Ruthenica, 2022, vol. 32, No. 2: 85-92.
Published online April 1, 2022.

http: ruthenica.net

Bathyal Rissoidae (Gastropoda: Rissooidea) off the Russian Far East coast of the Sea of Japan, with redescription of *Punctulum reticulatum* Golikov, 1986

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ABSTRACT. Examination of unsorted microgastropod samples collected during the joint Russia-German research "Sea of Japan Biodiversity Studies (SoJaBio) Expedition" in 2010 and preserved in the National Scientific Center of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, resulted in the finding of six species of the family Rissoidae. Among them, "*Alvania*" *nihonkaiensis* Hasegawa, 2014 is newly recorded both in Russian waters and on the northern slope of the Sea of Japan, and *Punctulum reticulatum* Golikov, 1986 was rediscovered for the first time since its original description. Geographical and vertical distributions of each species and their significance are updated and discussed.

https://doi.org/10.35885/ruthenica.2022.32(2).5:

Батиальные Rissoidae (Gastropoda: Rissooidea) российского дальневосточного побережья Японского моря, с переописанием *Punctulum reticulatum* Golikov, 1986

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РЕЗЮМЕ. В результате изучения несортированных проб микрогастропод, собранных во время совместной Российско-Германской экспедиции "Sea of Japan Biodiversity Studies (SoJaBio) Expedition" в 2010 г. и хранящихся в Национальном научном центре морской биологии ДВО РАН, Владивосток, обнаружено шесть видов семейства Rissoidae. Среди них "*Alvania*" *nihonkaiensis* Hasegawa, 2014 впервые отмечена в Российских водах и на северном склоне Японского моря, а *Punctulum reticulatum* Golikov, 1986 впервые найден после первоописания. Уточняется и обсуждается географическое и вертикальное распределение каждого вида.

Introduction

The family Rissoidae is a group of minute gastropods with high taxonomic diversity, represented by a large number of species in various habitats from intertidal to abyssal depths throughout the world's oceans. However, knowledge of their taxonomy in deep waters, especially in the Northwest Pacific, had been limited until Hasegawa [2014] published a detailed taxonomic review of the family in the Sea of Japan and adjacent waters (parts of the Okhotsk Sea and the Northwest Pacific). That study was based mainly on material collected by a deep-water survey carried out by the National Museum of Nature and Science, Tsukuba, during the years 2009–2013 on the Japan-side (southeastern) slope of the sea [Saito *et al.*, 2014], as well as some additional specimens collected from Russian waters and preserved in Russian museums. Another deep-water survey program, called the "Sea of Japan Biodiversity Studies (SoJaBio) Expedition", was carried out in 2010 on the Russian (northern) slope as a joint Russian-German project [Malyutina, Brandt, 2013]. Although taxonomic studies based on the latter expedition were published in 2013 as a special issue of the journal *Deep-Sea Research II*, shell-bearing heterobranchs were the only gastropods treated [Chaban, Chernyshev, 2013] and there was only a brief mention that 12 "prosobranchs" were collected during the survey [Malyutina, Brandt, 2013].

In 2014 I had an opportunity to examine gastropod specimens preserved in the museum of the A.V. Zhirmunsky Institute of Marine Biology (now the National Scientific Center of Marine Biology; NSCMB) at the Far Eastern Branch of the Russian Academy of Sciences in Vladivostok, and found among its collections some vials containing unsorted minute gastropods that were collected during the SoJaBio Expedition. Examination of this material revealed a considerable number of rissoid specimens. Although some rissoids from Russian waters,

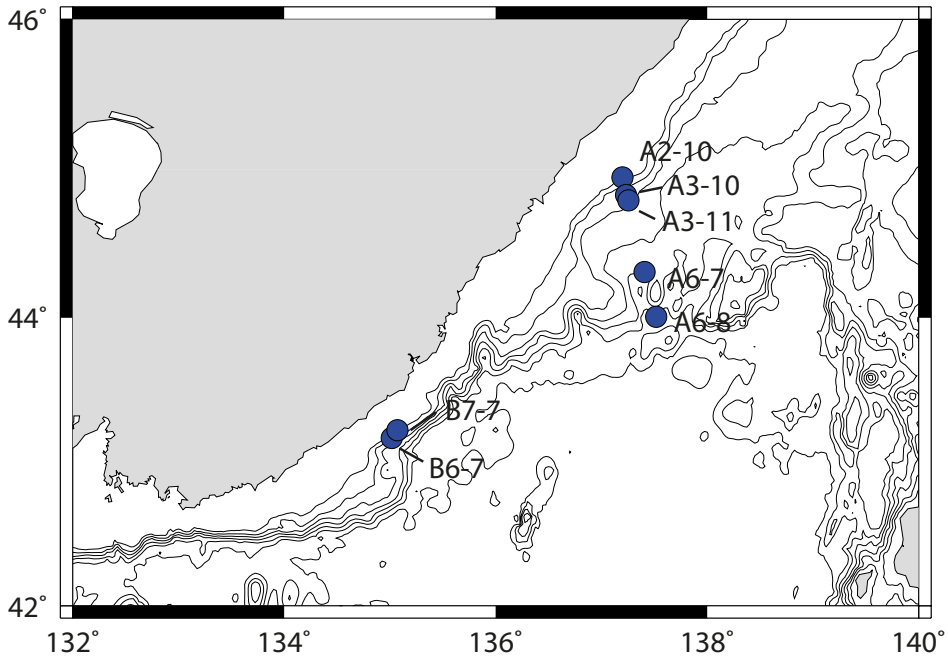

FIG. 1. A map showing the SoJaBio stations at which species of Rissoidae occurred.

РИС. 1. Карта станций SoJaBio, на которых были собраны Rissoidae.

including the Far Eastern region, were treated by Hasegawa [2014] as mentioned above, the material from the SoJaBio expedition is specially important in understanding the species composition and vertical distribution of each species on the northern slope of the Sea of Japan, because of the survey's systematically designed sampling method. Furthermore, one species, *Punctulum reticulatum* Golikov, 1986, that had been known only from the type material [Hasegawa, 2014], was discovered in the material.

Materials and methods

The main body of the material examined in the present study was collected during the sampling program "SoJaBio Expedition" [Malyutina, Brandt, 2013] and stored in the NSCMB, Vladivostok. Minute gastropods were found mixed and preserved in ethanol in vials by stations (six in total within a depth range of 455 to 2555 m; Table 1, Fig. 1). Rissoid specimens were sorted out and identified to species under a stereomicroscope in the NSCMB laboratory, though without destructive treatments such as examination of radula and soft parts or drying for SEM. Shells of representative specimens were photographed using a Nikon D300 digital camera with a reversed AF Nikkor 20 mm F2.8 lens and a PN-11 extension ring. At least 10 shots in gradually changing focus planes were taken and combined with the aid of the focus-stacking software CombineZP. All the combined images were processed with Adobe Photoshop.

Additional records of each species from Russian Far East waters are cited from Hasegawa [2014].

Institutional abbreviations for registration of specimens: MIMB – Museum of A.V. Zhirmunsky National Scientific Center of Marine Biology (formerly Institute of Marine Biology), Far Eastern Branch of the Russian Academy of Sciences, Vladivostok; NSMT – National Museum of Nature and Science, Tsukuba, Japan; ZIN – Zoological Institute, Russian Academy of Sciences, St. Petersburg.

Results

Six species in two genera of the family Rissoidae were recognized in the SoJaBio material collected from the northern slope of the Sea of Japan at bathyal depths and preserved in the NSCMB (Table 2). Results are summarized in the Taxonomy section, with some remarks on taxonomy and distribution and comparison with the results of Hasegawa [2014]. Because *Punctulum reticulatum* Golikov, 1986 was rediscovered for the first time since its original description, a more detailed description and synonymy are given.

Taxonomy

Family Rissoidae Gray, 1847

Genus *Alvania* Risso, 1826: 140

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

Remarks. Criscione *et al.* [2017] suggested in their molecular phylogenetic study that all the rissoid species examined by them from bathyal depths in the Sea of Japan, e.g. *Alvania* cf. *akibai*, *Frigidoalvania asura*, *Puctulum flavum* and *P. tanseimaruae*, formed

Table 1. Station data of material treated in the present study from SoJaBio expedition.

Табл. 1. Данные о станциях экспедиции SoJaBio, на которых был собран материал, рассмотренный в данной статье.

Station	Date	Position in		Position out		Depth (m)
		Latitude (N)	Longitude (E)	Latitude (N)	Longitude (E)	
A 2-10	13 August 2010	44°56.9197’	137°11.8947’	44°57.0193’	137°11.9896’	455-456
A 3-10	14 August 2010	44°49.8620’	137°13.9974’	44°50.0210’	137°14.0932’	1354-1356
A 3-11	14 August 2010	44°47.6338’	137°15.3182’	11°47.8110’	137°15.3922’	1494-1525
A 6-7	14 August 2010	44°00.2607’	137°31.1584’	44°19.2650’	137°24.1206’	2511-2534
A 6-8	14 August 2010	44°18.6270’	137°24.4079’	44°18.4712’	137°24.3985’	2545-2555
B 6-7	24 August 2010	43°10.3999’	135°00.9751’	43°10.2513’	135°00.9239’	1001-1011
B 7-7	25 August 2010	43°13.4578’	135°04.3295’	43°13.5809’	135°04.1939’	470-528

Table 2. Occurrence of species. + indicates the occurrence of the species from each station in SoJaBio Expedition.

Табл. 2. Распределение видов по станциям. + обозначает нахождение вида на станции экспедиции SoJaBio.

Species	Stations (depths: m)						
	A-2-10 (455-456)	A-3-10 (1354-1356)	A-3-11 (1494-1525)	A-6-7 (2511-2534)	A-6-8 (2545-2555)	B-6-7 (1001-1011)	B-7-7 (470-528)
“Alvania” akibai	+					+	+
“Alvania” nihonkaiensis	+						
Frigidoalvania asura						+	+
Frigidoalvania tanseimaruae						+	+
Punctulum flavum		+	+	+	+	+	+
Punctulum reticulatum	+						+

a well-supported clade with small genetic distances, and are clearly separated from *Alvania sensu stricto*. It is thus apparent that the following two species cannot ultimately be assigned to the genus *Alvania*. However, they are here provisionally retained therein, both because of the incompleteness of our understanding of the phylogenetic relationships of genera in the family and the absence of an appropriate genus to accommodate them.

“Alvania” akibai (Yokoyama, 1926)
(Fig. 2A)

Rissoa (*Alvania*) *akibai* Yokoyama, 1926: 275, pl. 34, fig. 3 (see Hasegawa [2014] for more detailed synonymy).

Material examined. SoJaBio A 2-10, MIBM 39336 (Fig. 2A); SoJaBio B 6-7, MIBM 14492; SoJaBio B 7-7, MIBM 39342 [depth range: 455–1011 m].

Additional material examined (cited from Hasegawa, 2014). ZIN, 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*., 2001: 158).

Distribution. Off Primorsky Krai coast on the northern slope, and from Musashi Bank to off Shimane Prefecture on the southeastern slope in the Sea of Japan, within the depth range of 220–1011 m.

Remarks. This species was originally described based on fossils from the Pliocene Sawane Formation on Sado Island in the Sea of Japan, and is characterized by the peculiar pockmarked protoconch sculpture [Hasegawa, 2014: fig. 37D]. Its previously known vertical distribution range was 220–635 m, and that is significantly extended to 1011 m in the present study.

“Alvania” nihonkaiensis Hasegawa, 2014
(Fig. 2B)

Alvania nihonkaiensis Hasegawa, 2014: 132–135, figs 38 D–I, 39 D–F, 40 C–D, 43–45, 49H; table 8.

Material examined. SoJaBio A 2-10, MIBM 39337 (depth range: 455–456 m).

Distribution. Off Primorsky Krai coast on the northern slope, and from off Rebun Island south to off Oki Island on the southeastern slope in the Sea of Japan; off Abashiri in the Okhotsk Sea, within the depth range of 176–635 m.

Remarks. As with the preceding one, this species is also characterized by its distinct protoconch morphology, in this case a zigzag sculpture. Although only one juvenile specimen was recognized among the present material, it was confidently identified based on this character. This is the first record of this

species from the northern slope of the Sea of Japan, as well as in any Russian waters.

Genus *Frigidoalvania* Warén, 1974: 125

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

Remarks. Although Criscione *et al*. [2019] suggested that this genus is genetically closely related to *Punctulum*, as noted above, it is provisionally retained as distinct because of differences in some morphological characters, including details of the anatomy and metapodial tentacles [Ponder, 1984], and the radula [Hasegawa, 2014: 82].

Frigidoalvania asura (Yokoyama, 1926) (Fig. 2 C–D)

Rissoa (Apicularia?) asura Yokoyama, 1926: 273, pl. 33, fig. 15 (see Hasegawa [2014] for more detailed synonymy).

Material examined. SoJaBio B 6-7, MIBM 14992; SoJaBio B 7-7, MIBM 39340 (Fig. 2 C–D) [depth range: 470–1011 m].

Additional material examined (cited from Hasegawa, 2014). ZIN 33623, off SW Sakhalin, N. Sea of Japan, 202–222 m, 49°14.8'N, 141°09.7'E, 100 m; ZIN 33625, Peter the Great Bay, 42°18.8'N, 131°09.5'E, 247 m; ZIN 36609, Peter the Great Bay, 42°15.4'N, 130°44.6'E, 140 m; ZIN 36610, Peter the Great Bay, 42°28.0'N, 131°40.5'E, 125 m; ZIN 36611, Peter the Great Bay, 42°25.7'N, 132°36.8'E, 157–140 m; ZIN 36612, Peter the Great Bay, 42°33.0'N, 132°51.0'E, 133 m; ZIN 36613, Peter the Great Bay, 42°35.3'N, 132°51.1'E, 110 m; ZIN 36614, Peter the Great Bay, 42°35.7'N, 133°06.2'E, 143 m; ZIN 36615, Peter the Great Bay, 42°38'N, 132°43.2'E, 100 m [depth range: 100–247 m].

Distribution. Widely distributed in the Northwest Pacific, from the eastern part of the Okhotsk Sea to the southernmost part of the Sea of Japan, and to Sagami Bay along the Pacific coast. Depth range in the Sea of Japan is 100–1011 m.

Remarks. Although this species was considered by Hasegawa [2014] to be widely distributed in the North Pacific and its marginal seas, there are considerable differences in the shape and sculpture of the shell between geographic areas, even within the Sea of Japan. More detailed analysis using molecular techniques may reveal genetic and thus taxonomic distinctions.

Frigidoalvania tanseimaruae Hasegawa, 2014 (Fig. 2 E–F)

Frigidoalvania tanseimaruae Hasegawa, 2014: 93–97, figs 4 G–K, 6 E–F, 10–13, 49B; table 5.

Material examined. SoJaBio B 6-6, MIBM 39347; SoJaBio B 6-7; SoJaBio B 7-7 [depth range: 470–1011 m]

Additional material examined (cited from Hasegawa, 2014). 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.

Distribution. Off Primorsky Krai coast on the northern slope, and from off southwestern Hokkaido to off Oki Island on the southeastern slope in the Sea of Japan, 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.

Remarks. This species is superficially similar to some in the genus *Punctulum* through its rather thin periostracum and distinct teleoconch sculpture, but can be assigned to *Frigidoalvania* because of the close similarities in protoconch and radula characters to *F. asura* [Hasegawa, 2014]. The intermediate state of characters of this species, however, may reinforce the closeness of the two nominal genera.

Genus *Punctulum* Jeffreys, 1884: 122

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

Punctulum flavum (Okutani, 1964) (Fig. 2 G–I)

Microstelma flava Okutani, 1964: 389–390, pl. 6, fig. 5 (see Hasegawa [2014] for more detailed synonymy).

Material examined. SoJsBio A 2-10, MIBM 14270 (Fig. 2 G–H); SoJsBio A 3-10, MIBM 39344; SoJsBio A 3-11, MIBM 39335; SoJaBio A 6-7, MIBM 39334 (Fig. 2 I–J); SoJaBio A6-8, MIBM 14412; SoJaBio B 6-6, MIBM 39346; SoJaBio B 6-7, MIBM 14492; SoJaBio B 7-6, MIBM 39345; SoJaBio B 7-7, MIBM 39341 [depth range: 470–2555 m].

Additional material examined (cited from Hasegawa, 2014). 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.

Distribution. Off the Primorsky Krai coast on the northern slope, and from off Rebun Island to the southernmost part of the southeastern slope in the Sea of Japan; the western Okhotsk Sea and Pacific coast of the Japanese archipelago south to Kyushu. Depth range in the Sea of Japan is 200–2027 m.

Remarks. On both the northern and southeastern slopes of the Sea of Japan, two distinct phenotypes have been recognized in this species that are distinguished by the depth of their habitat [Hasegawa, 2014]. Down to ca. 1,000 m, specimens possess a low conical shell, with strong axial and spiral sculpture (the "shallow-water form"; Fig. 2G, H), while those from deeper stations possess a more inflated shell with very much weaker sculpture (the "deep-water form"; Fig. 2I, J). Furthermore, there is a correlation between the size of the protoconch and depth, with the "deep-water form" tending to have a larger protoconch. These two forms are still considered conspecific here because of the presence of intermediate forms at around 1,000 m. However, Criscione *et al*. [2019] indicated the presence of two genetically slightly distinct specimens identified as *P. flavus* and *P.* cf. *flavus* in their analysis and if the latter corresponds to the "deep-water form", the two may be separable as distinct species.

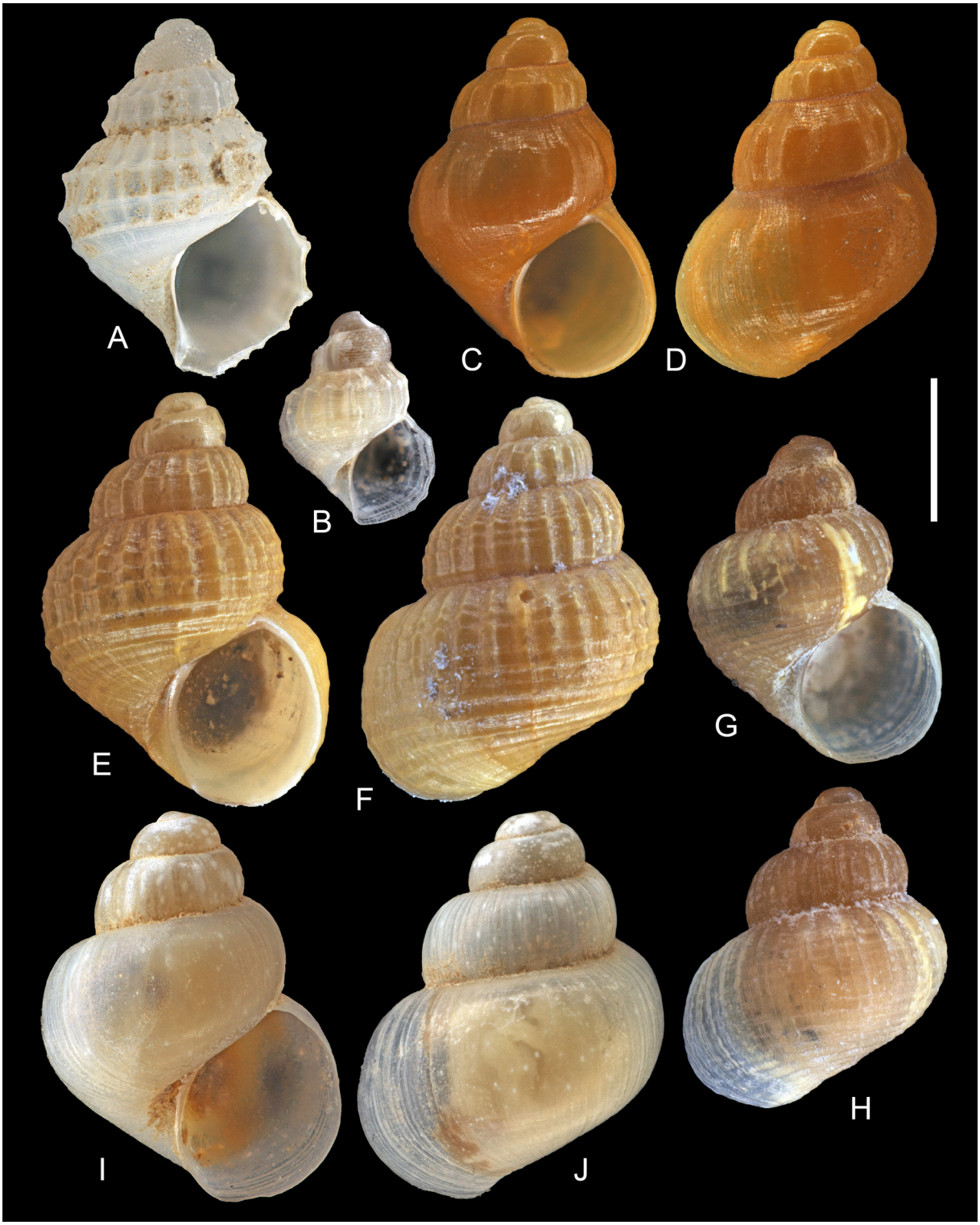

FIG. 2. Species of Rissoidae. **A.** *Punctulum akibai* (Yokoyama, 1926), SoJaBio stn. A2-10 (455-456 m), MIBM 39336. **B.** *Punctulum nihonkaiensis* (Hasegawa, 2014), SoJaBio stn. A2-10 (455-456 m), MIBM 39337. **C-D.** *Frigidoalvania asura* (Yokoyama, 1926), SoJaBio stn. B7-7 (470-528 m), MIBM 39340. **E-F.** *Frigidoalvania tanseimaruae* Hasegawa, 2014, SoJaBio stn. B6-7 (1,001-1,011 m). **G-J.** *Punctulum flavum* (Okutani, 1964); G-H, "shallow-water form", SoJaBio stn. A2-10 (455-456 m), MIBM 14270; I-J, "deep-water form", SoJaBio stn. A6-7 (2,511-2,534 m), MIBM 39334. All at the same scale; scale = 1 mm.

РИС. 2. Виды Rissoidae. **A.** *Punctulum akibai* (Yokoyama, 1926), SoJaBio ст. A2-10 (455-456 м), MIBM 39336. **B.** *Punctulum nihonkaiensis* (Hasegawa, 2014), SoJaBio ст. A2-10 (455-456 м), MIBM 39337. **C-D.** *Frigidoalvania asura* (Yokoyama, 1926), SoJaBio ст. B7-7 (470-528 м), MIBM 39340. **E-F.** *Frigidoalvania tanseimaruae* Hasegawa, 2014, SoJaBio ст. B6-7 (1001-1011 м). **G-J.** *Punctulum flavum* (Okutani, 1964); G-H, "мелководная форма", SoJaBio ст. A2-10 (455-456 м), MIBM 14270; I-J, "глубоководная форма", SoJaBio ст. A6-7 (2511-2534 м), MIBM 39334. Все раковины в одном масштабе, масштабная линейка = 1 мм.

Punctulum reticulatum Golikov, 1986 (Fig. 3)

Punctulum reticulatum Golikov, 1986: 88–89, fig. 4; Kantor, Sysoev, 2006: pl. 36, fig. J (holotype); Hasegawa, 2014: fig. 48 F–H (holotype).

Type material. *Punctulum reticulatum* Golikov, 1986, holotype, ZIN 36574/3 (dried shell; Fig. 3 G–I); paratype, off Primorsky Krai, 380–312 m, ZIN 36576/5 (shell completely dissolved in preservative).

Type locality. Off the coast of Primorsky Krai near Rynda Bay in the Sea of Japan (44°48'N, 136°40'E) at a depth of ca. 430 m on a silty ground with a sandy area.

Material examined. SoJaBio A 2-10, MIBM 39338 (Fig. 3 A–D); SoJaBio B 7-7, MIBM 39343 (Fig. 3 E–F) [depth range: 455–528 m].

Distribution. Off the coast of southern and middle Primorsky Krai, at depths from 240 to 880 m [Golikov, 1986]. Because there have been no records of this species from Japanese territorial waters [Hasegawa, 2014], it is probably endemic to the northern slope of the Sea of Japan.

Original description. "Раковина маленькая, хрупкая, с 4,5 выпуклыми, закругленными оборотами, разделенными тонким вдавленным швом. Периостракум тонкий, шелушащийся, бледно-лимонно-желтого цвета. Зародышевая раковина из 1,5 выпуклых закругленных оборотов, покрыта тончайшей спиральной исчерченностью, составленной 15 нитевидными ребрышками. Последний оборот с закругленной периферией и выпуклым основанием занимает 0,77 высоты раковины. Осевая скульптура представлена тонкими линиями роста и узкими осевыми складками, расположенными с промежутками, примерно в 2 раза превышающими их ширину, распространяющимися на всю высоту оборотов, но не заходящими на основание раковины. На последнем и предпоследнем оборотах расположено по 28 таких складок. Спиральная скульптура состоит из приподнятых, волнистых на осевых складках ребрышек, расположенных с промежутками в 2–3 раза более широкими, чем их толщина. На последнем обороте расположено 10 таких ребрышек, а на предпоследнем обороте их 5. Пупок не полностью прикрыт отворотом внутренней губы. Устье с сомкнутым краем, почти округлое, слегка выступает у нижнего париетального края. "

[The shell is small, fragile, with 4.5 convex, rounded whorls separated by a thin, depressed suture. Periostracum thin, scaly, pale lemon yellow in color. The embryonic shell consists of 1.5 convex rounded whorls, covered with the finest spiral striation, composed of 15 threadlike ribs. The last whorl has a rounded periphery and a convex base that occupies 0.77 of the shell height. Axial sculpture is represented by thin growth lines and narrow axial ribs, located at intervals of approximately twice their width, extending over the entire height of the whorls but not to the base of the shell. On both the last and the penultimate whorls there are 28 such ribs. The spiral sculpture consists of raised cords that are made wavy by the axial ribs, spaced at intervals 2–3 times wider than their thickness. On the last whorl there are 10 such cords, and on the penultimate whorl there are five. The umbilicus is not completely covered by the folding of the inner lip. The aperture has a contracted margin, almost rounded, and protrudes slightly at the inferior parietal margin.]

Re-description (in accordance with Hasegawa [2014]). Shell minute, 2.7 mm shell length in holotype, moderately thick for genus, low conical in shape, with relatively small spire and covered by thick, rather smooth and light yellowish periostracum. Protoconch (Fig. 3D) dome-shaped, consisting of 1.5 whorls, with flat spiral cords, 15 in number at end of protoconch. Terminus of protoconch slightly thickened and clearly demarcated from teleoconch whorls. Teleoconch of ca. 2.0–2.5 convex whorls, with deeply constricted suture and weak angulation at shoulder. Relatively small spire occupying 25–28% of shell length. Surface rather smooth, with widely spaced 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. On initial part of first teleoconch whorl, very fine but distinct and somewhat granulate spiral threads present, gradually disappearing on later whorls. 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 slit-like and only narrowly perforate.

Remarks. This species apparently belongs to the clade containing *P. flavum* and *P. tanshumaruae* Hasegawa, 2014 [Criscione *et al*., 2019] because of the close similarity in the morphology of the protoconch. However, it can easily be distinguished from other species by the teleoconch sculpture, and is probably endemic to the Russian Far East.

Discussion

The Sea of Japan has experienced a number of large-scale extinctions since the Lower Pleistocene due to its extremely closed environment and declines in the sea level during the glacial periods, and its Recent fauna is known to be extremely poor both in diversity and endemicity, especially in deep water [Nishimura, 1968]. However, it has become clear [e.g., Hasegawa, 2014] that a considerable number of endemic species survived the deteriorated environment in the so called "intermediate waters", assumed to have been between depths of ca. 200 and 500 m where salinity and dissolved oxygen values

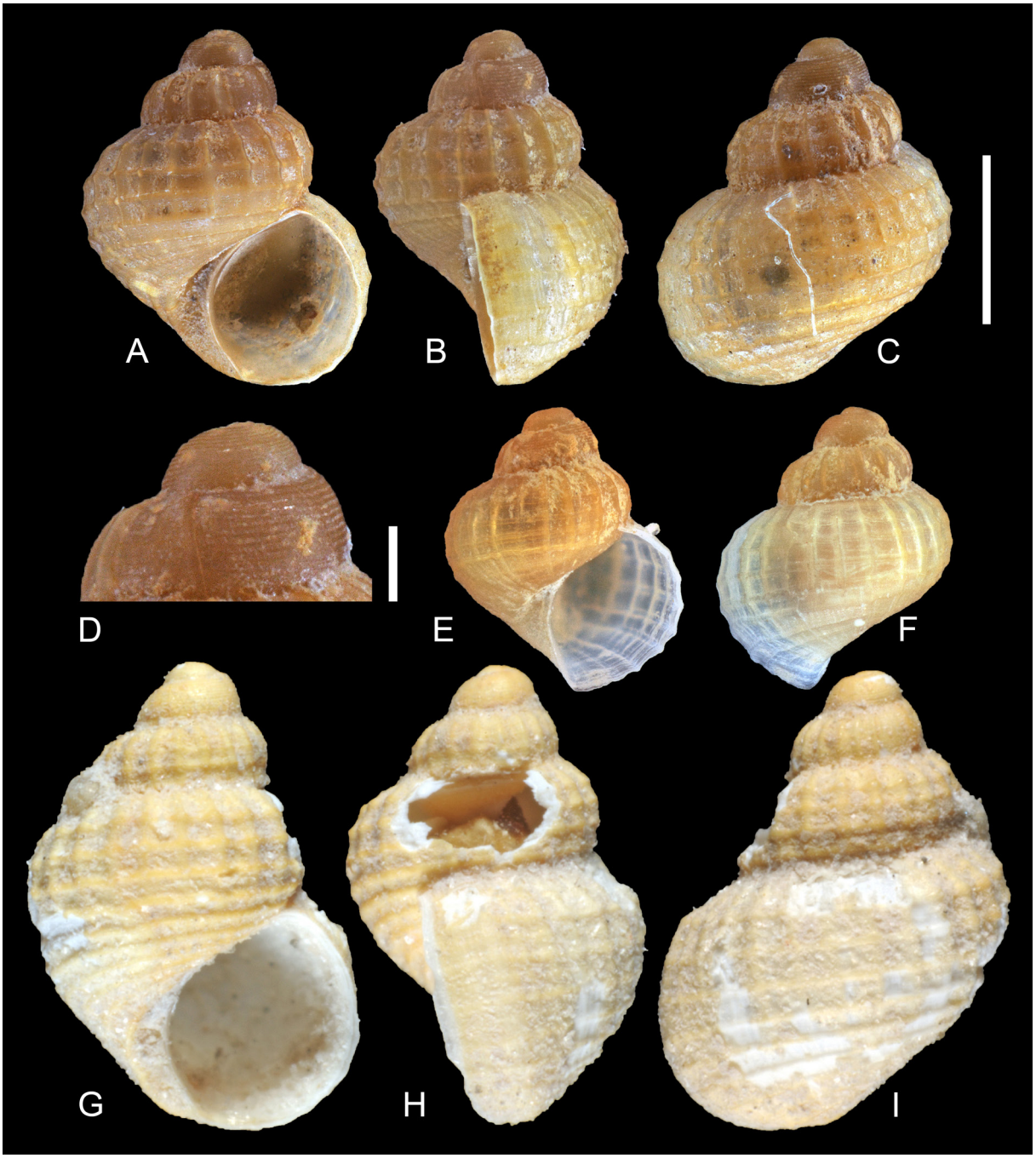

FIG. 3. *Punctulum reticulatum* Golikov, 1986. **A-D.** SoJaBio stn. A2-10 (455–456 m), MIBM 39338. **E-F.** SoJaBio stn. B7-7 (470–528 m), MIBM 39343. **G-I.** Holotype, ZIN 36574/3. All at the same scale, scale = 1 mm; except for D, scale, 200 µm.

РИС. 3. *Punctulum reticulatum* Golikov, 1986. **A-D.** SoJaBio ст. A2-10 (455–456 м), MIBM 39338. **E-F.** SoJaBio ст. B7-7 (470–528 м), MIBM 39343. **G-I.** Голотип, ZIN 36574/3.

remained normal throughout these periods [e.g., Itaki *et al*., 2004]. Furthermore, evidence is accumulating that deep-water organisms have adopted various distribution patterns within the Sea of Japan since the Lower Pleistocene [Hasegawa, 2014; Amano *et al*., 2021], probably reflecting the complicated geological history of the sea. It is thus important to clarify and compare deep-sea faunas in various parts of the sea to understand the process by which they formed. In the present study, some species were shown to commonly inhabit both the northern and southeastern slopes of the Sea of Japan, whereas others are probably endemic to one or the other. Two species, *Punctulum soyomaruae* Hasegawa, 2014 and *P. tanshumaruae* are so far known only from the southeastern slope, whereas *P. reticulatus* is from the northern slope, and *Alvania yamatoensis* Hasegawa, 2014 is probably endemic to the Yamato Bank at the center of the Japan Basin. The differences in their distributions can be explained either by local specia-

tion within the sea or survival in local refuges during the glacial environmental degradation, but further research will be necessary to clarify this.

Concerning vertical distributions of rissoids in the Sea of Japan, species diversity declines significantly with depth on both the northern and southeastern slopes [Hasegawa, 2014; present study]. It was reconfirmed that *P. flavum* has the widest vertical distribution range, and is the only species of the family found below 1,500 m. This is consistent with the theory that most organisms living at depths of 500 m and beyond became almost extinct during the glacial periods, and that those presently found there re-established themselves after the restoration of the environment [e.g., Itaki *et al.*, 2004].

Following the present study, the only remaining area to be surveyed in the Sea of Japan is off the western Korean Peninsula. Although only fragmentary information is available, the deep-sea fauna of this area might be significantly different even from that of the adjacent area off the western Honshu coast of Japan across the Tsushima Basin [Min, 2004; Amano *et al.*, 2021], and a detailed survey will be important to clarify the formation of the entire fauna of the sea.

Acknowledgements

I wish to express my sincere thanks to Dr. K. A. Lutaenko and Mrs. N. V. Kameneva of the A.V. Zhirmunsky National Scientific Center of Marine Biology, Vladivostok, for kind support during my stay in the institute, and for permission to study the rissoid material deposited in the institute. Thanks are also due to Mr. Paul Callomon of Academy of Natural Sciences of Drexel University, Philadelphia, for linguistic correction. The author is grateful to anonymous referees for their remarks and suggestions. This work was supported in part by JSPS KAKENHI Grant Numbers JP23570126, and JP21K06311.

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