Fig. 19B–D, protoconch); NSMT-Mo 102132, SO07-K1, 2137–2183 m (*ca.* 40+16e: Figs. 15K, M); NSMT-Mo 102144, WA06-H480, 480–481 m (1e). Tosa Bay: NSMT-Mo 102128, KH-02-3 TB-3, 1042–1045 m (1+1e); NSMT-Mo 102123, KT-99-18 BT-3, 1291–1298 m (1); NSMT-Mo 102124, KT-99-18 BT-4, 1501–1516 m (14+4e: Fig. 15I); NSMT-Mo 102125, KT-99-18 BT-6, 2072–2075 m (8+1e: Fig. 15J); NSMT-Mo 102126, KT-99-18 BT-8, 2035–2043 m (1); NSMT-Mo 102127, KT-99-18 BT-9, 1947–2023 m (2+1e); NSMT-Mo 90226, KT-00-8 BT-2, 742–776 m (7+1e: Fig. 15G–H). Suruga Bay: NSMT-Mo 102129, SH-BT93-1, 870–950 m (>100e: Figs. 15D–F, 18E–F); NSMT-Mo 102130, SH-DG93-11, 760–820 m (3e). Okhotsk Sea: IORAN, non-registered, R/V *Vityaz* st. 1735, 51°15.0′N, 150°23.0′E, 1186–1130 m (1e).

Distribution. From off Rebun Island south to western part of the Sea of Japan, western part of Okhotsk Sea, and Pacific coast of Japanese archipelago, from off Hokkaido south to Hyuga-nada, east of Kyushu (Fig. 23), at depths of 200–2027 m in the Sea of Japan and 480–2075 m in the Pacific (Figs. 24, 25).

Diagnosis. Shell (Figs. 15–20) small, 2.30 mm SL (mean of 15 specimens from Sea of Japan; Table 6), moderately thick and solid for size, low conical in shape, with yellowish periostracum. Protoconch dome-shaped, consisting of 1.0–1.2 whorls, with weak and flat spiral cords, 15–18 in number at end of protoconch (Fig. 19–20). Thickness of spiral cords almost equal to interspaces. End of protoconch slightly thickened, rather clearly demarcated from teleoconch.


A
B
×140 100μm
C
500μm
D
E
F
G
H
I
J
L
M
×150 100μm
K

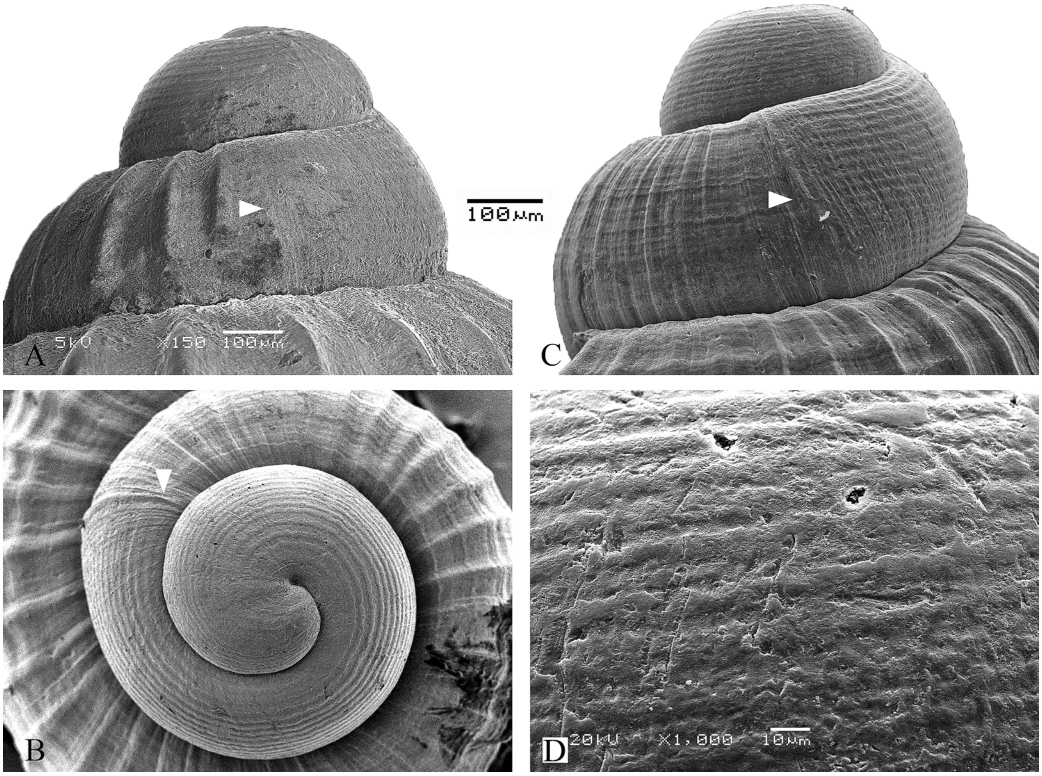


Fig. 19. SEM of protoconch of *Punctulum flavum* from the Pacific Ocean. A, paratype of *Microstelma flava*, NSMT-Mo 69584, from the type locality (Sagami Bay, 550 m); B–D, NSMT-Mo 102143, off Sanriku, 894–935 m (D, enlarged lateral view of the first proconch whorl). A–C at same scale. Arrowheads indicate demarcation between protoconch and teleoconch.

Teleoconch of *ca.* 2.5 convex whorls, with deeply constricted suture. Spire relatively small, occupying *ca.* 30% of shell length. Surface slightly glossy in fresh specimens, but often covered by yellowish rust, with distinct axial and spiral sculpture. Axial sculpture consisting of straight thick ribs that appear at initial part of teleoconch and usually persist to last whorl, and indistinct microscopic growth lines. Thickness of axial ribs highly variable; considerably thick and widely spaced in holotype, but usually finer and more numerous in most localities; number of axial ribs on last whorl 18 in holotype (Fig. 15C), but more than 35 in specimens from Suruga Bay (Fig. 15F). Spiral cords rather weak and narrow, but becoming more distinct toward base in holotype and specimens from temperate Pacific; spiral cords stronger in some northern localities and in the Sea of Japan. Last whorl large in proportion and well inflated. Aperture oval to almost evenly rounded, angulate at posterior end. Inner lip moderate in thickness; outer lip orthocline to slightly prosocline, with very weak apertural varix behind lip in some fully mature specimens. Umbilical chink narrowly to moderately perforate. Operculum (Fig. 49C) thin, chitinous, paucispiral, oval

Fig. 18. SEM of shells of *Punctulum flavum*. A–C, NSMT-Mo 102137, off Sanriku (Pacific), 1002–1069 m (C, enlarged adapical part of the last whorl); D, paratype of *Microstelma flava*, NSMT-Mo 69584, from the type locality (Sagami Bay, Pacific); E–F, NSMT-Mo 102129, Suruga Bay (Pacific), 870–950 m; G–H, NSMT-Mo 102156, off Esashi, 787–854 m; I–K, NSMT-Mo 102100, Yamato Bank, 1341–1360 m (K, enlarged adapical part of the last whorl); L–M, NSMT-Mo 102101, Yamato Bank, 1696–1768 m. All at same scale, except C, K.

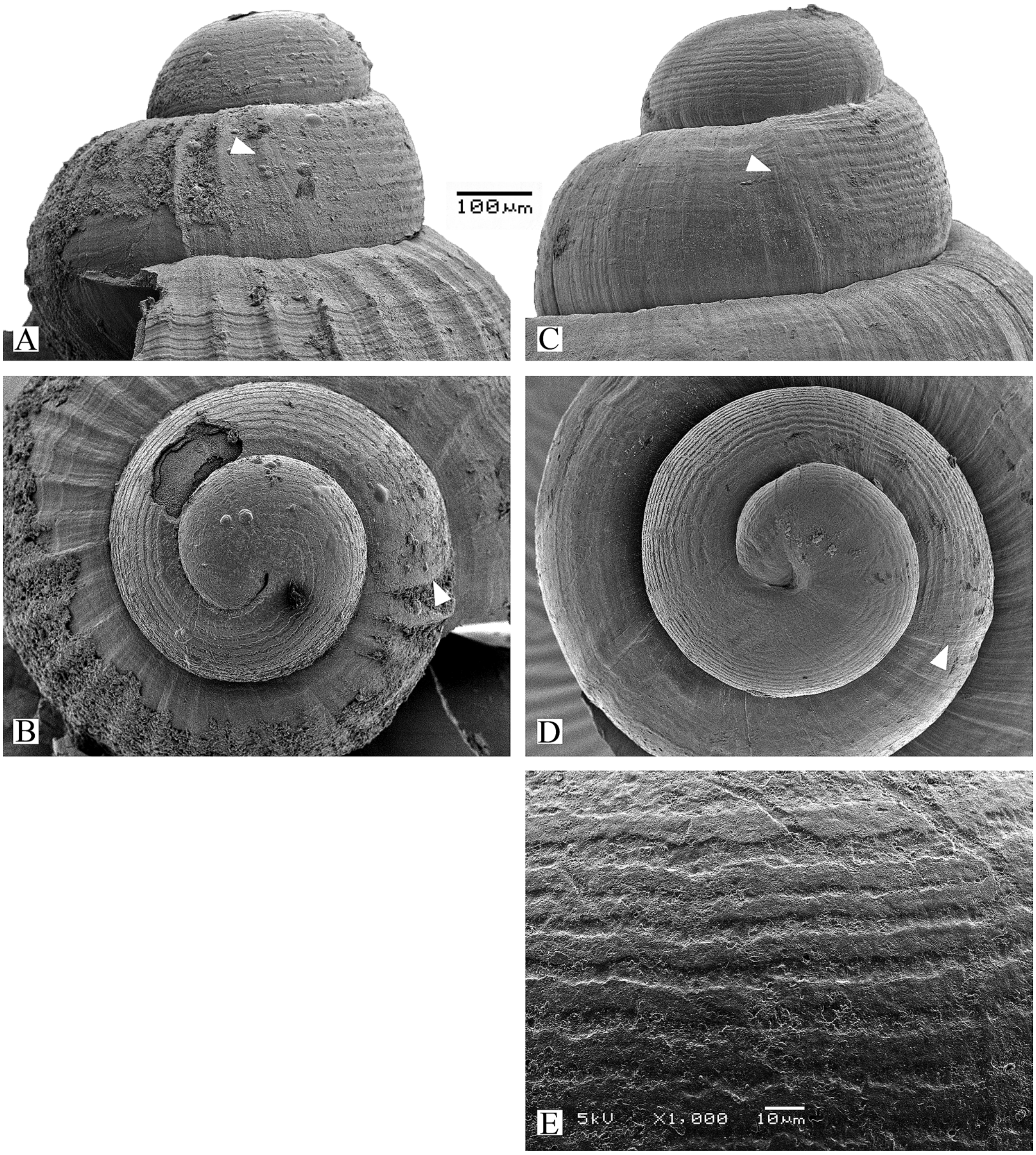


Fig. 20. SEM of protoconch of *Punctulum flavum* from the Sea of Japan. A–B, NSMT-Mo 95835, off Oki Islands, 598–601 m ("shallow-water form"); C–E, NSMT-Mo 95844, off Oki Islands, 1497–1500 m ("deep-water form") (E, enlarged lateral view of the first protoconch whorl). A–D at same scale. Arrowheads indicate demarcation between protoconch and teleoconch.

to leaf-shaped, with convex outer ridge. Head-foot unpigmented, lacking pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe and projections. Radula (Fig. 22) taenioglossate, 124 μm in width for 2.4 mm SW. Central teeth of cusp formula 4–6+1+4–6, with narrowly elongate tongue-like central cusp and triangular cutting edge; one to two pair(s) of well-developed basal denticles; U-shaped basal extension rather indistinct and irregular in shape. Lateral teeth of cusp formula 5–6+1+5–5, with triangular primary cusp; inner and outer cusps nearly same in strength. Inner marginal teeth sickle-shaped, rather broad; distal end rapidly

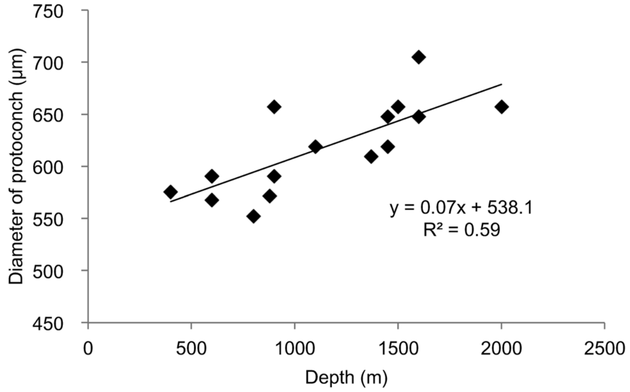


Fig. 21. Relationship between the diameter of protoconch and habitat depth of *Punctulum flavum* in the Sea of Japan.

sharpen and curved, with rather long and large cusps only on outer edge. Outer marginal teeth more slender than inner marginal teeth, tusk-like, with 4 cusps only on inner side.

Variations. There is an extremely wide range of variation among the material examined in the present study, and it is probable that more than one species is involved in this "species", especially in the Pacific coast localities. However, it was very difficult to distinguish those forms clearly from each other, because of the presence of intermediate forms. Furthermore, all the specimens that were identified herein as this species share a nearly identical protoconch morphology, except for the size (see below). Accordingly they are rather provisionally regarded as phenotypes of a single species. Pacific coast of temperate Honshu: specimens from this area are rather uniform in shell characters, especially in general shell shape. Strength of axial ribs is variable as described above, but spiral cords are always thin and weak or indistinct. Specimens from deeper waters tend to possess much weaker sculpture (Fig. 15J: Kumano-nada, 2072–2075 m), and this phenomenon was observed in other areas. Pacific coast of northern Japan: although specimens from shallow waters (*e.g.*, Hasegawa, 2009: fig. 65; off Hitachi, Ibaraki Pref., 481–480 m) generally agree well with the holotype from Sagami Bay, those from deeper stations off the Sanriku coast (at 1000 m and deeper) are highly variable both in shape and sculpture. They are sometimes more elongate in shape and possess stronger spiral cords (Figs. 15M, N–O). These forms often occur sympatrically, and seem to be continuous in morphology within a population. Sea of Japan: specimens collected from the Sea of Japan could roughly be classified into two forms: those from shallower stations (usually less than 1000 m) possess a low conical shell, with strong axial and spiral sculpture and rather thick yellowish brown periostracum ("shallow-water form"; Figs. 16A–M), while others from deeper stations (usually deeper than 1000 m) possess a more inflated shell with weaker sculpture and relatively thin, translucent periostracum ("deep-water form"; Fig. 17). Although some specimens have an almost completely smooth teleoconch (Fig. 17N–P), most of the "deep-water form" have a similar pattern of sculpture on the initial teleoconch whorls to the "shallow-water form" (Fig. 17C). Furthermore, although the "deep-water form" tends to have a larger protoconch than the "shallow water form" (compare Figs. 20A–B and 20C–D), it was found that there is a correlation between the size of protoconch and depth of habitat (Fig. 21), at least in the Sea of Japan. Sculpture on the protoconch is nearly identical in both forms. Accordingly, these different-looking forms are regarded as phenotypes of single species. Okhotsk Sea: specimens referable to this species were only found in the eastern part of Okhotsk

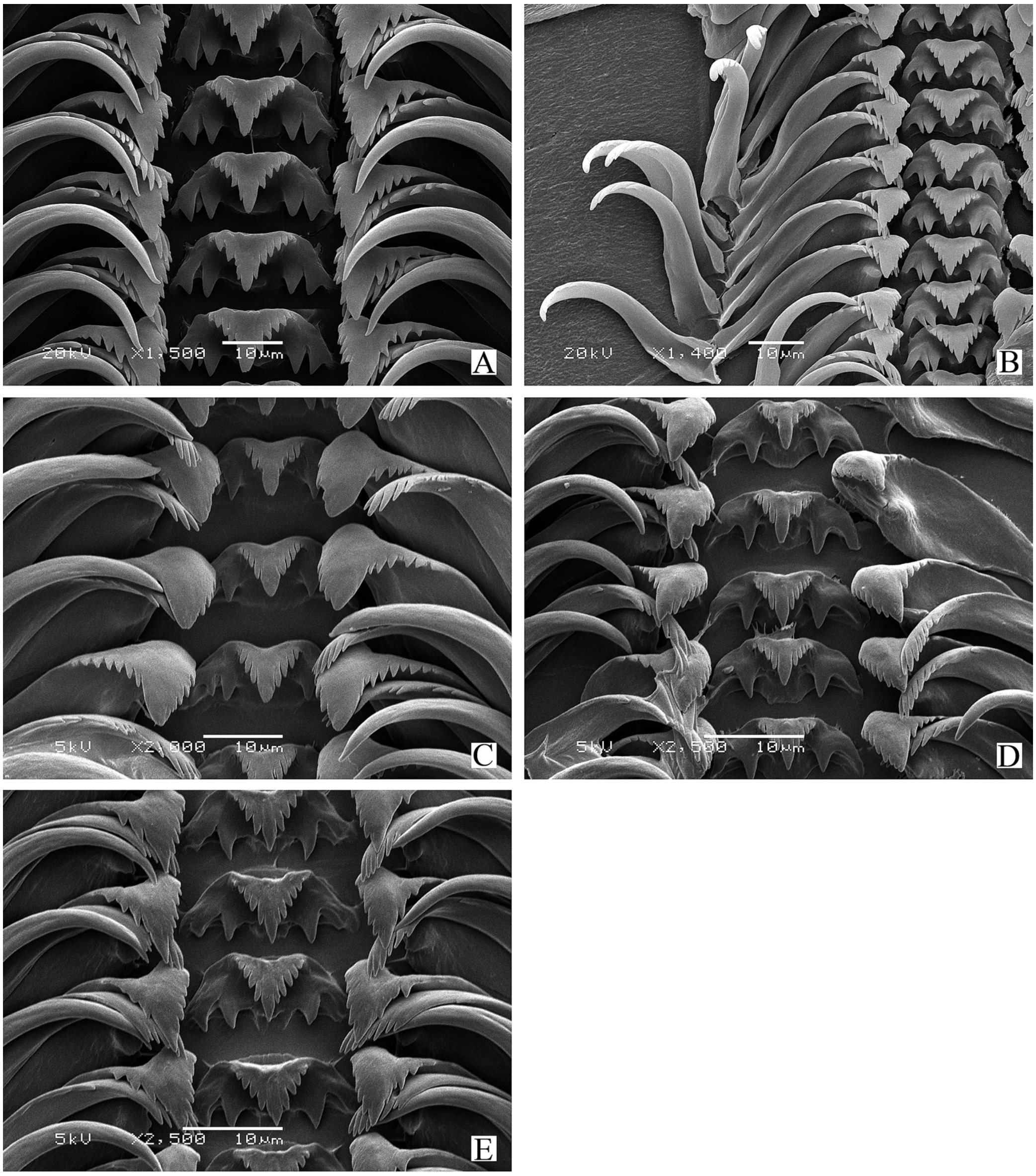


Fig. 22. SEM of radulae of *Punctulum flavum*. A–B, NSMT-Mo 102143, off Sanriku (Pacific), 894–935 m; C–D, NSMT-Mo 95838, off Oki Islands, 600–604 m ("shallow-water form"); E, NSMT-Mo 95844, off Oki Islands, 1497–1500 m ("deep-water form"). Images in the right column (A, C, E), females; those in the left column (B, D), males.

Sea in limited numbers. *P. delicatum* (Fig. 16P–Q) and *P. ochotense*, which were described from exactly the same station near the southern tip of Kamchatka Peninsula, fall within the range of variation of the present species as defined herein, and are regarded as junior synonyms. However, the types (holotype and several paratypes collected together) of both taxa are considerably damaged due to crystallization in the preservative, and not suitable for detailed taxonomic examination. Considering the fact that there is no record of this (or at least any similar) species in the western part of the Okhotsk Sea, additional information may be necessary to confirm the identifi-

Table 6. Measurements of *Punctulum flavum*. *: shell dissolved for radula preparation; **: holotype of *P. ochotense*; ***: holotype of *P. delicatum*.

Category	Register no.	Station	Locality	Depth (m)	SL	SW	SL/SW	AL	Figures
Holotype	UMUT RM 8817		Sagami Bay	550	3.05	2.27	1.34	1.39	15A–C
Pacific	NSMT-Mo 102144	WA06-H480	Off Hitachi	481–480	2.91	2.29	1.27	1.51	
	NSMT-Mo 102129	SH-BT93-1	Suruga Bay	870–950	2.68	2.14	1.25	1.38	15D–F
	NSMT-Mo 90226	KT-00-8 BT-2	Tosa Bay	742–776	2.68	2.06	1.30	1.37	15G–H
	NSMT-Mo 102124	KT-99-18 BT-4	Hyuga-nada	1501–1516	2.59	2.00	1.30	1.35	
	NSMT-Mo 102125	KT-99-18 BT-6	Kumano-nada	2072–2075	2.57	2.05	1.25	1.37	15J
	NSMT-Mo 102142	KH-69-2-13	Off Sanriku	620–640	3.19	2.45	1.30	1.57	
	NSMT-Mo 102142	KH-69-2-13	Off Sanriku	620–640	2.58	2.10	1.23	1.31	
	NSMT-Mo 102137	KH-01-2 TD-2	Off Sanriku	1002–1069	2.96	2.21	1.34	1.50	15N–O
	NSMT-Mo 102138	KT-07-29 M-1	Off Sanriku	1039–1041	2.44	1.94	1.26	1.27	15L
	NSMT-Mo 102132	SO07-K1	Off Sanriku	2137–2183	3.20	2.53	1.26	1.61	
	NSMT-Mo 102132	SO07-K1	Off Sanriku	2137–2183	3.11	2.30	1.35	1.50	
	NSMT-Mo 102132	SO07-K1	Off Sanriku	2137–2183	2.76	2.20	1.25	1.43	15K
	NSMT-Mo 102132	SO07-K1	Off Sanriku	2137–2183	2.65	1.89	1.40	1.26	15M
	NSMT-Mo 102124	KT-99-18 BT-4	Hyuga-nada	1501–1516	2.36	1.83	1.29	1.23	15I
	NSMT-Mo 102144*	SO07-C7	Off Sanriku	894–935	3.08	2.40	1.28	1.49	
	NSMT-Mo 102144*	SO07-C7	Off Sanriku	894–935	2.45	1.89	1.30	1.20	
Mean (*n* = 16)					2.78	2.15	1.29	1.40	
Sea of Japan (shallow-water from)	NSMT-Mo 102090	SO07-C4-B2	Off Iwanai	843–760	2.08	1.62	1.28	1.13	16G–H
	NSMT-Mo 95840	TS09-OW08	Off Oki Is.	897–908	2.88	2.11	1.36	1.37	
	NSMT-Mo 102152	KT-11-9 K4	Off Kasumi	603–613	2.43	1.91	1.27	1.16	16L–M
	NSMT-Mo 102090	SO07-C4-B2	Off Iwanai	843–760	2.15	1.69	1.27	1.11	
	NSMT-Mo 102090	SO07-C4-B2	Off Iwanai	843–760	2.52	2.03	1.24		
	NSMT-Mo 102156	KT-11-9 E4	Off Esashi	787–854	2.24	1.77	1.27	1.14	16A–D
	NSMT-Mo 102090	SO07-C4-B2	Off Iwanai	843–760	2.39	1.76	1.36	1.25	
	NSMT-Mo 102146	TS12-OW02	Off Oki Is.	301–301	2.10	1.59	1.32	1.04	16E–F
	NSMT-Mo 95835	TS09-OW28	Off Oki Is.	601–598	2.27	1.81	1.25	1.17	
	NSMT-Mo 102098	KT-10-8 R3	Rebun I.	615–594	2.06	1.98	1.04	1.30	16J–K
	NSMT-Mo 102157	TS09-ZY18	Off Oki Is.	237–235	2.07	1.65	1.25	-	16I
	NSMT-Mo 95837	TS09-OW31	Off Oki Is.	888–900	2.38	1.94	1.23	1.20	17H–I
	NSMT-Mo 95837*	TS09-OW31	Off Oki Is.	888–900	2.11	1.73	1.22	1.18	
	NSMT-Mo 95838*	TS09-OW38	Off Oki Is.	600–604	2.84	2.08	1.37	1.37	
	NSMT-Mo 95838	TS09-OW38	Off Oki Is.	600–604	2.04	1.68	1.21	1.06	
Mean (*n* = 15)					2.30	1.82	1.26	1.19	
Japan Sea (dee-water from)	NSMT-Mo 95844	TS09-OW37	Off Oki Is.	1500–1497	2.53	1.94	1.30	1.30	17J–K
	NSMT-Mo 102091	SO07-C4-B1	Off Iwanai	1607–1369	2.34	1.82	1.29	1.29	17L–M
	NSMT-Mo 102091	SO07-C4-B1	Off Iwanai	1607–1369	1.88	1.55	1.21	1.03	17G
	NSMT-Mo 102100	SO07-C2-B	Yamato Bank	1360–1341	1.95	1.64	1.19	1.08	17D–F
	NSMT-Mo 102100	SO07-C2-B	Yamato Bank	1360–1341	2.24	1.80	1.24	1.22	17A–C
	NSMT-Mo 102101*	SO08-C3-B	Yamato Bank	1360–1341	2.52	2.07	1.22	1.27	17N–P
	NSMT-Mo 95844	TS09-OW37	Off Oki Is.	1500–1497	2.01+α	1.85	-	1.19	
Mean (*n* = 6)					2.24	1.80	1.24	1.20	
Okhotsk Sea	ZISP 54204/1		Off Paramushir I.	500	2.62	2.11	1.24	1.35	16N–O
	ZISP 54202/1		Off Paramushir I.	500	2.25	1.74	1.29	1.17	16P–Q

cation.

Remarks. This highly variable species can be recognized by its low-conical, umbilicate shell with thick, yellowish periostracum and strong axial and spiral sculpture at least on the initial part of the teleoconch whorls. Protoconch characters are also rather stable among the specimens examined, with regularly spaced numerous flat spiral cords with interspaces of similar width as the cord. This type of protoconch sculpture has not been observed in any previously known species in this and allied genera, but is shared by several Japanese bathyal species, as described below. These species seem to form a natural group, which may be endemic to the

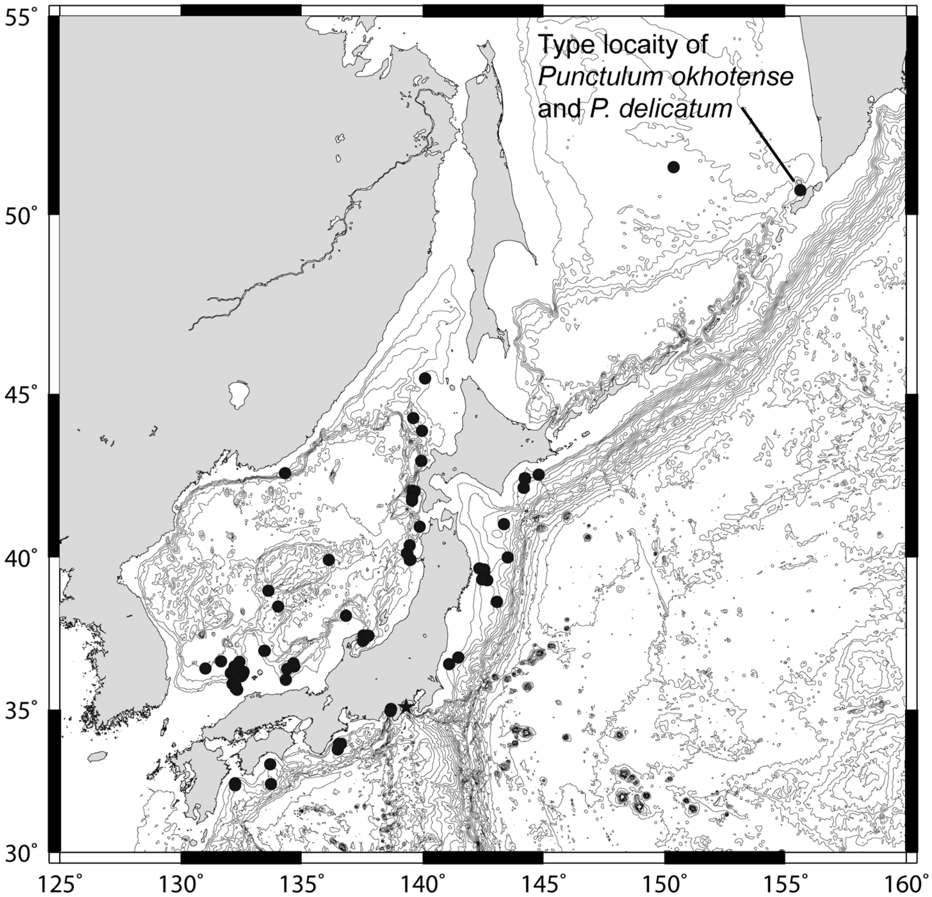


Fig. 23. Geographical distribution of *Punctulum flavum*. Asterisk: type locality of *Microstelma flava*.

northwestern Pacific. In other aspects of shell morphology, they closely resembles *P. wyvillethomsoni*, which is distributed from northeastern Greenland east to Franz Josef Land in the Barents Sea (Bouchet and Warén, 1993) and the East Siberian Sea (Golikov *et al.*, 2001a), but the latter has a completely smooth protoconch.

***Punctulum soyomaruae* n. sp.**

[New Japanese name: Hesoaki-watazoko-tsubo]

(Figs. 26A–I, 27A–C, 28A–C, 30A–B, 31–32, 49D; Table 7)

Type material. Holotype, NSMT-Mo 102216, SO07-C4-B2, 760–843 m (type locality) (Figs. 26A–E, 27A–C). Paratypes, NSMT-Mo 102194, from the type locality (4+1d and 2 radula preparations mounted on SEM stub: Fig. 26H–I, shell; Fig. 30A–B, radulae; Fig. 49D, operculum).

Type locality. Off Esashi, southwestern Hokkaido, 42°53.7′N, 139°59.4′E–42°54.3′N, 140°01.1′E, 843–800 m (Figs. 31–32).

Additional material examined: NSMT-Mo 102196, KT-10-08 Es2, 670–671 m (5); NSMT-Mo 102197, KT-10-08 Es3, 821–839 m (1+1e); NSMT-Mo 102096, KT-10-08 T2, 679–715 m (1); NSMT-Mo 102097, KT-10-08 T3, 839–851 m (1); NSMT-Mo 102195, KT-11-9 E4, 787–

854 m (1+1d: Fig. 26F–G, shell; Fig. 28A–C, protoconch); NSMT-Mo 102198, KT-11-9 T5, 790–808 m (1d).

Distribution. From off southwestern Hokkaido south to Toyama Bay, in a depth range of 679–839 m (Fig. 31: circles; Fig. 32).

Diagnosis (based mainly on holotype). Shell (Figs. 26A–I, 27A–C) small, 2.44 mm SL (mean of 6 specimens; Table 7), moderately thick, depressed conical in shape, with small spire, and covered by thick, slightly fibrous and yellowish tan periostracum. Protoconch (Fig. 28A–C) dome-shaped, consisting of 1.4–1.5 whorls, with rather strong and flat spiral cords, 14–15 in number at end of protoconch, and irregular axial threads in the interspaces. Thickness of spiral cords wider than interspaces (Fig. 28C). End of protoconch slightly thickened, and rather clearly demarcated from teleoconch (Fig. 28A: arrowhead). Teleoconch of *ca.* 2.2 convex whorls, with deeply constricted suture. Spire very small, occupying *ca.* 20% of shell length. Surface slightly rough, and often covered by yellowish rust, with distinct axial and spiral sculpture. Axial sculpture consisting of straight, rather thin but strong ribs, and indistinct microscopic growth lines. Axial ribs appearing at initial

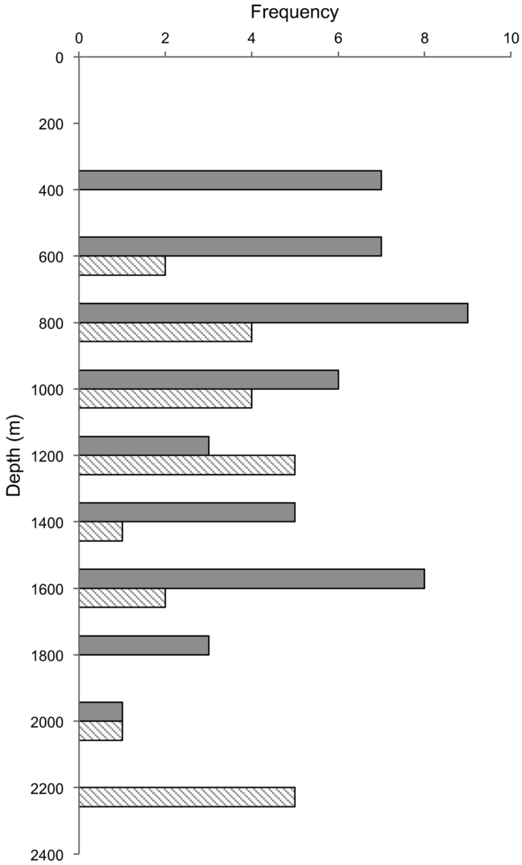


Fig. 24. Vertical distribution of *Punctulum flavum* in the Sea of Japan (grey bars) and off the Pacific coast of Honshu (crosshatched bars). Number of sampling stations within 100 m of depth.

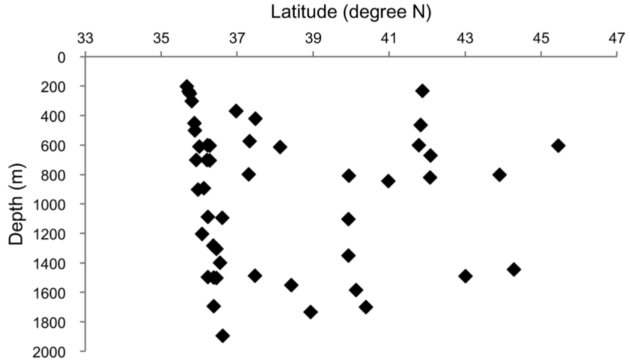


Fig. 25. Relationship between the depth and latitude in the distribution of *Punctulum flavum* in the Sea of Japan (excluding Russian territorial waters).

Fig. 26. Shells of *Punctulum soyomaruae* n. sp. and *P. sanrikuense* n. sp. A–I, *P. soyomaruae* n. sp.; A–E, holotype, NSMT-Mo 102216, off Esashi, 760–843 m; F–G, NSMT-Mo 102195, off Esashi, 787–854 m; H–I, paratype, NSMT-Mo 102194, from the type locality. J–O, *P. sanrikuense* n. sp., J–K, holotype, NSMT-Mo 102217, off Sanriku (Pacific), 894–935 m; L–O, paratype, NSMT-Mo 102204, off Sanriku (Pacific), 2137–2183 m. All at the same scale (scale bar = 1 mm), except E (scale bar = 200 μm).

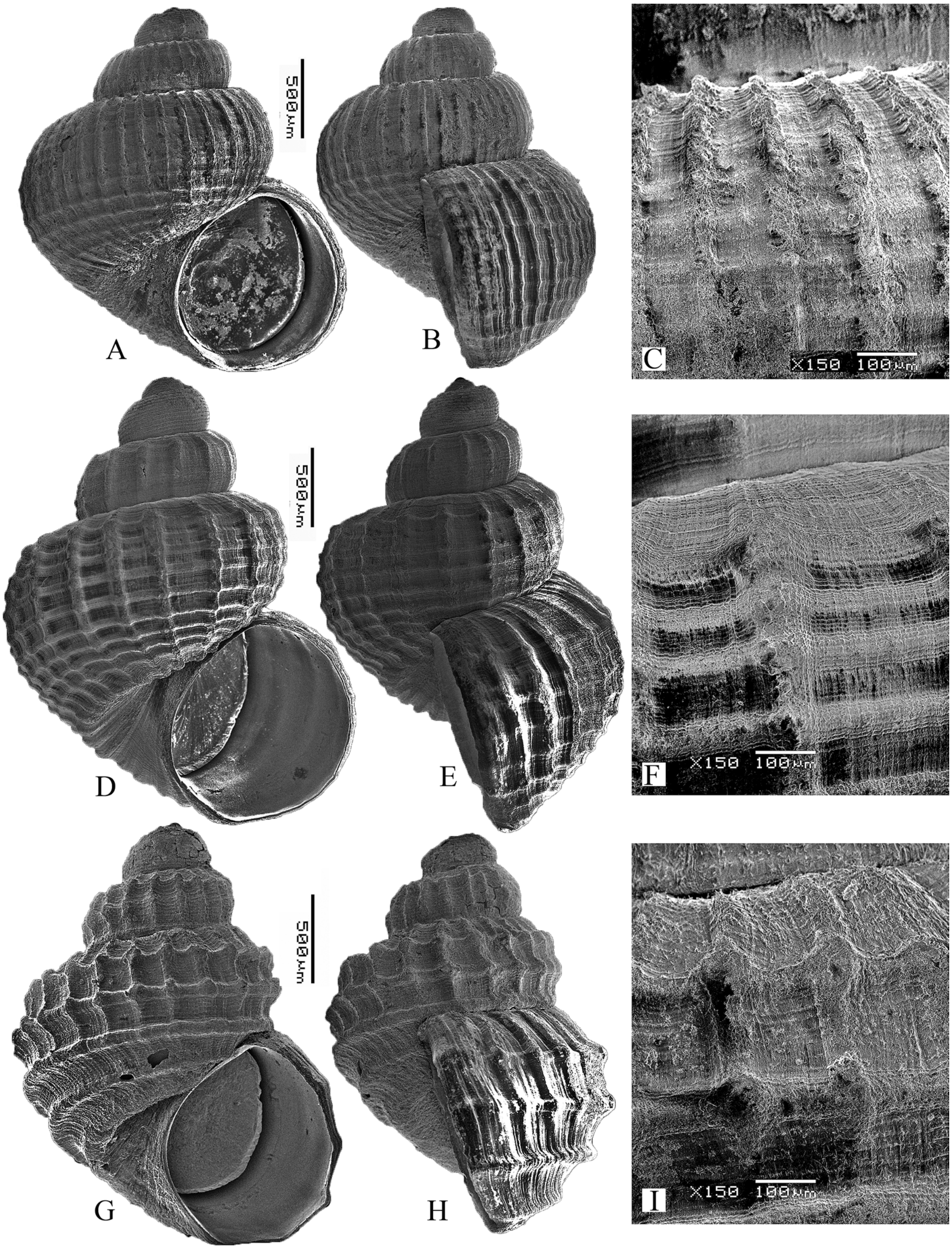


Fig. 27. SEM of shells of *Punctulum* spp. A–C, *P. soyomaruae* n. sp., holotype, NSMT-Mo 102216, off Esashi, 760–843 m. D–F, *P. sanrikuense* n. sp., holotype, NSMT-Mo 102217, off Sanriku (Pacific), 894–935 m. G–I, *P. tanshumaruae* n. sp., holotype, NSMT-Mo 102219, off Kasumi, 370–411 m. C, F, I, enlarged adapical part of the last whorl of A, D, G, respectively.

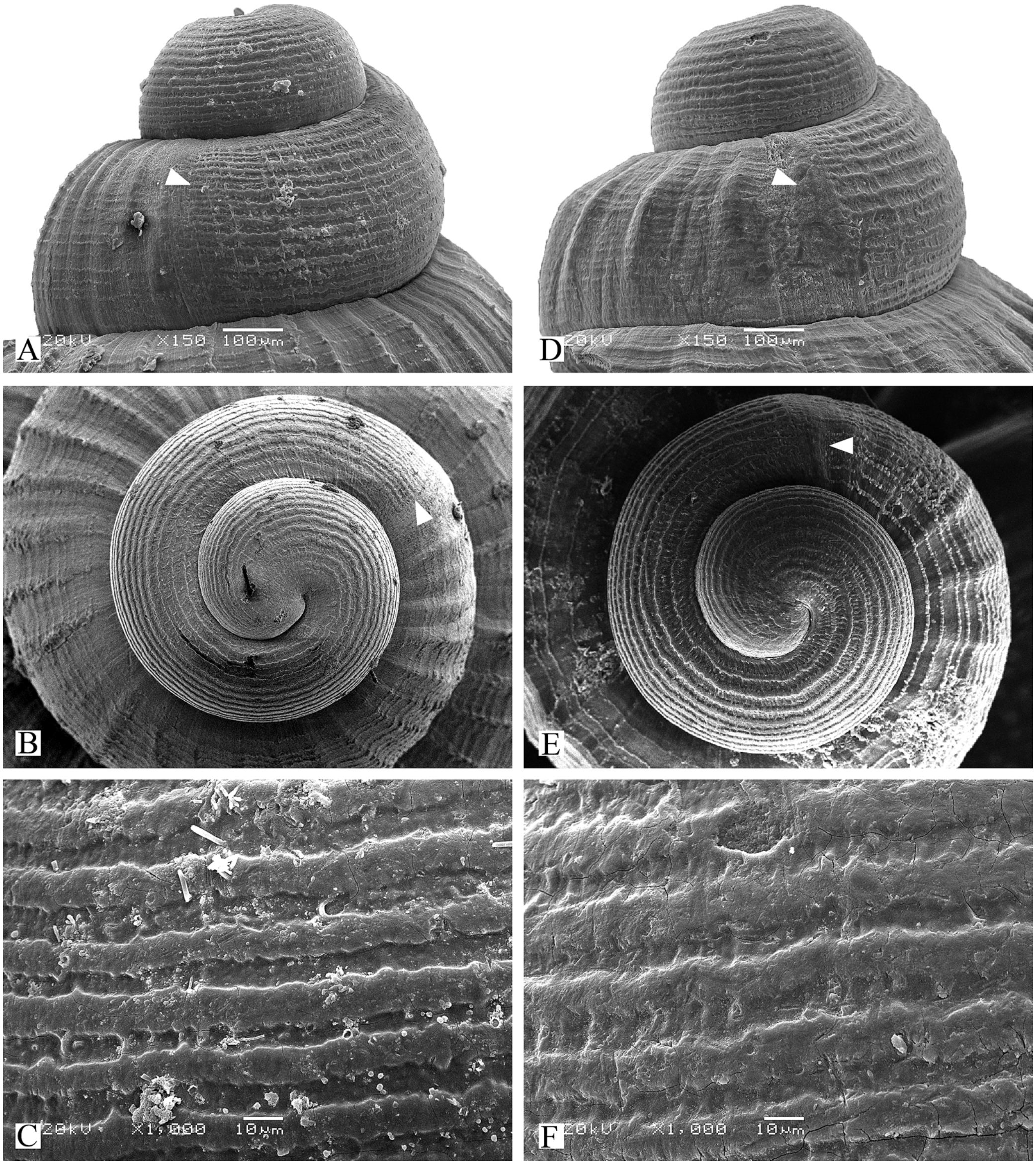


Fig. 28. SEM of protoconchs of *Punctulum* spp. A–C, *P. soyomaruae* n. sp., NSMT-Mo 102195, off Esashi, 787–854 m. D–F, *P. sanrikuense* n. sp., paratype, NSMT-Mo 102205, off Sanriku (Pacific), 894–935 m. C, F, enlarged lateral views of the first protoconch whorl of A, D, respectively. A–B and D–E at the same scale. Arrowheads indicate demarcation between protoconch and teleoconch.

part of teleoconch, gradually becoming stronger on first protoconch whorl and persisting to last whorl. Axial ribs reaching from suture to suture on spire whorls and from suture to umbilicus on last whorl; periostracum becoming fibrous on axial ribs. Spiral sculpture consisting of cords and minute but distinct secondary threads (Fig. 27C). Spiral cords always weaker than axial ribs, strongest below periphery and becoming weaker and indistinct toward suture. Last whorl large in proportion and extremely inflated. Aperture oval to almost evenly rounded, only slightly angled at posterior end. Inner lip rather thin; outer lip slightly prosocline, with very weak apertural varix

Table 7. Measurements of *Punctulum* spp. *: shell dissolved for radula preparation.

Species	Type status	Register no.	Station	Locality	Depth (m)	SL	SW	SL/SW	AL	Figures
P. soyomaruae n. sp.	Holotype	NSMT-Mo 102216	SO07-C4-B2	Off Iwanai	843–760	2.38	2.16	1.10	1.19	26A–E
P. soyomaruae n. sp.	Paratype	NSMT-Mo 102194	SO07-C4-B2	Off Iwanai	843–760	2.09	1.93	1.08	1.10	26H–I
P. soyomaruae n. sp.	Paratype	NSMT-Mo 102194	SO07-C4-B2	Off Iwanai	843–760	2.14	1.85	1.16	1.21	
P. soyomaruae n. sp.		NSMT-Mo 102195	KT-11-9 E4	Off Esashi	787–854	3.10	2.56	1.21	1.47	26F–G
P. soyomaruae n. sp.		NSMT-Mo 102194*	SO07-C4-B2	Off Iwanai	843–760	2.75	2.45	1.12	1.31	30A
P. soyomaruae n. sp.		NSMT-Mo 102194*	SO07-C4-B2	Off Iwanai	843–760	2.15	1.87	1.15	1.27	30B
Mean ($n = 6$)						2.44	2.14	1.14	1.26	
P. sanrikuense n. sp.	Holotype	NSMT-Mo 102217	SO07-C7	Off Sanriku	894–935	2.95	2.26	1.31	1.32	26J–K
P. sanrikuense n. sp.	Paratype	NSMT-Mo 102204	SO07-K1	Off Sanriku	2137–2183	3.07	2.60	1.18	1.61	26L–O
P. sanrikuense n. sp.		NSMT-Mo 102205*	SO07-C7	Off Sanriku	894–935	2.87	2.42	1.19	1.35	30C
P. sanrikuense n. sp.		NSMT-Mo 102205*	SO07-C7	Off Sanriku	894–935	2.43	2.10	1.16	1.22	30D
Mean ($n = 4$)						2.83	2.35	1.21	1.38	
P. tanshumaruae n. sp.	Holotype	NSMT-Mo 102214	KT-11-9 K3	Off Kasumi	370–411	2.83	1.91	1.48	1.21	33A–E
P. tanshumaruae n. sp.	Paratype	NSMT-Mo 102214	KT-11-9 K3	Off Kasumi	370–411	2.47	1.86	1.33	1.04	33F
P. tanshumaruae n. sp.		NSMT-Mo 102214*	KT-11-9 K3	Off Kasumi	370–411	2.77	1.94	1.43	1.21	
P. tanshumaruae n. sp.		NSMT-Mo 102214*	KT-11-9 K3	Off Kasumi	370–411	2.06	1.55	1.33	1.06	30F
Mean ($n = 4$)						2.53	1.82	1.39	1.13	
P. tanshumaruae n. sp.	(Pacific)	NSMT-Mo 102221	KT-12-8 A-1	Off Sanriku	498–459	2.56	2.04	1.25	1.29	33G–J
P. tanshumaruae n. sp.		NSMT-Mo 102221	KT-12-8 A-1	Off Sanriku	498–459	2.69	2.01	1.34	1.24	33K
P. tanshumaruae n. sp.		NSMT-Mo 102221	KT-12-8 A-1	Off Sanriku	498–459	2.59	1.98	1.31	1.18	
Mean ($n = 3$)						2.61	2.01	1.30	1.24	

behind lip in mature specimens. Umbilical chink widely perforate, and encircled by weak angulation. Operculum (Fig. 49C) thin, chitinous, paucispiral, oval, with convex outer ridge. Head-foot unpigmented, lacking pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe and projections. Radula (Fig. 30A–B) taenioglossate, 99.9 μm in width for 2.4 mm SW. Central teeth of formula 5+1+5, with tongue-like central cusp and triangular cutting edge; one pair of well-developed basal denticles, sometimes with additional pair of weak outer denticles; U-shaped basal extension indistinct. Lateral teeth of cusp formula 5+1+5–6, with broad primary cusp; inner cusps short and broad, and crowded on distal portion, whereas outer cusps sharper and more sparse. Inner marginal teeth sickle-shaped, relatively narrow, with 5–6 rather long and large cusps only on outer edge. Outer marginal teeth more slender than inner marginal teeth, tusk-like, with 3 cusps only on inner side.

Variations. No significant variations in shell morphology were observed among the material examined, although some specimens possess a slightly more elevated spire (Fig. 26F–G) than the holotype.

Etymology. Named after the R/V *Soyo-maru*, of the JFA, in recognition of her long-term contribution to marine science, especially Malacology.

Remarks. This species can easily be distinguished from all the previously known species in the genus by its depressed shape and characteristic sculpture. SL/SW value is 1.14 (mean of 6 specimens) and it is the smallest among the species treated in the present paper (Table 7). In protoconch sculpture, it closely resembles *P. flavum*, suggesting a probable affinity to that species, in spite of the relatively large differences in teleoconch features.

Examination of additional material from areas other than the Sea of Japan resulted in the finding of very similar specimens from the Pacific coast of northern Honshu. The Pacific specimens resemble the present species in their general shape, wide umbilicus and strong spiral ribs, and especially in the details of the protoconch microsculpture (compare Figs. 28A–C and 28D–F), and are apparently allied to this species. However, the range of variation in shell characters is very narrow and rather uniform in each area, and there are consistent differences between them,

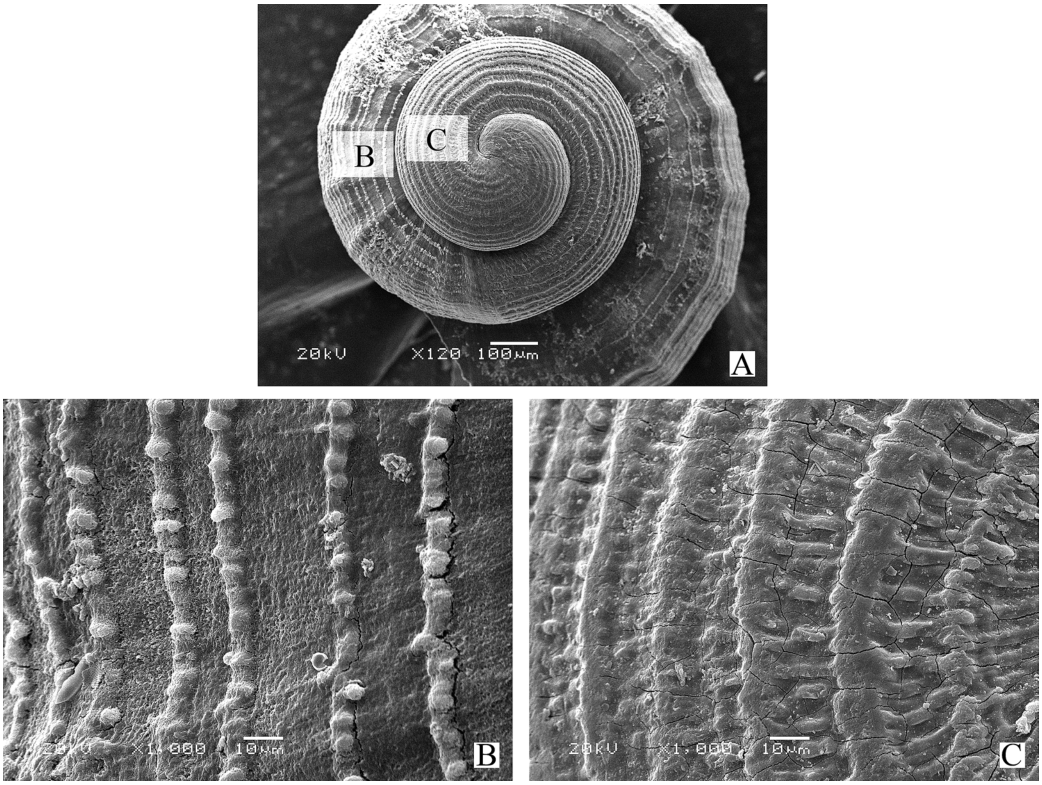


Fig. 29. Protoconch and early teleoconch microsculpture of *Punctulum sanrikuense* n. sp., paratype, NSMT-Mo 102205, off Sanriku (Pacific), 894–935 m.

especially in sculpture (see below). Accordingly, the Pacific population is here described as a distinct new species, although they are apparently closely related to each other, and represent counterparts in both areas.

Punctulum sanrikuense n. sp.

[New Japanese name: Sanriku-watazoko-tsubo]

(Figs. 26J–O, 27D–F, 28D–F, 29, 30C–D, 31–32, 49E; Table 7)

Type material. Holotype, NSMT-Mo 102217, SO07-C7, 894–935 m (type locality) (Figs. 26J–K, 27D–F). Paratypes, NSMT-Mo 102205, from the type locality (*ca.* 20+2d+6e and 2 radula preparations mounted on SEM stub: Fig. 28D–F, protoconch; Fig. 29A–C, shell microsculpture; Fig. 30C–D, radulae; Fig. 49E, operculum); NSMT-Mo 102204, SO07-K1, 2137–2183 m (5: Fig. 26 L–O).

Type locality. Off Miyako, Sanriku, 39°36.70′N, 142°33.30′E–39°35.90′N, 142°34.00′E, 894–935 m.

Additional Material examined: NSMT-Mo 102199, KH-69-2-13, 620–640 m (1+1e); NSMT-Mo 102206, KH-01-2 KC-0, 1134–1219 m (3d); NSMT-Mo 102200, KH-01-2 TD-2, 1002–1069 m (14); NSMT-Mo 102203, KT-07-29 M-1, 1039–1041 m (14); NSMT-Mo 102202, KT-07-29 M-2, 1528–1603 m (1); NSMT-Mo 102201, KT-08-27 K-2, 1853–1906 m (2).

Distribution. Off Kushiro, eastern Hokkaido, and the Sanriku coast of the Pacific Ocean, south to off Kinkazan, Miyagi Pref., at depths of 620–2183 m (Fig. 31: triangles; Fig. 32).

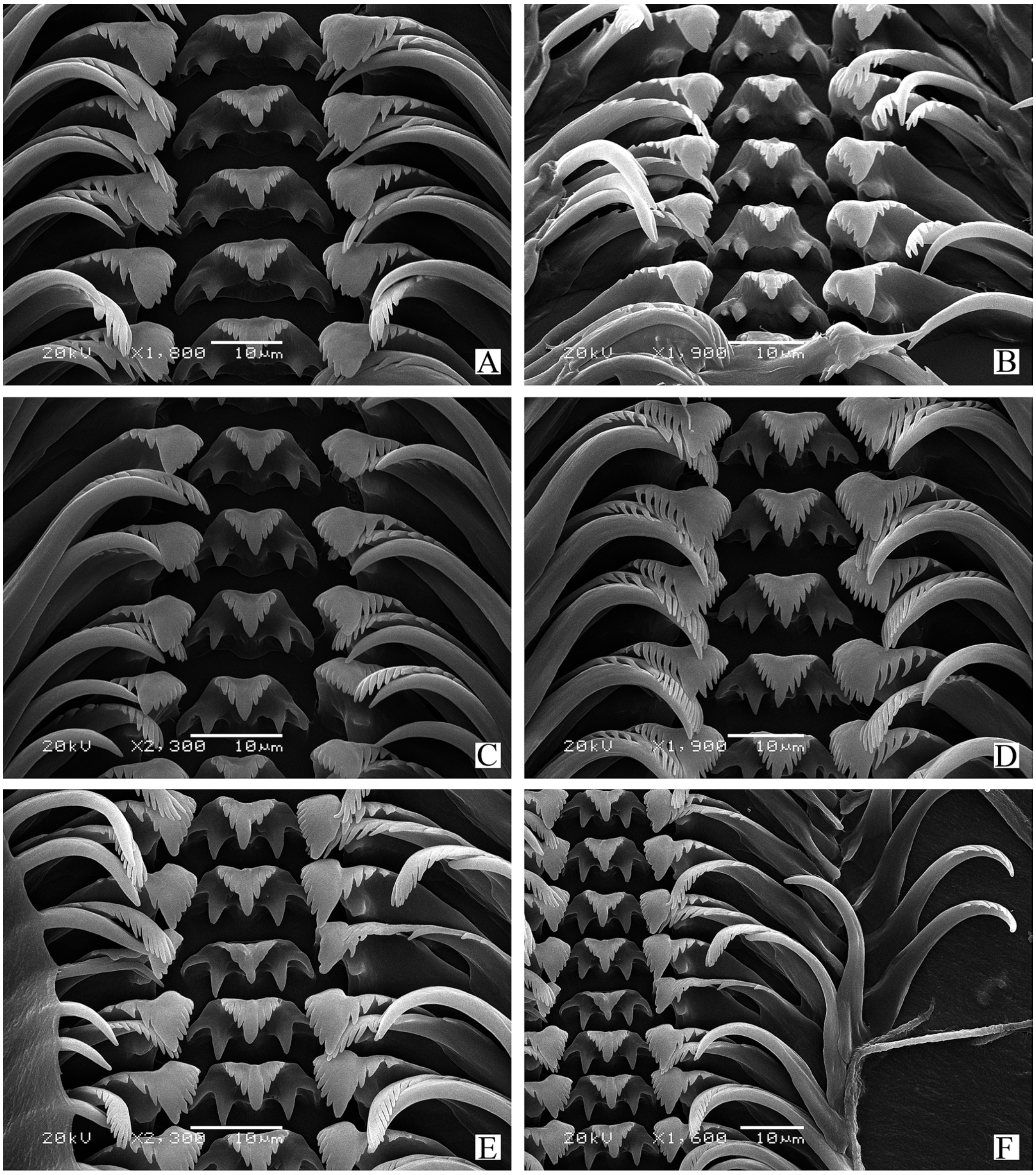


Fig. 30. SEM of radulae of *Punctulum* spp. A–B, *P. soyomaruae* n. sp., NSMT-Mo 102194, off Iwanai, 843–760 m. C–D, *P. sanrikuense* n. sp., NSMT-Mo 102205, off Sanriku (Pacific), 894–935 m. E–F, *P. tanshumaruae* n. sp., NSMT-Mo 95844, off Oki Islands, 1497–1500 m. Images in the right column (A, C, E), females; those in the left column (B, D), males.

Diagnosis (based mainly on holotype). Shell (Figs. 26J–O, 27D–F) small, 2.83 mm SL (mean of 4 specimens; Table 7), moderately thick, conical in shape, with relatively small spire, and covered by thick, rather smooth and yellowish brown periostracum. Protoconch (Fig. 28D–F) dome-shaped, consisting of 1.3 whorls, with strong and flat spiral cords, 14 in number at end of protoconch, and crowded numerous irregular axial threads in the interspaces (Fig. 29C). Thickness of spiral cords variable but usually wider than interspaces (Fig. 28F). End of protoconch slightly thickened, and clearly demarcated from teleoconch. Teleoconch of *ca.* 2.45 con-

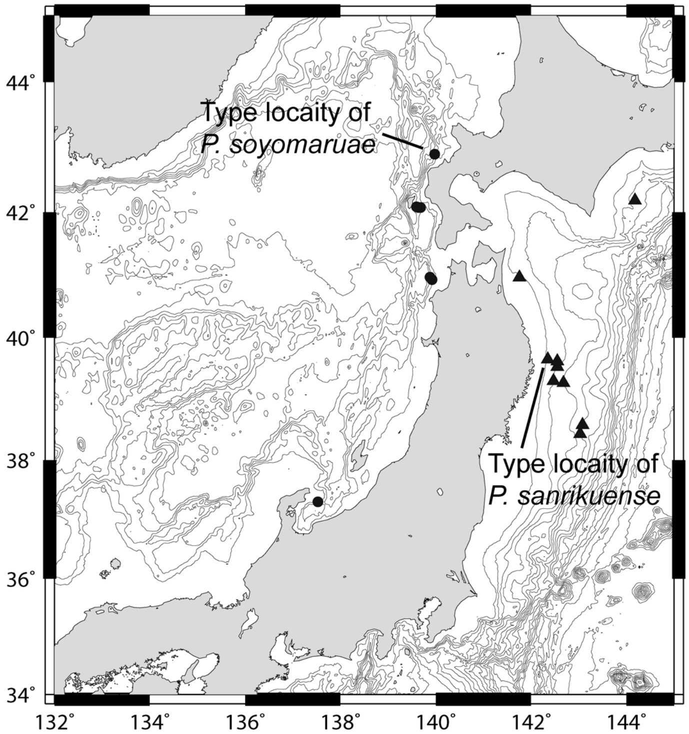


Fig. 31. Geographical distributions of *Punctulum soyomaruae* n. sp. (circles) and *P. sanrikuense* n. sp. (triangles).

vex whorls, with deeply constricted suture and weak angulation at shoulder. Spire relatively small, occupying 31–32% of shell length. Surface rather smooth, and covered by yellowish rust, with distinct axial and spiral sculpture of nearly same strength, forming rough lattice-like appearance. Axial sculpture consisting of straight, strong, round ribs that gradually appear on later part of first teleoconch whorl and persist to last whorl, and indistinct microscopic growth lines. Axial ribs reaching from suture to suture on spire whorls and from suture to umbilicus on last whorl; periostracum not fibrous on axial ribs. Spiral sculpture consisting of strong, rounded spiral cords and minute but distinct numerous secondary spiral threads (Fig. 27F). On initial part of first teleoconch whorl, very fine but distinct and somewhat granulate spiral threads present, gradually disappearing on later whorls (Fig. 29B). Spiral cords strongest below periphery, becoming slightly weaker and thinner toward suture and umbilicus. Last whorl large and inflated. Aperture oval to almost evenly rounded, only slightly angled at posterior end. Inner lip rather thin; outer lip slightly prosocline, with very weak apertural varix behind lip in mature specimens. Umbilical chink widely perforate, and encircled by strong angulation, distinctly denticulate at crossing with axial ribs. Operculum (Fig. 49E) thin, chitinous, paucispiral, oval, with convex outer ridge. Head-foot unpigmented, lacking pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe and projections. Radula (Fig. 30C–D) small for size, 73 μm in width for 2.4 mm SW. Central teeth of formula 5–6+1+5–6, with tongue-like central cusp and triangular cutting edge; one pair of well-developed basal denticles present, sometimes with one additional pair of weak outer denticles; U-shaped basal extension indistinct. Lateral teeth of cusp formula 7–9+1+4–6, with broad primary cusp with crowded short cusps on inner side; outer cusps longer, sparser and situated at more proximal part. Inner marginal teeth sickle-shaped, relatively narrow, with 6 rather long and large cusps only on outer edge. Outer marginal teeth more slender than inner marginal teeth, tusk-like; cusps on outer marginal not visible on mounts, outer side simple.

Variations. Specimens from deeper stations (Fig. 26 L–O: 2137–2183 m) possess a slightly broader shell with a smaller spire than those from shallower stations (Fig. 26J–K: 818–815 m). Otherwise no significant variations in shell morphology were observed among the material examined.

Etymology. Named after the type locality, the Sanriku region of northeastern Honshu, Japan.

Remarks. As noted in the remarks of the preceding species, this species closely resembles *P. soyomaruae* n. sp. in overall conchological features, and is probably derived from the same origin. However, there are some consistent differences between the two forms, such as a taller shell with angulation both at the shoulder and around the umbilicus, stronger sculpture, and granulated minute spiral threads on the initial teleoconch whorls in the present new species. The two forms are regarded herein as separate species.

***Punctulum tanshumaruae* n. sp.**

[New Japanese name: Tanshu-watazoko-tsubo]

(Figs. 27G–I, 30E–F, 33, 35–36; Table 7)

Type material. Holotype, NSMT-Mo 102219, KT-11-9 K-3, 370–411 m (type locality) (Figs. 27G–I, 33A–E). Paratypes, NSMT-Mo 102214, from the type locality (6+2d and 2 radula preparations on SEM stub: Fig. 33F, shell; Fig. 35A–B, protoconch; Fig. 30E–F, radulae; Fig. 49F, operculum).

Type locality. Off Kasumi, Hyogo Pref., 35°54.9′N, 134°18.6′E–35°55.2′N, 134°20.1′E, 411–370 m.

Additional material examined. Pacific coast of Honshu: NSMT-Mo 102221 and Atmosphere and Ocean Research Institute, the University of Tokyo, non-registered, KT-12-18 A-1, off Hachinohe, Aomori, 459–498 m (25 in total: Figs. 33G–K).

Distribution. Known only from two localities; off Hyogo Pref., Sea of Japan, at a depth of 370–411 m, and off Aomori, Pacific coast of NE Honshu, at a depth of 370–498 m (Fig. 36).

Diagnosis (based mainly on holotype). Shell (Figs. 27G–I, 33) small, 2.53 mm SL (mean of 4 specimens from type locality; Table 7), rather thick, elongate conical in shape, with relatively narrow spire, and covered by thick, rough and

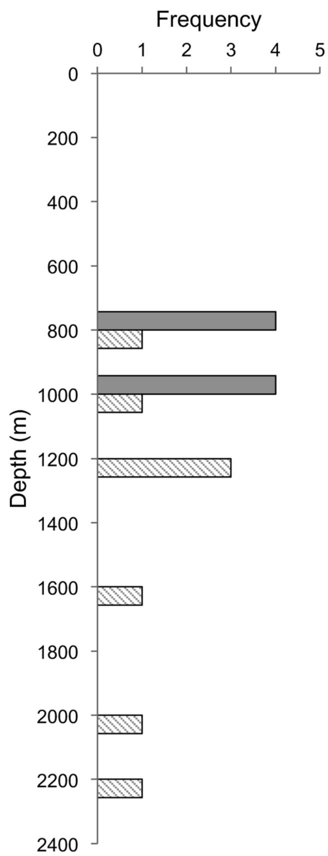


Fig. 32. Vertical distributions of *Punctulum soyomaruae* n. sp. in the Sea of Japan (grey bars) and *P. sanrikuense* n. sp. off the Pacific coast of Honshu (crosshatched bars). Number of sampling stations within 100 m of depth.

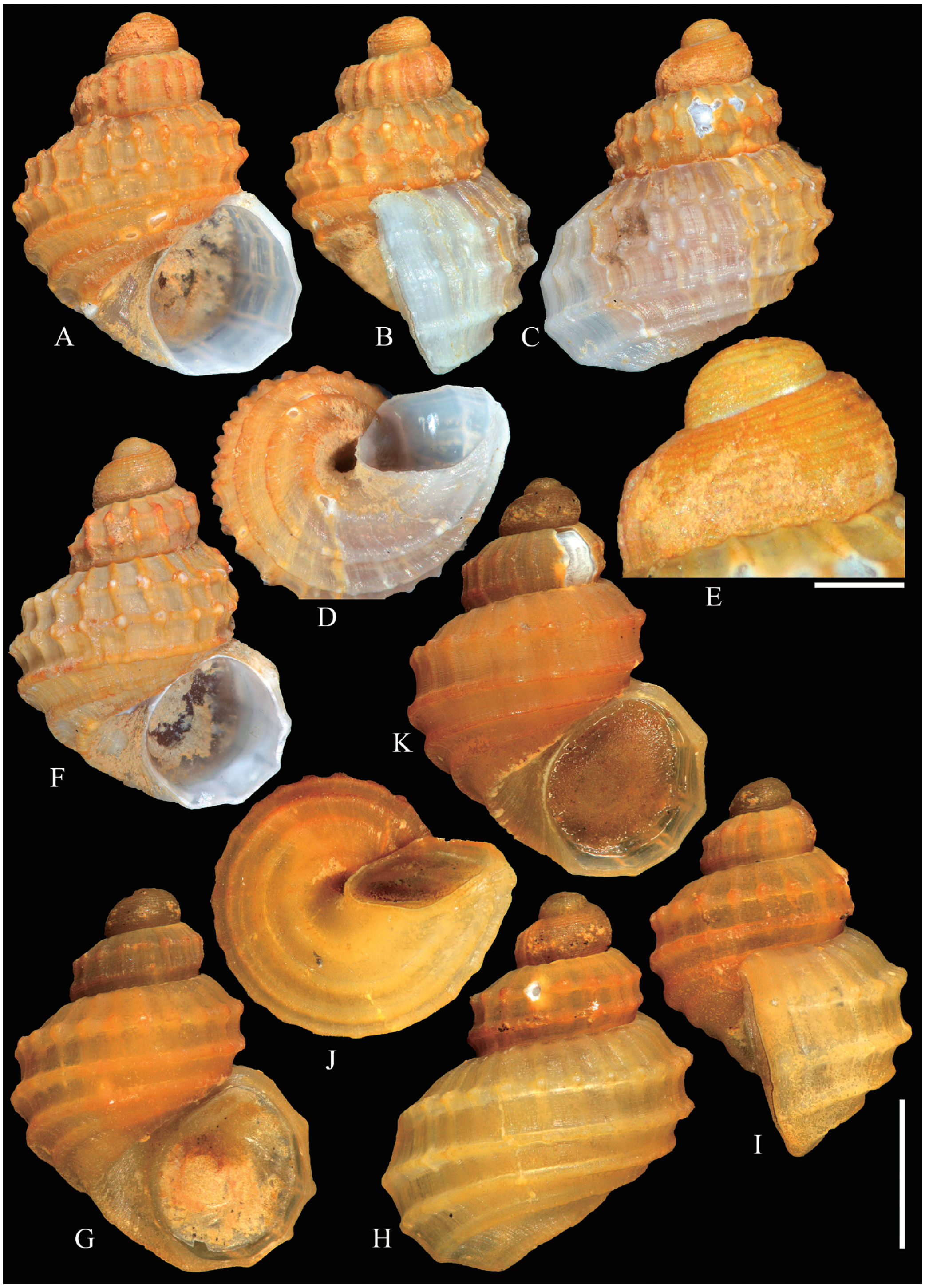


Fig. 33. Shells of *Punctulum tanshumaruae* n. sp. A–E, holotype, NSMT-Mo 102219, off Kasumi, 370–411 m; F, paratype, NSMT-Mo 102214, from the type locality; G–J, K, NSMT-Mo 102221, off Sanriku (Pacific), 459–498 m (2 examples). All at the same scale (scale bar = 1 mm), except E (scale bar = 200 μm).

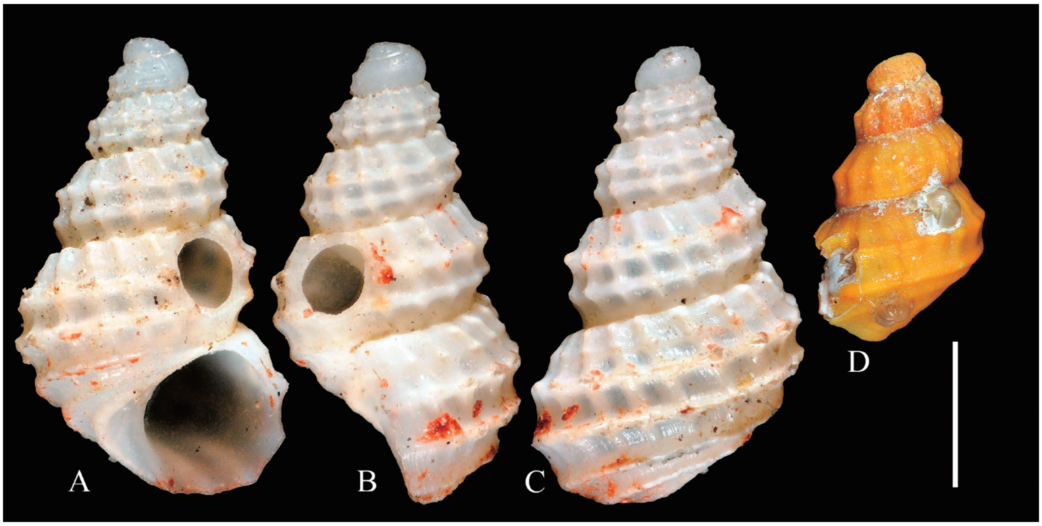


Fig. 34. Shells of *Alvania lusoria*. A–C, holotype of *Rissoa* (*Alvania*) *lusoria*, UMUT CM 23131, Pliocene fossil, Sawane Formation, Sado Island; D, possible Recent representative, KT-11-9 M2, Musashi Bank, 198–206 m. All at the same scale (scale bar = 1 mm).

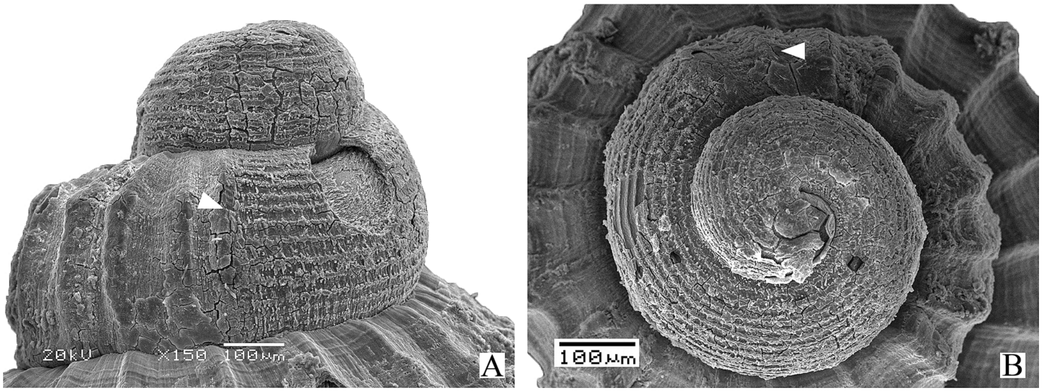


Fig. 35. SEM of protoconchs of *Punctulum tanshumaruae* n. sp. A–B, paratype, NSMT-Mo 102214, off Kasumi, 370–411 m. Arrowheads indicate demarcation between protoconch and teleoconch.

yellowish brown periostracum. Protoconch (Fig. 35) dome-shaped, consisting of 1.4 whorls, with strong and flat spiral cords, 14 in number at end of protoconch. Thickness of spiral cords almost equal to interspaces. Microsculpture of protoconch not observable due to condition of all specimens examined. End of protoconch slightly thickened, and clearly demarcated from teleoconch. Teleoconch of *ca.* 2.1 moderately convex whorls, with deeply constricted suture. Spire relatively small, occupying *ca.* 31% of shell length. Surface rough due to presence of many fine spiral ribs as described below, and usually covered by yellowish rust in fresh condition, with distinct axial and spiral sculpture, forming extremely coarse lattice-like appearance. Axial sculpture consisting of straight, rather thin but strong, rounded ribs and indistinct microscopic growth lines. Axial ribs appearing at beginning of first teleoconch whorl and persisting to last whorl; reaching from suture to suture on spire whorls but absent on basal part of last whorl. Spiral sculpture consisting of extremely strong and round spiral cords that gradually appear on first teleoconch whorl, 2 in

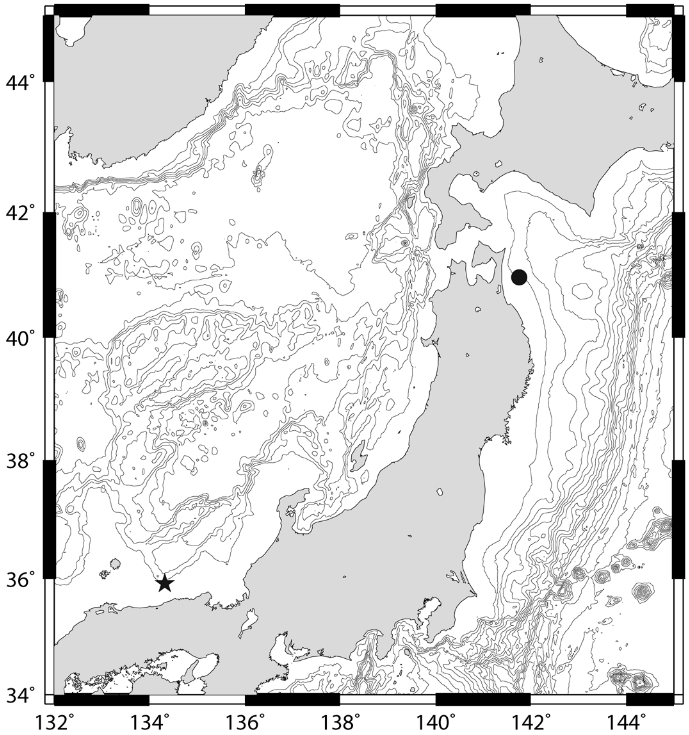


Fig. 36. Geographical distribution of *Punctulum tanshumaruae* n. sp. Asterisk: type locality.

number on penultimate whorl and 4 on last whorl except for keel around umbilicus, and rather widely spaced minute but distinct secondary spiral threads (Fig. 27I). Intersection of axial ribs and spiral cords becoming nodulous. Last whorl large and inflated. Aperture oval, and angled at posterior end. Inner lip rather thin; outer lip prosocline, with weak apertural varix behind lip in mature specimens. Umbilical chink rather widely perforate, and encircled by strong angulation that is distinctly denticulate where crossing axial ribs. Operculum (Fig. 49E) thin, chitinous, paucispiral, oval, with convex outer ridge. Head-foot unpigmented, lacking pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe and projections. Radula (Fig. 30E–F) small for size, 75 μm in width for 2.8 mm SW. Central teeth of formula 3–5+1+3–5, with elongate tongue-like central cusp and triangular cutting edge; one pair of well-developed basal denticles present; U-shaped basal extension indistinct. Lateral teeth of cusp formula 5–7+1+3–4, with broad primary cusp with crowded short cusps on inner side; outer cusps, sparse and situated at more proximal part. Inner marginal teeth sickle-shaped, relatively narrow, with 9 rather long and large cusps only on outer edge. Outer marginal teeth more slender than inner marginal teeth, tusk-like, with 5 cusps only on inner side.

Variations. No significant variations in shell morphology were observed among the type material, which was collected together at the same station. Specimens from off the Sanriku coast in the Pacific agree well with the type material from the Sea of Japan, but differ slightly in possessing a larger shell with weaker axial ribs. However, the differences are very small, and there is no positive reason to separate them as different species.

Etymology. Named after the T/V *Tanshu-maru*, of Hyogo Pref., in recognition of her considerable contribution to fisheries science in the Sea of Japan and off the Sanriku coast.

Remarks. This species apparently belongs in a species group that comprises *P. flavum*, *P. soyomaruae* n. sp. and *P. sanrikuense* n. sp., based on the close similarities in the morphology of the protoconch and radula. Among those species, it somewhat resembles *P. sanrikuense* n. sp. in possessing coarse lattice-like sculpture, but is easily distinguished by having only 4 spiral cords on the last whorl (versus 9 in *P. sanrikuense* n. sp.). Among other named species, the present new species might most closely be allied to *Rissoa* (*Alvania*) *lusoria* Yokoyama (1926: 273, pl. 33, fig. 18), which was described based on a Pliocene fossil from the Sawane Formation, Sado Island, in possessing the same number of thick spiral cords and strong axial ribs on the last whorl. *R. lusoria* is, however, distinguished from the present new species by its tall conical shell with a very narrow umbilicus. Furthermore, a single immature and incomplete specimen that agrees well with the holotype of *R. lusoria* was collected from KT-11-9 M2, Musashi Bank, 198–206 m, during the present project, and it clearly differs from the present new species. The holotype and the probable Recent representative of *R. lusoria* are illustrated in Figs. 34A–C and 34D, respectively, for comparison.

The present new species was recorded only at two distantly separated stations in the Sea of Japan and the Pacific. In spite of the fact that both localities are separated by the Japanese Archipelago with only a shallow connection at Tsugaru Strait, there are no considerable differences between the specimens from either locality, in clear contrast to the case of *P. soyomaruae* n. sp. and *P. sanrikuense* n. sp., and they are considered to be conspecific (see "Discussion" part).

Punctulum reticulatum Golikov, 1986
(Fig. 48F–H)

Punctulum reticulatum Golikov, 1986: 88–89, fig. 4 [type locality: off Primorsky Krai, near Rynda Bay in the Sea of Japan, 44°48′N, 136°40′E, 373–494 m]; Kantor and Sysoev, 2006: pl. 36, fig. J (holotype).

Type material. *Punctulum reticulatum* Golikov, 1986; holotype, ZISP 36574/3 (dried shell: Fig. 48F–H); "paratype", ZISP 36576/5, off Primorsky Krai, 380–312 m (shell completely dissolved in preservative).

Material examined. No specimens that were identifiable as this taxon were found in the present material.

Remarks. This nominal taxon was described based on single specimen collected from the Russian coast of the northern Sea of Japan. The holotype is now preserved as a dry specimen in the ZISP, but it had probably deteriorated while in alcohol, and is not suitable for detailed taxonomic examination (Fig. 48F–H). One other example of this species is preserved as a "paratype" in the ZISP type collection, although the paratype is not mentioned in the original description. Furthermore, the shell of the latter specimen has been completely dissolved in the preservative. The holotype of *P. reticulatum* was said to possess numerous spiral ribs on the protoconch (Golikov, 1986), like all the other species assigned to the genus *Punctulum* in the present paper, including *P. flavum*. However, it differs from *P. flavum* in possessing significantly thicker spiral cords. It most closely resembles *Frigidoalvania flavida* Golikov and Sirenko, 1998, described from the Okhotsk Sea coast of Paramushir Island, at a depth of 500 m, although the holotype of this taxon (ZISP 54239; Fig. 48I–K) also deteriorated in its preservative. It is thus necessary to obtain additional material to clarify the relationship among these taxa.

Genus ***Alvania*** Risso, 1826: 140

Type species. *Alvania europea* Risso, 1826, subsequent designation by Nevill (1885: 105).

Remarks. It has been proved that the genus *Alvania* as currently recognized is a polyphyletic mixture of groups, as noted in the remarks for the genus *Punctulum*. The species included in this genus in the present paper differ considerably from the type species of the genus, and probably belong to different genera. However, because of the absence of appropriate genera, they are only provisionally placed here, until a firmer framework is established for the family.

Alvania akibai (Yokoyama, 1926)
[New Japanese name: Akiba-tsubo]
(Figs. 37, 38A–C, 39A–C, 40A–B, 41–42, 49G; Table 8)

Rissoa (*Alvania*) *akibai* Yokoyama, 1926: 275, pl. 34, fig. 3 [type locality: Upper horizon, Sawane Formation, Sado Island, Pliocene].

Alvania (*Arsenia*) *akibai* — Hatai and Nisiyama, 1952: 241; Makiyama, 1958: pl. 45, fig. 13 [reproduction of the original plate].

Punctulum sp. — Golikov *et al*., 2001b: 158 [northern Sea of Japan, 373–494 m] (voucher specimen: Fig. 37K–L).

Type material. *Rissoa* (*Alvania*) *akibai* Yokoyama, 1926, lectotype (figured syntype), here designated, UMUT CM 23137 (Fig. 37M–N); paralectotypes, UMUT CM 23136 (2 specimens; labeled as "figured syntype", but none of them agree with the original figure) (Fig. 37O–P).

Material examined. NSMT-Mo 102177, KT-11-9 E1, 220–247 m (8+1d: Figs. 37A–D, 38A–C); NSMT-Mo 102174, KT-11-9 E3, 563–635 m (2); NSMT-Mo 102175, KT-11-9 K3, 370–411 m (12+2e and 2 radula preparations mounted on SEM stub: Figs. 37E–F, I–J, shells; Fig. 40A–B, radulae; Fig. 49G, operculum); NSMT-Mo 102179, KT-11-9 K4, 603–613 m (2: Fig. 37G–H); NSMT-Mo 102176, KT-11-9 M3, 407–413 m (3+1d: Fig. 39A–C, protoconch); NSMT-Mo 102178, KT-11-9 N4, 603–622 m (1+1d); ZISP, non-registered, off Primorsky Krai, 44°48.5′N, 136°46.0′E, 373–494 m (voucher specimen of *Punctulum* sp. *fide* Golikov *et al*., 2001b: 158).

Distribution. From Musashi Bank south to off Shimane Pref., and off Primorsky Krai coast in northern Sea of Japan, at depths of 220–635 m. Probably endemic to the Sea of Japan.

Diagnosis. Shell (Figs. 37, 38A–C, 39A–C) moderate in size for genus, 3.49 mm SL (mean of 7 specimens; Table 8), rather thick and solid, conical in shape, somewhat translucent white with thin periostracum. Protoconch dome-shaped, large, *ca.* 630 μm in width (Fig. 39B), consisting of 1.5 whorls, with peculiar pockmarked sculpture consisting of densely placed minute pits of rather irregular shape (Fig. 39A–C). End of protoconch clearly demarcated from teleoconch. Teleoconch of 3.1 convex whorls, with deeply constricted suture. Spire moderately small, occupying *ca.* 35% of shell length. Surface slightly glossy, with distinct axial and spiral sculpture. Axial sculpture consisting of straight, rather thin but strong ribs that appear at beginning of first teleoconch whorl and persist to last whorl; reaching from suture to suture on spire whorls but gradually disappearing toward base on last whorl. Spiral cords also rather thin but distinct, as strong as axial ribs, and widely spaced, with numerous minute secondary threads in interstices. Number of spiral cords variable from 2 to 3 on penultimate whorl, 8 to 9 on last whorl; spiral cords on base attenuating in some specimens. Last whorl large in proportion and well inflated. Aperture oval and angled at posterior end. Inner lip moderate in thickness; outer lip slightly prosocline, usually without apertural varix, but sometimes with weak apertural varix behind lip in fully mature specimens (Fig. 37I–J). Umbilical chink very narrow and slit-like. Operculum

Fig. 37. Shells of *Alvania akibai*. A–D, NSMT-Mo 102177, off Esashi, 220–247 m; E–F, I–J, NSMT-Mo 102175, off Kasumi, 370–411 m (2 examples); G–H, NSMT-Mo 102179, off Kasumi, 603–613 m; K–L, ZISP, non-registered, off Primorsky Krai, 373–494 m; M–N, lectotype of *Rissoa* (*Alvania*) *akibai*, UMUT CM 23137, Pliocene fossil, Sawane Formation, Sado Island; O–P, paralectotype, UMUT CM 23136, from the type locality (= *A.* sp; not *A. akibai*). All at the same scale (scale bar = 1 mm), except D (scale bar = 200 μm).

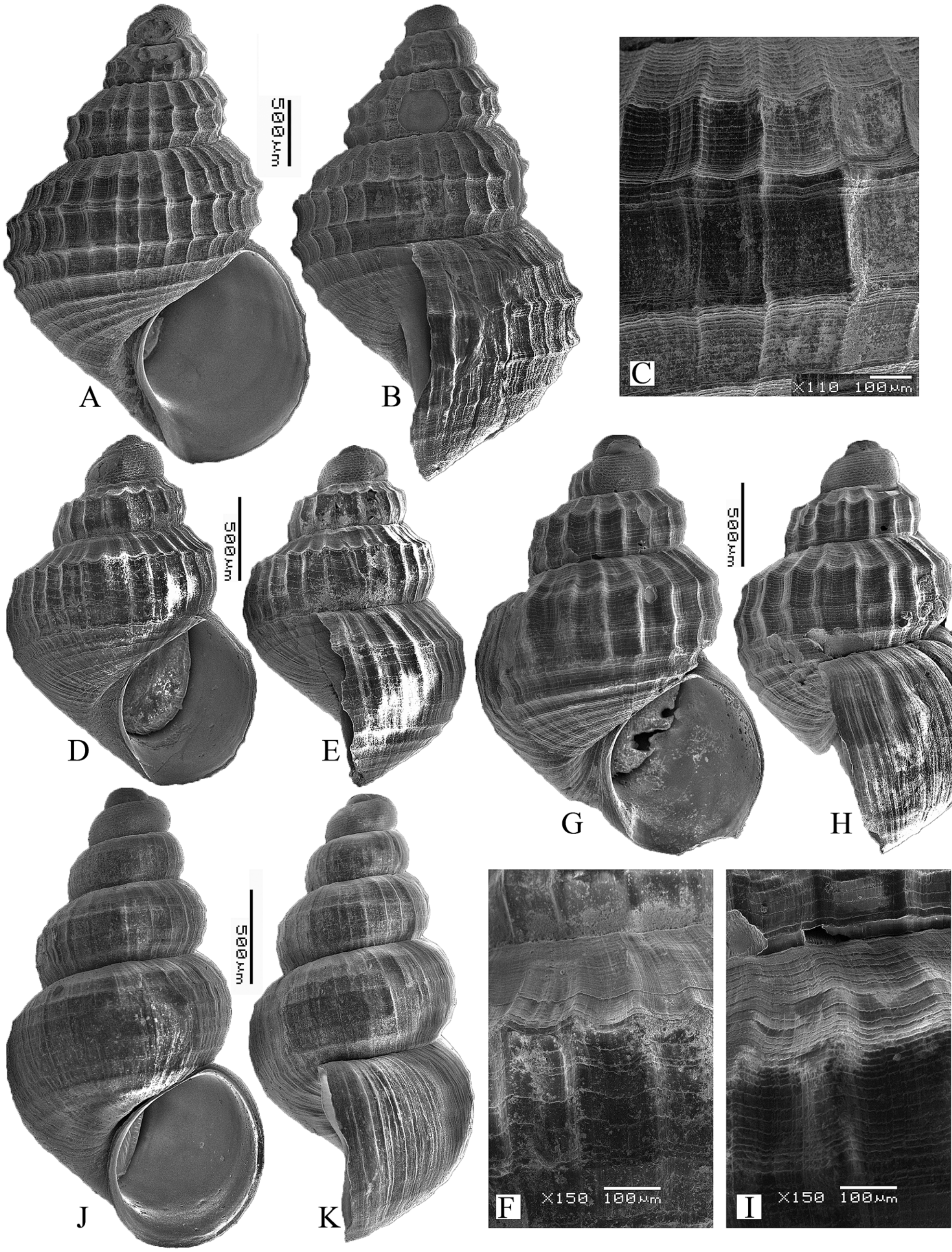


Fig. 38. SEM of shells of *Alvania* spp. A–C, *A. akibai*, NSMT-Mo 102177, off Esashi, 220–247 m. D–I, *A. nihonkaiensis* n. sp.; D–F, holotype, NSMT-Mo 102218, Toyama Bay, 383–460 m; G–I, NSMT-Mo 102207, Okhotsk Sea, 176–177 m. J–K, *A. yamatoensis* n. sp.; holotype, NSMT-Mo 102220, Yamato Bank, 316–328 m. C, F, I, enlarged adapical parts of the last whorl of A, D, G, respectively.

(Fig. 49G) thin, chitinous, paucispiral, oval, with more convex outer ridge. Head-foot unpigmented, with distinctly pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe and projections. Radula (Fig. 40A–B), 126 μm in width for 2.2 mm SW. Central teeth of cusp formula 4–6+1+4–6, with narrowly elongate tongue-like central cusp and triangular cutting

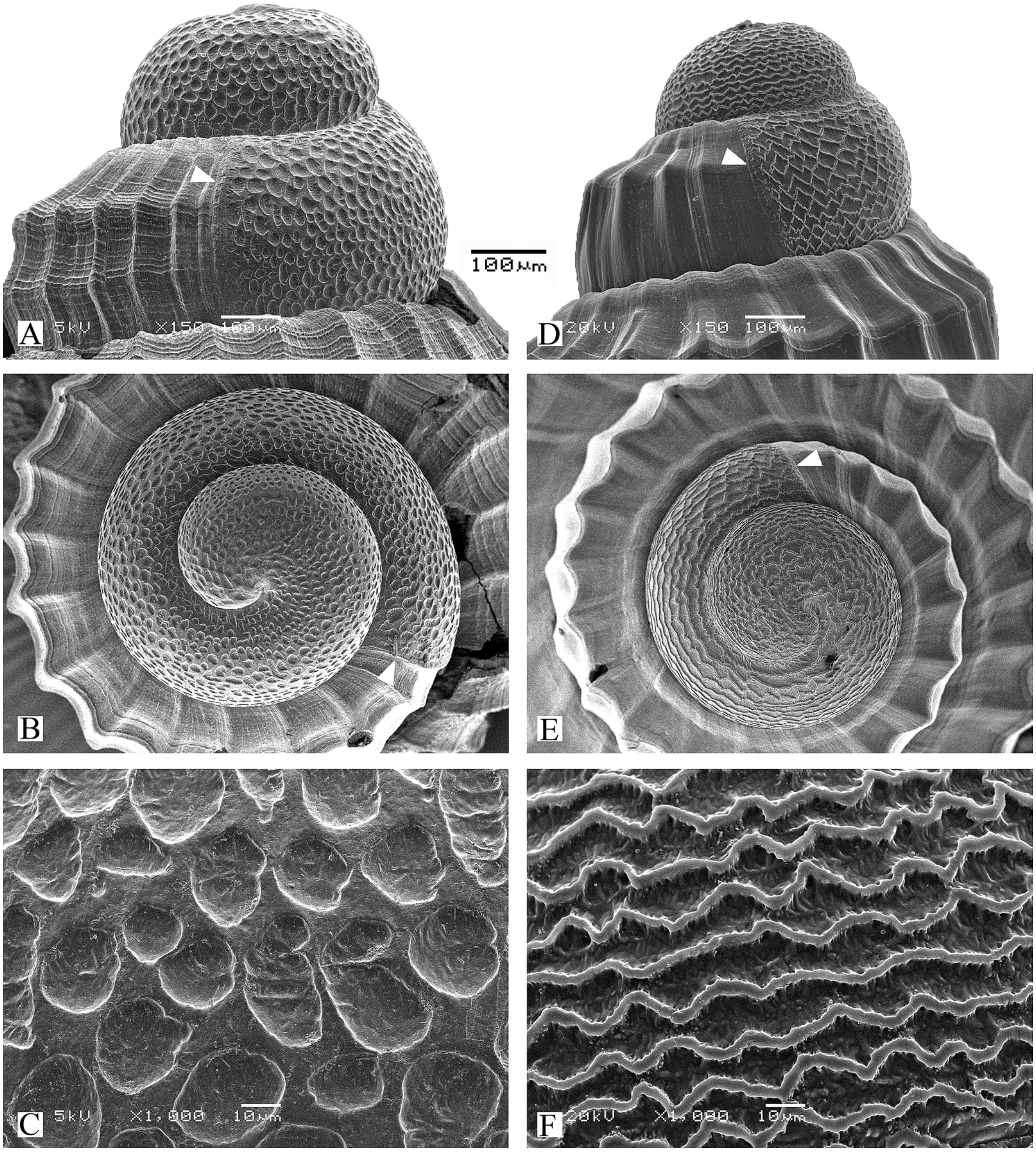


Fig. 39. SEM of protoconch of *Alvania* spp. A–C, *A. akibai*, NSMT-Mo 102176, Musashi Bank, 407–413 m. D–F, *A. nihonkaiensis* n. sp., NSMT-Mo 102209, Toyama Bay, 207–258 m. C, F, enlarged lateral views of the first protoconch whorl of A, D, respectively. A–B and D–E at the same scale. Arrowheads indicate demarcation between protoconch and teleoconch.

edge; two to three pairs of well-developed basal denticles; U-shaped basal extension indistinct. Lateral teeth of cusp formula 6–8+1+6–7; broad primary cusp with smaller and rather irregularly shaped cusps on inner side, and sparse and significantly large outer cusps situated at more proximal part. Inner marginal teeth sickle-shaped, with 6–8 rather long and large cusps only on outer edge. Outer marginal teeth more slender than inner marginal teeth, tusk-like, with 4 cusps only on inner side.

Variations. This species is not very variable, at least among the material examined. The size is generally large relative to the other species here treated, and often exceeds 3.5 mm in SL,

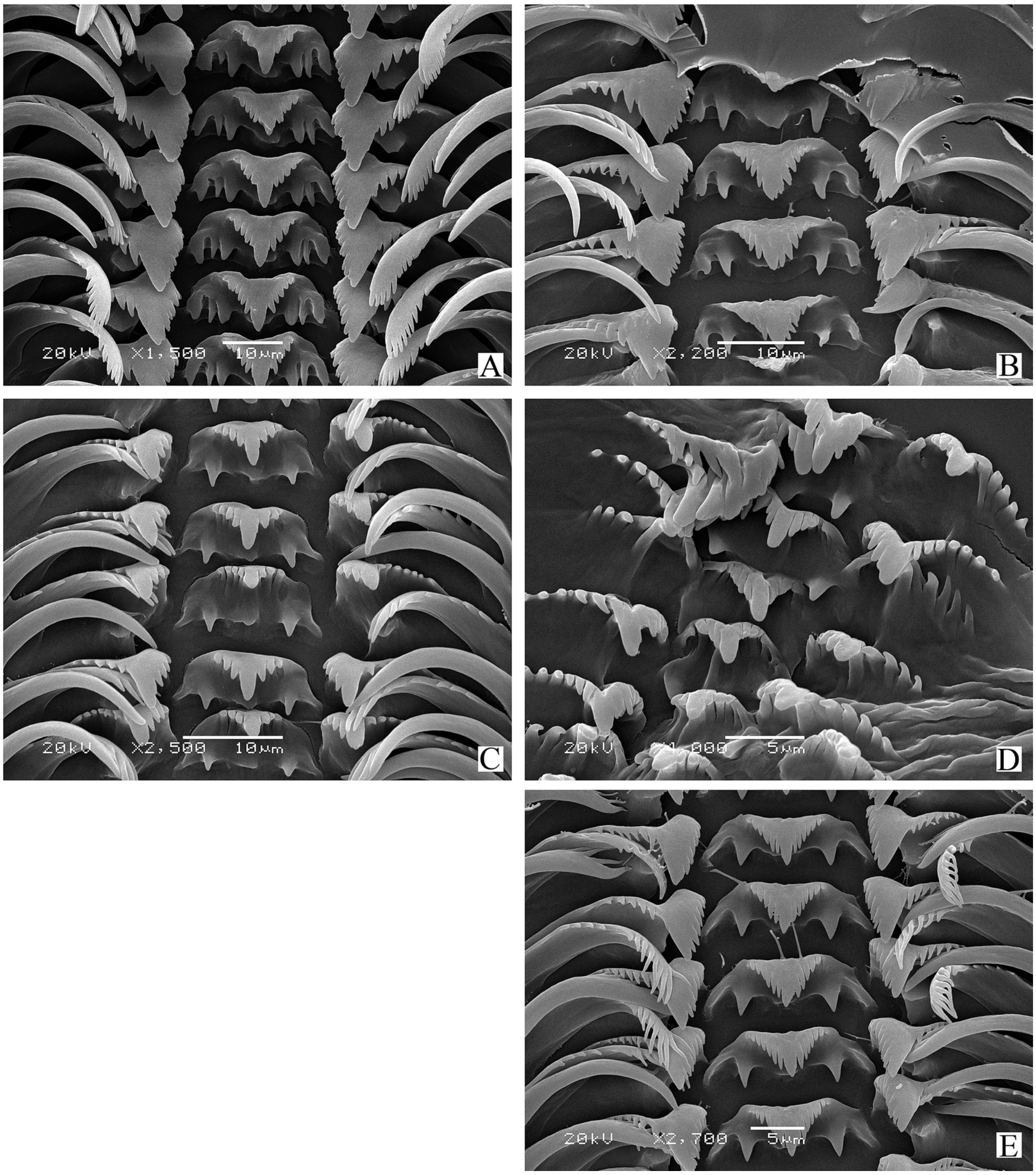


Fig. 40. SEM of radulae of *Alvania* spp. A–B, *A. akibai*, NSMT-Mo 102175, off Kasumi, 370–411 m. C–D, *A. nihonkaiensis* n. sp., paratype, NSMT-Mo 102210, Toyama Bay, 383–460 m. E, *A. yamatoensis* n. sp., NSMT-Mo 102083, Yamato Bank, 316–328 m. Images in the right column (A, C), females; those in the left column (B, D, E), males.

although some specimens seem to be mature at a smaller size (Fig. 37I–J: 3.05 mm SL). The number and strength of spiral cords are slightly variable, although those of the axial ribs are rather consistent.

Remarks. *Rissoa* (*Alvania*) *akibai* Yokoyama, 1926 was described based on three specimens (syntypes) collected from the Pliocene Sawane Formation. Examination of the syntypes revealed that they comprise two apparently distinct species; one is conspecific with the species treated here, and the other is probaly allied to *Alvania maya* (Yokoyama, 1926) in protoconch

Table 8. Measurements of *Alvania* spp. *: shell dissolved for radula preparation; **paralectotype of *Rissoa akibai.*

Species	Type status	Register no.	Station	Locality	Depth (m)	SL	SW	SL/SW	AL	Figures
A. akibai	Lectotype	UMUT CM 23136a		Sado I., Pliocene		3.45	2.18	1.58	1.56	37M–N
A. sp. (cf. *maya*)	**	UMUT CM 23136b		Sado I., Pliocene		3.06	1.91	1.60	1.30	37O–P
A. akibai		NSMT-Mo 102177	KT-11-9 E1	Off Esashi	220–247	3.81	2.60	1.47	1.86	37A–D
A. akibai		NSMT-Mo 102179	KT-11-9 K4	Off Kasumi	603–613	3.48	2.62	1.33	1.77	37G–H
A. akibai		NSMT-Mo 102175	KT-11-9 K3	Off Kasumi	370–411	3.05	2.17	1.41	1.51	37I–J
A. akibai		NSMT-Mo 102175	KT-11-9 K3	Off Kasumi	370–411	3.61	2.55	1.42	1.65	37E–F
A. akibai		NSMT-Mo 102175*	KT-11-9 K3	Off Kasumi	370–411	3.29	2.22	1.48	1.58	
A. akibai		NSMT-Mo 102175*	KT-11-9 K3	Off Kasumi	370–411	2.75	1.90	1.45	1.37	
A. akibai		ZISP non-registered		Off Primorsky Krai	373–494	3.88	2.87	1.35	1.88	37K–L
Mean (n = 7)						3.49	2.49	1.40	1.70	
A. nihonkaiensis n. sp.	Holotype	NSMT-Mo 102210	KT-11-9 T3	Toyama Bay	383–460	2.15	1.52	1.41	1.04	43A–D
A. nihonkaiensis n. sp.	Paratype	NSMT-Mo 102210	KT-11-9 T3	Toyama Bay	383–460	2.09	1.56	1.34	1.00	43K
A. nihonkaiensis n. sp.	Paratype	NSMT-Mo 102218	KT-11-9 T3	Toyama Bay	383–460	2.14	1.53	1.40	1.05	
A. nihonkaiensis n. sp.		NSMT-Mo 95826	TS09-ZY18	Off Oki Is.	237–235	1.79	1.29	1.39	0.83	
A. nihonkaiensis n. sp.		NSMT-Mo 102082	KT-10-8 R2	Off Rebun I.	402–393	2.08	1.38	1.51	0.88	43I–J
A. nihonkaiensis n. sp.		NSMT-Mo 102081	KT-10-8 T1	Off Tsugaru	350–315	2.47	1.68	1.47	1.11	43G–H
A. nihonkaiensis n. sp.		NSMT-Mo 102211	KT-11-9 E3	Off Esashi	563–635	1.86	1.30	1.43	0.99	43E–F
A. nihonkaiensis n. sp.		NSMT-Mo 102210*	KT-11-9 T3	Toyama Bay	383–460	1.91	1.36	1.40	0.97	
A. nihonkaiensis n. sp.		NSMT-Mo 102210*	KT-11-9 T3	Toyama Bay	383–460	2.14+α	1.67	—		
A. nihonkaiensis n. sp.		NSMT-Mo 102207	SO07-C5-B	Okhotsk Sea	177–176	2.55	1.78	1.43	1.15	43 L
Mean (n = 9)						2.06	1.45	1.42	0.98	
A. yamatoensis n. sp.	Holotype	NSMT-Mo 102083	TS10-T55	Yamato Bank	316–328	2.52	1.41	1.79	0.97	46A–D
A. yamatoensis n. sp.	Paratype	NSMT-Mo 102083	TS10-T55	Yamato Bank	316–328	2.76	1.39	1.99	0.94	46E–G
A. yamatoensis n. sp.		NSMT-Mo 102083*	TS10-T55	Yamato Bank	316–328	2.39	1.35	1.77	0.92	
A. yamatoensis n. sp.		NSMT-Mo 102083*	TS10-T55	Yamato Bank	316–328	1.79	1.10	1.63	0.61	
Mean (n = 4)						2.37	1.31	1.79	0.86	

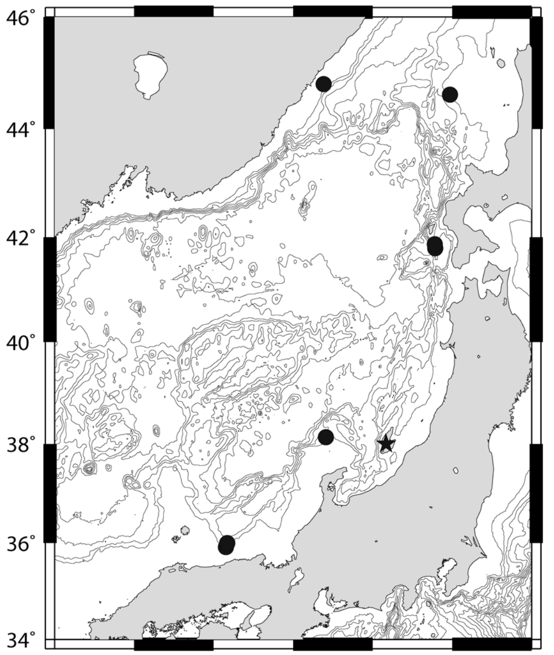


Fig. 41. Geographical distribution of *Alvania akibai*. Asterisk: type locality of *Rissoa* (*Alvania*) *akibai*.

and teleoconch characters. The illustrated syntype (Yokoyama, 1926: pl. 34, fig. 3) belongs to the former, and it is here designated as lectotype in order to avoid taxonomical confusion.

This species is characterized by the relatively large and white shell with distinct clathrate sculpture, and especially by the peculiar pockmarked protoconch sculpture, which can be easily observed under a light microscope (Fig. 37D).

Alvania nihonkaiensis **n. sp.**

[New Japanese name: Hakuboku-tsubo]

(Figs. 38D–I, 39D–I, 40C–D, 43–45, 49H; Table 8)

Type material. Holotype, NSMT-Mo 102218, KT-11-9 T3, 383–460 m (type locality) (Figs. 38D–F, 43A–D). Paratypes, NSMT-Mo 102210, from the type locality (7 and 2 radula preparations mounted on SEM stub: Fig. 43K, shell; Fig. 40C–D, radulae; Fig. 49H, operculum), NSMT-Mo 102213, from the type locality (9+3e).

Type locality. Toyama Bay, 37°29.18′N, 137°33.25′E–37°29.35′N, 137°31.96′E, 383–443 m.

Additional Material examined (Sea of Japan). NSMT-Mo 102082, KT-10-08 R2, 393–402 m (1+1e: Fig. 43I–J); NSMT-Mo 102081, KT-10-08 T1, 315–350 m (2: Fig. 43G–H); NSMT-Mo 102208, KT-11-9 E1, 220–247 m, (1); NSMT-Mo 102211, KT-11-9 E3, 563–635 m (1: Fig. 43E–F); NSMT-Mo 102212, KT-11-9 K2, 203–205 m (1 specimen mounted on SEM stub; protoconch examined by SEM); NSMT-Mo 102209, KT-11-9 T2, 207–258 m (1 specimen mounted on SEM stub; protoconch examined by SEM: Fig. 39D–F); NSMT-Mo 95826, TS09-ZY18, 235–237 m (2).

Additional Material examined (other area). Okhotsk Sea: NSMT-Mo 102207, SO07-C5-B, 176–177 m (7+1d: Figs. 38G–I, 43 L).

Distribution. From off Rebun Island south to off Oki Islands along the Japanese coasts, and off Abashiri in Okhotsk Sea, at depths of 176–635 m, with the mode around 400 m.

Diagnosis (based mainly on holotype). Shell (Figs. 38D–I, 39D–F, 43) small, 2.06 mm SL (mean of 9 specimens from Sea of Japan; Table 8), rather thin and fragile, conical in shape, opaque white with very thin yellowish periostracum. Protoconch dome-shaped, relatively small, 477 μm in width in holotype, consisting of 1.25 whorls, with sculpture of numerous spirally arranged short raised lines that form zig-zag pattern (Fig. 39D–F). End of protoconch clearly demarcated from teleoconch. Teleoconch of *ca.* 2.25–2.45 convex whorls, with strongly angulate shoulder and deeply constricted suture. Spire moderately large, occupying *ca.* 33% of shell length. Surface slightly glossy but fragile, and becoming chalky in preservative in most specimens, with weak axial and spiral sculpture. Axial sculpture consisting of regularly spaced straight, rather thin but distinct ribs that appear at beginning of first teleoconch whorl and persist to last whorl; ribs reaching from suture to suture on spire whorls but gradually disappearing toward base on last whorl, where wrinkle-like growth lines

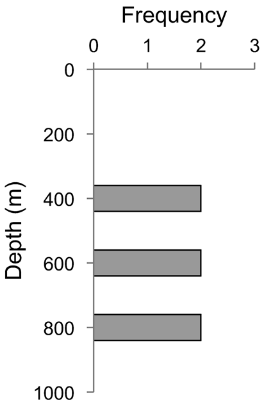


Fig. 42. Vertical distribution of *Alvania akibai* in the Sea of Japan. Number of sampling stations within 100 m of depth.

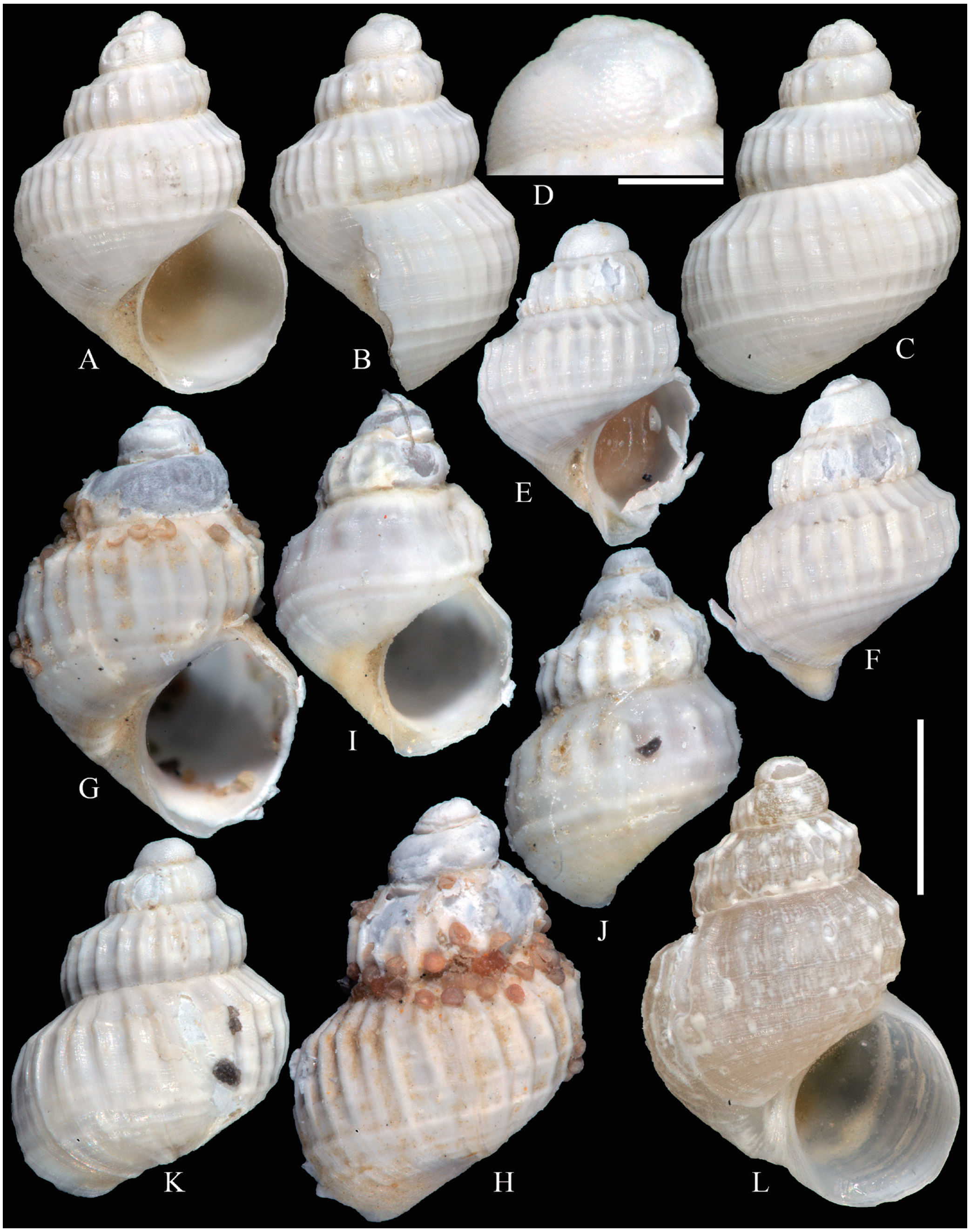


Fig. 43. Shells of *Alvania nihonkaiensis* n. sp. A–D, holotype, NSMT-Mo 102218, Toyama Bay, 383–460 m; E–F, NSMT-Mo 102211, off Esashi, 563–635 m; G–H, NSMT-Mo 102081, off Tsugaru, 315–350 m; I–J, NSMT-Mo 102082, off Rebun Island, 393–402 m; K, paratype, NSMT-Mo 102210, from the type locality; L, NSMT-Mo 102207, Okhotsk Sea, 176–177 m. All at the same scale (scale bar = 1 mm), except D (scale bar = 200 μm).

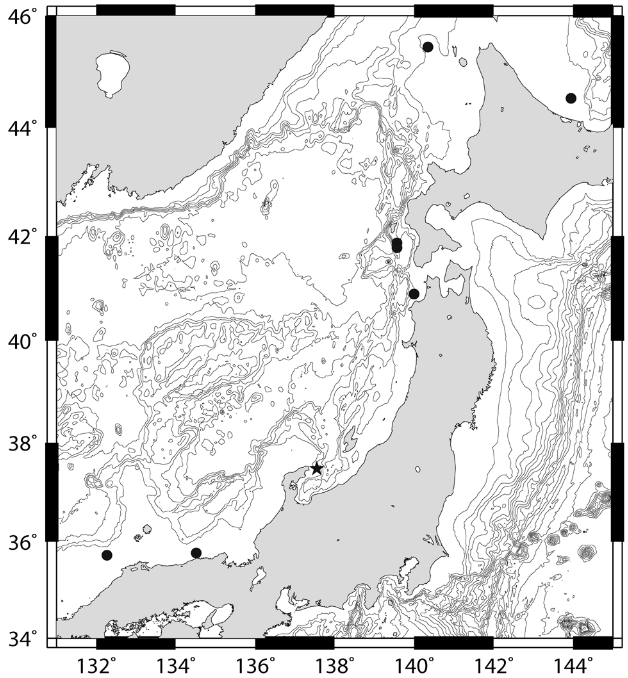


Fig. 44. Geographical distribution of *Alvania nihonkaiensis* n. sp. Asterisk: type locality.

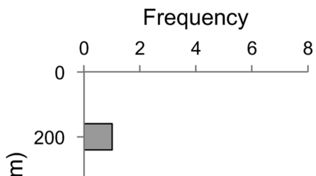


Fig. 45. Vertical distribution of *nihonkaiensis* n. sp. Number of sampling stations within 100 m of depth.

become more apparent. Spiral sculpture consisting of irregularly spaced thick cords and thread-like secondary threads. Spiral cords variable in strength, but always strongest at shoulder, becoming nodulous or spiculate at intersections with axial ribs, and below suture; several additional weaker and rather obscure threads present between them and on base, whereas no primary cords present between shoulder and suture. Secondary spiral threads usually widely spaced (Fig. 38F), but sometime more crowded, especially in specimens from Okhotsk Sea (Fig. 38I). Last whorl large in proportion and inflated. Aperture oval and angled at posterior end. Inner lip rather thin; outer lip prosocline, with no apertural varix in specimens examined. Umbilical chink very narrow and slit-like. Operculum (Fig. 49H) thin, chitinous, paucispiral, oval, with more convex outer ridge. Head-foot unpigmented, with distinctly pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe and projections. Radula (Fig. 40C–D), 71 μm in width for 1.7 mm SW. Central teeth of cusp formula 5+1+5, with narrowly elongate tongue-like central cusp and short triangular cutting edge; one pair of well-developed basal denticles; U-shaped basal extension present but irregular in shape. Lateral teeth of cusp formula 5+1+5; broad primary cusp with larger cusps on inner side, and sparse short outer cusps situated at more proximal part. Inner marginal teeth sickle-shaped, with

4 long and large cusps only on outer edge. Outer marginal teeth more slender than inner marginal teeth, tusk-like, with 3 moderate cusps only on inner side.

Variations. Despite their wide distribution, specimens from the Sea of Japan are rather uniform in conchological characters, except for the strength of the sculpture. The axial ribs tend to become stronger and more widely spaced in northern areas (Figs. 43G–H and I–J) than in southern areas (Fig. 43A–C). Although the strength and number of primary spiral cords are rather variable, two of them, one on the shoulder and other below the suture, are always strongest. On the other hand, specimens from the Okhotsk Sea superficially look different from those in the Sea of Japan, in possessing more obscure primary sculpture and crowded secondary spiral threads (Figs. 38G–I, 43 L). However, the pattern of their sculpture generally agrees with the diagnosis of this species as described above, and they have a distinct zigzag sculpture on the protoconch, ensuring conspecificity with the present new species.

Etymology. Named after the type locality, Nihon-kai (= the Sea of Japan), in Japanese.

Remarks. This species can be distinguished from other known species in the northwestern Pacific by the chalky white shell with distinct sculpture as mentioned in the "Variation", and also by the zigzag sculpture on the protoconch. Among the deep-sea rissoids, only two species are known to have a similar zigzag sculpture on the protoconch: *Alvania jeffferysi* (Waller, 1864) and *Bentonellania gofasi* Lozouet, 1990, both from the northeastern Atlantic (Bouchet and Warén, 1993: 642). However, the latter two species are very different in teleoconch features, and not comparable to the present new species.

Alvania yamatoensis **n. sp.**

[New Japanese name: Yamato-yase-tsubo]

(Figs. 38J–K, 40E, 46–47; Table 8)

Type material. Holotype, NSMT-Mo 102220, TS10-T55, 316–328 m (type locality) (Figs. 38J–K, 46A–C). Paratypes, NSMT-Mo 102083, from the type locality (4+2d+7e and 2 radula preparations mounted on SEM stub: Fig. 46E–G, shell; Fig. 47A–D, protoconch and microsculpture; Fig. 40E, radula).

Type locality. Yamato Bank, 39°04.45′N, 134°41.45′E–39°04.29′N, 134°40.90′E, 316–328 m.

Distribution. Known only from the type locality.

Diagnosis. Shell (Figs. 38J–K, 46–47) small, 2.37 mm SL (mean of 4 specimens; Table 8), rather thick for size, elongate conical in shape, opaque white with very thin yellowish periostracum, but outer surface of teleoconch eroded in most specimens. Protoconch dome-shaped, relatively small, 425 μm in width in holotype, consisting of 1.25 whorls, with coarse raised spiral lines of rather irregular shape and minute raised dots scattered in interspaces (Fig. 47A–D). End of protoconch clearly demarcated from teleoconch. Teleoconch of *ca.* 2.25–2.45 convex whorls, with strongly angulate shoulder and deeply constricted suture. Spire high, occupying 44% of shell length. Surface rather rough and coarse, with weak axial and spiral sculpture forming indistinct lattice-like appearance. Axial sculpture consisting of straight, coarse, low and rather indistinct ribs, and indistinct irregular growth lines. Axial ribs gradually appearing on first teleoconch whorl and usually persisting to, or sometimes gradually attenuating on last whorl; reaching from suture to suture on spire whorls and from suture to umbilicus on last whorl, if present. Spiral sculpture consisting of very low and indistinct cords, 6 on penultimate whorl and 10 on last whorl, and numerous indistinct microscopic secondary threads. Last whorl moderate in propor-

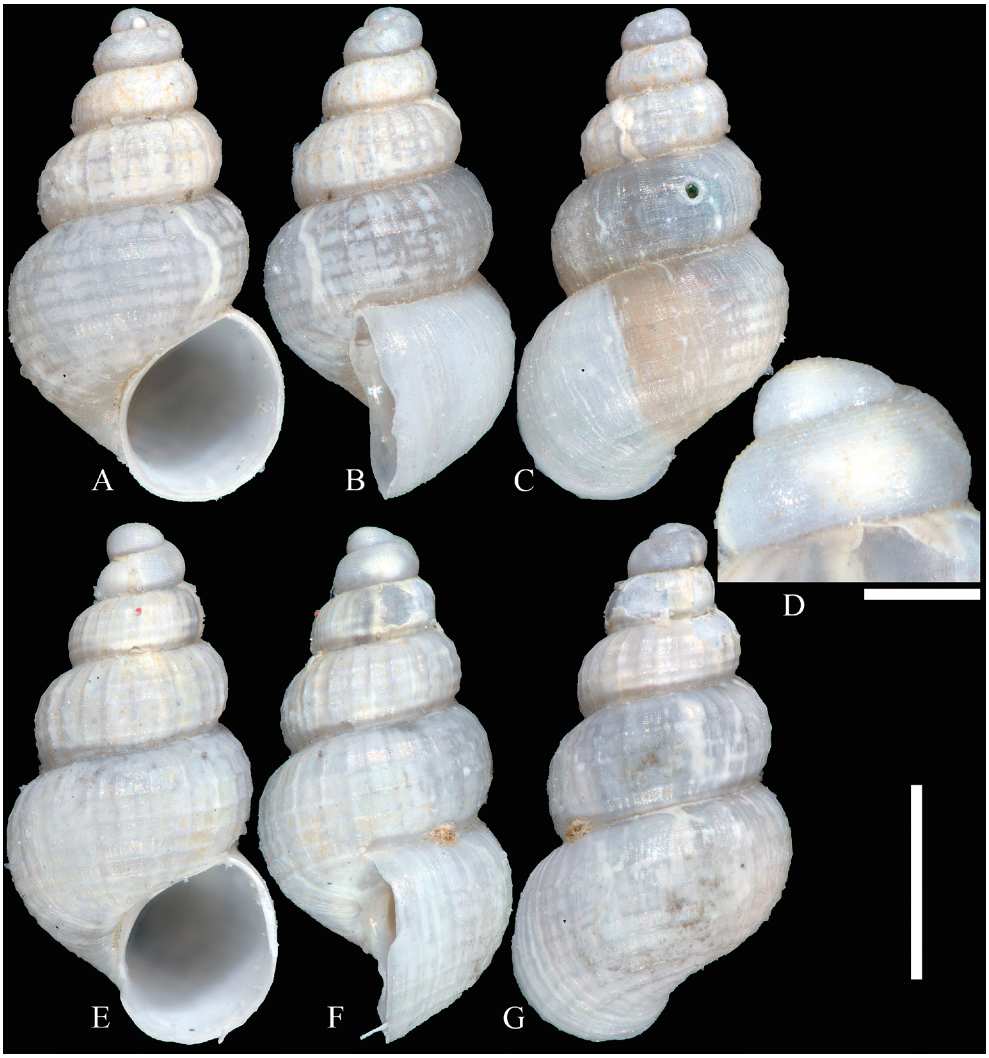


Fig. 46. Shells of *Alvania yamatoensis* n. sp. A–D, holotype, NSMT-Mo 102220, Yamato Bank, 316–328 m; E–G, paratype, NSMT-Mo 102083, from the type locality. All at the same scale (scale bar = 1 mm), except D (scale bar = 200 μm).

tion and weakly inflated. Aperture evenly rounded and weakly angled at posterior end. Inner lip rather thin; outer lip slightly prosocline, with no apertural varix among specimens examined. Umbilicus imperforate, or very narrow slit-like. Operculum thin, chitinous, paucispiral, oval, with more convex outer ridge. Head-foot unpigmented, with distinctly pigmented eyes. Penis slender, evenly tapering to tip, lacking glandular lobe and projections. Radula (Fig. 40E), 72 μm in width for 1.4 mm SW. Central teeth of cusp formula 5–6+1+5–6, with narrowly elongate central cusp and short triangular cutting edge; one pair of well-developed basal denticles; U-shaped basal extension indistinct. Lateral teeth of cusp formula 7–8+1+6–8; broad primary cusp with more crowded cusps on inner side, and sparse outer cusps situated at more proximal part; inner and outer marginal cusps on lateral teeth nearly in same size. Inner marginal teeth sickle-shaped, with more than 10 cusps only on outer edge; distal 6–7 cusps extremely long, but 4 proximal

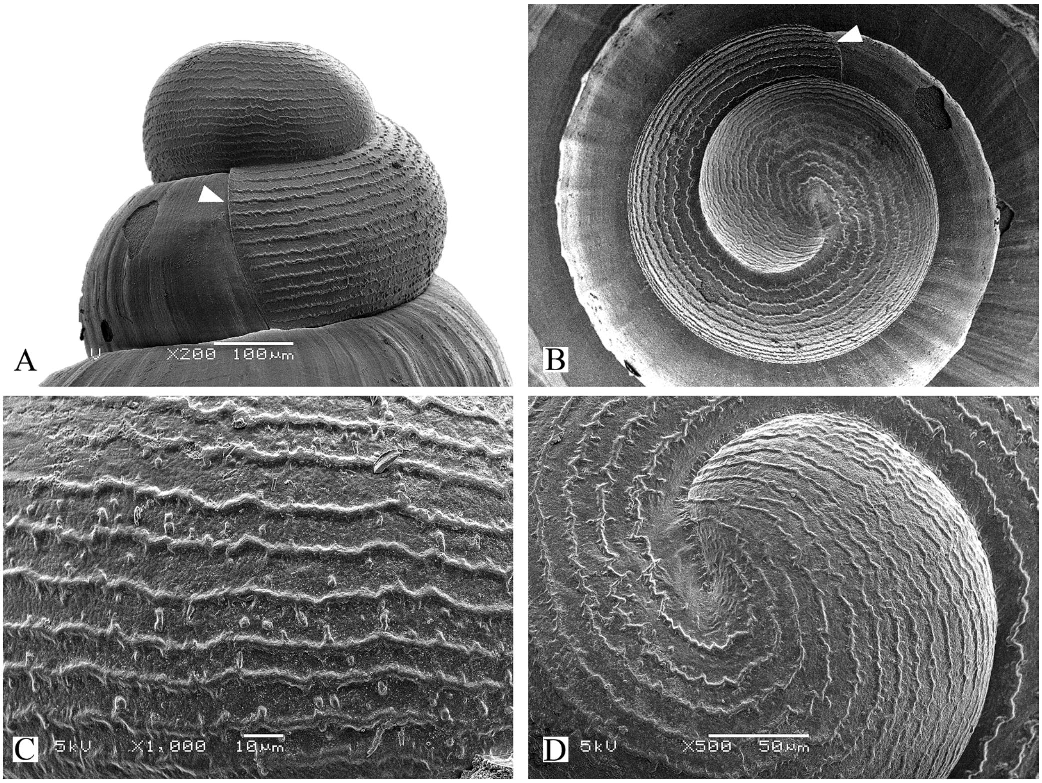


Fig. 47. SEM of protoconch of *Alvania yamatoensis* n. sp., paratype, NSMT-Mo 102083, Yamato Bank, 316–328 m (c, enlarged lateral view of the first protoconch whorl). A–B at the same scale. Arrowheads indicate demarcation between protoconch and teleoconch.

cusps short. Outer marginal teeth more slender than inner marginal teeth, tusk-like, with 4 long cusps only on inner side.

Variations. No significant variations in shell morphology were observed among the material examined, which was collected together at the same station.

Etymology. Named after the type locality, Yamato Bank, which is located in the center of the Sea of Japan.

Remarks. In overall teleoconch features, the present new species more closely resembles some species in the genus *Onoba* H. and A. Adams, 1852 (type species: *Turbo semicostatus* Montagu, 1803, western Europe and the Mediterranean Sea) than *Alvania*, particularly in its elongate conical shape. However, because of the difficulty in distinguishing two genera by conchological characters (Bouchet and Warén, 1993: 659), and considering the presence of similar species, such as *A. jeffreysi* and *A. pseudoareolata* Warén, 1974, the present new species is provisionally included in the genus *Alvania*.

This new species is characterized by the elongate white shell with thick but weak spiral cords, and can be distinguished from any other species in the family known from the northwestern Pacific, including Russian waters. Among the species in northern Atlantic, the present new species most closely resembles in protoconch sculpture *Alvania verrilli* (Friele, 1886) (Bouchet and Warén, 1993: fig. 1463), which has a similarly elongate shell but with strong axial ribs and a distinctly thickened outer lip. In the general shape of the teleoconch, it resembles *A. jeffreysi* and

Fig. 48. Shells of additional rissoid species in the Sea of Japan and adjacent waters. A–E, *Alvania awa*; A–C, holotype of *Alvania awa*, UMUT CM 8513, Pliocene fossil, Kubo Formation, Aomori Pref.; D, E, voucher specimens of "*Alvania* cf. *awa*" *fide* Ito (1985), off Sado Island, 200–300 m. F–H, *Punctulum reticulatum*, holotype, ZISP 36574/3, off Primorsky Krai, 430 m. I–K, *Frigidoalvania flavida*, holotype, ZISP 54239, Okhotsk Sea, 500 m. All at the same scale (scale bar = 1 mm).

Table 9. Measurements of additional species of Rissoidae *Alvania* spp. *: syntype of *Rissoa (Alvania) sitta*. Abbreviations: *A.*, *Alvania; F.*, *Frigidoalvania*; *P.*, *Punctulum*.

Species	Type status	Register no.	Locality	Depth (m)	SL	SW	SL/SW	AL	Figures
F. sitta	Syntype*	UMUT CM 23133	Sado I., Pliocene		4.52	2.82	1.60	1.85	14A–B
F. sitta		RFM no. 346	Off Kasumi	175	3.50	2.32	1.51	1.42	14D
F. sitta		RFM no. 346	Off Kasumi	175	4.20	2.61	1.61	1.67	14C
F. sitta		ZISP 42529	Peter the Great Bay	120	3.02	2.12	1.42	1.13	14E–F
F. sitta		ZISP 36760	Off Cape Povorotniy	67	3.62	2.40	1.51	1.40	14G
F. sitta		ZISP 28639	Peter the Great Bay	74	3.04	2.06	1.48	1.21	14H–I
F. sitta		ZISP 33510	Okhotsk Sea	144	2.36	1.49	1.58	ND	14J
A. awa	Holotype	UMUT CM 8513	Aomori Pref., Pliocene		2.59	1.66	1.56	0.96	48A–C
A. awa		RFM no. 347	Off Sado I.	200–300	2.35	1.69	1.39	1.06	48D
A. awa		RFM no. 347	Off Sado I.	200–300	2.22	1.55	1.43	1.02	48E
P. reticulutum	Holotype	ZISP 36574/3	Off Primorsky Krai	430	2.75	2.04	1.35	1.34	48F–H
P. flavidum	Holotype	ZISP 54239	Okhotsk Sea	500	2.90	1.99	1.46	1.24	48I–K

A. pseudoareolata, but differs in sculpture patterns both on the protoconch and teleoconch. Among the species distributed in the northwestern Pacific, *Alvania maya* (Yokoyama, 1926) [= "*Boreocingula castanea*" *fide* Golikov *et al.*, 2001b (*non Alvania castanella* Dall, 1887); = "*Alvania mighelsi*" *fide* Kantor and Sysoev, 2006: pl. 33, fig. A (*non Rissoa mighelsi* Stimpson, 1851)] may be comparable to the present species. However, *A. maya* is an exclusively sublittoral inhabitant, which has not been recorded from bathyal depths, and has a stouter fusiform shell with more distinct spiral and axial sculpture. There are several undescribed species that are similar to *A. maya*, and also to the present new species, in the sublittoral and upper bathyal zones around the Japanese Archipelago, including the one illustrated by Hasegawa (2009: fig. 66A–C), and they will be treated in a separate paper (Hasegawa, in preparation).

Alvania awa Chinzei, 1959
[New Japanese name: Awa-tsubo]
(Fig. 48A–E)

Alvania awa Chinzei, 1959: 109, pl. 10, figs. 1–3 [Kubo Formation, Aomori Pref., Pliocene].
Alvania sp. cf. *awa* Chinzei — Ito, 1985: 26, pl. 2, fig. 2 [off Sado and Awashima Islands, 200–300 m]

Type material. *Alvania awa* Chinzei, 1959, holotype, UMUT CM 8513 (Fig. 48A–C).

Material examined. No specimens that were identifiable as this taxon were found in the present material.

Additional material examined. Voucher material of previous records and additional specimens preserved in museums were examined as follows: RFM no. 39 (2 specimens: Figs. 48D–E).

Distribution. Recent specimens are known only from off Sado and Awashima Islands in the Sea of Japan.

Remarks. *A. awa* was originally described based on Pliocene fossils from Aomori Pref., and Recent examples comparable to this species were recorded by Ito (1985) from off Sado and Awashima Island, both in Niigata Pref., in the Sea of Japan, at bathyal depths. Voucher specimens of latter form were found in the Ito collection in the RFM (Figs. 48D–E), and compared with the type material of *A. awa*. The holotype of *A. awa* (Fig. 48A–C) is slightly more elongate in shape with a larger spire and more numerous axial ribs, but otherwise very similar to the Recent specimens (Figs. 48D–E). The Kubo Formation, the type locality of *A. awa*, belongs to the Pliocene Sannohe group, and is dominated by "Omma-Manganji" elements, which characterize a Pliocene semi-closed Sea of Japan endemic fauna (Chinzei, 1978). Although most of the

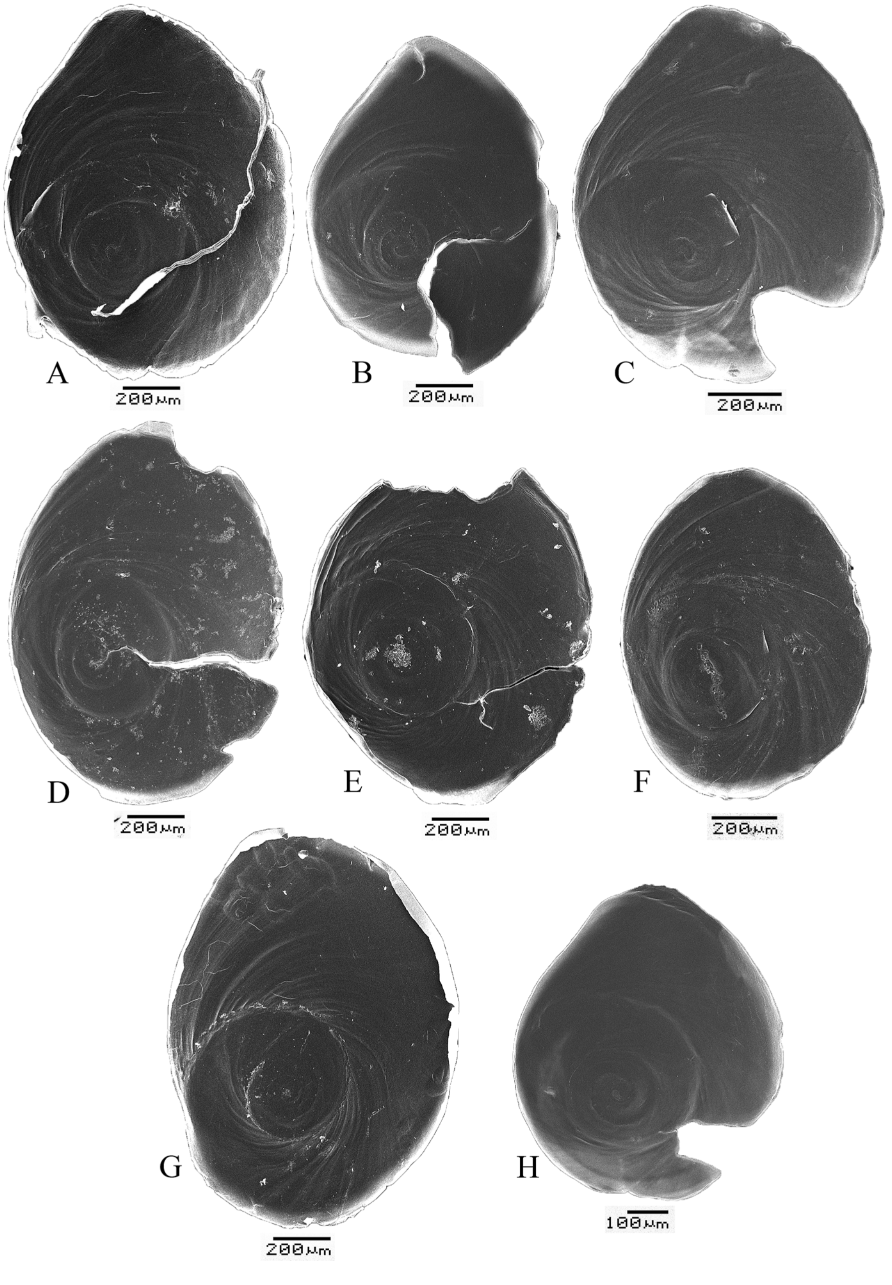


Fig. 49. SEM of opercula of rissoid species in the Sea of Japan. A, *Frigidoalvania asura*, NSMT-Mo 102087, Toyama Bay, 315–350 m. B, *F. tanseimaruae* n. sp., paratype, NSMT-Mo 102182, off Iwanai, 843–760 m. C, *Punctulum flavum*, NSMT-Mo 95838, off Oki Islands, 600–604 m. D, *P. soyomaruae* n. sp., paratype, NSMT-Mo 102194, off Esashi, 760–843 m. E, *P. sanrikuense* n. sp., paratype, NSMT-Mo 102205, off Sanriku, 818–815 m. F, *P. tanshumaruae* n. sp., paratype, NSMT-Mo 102214, off Kasumi, 411–370 m. G, *Alvania akibai*, NSMT-Mo 102175, off Kasumi, 370–411 m. H, *A. nihonkaiensis* n. sp., paratype, NSMT-Mo 102210, Toyama Bay, 383–443 m.

"Omma-Manganji" elements became extinct during Early Pleistocene (0.9–0.8 Ma), some species in the intermediate waters survived (Amano, 2007). Chinzei (1959) reported that 12 (31%) among 39 molluscan species recorded from the Kubo formation were considered to be conspecific with Recent representatives. It is therefore appropriate to identify the Recent examples with the fossil taxon, although examination of additional material is necessary to confirm this.

Discussion

More than 660 rissoid specimens obtained from the Sea of Japan at bathyal depths during the present project, were classified into eight species, including five new species (Fig. 50). In addition, examination of voucher material of previous studies resulted in the recognition of three more species in this area. Prior to the present study, eight rissoid species had been recorded from the Sea of Japan at bathyal depths, but they were re-classified into five species (excluding one that was excluded from the family) based on the examination of voucher material (see Appendix). As a result, 11 species in total are presently known to be distributed in this area. Most of these species have not been found at depths shallower than 200 m, despite extensive examination of dredged material collected from such depths (Hasegawa, personal observation), at least in the waters along the Japanese coasts. The exclusively bathyal distributions of these species exclude the possibility that they might be conspecific with ambiguous nominal taxa that were described from the Sea of Japan by A. Adams, because the latter were all based on material collected at depths of less than 115 m (see Introduction).

Two modes of adaptation to a bathyal environment are supposed for these species. All the species classified into the genera *Frigidoalvania* and *Punctulum* lack pigmented eyes, suggesting a long-term and specialized adaptation of these groups to a bathyal environment. On the other hand, all the species tentatively classified into the genus *Alvania* possess distinct black eyes, suggesting a shallow water origin. This is in accordance with the fact that many of the species in the genus *Alvania*, including type species, are known to inhabit shallow waters. In any cases, their habitats are restricted to the bathyal depths, as shown in Fig. 50.

The abundance of rissoid species in the bathyal zone of the Sea of Japan can be correlated to the geological history of the sea. It has been proved that the Sea of Japan underwent drastic environmental changes during glacial ages in the Late Tertiary to the Early Quaternary. The sea is presently connected to adjacent seas through only four narrow straits (Fig. 51); the deepest ones being the Korea/Tsushima Strait in the west and Tsugaru Strait in the east, which function as the entrance and exit of the Tsushima Current, respectively. Although the deepest parts of both straits are less than 140 m, sea level dropped as low as 130–135 m during the Last Glacial Maximum (LGM) *ca.* 20,000 years ago (Tanimura, 1981; Oba, 1988). Considerable decrease in the water circulation in this period resulted in extreme low salinity in the surface water and anoxia in the bottom water, and thus caused a large-scale extinction in the Sea. Prior to this event, during the Late Miocene (Pliocene), a unique cold-water fauna, so called Omma-Manganji fauna that contains many endemic species, had formed in the Sea of Japan. Most of these endemic species suffered extinction during the LGM (Chinzei, 1978; Amano, 2007). However, analysis of sediment micro- and nano-fossils (such as radiolarians and foraminiferans) revealed the presence of intermediate water with normal salinity and dissolved oxygen values between the depths of *ca.* 200 and 500 m throughout this period (*e.g.*, Itaki *et al.*, 2004), and this could have functioned as a refuge for a part of the deep-water fauna. The rissoids treated here may thus represent such relict species. Most of these species are considered to be endemic to the Sea of Japan and adjacent

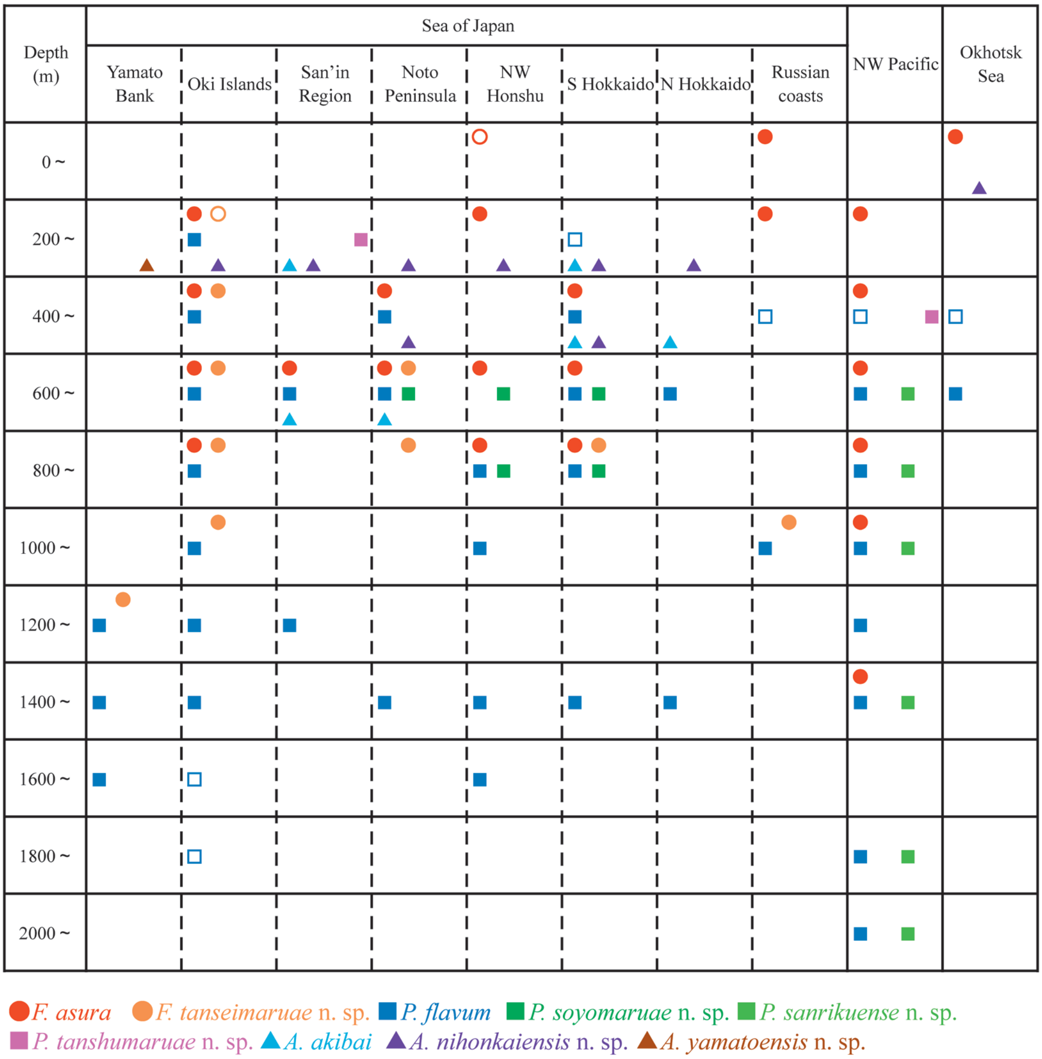


Fig. 50. Summary of geographical distributions of bathyal rissoid species in the Sea of Japan and neighboring seas. Circles, *Frigidoalvania* spp.; squares, *Punctulum* spp.; triangles, *Alvani* spp. Open symbols (squares and circles): represented only by empty shell(s).

areas, and at least four (*F. asura*, *F. sitta*, *A. akibai* and *A. awa*) each have a close (considered to be conspecific in the present study) counterpart in the Late Miocene Sea of Japan. In addition, the number of species is largest between the depths of 200 and 800 m (Fig. 50), which corresponds to the depths of the intermediate water during the LGM. On the other hand, only two species occurred below 1000 m, and they can be considered to have adapted secondarily to this newly provided environment after the LGM. Similar relationships between species diversity and depth of habitats in the Sea of Japan can be seen in other gastropod groups, especially in the Buccinidae. Although more than 29 species of the genus *Buccinum* have been recorded mainly from the continental slope and upper bathyal depths in the Sea of Japan (Higo *et al.*, 1999; Gulbin and Chaban, 2007; Hasegawa, unpublished results), only two (*B. tsubai* Kuroda in Teramachi, 1933 and *B. tenuissimum* Kuroda in Teramachi, 1933) occur below 1000 m

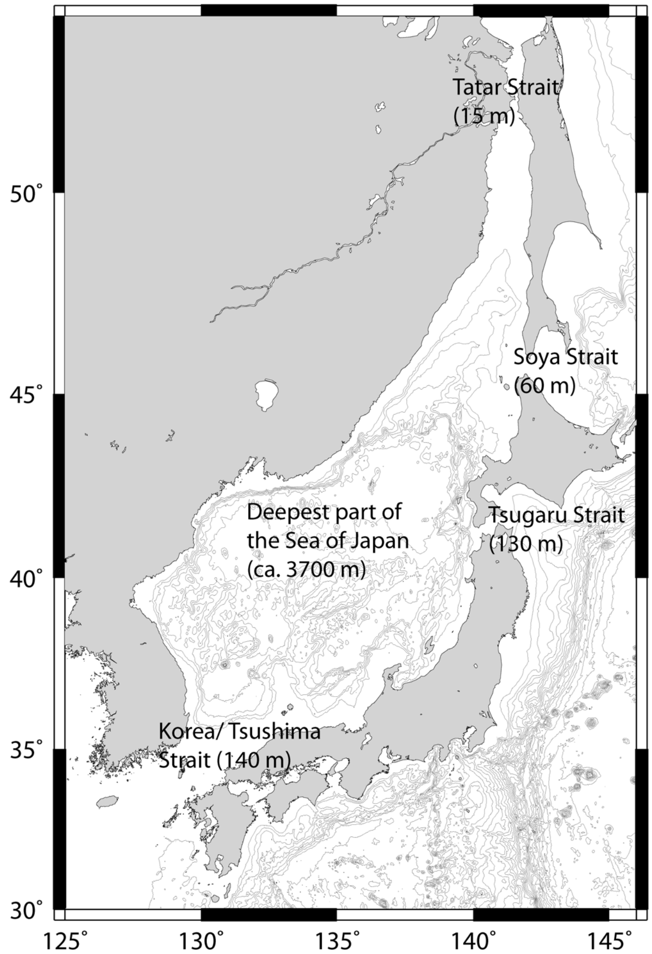


Fig. 51. Map showing the geographical overview of the Sea of Japan. Numbers in parentheses indicate the depths of the deepest part of each strait.

(Hasegawa, unpublished results). Species adapted to the bottom water tend to show very wide vertical distributions, not only in the Sea of Japan but also in the Pacific waters, as exemplified by *P. flavum* (200–2027 m in the Sea of Japan and 480–2075 m in the Pacific), and the buccinid *Neptunea intersculpta* (Sowerby, 1899), which inhabits depths of 160–1600 m in the Sea of Japan and 250–650 m in the Pacific (Hasegawa, 1999; Hasegawa, unpublished results).

Regarding geographical distributions, some species are currently known only from the Sea of Japan (*F. tanseimaruae* n. sp., *P. soyomaruae* n. sp., *A. akibai*, and *A. yamatoensis* n. sp.), but others are considered to be also distributed in other areas, such as the Pacific coasts of Japan (*P. tanshumaruae* n. sp.), Okhotsk Sea (*A. nihonkaiensis* n. sp.), and both areas (*F. asura* and *P. flavum*) (Fig. 50). Among these, the last two (*F. asura* and *P. flavum*) show especially wide geographical distributions, with a wide range of intraspecific variations, and are suspected to be mixtures of several different species. To a greater or lesser extent, if a species is distributed in geographically separated areas (*i.e.*, the Sea of Japan, the Pacific coast of Japan, and Okhotsk Sea, or even in the same area at different depths), specimens from different populations often show some differences in shell morphology. It is generally difficult to evaluate objectively the

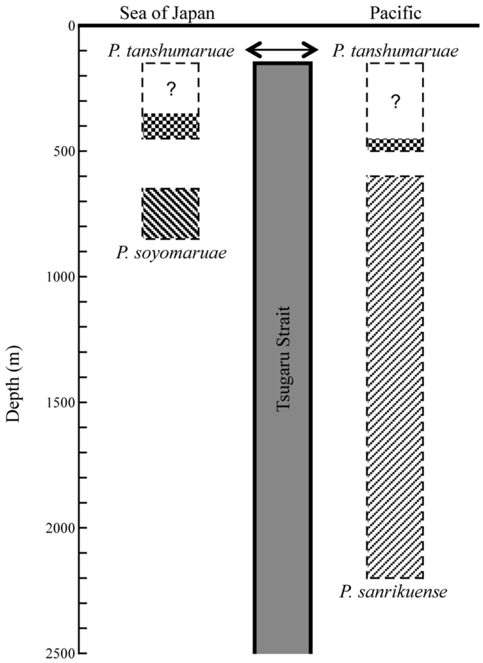


Fig. 52. Comparison of vertical distributions of *Punctulum* spp. between the Sea of Japan and the Pacific coast of northern Honshu, which are separated by the Tsugaru Strait (central bar).

extent of genetic separation on the basis of morphology alone. In the present study, definition of species was done rather subjectively by integrating ranges of variation, presence of important shared characters, and absence of probable intermediate forms. The difficulty in this evaluation is represented by the cases of *P. tanshumaruae* n. sp. and the *P. soyomaruae* n. sp./*sanrikuense* n. sp. complex. In both cases, apparent counterparts are distributed both in the Sea of Japan and the Pacific coast off northeastern Honshu at similar depths. By considering the ranges of variation and the extent of differences between the populations, the former is regarded as a single species and the latter as different species. In making this decision, vertical distributions of these populations were also taken into consideration (Fig. 52). *P. tanshumaruae* n. sp. is apparently a very rare species, compared to most others treated in this paper, and is represented in the present material only by one station each in the Sea of Japan and the Pacific, at relatively shallower depths of *ca.* 400 to 500 m. It might have a wider vertical distribution with a shallower upper limit close to the depth of Tsugaru Strait, which would make gene flow between both populations possible, in connection with fluctuations in sea level. On the other hand, the vertical distributions of *P. soyomaruae* n. sp./*sanrikuense* n. sp. are significantly deeper than *P. tanshumaruae* n. sp. (670–854 m for *P. soyomaruae* n. sp. in the Sea of Japan, and 620–2183 m for *P. sanrikuense* n. sp. in the Pacific), and it is highly probable that the populations in both areas have been separated since the formation of the Sea of Japan by the rise of Tohoku Backbone Ranges in the end of the Pliocene (Chinzei, 1978). Future molecular analyses will certainly be necessary to clarify the precise relationships among these forms.

Acknowledgments

I wish to express my sincere thanks to the captains and the crews of the research and training vessels involved in the present project, especially the R/V *Tansei-maru* and T/V *Tanshu-maru*, for their cooperation in the sampling. Thanks are also due to Drs. Ikuko Yosho, Taro Hirose and Yoichi Kogure (FRA) for arranging cruises and facilitating the samplings by T/V *Tanshu-maru*. Drs. Boris Sirenko (ZISP), Elena Krylova (IORAN), Takenori Sasaki (UMUT) and Mr. Toshiki Noguchi (RFM) kindly facilitated the examination of specimens under their care. Chifumi Hasegawa sorted out part of material from sediment samples, made measurements and put most of the data in order. Additional material was provided by Dr. Tadashi Akiyama (Okayama University), and Dr. Yasunori Kano (Atmosphere and Ocean Research Institute, the University of

Tokyo). Mr. Paul Callomon (Academy of Natural Sciences, Philadelphia) made linguistic corrections. This work would not have been possible without the help of these people. This work is a contribution from the project "Research on Deep-sea Fauna of the Sea of Japan", and supported in part by a Grant-in-Aid for Scientific Research from the Japan Society for the Promotion of Science (No. 23570126), especially for foreign travel expenses.

References

Amano, K., 2007. The Omma-Manganji fauna and its temporal change. *Fossils*, *the Palaeontological Society of Japan*, (85): 6–12. (In Japanese with English abstract.)

Anistratenko, V., 2005. Morphology and taxonomy of Late Badenian to Sarmatian *Mohrensternia* (Gastropoa: Rissooidea) of the Central Parathys. *Acta Geologica Polanica*, **55**: 371–392.

Bartsch, P., 1941. The nomenclatorial status of certain northern turritid mollusks. *Proceedings of the Biological Society of Washington*, **54**: 1–14, pl. 1.

The Committee for Celebrating Dr Okutani's Retirement from Tokyo University of Fisheries, 1996. Bibliography on the Malacological Works of Dr Takashi Okutani 1955–1994. 101 pp., 9 pls. Published by the Committee, Tokyo.

Bouchet, P. and A. Warén, 1993. Revision of the Northeast Atlantic bathyal and abyssal Mesogastropoda. *Bolletino Malacologico*, Supplemento, (3): 579–840.

Chinzei, K., 1959. Molluscan fauna of the Pliocene Sannohe Group of Northeast Honshu, Japan. 1. The faunule of the Kubo Formation. *Journal of the Faculty of Science*, *University of Tokyo*, Section II, **12** (2): 103–132.

Chinzei, K., 1978. Neogene mollouscan faunas in the Japanese islands: an ecologic and zoogeographic synthesis. *Veliger*, **21**: 155–170.

Dall, W. H., 1919. Descriptions of new species of Mollusca from the North Pacific Ocean in the collection of the United States National Museum. *Proceedings of the United States National Museum*, **56** (2295): 293–371.

Gofas, S., 2007. Rissoidae (Mollusca: Gastropoda from northeast Atlantic seamounts. *Journal of Natural History*, **41**: 779–885.

Gofas, S. and A. Warén, 1982. Taxonomie de quelques especes du genre *Alvania* (Mollusca, Gastropoda) des côtes iberiques et marocaines. *Bollettino Malacologico*, **18**: 1–16. (In French with English abstract.)

Golikov, A. N., 1986. New species of gastropods from the suborder Rissooidei. *In*: Scarlato, O. A. (ed.), Morphological and Ecological Bases of the Mollucan Taxonomy. *Proceedings of the Zoological Institute*, *Leningrad*, **148**: 86–89. (In Russian with English abstract.)

Golikov, A. N, and O. A. Scarlato, 1985. Shell-bearing gastropod and bivalve molluscs of the shelf of southern Sakhalin and their ecology. *In*: Biocenoses and Fauna of the Shelf of Southern Sakhalin. *Issledovaniya Fauny Morei*, **30** (38): 360–487. (In Russian with English abstract.)

Golikov, A. N. and B. I. Sirenko, 1998. Prosobranch gastropods of the continental slope of Kurile Islands. *Ruthenica*, **8**: 91–135. (In Russian with English abstract.)

Golikov, A. N., B. I. Sirenko and E. M. Chaban, 2001a. Subclass Pectinibranchia. *In*: Sirenko, B. I. (ed.), List of species of free-living invertebrates of Eurasian arctic seas and adjacent deep waters. *Explorations of the Fauna of the Seas*, *Zoological Institute*, *Russian Academy of Sciences*, **51** (59): 104–108.

Golikov, A. N., B. I. Sirenko, V. V. Gulbin and E. M. Chaban, 2001b. Checklist of shell-bearing gastropods of the northwestern Pacific. *Ruthenica*, **11**: 153–173.

Gulbin, V. V. and E. M. Chaban, 2007. Catalogue of the shell-bearing gastropods in the Russian waters of the Sea of Japan. Part 2. *The Bulletin of the Russian Far East Malacological Society*, **11**: 5–30.

Habe, T., 1954. Report on the Mollusca chiefly collected by the S.S. *Soyo-Maru* of the Imperial Fisheries Experimental station on the continental shelf bordering Japan during the years 1922–1930. Part 1. Cephalaspidea. *Publications of the Seto Marine Biological Laboratory*, **3**: 301–318, pl. 38.

Hasegawa, K., 1995. Occurrences of *Amphithalamus* (*Amphithalamus*) *fulcira* (Laseron, 1956) (Mollusca: Gastropoda) in Japanese waters: the first record of the family Anabathronidae from the Northwest Pacific. *Bulletin of the National Science Museum*, *Tokyo*, Series A, **21**: 143–155.

Hasegawa, K., 2000. Rissoidae. *In*: Okutani, T. (ed.), *Marine Mollusks in Japan*, pp. 148–161. Tokai University Press, Tokyo.

Hasegawa, K., 2001. Deep-sea gastropods of Tosa Bay, Japan, collected by the R/V *Kotaka-Maru* and *Tansei-Maru* during the Years 1997–2000. *In*: Fujita, T., H. Saito and M. Takeda (eds.), Deep-sea Fauna and Pollutants in Tosa Bay. *National Science Museum Monographs*, (20): 121–165.

Hasegawa, K., 2005. A preliminary list of deep-sea gastropods collected from the Nansei Islands, southwestern Japan. *In*: Hasegawa, K., G. Shinohara and M. Takeda (eds.), Deep-sea Fauna and Pollutants in Nansei Islands. *National Science Museum Monographs*, (29): 137–190.

Hasegawa, K., 2006. Sublittoral and bathyal shell-bearing gastropods chiefly collected by the T/V *Rinkai-Maru* of the University of Tokyo around the Miura Peninsula, Sagami Bay, 2001–2004. *Memoirs of the National Science Museum*, (40): 225–281.

Hasegawa, K., 2009. Upper bathyal gastropods of the Pacific coast of northern Honshu, Japan, chiefly collected by R/V *Wakataka-maru*. *In*: Fujita, T. (ed.), Deep-sea Fauna and Pollutants off Pacific Coast of Northern Japan. *National Museum of Nature and Science Monographs*, (39): 225–383.

Hasegawa, K. and T. Okutani, 2011. A review of bathyal shell-bearing gastropods in Sagami Bay. *Memoir of the National Museum of Nature and Science*, (47): 97–144.

Hatai, K. and S. Nisiyama, 1952. Check list of Japanese Tertiary marine Mollusca. *The Science Reports of the Tohoku University*, *Sendai*, *Japan*, Second Series (Geology), Special Volume (3): 1464.

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

Hirose, T., I. Yosho, S. Shirai, T. Minami and K. Niu, 2006. Development of a large-sized dredge 'Beni-Zuwai Type I' for deep sea bottom sampling. *Bulletin of the Fisheries Research Agency of Japan*, (17): 69–82. (In Japanese with English abstract.)

Horikoshi, M., T. Fujita, M. Takeda, M. Okiyama, S. Ohta, E. Tsuchida and M. Yamamoto, 1982. Preliminary compilation of the results obtained by the "Survey of continental shelf bordering Japan" carried out on board the S/S *Soyo-Maru* during 1923–1930. Report for a part of the result of Grant-in-aid for Co-operative Research (A), Ministry of Education, Science and Culture: "Studies on Off-shore and Deep-sea Faunas in the West Pacific and Indian Oceans" (Proj. No. 0053033), 252 pp.

Itaki, T., K. Ikehara, I. Motoyama and S. Hasegawa, 2004. Abrupt ventilation changes in the Japan Sea over the last 30 ky: evidence from deep-dwelling radiolarians. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **208**: 263–278.

Ito, K., 1967. A catalogue of the marine molluscan shell-fish collected on the coast of and off Tajima, Hyogo Prefecture. *Bulletin of the Japan Sea Regional Fisheries Research Laboratory*, (18): 39–91. (In Japanese with English abstract.)

Ito, K., 1985. Distribution of the molluscan shells in the surrounding areas of Sado and Awa Isls [sic], Niigata Prefecture. *Bulletin of the Japan Sea Regional Fisheries Research Laboratory*, (35): 23–127. (In Japanese with English abstract.)

Ito, K., 1989. Distribution of molluscan shells in the coastal areas of Chuetsu, Kaetsu and Sado Island, Niigata Prefecture, Japan. *Bulletin of the Japan Sea Regional Fisheries Research Laboratory*, (39): 37–133. (In Japanese with English abstract.)

Ito, K., 1990. Distribution of molluscan shells in Wakasa Bay, Japan. *Bulletin of the Japan Sea Regional Fisheries Research Laboratory*, (40): 79–211. (In Japanese with English abstract.)

Ito, K., 1999. Ito Katsuchiyo-shi Kiso Korekushon. Kaisan-kairui So-mokuroku [A Catalogue of Marine Shells in the Collection Donated by Katsuchiyo Ito]. 133 pp. Ryotsu Kyodo Hakubutsukan [Ryotsu Folk Museum], Sado, Niigata. (In Japanese; title translated.)

Ito, K., Y. Matano, Y. Yamada and S. Igarashi, 1986. Shell species caught [*sic*] S/S Rokko-Maru off the coast Ishikawa Prefecture. *Bulletin of Ishikawa Prefectural Fisheries Experimental Station*, (4): 1–179. (In Japanese with English abstract.)

Jeffreys, J. G., 1884. On the Mollusca procured during the Lightning and Porcupine expeditions. Part VII. *Proceedings of the Zoological Society of London*, 1884: 111–149, pls. 9–10.

Kantor, Yu. I. and A. V. Sysoev, 2006. Marine and Brackish Water Gastropoda of Russia and adjacent Countries: an Illustrated Catalogue. 371 pp., 140 pls. KMK Scientific Press Ltd., Moscow.

Kato, F., 1979. Studies on the distribution of four species of edible deep sea whelk (Mollusca, Bccinidae) in the Japan Sea. *Bulletin of the Japan Sea Regional Fisheries Research Laboratory*, (30): 15–27.

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

Laseron, C. F., 1956. The families Rissoinidae and Rissoidae (Mollusca) from the Solanderian and Dampierian Zoogeographical Provinces. *Australian Journal of Marine and Freshwater Research*, **7**: 388–484.

Makiyama, J., 1958. Matajiro Yokoyama's Tertiary fossils from various localities in Japan. Part II. *Palaeontological Society of Japan Special Papers*, (4): 1–6, 57 pls.

Nevill, G., 1885. Hand List of Mollusca in the Indian Museum, Calcutta. Part II. Gastropoda. Prosobrachia–Neurobranchia (contd.). x+306 pp. Office of Superintendent of Government Printing, Calcutta.

Nordsieck, F., 1972. Die europäischen Meeresschnecken. Opisthobranchia mit Pyramidellidae Rissoacea. xiii+327 pp. Gustav Fischer Verlag, Stuttgart.

Oba, T., 1988. Comment for sea level change. *The Quaternary Research*, **26**: 243–250. (In Japanese with English abstract.)

Ogasawara, K., K. Masuda and Y. Matoba (eds.), 1986. Neogene and Quaternary Molluscs from the Akita Oil-field, Japan. 310 pp., 85 pls. Commemorative Association of Professor Taisuke Takayasu's retirement and Supporters' Fundation [*sic*] of Mineral Industry Museum, Mining College, Akita University, Akita.

Okutani, T., 1964. Report on the archibenthal and abyssal gastropod Molluca mainly collected from Sagami Bay and adjacent waters by the R. V. *Soyo-Maru* during the years 1955–1963. *Journal of the Faculty of Science*, *University of Tokyo*, Section II, **15**: 371–447, pls. 1–7.

Ponder, W. F., 1967. The classification of Rissoacea and Orbitestellidae with descriptions of some new taxa. *Transactions of the Royal Society of New Zealand*, Zoology, **9**: 193–224.

Ponder, W. F., 1983. Rissoaform gastropods from the Antarctic and sub-Antactic. The Eatoniellidae, Rissoidae, Barleeidae, Cingulopsidae, Orbitestellidaea and Rissoellidae (Mollusca: Gastropoda) of Signy Island, South Orkney Island, with a review of the Antarctic and sub-Antactic (excluding southern South America and the New Zealand sub-Antarctic islands) species. *British Antarctic Survey*, *Scientific Reports*, (108): 1–95.

Ponder, W. F., 1985. A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). *Records of the Australian Museum*, Supplement, (4): 1–221.

Ponder, W. F. and R. de Keyzer, 1992. A revision of the genus *Diala* (Gastropoda: Cerithioidea: Dialidae). *Invertebrate Taxonomy*, *an Australian Journal of Scientific Research*, **6**: 1019–1075.

Ponder, W. F. and T. M. Worsfold, 1994. A review of the rissoiform gastropods of southwestern South America. *Contributions in Science*, *Natural History Museum of Los Angeles County*, (445): 1–63.

Risso, A., 1826. Des principals productions de l'Europe Méridionale. *Histoire Naturelle*, **4**: 1–439, pl. 1–12. (Not seen by the present author.)

Rolán, E., 2005. Malacological Fauna from the Cape Verde Archipelago. Part 1. Polyplacophora and Gastropoda. 455 pp. ConchBooks, Hackenheim.

Sirenko, B. I., 2009. The prosobranchs of the gastropods (Mollusca, Gastropoda, Prosobranchia) of the Chukchi Sea and Bering Strait, their species composition and distribution. *In*: Sirenko, B. I. (ed.), Ecosystems and Biological resources of the Chukchi Sea and Adjacent Areas. *Explorations of the Fauna of the Seas*, *Zoological Institute*, *Russian Academy of Sciences*, **64** (72): 104–153. (In Russian with English abstract.)

Tanimura, Y., 1980. Late Quaternary diatoms and paleoceanography of the Sea of Japan. *The Quaternary Research*, **20**: 231–242. (In Japanese with English abstract.)

Tsuchida, E. and I. Hayashi, 1994. Characteristics of lower-sublittoral and bathyal molluscs in the western area of the Sea of Japan. *Bulletin of the Japan Sea National Fisheries Research Institute*, (44): 81–129.

Tsuchida, E. and S. Hori, 1996. Marine mollusks around Mishima and Tsunoshima Islands, Japan Sea collected by the R/V *Tansei-Maru*. *Bulletin of the National Science Museum*, Series A (Zoology), **22**: 219–262.

Warén, A., 1973. Revision of the Rissoidae from the Norwegian North Atlantic Expedition 1876–78. *Sarsia*, (53): 1–13.

Warén, A., 1974. Revision of the Arctic-Atlantic Rissoidae (Gastropoda, Prosobranchia). *Zoologica Scripta*, **3**: 121–135.

Yokoyama, M., 1926. Fossil shells from Sado. *Journal of the Faculty of Science*, *Imperial University of Tokyo*, Section II Geology, Mineralogy, Geography, Seismology, **1**: 249–312, pls. 32–37.

Appendix

Summary of previous records of rissoids at bathyal depths (deeper than 200 m) in the Sea of Japan

Alvania ferruginea A. Adams, 1861 – Golikov *et al.*, 2001b: 158 [northern Sea of Japan: 8–250 m] (= *Frigidoalvania sitta*; *non Alvania ferruginea* A. Adams, 1861).

Alvania asura (Yokoyama) – Ito, 1967: 50 [off Tajima, Hygo Pref.: *ca.* 300–400 m]; Ito, 1985: 26, pl. 2, figs. 1–1–2 [Awashima Island: 200–250 m; Suizu, Sado Island: 200–300 m; Akadama, Sado Island: 200–250 m]; Ito *et al.*, 1986: 8–9, pl. 4, fig. 4 [off Ishikawa Pref.: 100–264 m]; Ito, 1999: 18 [off Kasumi, Hygo Pref.: 350–400 m] (= *Frigidoalvania asura*).

Alvania cf. *awa* Chinzei – Ito, 1985: 26, pl. 2, fig. 2 [Awashima Island: 200 m; Suizu, Sado Island: 200–300 m; Akadama, Sado Island: 200–250 m]; Ito, 1999: 18 [off Sado, Niigata Pref.: 200–300 m] (= *Alvania awa*).

Alvania sitta (Yokoyama, 1926) – Ito *et al.*, 1986: 9, pl. 4, fig. 4 [E off Ishikawa Pref.: 200–204 m] (= *Frigidoalvania sitta*).

Lucidestea oranata [sic = *ornata*] (Gorokov [sic = Gorikov] & Kussakin) – Ito, 1999: 19 [Toyama Bay: 300–400 m] (= *Menestho* sp. [Pyramidellidae]; *non Falsisetia ornata* Golikov and Kussakin in Golikov and Scarlato, 1967; voucher specimens examined, RFM no. 386).

Frigidalvania janmayeni (Friele, 1878) – Golikov *et al.*, 2001b: 158 [northern Sea of Japan: 8–890 m]. (= *Frigidoalvania asura*; *non Rissoa janmayeni* Friele, 1878).

Punctulum reticulatum Golikov, 1986: 88–89, fig. 4 [type locality: off Primorsky Krai, near Rynda Bay, 430 m in the Sea of Japan]; Golikov *et al.*, 2001b: 158 [northern Sea of Japan: 240–880 m] (valid).

Punctulum sp. – Golikov *et al.*, 2001b: 158 [northern Sea of Japan: 373–494 m] (= *Alvania akibai*).