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New records of *Cuspidaria trosaetes* Dall, 1925 (Bivalvia: Anomalodesmata: Cuspidariidae) in the Sea of Japan with notes on the genus *Nordoneaera*

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ABSTRACT. For the first time carnivorous bivalve mollusc *Cuspidaria trosaetes* Dall, 1925 was recorded in the north-western Sea of Japan. There was only one species of *Cuspidaria*, *C. ascoldica*, previously known in this region. Alive specimens of *C. trosaetes* were collected in the Tatarsky Strait on the continental slope on muddy sediment at the depths of 531–589 m. Stomach contents of *C. trosaetes* consist of foraminifers, copepods and rissoid gastropods. *Cuspidaria trosaetes* was selected as a type species of a monotypic subgenus *C.* (*Nordoneaera*) Okutani, 1985, which is now considered a separate genus, based on the presence of a thick shell without sculpture and with thick periostracum, as well as a short rostrum. The first obtained data on anatomy of *C. trosaetes* suggest its close affinity with the type species of the genus *Cuspidaria*, *C. cuspidata*. *Cuspidaria trosaetes* and *C. cuspidata* share such features as the presence of 5 pairs of septal pores, thin elongated posterior labial palps and the presence of two rows of papillae on the rim of the common siphonal sheath. Taking into account new data we propose to synonymize the monotypic genus *Nordoneaera* with the genus *Cuspidaria*.

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Новые находки *Cuspidaria trosaetes* Dall, 1925 (Bivalvia: Anomalodesmata: Cuspidariidae) в Японском море с замечаниями о роде *Nordoneaera*

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РЕЗЮМЕ. Хищный двустворчатый моллюск *Cuspidaria trosaetes* Dall, 1925 впервые обнаружен в российских водах северо-западной части Японского моря. Живые особи *C. trosaetes* собраны у материкового побережья Татарского пролива на илистом грунте в диапазоне глубин 531–589 м. Вид *C. trosaetes* был выделен в отдельный монотипический подрод *C.* (*Nordoneaera*) Okutani, 1985, ранг которого позднее был поднят до рода, на основании наличия крепкой, лишенной скульптуры раковины с толстым периостракумом и коротким ростром. Впервые полученные нами данные по анатомии *C. trosaetes* свидетельствуют о его близком родстве с типовым видом рода *Cuspidaria – C. cuspidata*. Оба вида имеют пять пар септальных пор, удлиненные тонкие задние лабиальные пальпы и два ряда папилл на дистальной части сифонального чехла. На основании анатомического сходства *C. trosaetes* и *C. cuspidata* мы предлагаем синонимизировать *Nordoneaera* с родом *Cuspidaria*.

Introduction

Cuspidaria Nardo, 1840 is the largest genus in the family Cuspidariidae (Bivalvia: Anomalodesmata) comprising more than 110 species (WoRMS, accessed on 17.01.2024) of carnivorous bivalves distributed worldwide from shelf to ultraabyssal trenches. The genus is morphologically and anatomically variable, and many attempts were conducted to systemize the diversity of *Cuspidaria.* As a result, several sections and subgenera were established, usually based on conchological characters only [Smith, 1885; Dall, 1886; Okutani, 1985]; some of these subgenera were subsequently elevated to the generic level. However, the anatomical characters of cuspidariids which are known as informative

Table 1. Collection sites of *C. trosaetes* in the Tatarsky Strait.

Табл. 1. Места сбора *C. trosaetes* в Татарском проливе.

Date	Station	Coordinates		Depth, m	Sediment (m – mud; p – pebble)	Number of specimens (alive/ paired valves)
		Start	End			
17.10.2016	RV "*Buhoro*", Stn. 109	47°77′000N 140°26′167E	47°77′833N 140°27′333E	531–531	m, p	5/2
04.06.2018	RV "*Buhoro*", Stn. 176	47°78′667N 140°28′667E	47°79′167N 140°29′167E	531–531	m, p	2/2
02.05.2019	RV "*Vladimir Safonov*", Stn. 78	47°21′500N 139°68′660E	47°20′333N 139°67′333E	579–589	m	1/0

taxonomic features [Allen, Morgan, 1981; Krylova, 1993; 1994], were not always considered.

Monotypic subgenus *Nordoneaera* was suggested on the basis of the presence of a thick smooth shell with thick periostracum as well as a short rostrum, and typified by *Cuspidaria trosaetes* Dall, 1925 [Okutani, 1985]. There has been no data on anatomy of this species so far. *Nordoneaera* has not been discussed since the time of its establishment and its status is still ambiguous. In the WoRMS (accessed on 17.01.2024) this taxon is used as a separate genus. Data on the anatomy of *C. trosaetes* would be essential for clarification of the taxonomic status of *Nordoneaera.*

Beside *C. trosaetes*, five species of the genus *Cuspidaria* are presently known from the Russian Far-Eastern seas, that are *C. arctica* (M. Sars, 1859) (Bering Sea, Sea of Okhotsk), *C. obtusirostris* Okutani, 1962 (Sea of Okhotsk), *C. ascoldica* Scarlato, 1972 (Sea of Japan), *C. cf. abyssopacifica* Okutani, 1975 (Sea of Okhotsk) and, probably, *C. glacialis* (Sars, 1878) (Bering Sea) [Filatova, 1957; Scarlato, 1981; Kafanov, 1991; Volova, Scarlato, 1991; Krylova, 1997; Kantor, Sysoev, 2005; Kamenev, 2013; 2018; Lutaenko, 2013]. There is one more record of *Cuspidaria* sp. from the bathyal zone of Peter the Great Bay (Sea of Japan) but there is no detailed information about this finding [Derjugin, 1939].

Cuspidaria trosaetes was earlier recorded from the Russian Far-Eastern seas from two different locations. The first record was from the vicinities of the Kuril Islands with no precise locality and depth of sampling [Higo *et al*., 1999]. The second record was from the Sea of Okhotsk near the southern coast of the Sakhalin Island at depths of 185–417 m where empty valves of *C. trosaetes* were collected [Lutaenko, 2009]. In addition, live specimens collected near the south-west coast of the Sakhalin Island in the Sea of Japan and identified as *C. glacialis* [Belan, Belan, 2008], may well be *C. trosaetes*, but there is no material to verify identification.

In cruises organized by TINRO in the north-western Sea of Japan during three trawl bottom surveys in 2016, 2018 and 2019 years we collected several alive specimens and empty valves of *C. trosaetes*.

In this paper we give new data on distribution and ecology of *C. trosaetes*, for the first time provide information on anatomy of this species and discuss the status of the genus *Nordoneaera*.

Material and methods

Material was obtained during expeditions in the Tatarsky Strait (Sea of Japan) organized by TINRO on RV "*Buhoro*" and RV "*Vladimir Safonov*". Bivalves were collected with bottom trawls (Table 1). Molluscs were preserved in 96% ethanol. For the morphological description the following measurements were taken with calipers (±0.1 mm): length of valve (L), height of valve (H), width of valve (W), the length of rostrum (R) and the distance from the beak to the end of rostrum (P) (Fig. 1). Gross anatomy was observed on preserved live-taken specimens. Anatomical details were examined using a scanning electronic microscope (KY-KY EM-6900LV) on critical-point dried, and gold-coated specimen. Stomach contents were examined in five specimens. Number of eggs was counted in one specimen. Three specimens and six paired valves are deposited in the ZMFU (Vladivostok) (no. 53066/Bv-8531, 53067/Bv-8532 и 53068/Bv-8533); soft parts of five specimens and two paired valves are stored in the IORAN (Moscow). Additionally, we examined specimens of *Cuspidaria glacialis* (Sars, 1878) collected during the 49-th cruise of RV "*Dmitry Mendeleev*" (stn. 4383, 74°21′N, 64°25′E, 128–160 m, Sigsbee trawl, 3 September 1993, Barents Sea).

Abbreviations of scientific organizations: IORAS – P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia; KhabarovskNIRO – Khabarovsk Branch of Russian Federal Research Institute of Fisheries and Oceanography, Khabarovsk, Russia; MFEH – V.K. Arseniev Museum of Far East History, Vladivostok, Russia; NMNH – National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; NSCMB FEB RAS – A.V. Zhirmunsky National

Scientific Center for Marine Biology, Vladivostok, Russia; TINRO – Pacific Branch of Russian Federal Research Institute of Fisheries and Oceanography, Vladivostok, Russia; ZMFU – Zoological Museum, Educational and Science Museum, Far Eastern Federal University, Vladivostok, Russia.

Systematic part

Superorder Anomalodesmata Dall, 1889
Superfamily Cuspidarioidea Dall, 1886

Family Cuspidariidae Dall, 1886
Cuspidaria Nardo, 1840

Type species: *Cuspidaria typus* Nardo, 1840 (= *Tellina cuspidata* Olivi, 1792) (by original designation).

Cuspidaria trosaetes Dall, 1925

Cuspidaria trosaetes Dall, 1925: 16, pl. 29, fig. 5; Furukawa, Kubota, 1947: 34; Kuroda, 1948: 9, pl. 1, fig. 6; Kuroda, Habe, 1952: 18; Ito, 1967: 70 pl. 10, fig. 13; Okutani, 1975: 75; Okutani, 1985: 147; Kafanov, 1991: 108; Higo *et al*., 2001: 185, fig. B1447.
Cuspidaria glacialis trosaetes – Habe, 1977: 21; Ito *et al*., 1986: 36, pl. 56, fig. 3.
Cuspidaria (*Nordoneaera*) *glacialis trosaetes* – Higo, Goto, 1993: 682.
Cuspidaria (*Cuspidaria*) *obtusirostris* – Lee, Kim, 2002: 173, fig. 351.
Cuspidaria glacialis – Belan, Belan, 2008: 118.
Cuspidaria (*Nordoneaera*) *trosaetes* – Tsuchida, Hayashi, 1994: 101, pl. 9, fig. 12; Poutiers, Bernard, 1995: 168; Higo *et al*., 1999: 529; Okutani, 2000: 1045, pl. 520, fig. 17; Lutaenko, 2009: 27, figs 1, 2; Okutani, Saito, 2017: 47, fig. 4H.

Type material. Holotype USNM 110770; 2 dry valves of the same specimen; https://collections.nmnh.si.edu/search/iz/?ark=ark:/65665/3affd314c1aef4050854d0e7cf36f60da (Fig. 2 A–E).

Type locality. Sea of Japan, north-west of Hokkaido, 45°40′00 N, 140°81′94 E, 594 m; mud, 22 September 1906, RV "*Albatross*", St. 4992 [Dall, 1925].

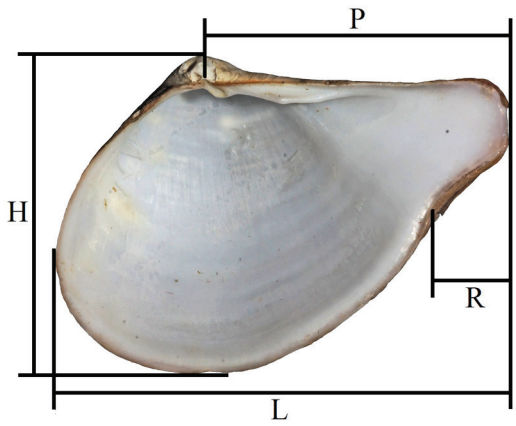

FIG. 1. Shell measurements: **L** – shell length; **H** – height; **R** – rostrum length; **P** – distance from beak to posterior end of rostrum.

РИС. 1. Схема промеров правой створки: **L** – длина; **H** – высота; **R** – длина рострума; **P** – расстояние от конца рострума до макушки.

Shell description (Fig. 2 F–J)**.** Shell to 35 mm long, relatively high (H/L = 0.62–0.67), thin-shelled, strong, inequilateral (Table 2): anterior side rounded, posterior side with broad and relatively short (R/L = 0.18–0.21) rostrum. Umbo prominent, inflated, beaks orthogyrate; situated slightly in front of midline of shell (P/L = 0.57–0.60). Anterodorsal margin very short, straight, meeting rounded anterior margin at an obtuse angle. Ventral margin rounded, becoming sinuous posteriorly. Posterodorsal margin nearly straight. Rostrum set off from disk by radial depression running from umbo to posteroventral corner of shell. Sculpture consists of coarse growth lines. Periostracum adherent, brownish, thin and glossy on the umbo, thicker and wrinkled on rostrum and in marginal region.

Internal ligament in oblique chondrophore located under beak. Left valve edentulous, right valve with posterior lateral long triangular tooth located just behind chondrophore. Interior white, glossy. Septal muscle scars look like two arcuate nearly parallel each other rows in upper region of shell.

Table 2. Measurements of the right valves of *Cuspidaria trosaetes*.

Табл. 2. Размеры правых створок *Cuspidaria trosaetes*.

N	L, mm	H, mm	W, mm	R, mm	P, mm	H/L	D/L	R/L	P/L
1	31.0	20.4	7.2	6.1	18.0	0.66	0.23	0.20	0.58
2	32.1	21.2	8.0	6.4	18.9	0.66	0.25	0.20	0.59
3	23.8	15.6	5.3	4.9	14.0	0.66	0.22	0.21	0.59
4	25.5	16.1	5.9	5.1	15.1	0.63	0.23	0.20	0.59
5	27.7	17.5	6.6	5.4	15.9	0.63	0.24	0.20	0.57
6	24.9	16.3	6.0	4.9	14.5	0.66	0.24	0.20	0.58
7	28.6	18.4	7.6	5.7	17.2	0.64	0.27	0.20	0.60
8	24.7	16.1	5.8	4.9	14.7	0.65	0.24	0.20	0.60
9	25.7	16.4	6.2	5.0	14.6	0.64	0.24	0.20	0.57
10	26.7	16.6	6.4	4.9	15.7	0.62	0.24	0.18	0.59

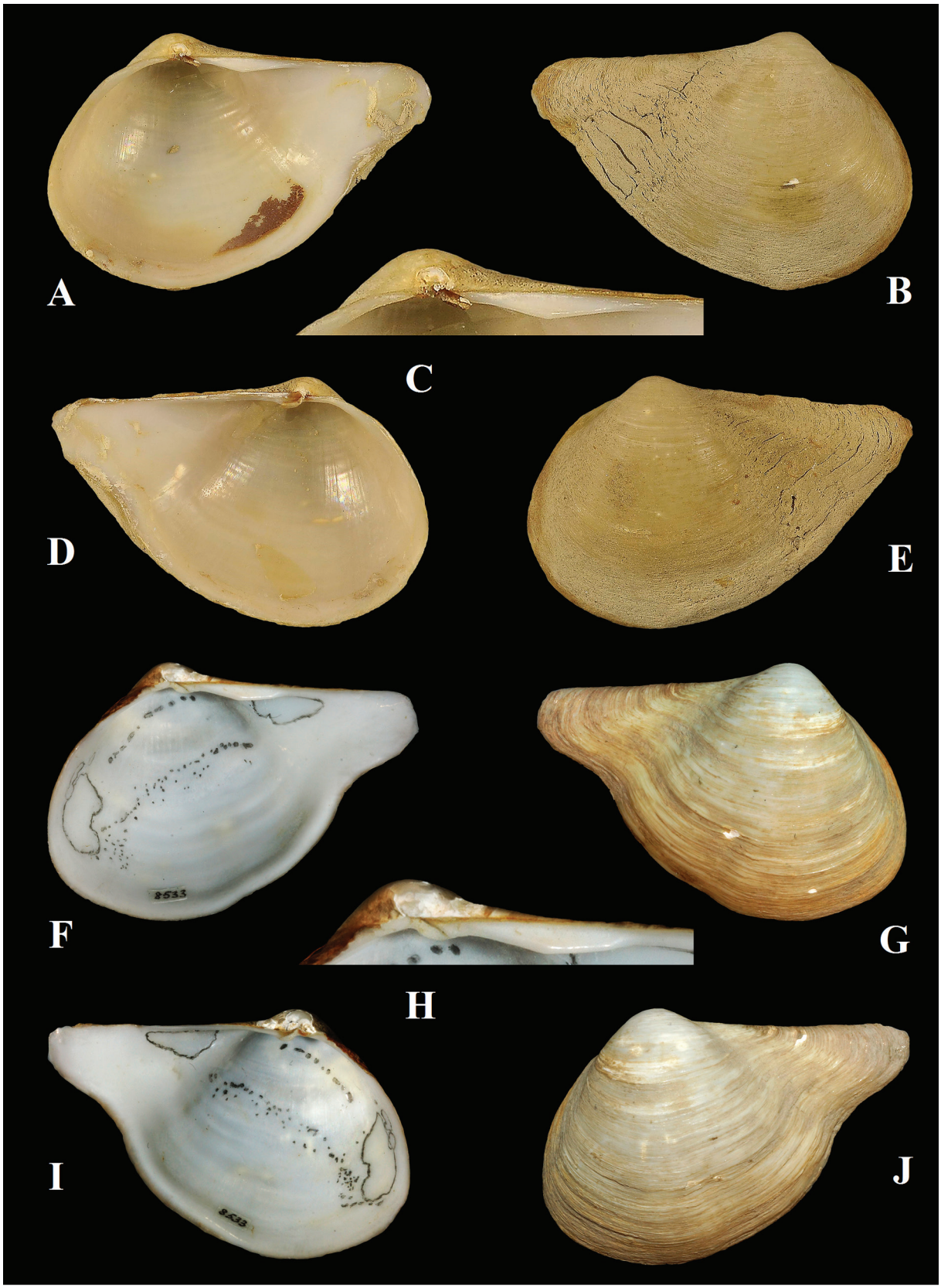

FIG. 2. *Cuspidaria trosaetes* Dall, 1925: **A–E**, holotype, Sea of Japan, depth 594 м, L = 25.0 mm, USNM 110770; A, right valve, interior view; B, right valve, exterior view; C, right hinge margin; D, left valve, interior view; E, left valve, exterior view; **F–J**, Tatarsky Strait, Sea of Japan, depth 531 м, L= 27.7 mm, ZMFU no. 53068/Bv-8533 (periostracum mainly deleted); F, right valve, interior view; G, right valve, exterior view; H, right hinge margin; I, left valve, interior view; J, left valve, exterior view..

Near-umbonal row shorter and consists of larger scars. Pallial line inconspicuous. Anterior adductor scar large, bean-shaped, elongated in dorso-ventral direction; posterior adductor scar smaller, triangular, situated at base of rostrum.

Variability. Variability can be seen in height of umbo, in length and broadness of rostrum, and in the size of posteroventral margin sinus [Dall, 1925; Ito, 1967; Okutani *et al*., 1988; Lutaenko, 2009; Okutani, Saito, 2017]. Specimens from the Tatarsky Strait correspond to the holotype very well and differ from it only by a slightly higher umbo and slightly deeper pallial sinus. Some valves from the Sea of Okhotsk have shorter rostrums, maybe because the valves were weared [Lutaenko, 2009]. The most constant characters of *C. trosaetes* are the straight postero-dorsal margin, short antero-dorsal margin and oblique chondrophor.

Anatomy. Septum thick, well developed; lateral septal muscles continuous, not divided into two parts; there are five pairs of septal pores, located at the same distance from each other (Fig. 3). Anterior labial palps short, posterior palps longer and narrower. On the common siphonal sheath below the ring of papillae on inside rim, there is additional ring of small irregular transparent processes (Fig. 4). There are no additional papillae between siphonal tentacles of exhalant siphon.

Remarks. *Cuspidaria trosaetes* is similar to *C. glacialis* (Fig. 5) and differs from it by a shorter and higher right lateral tooth and a lower umbo. Anatomically, *C. trosaetes* and *C. glacialis* are similar in the presence of 5 pairs of septal pores, continuous lateral septal muscles, labial palps of the type II [Allen, Morgan, 1981] and the presence of an additional ring of small irregular processes below the ring of papillae on the rim of the common siphonal sheath.

Ecology. *C. trosaetes* with the shell length of more than 30 mm is one of the largest species of the family. The species inhabits muddy and muddy-sandy sediments in the Sea of Japan near the Japanese archipelago [Dall, 1925; Okutani, Saito, 2017] and muddy sediments with admixture of pebbles in the Tatarsky Strait (this paper). We examined the stomach contents of five specimens of *C. trosaetes*, which consist of foraminifers, copepods and rissoid gastropods *Frigidoalvania asura* (Yokoyama, 1926) with shell length of up to 1.5 mm. One specimen of *C. trosaetes* collected in the beginning of May contained about 2000 oocytes with maximum diameter of 0.38 mm.

Distribution. The Sea of Japan: off Hokkaido and Honshu to the south until the Tottori Prefecture, 50−794 m [Dall, 1925; Ito, 1967, 1985, 1989; Okutani, Saito, 2017], the western part of the Tatarsky Strait, 531−589 m, probably off the south-western Sakhalin Island (46°99′N, 41°49′E), as *C. glacialis* [Belan, Belan, 2008]; the Sea of Okhotsk: off the Cape Aniva, 185−417 m [Lutaenko, 2009]; Pacific Ocean: the eastern coast of the Hokkaido and the south of the Kuril Islands [Higo *et al*., 1999] (Fig. 6). Also, we assume that *C. trosaetes* occurs in the Korea Strait, from where it was recorded as *C.* (*Cuspidaria*) *obtusirostris*; image in [Lee, Kim, 2002, p. 173, fig. 351].

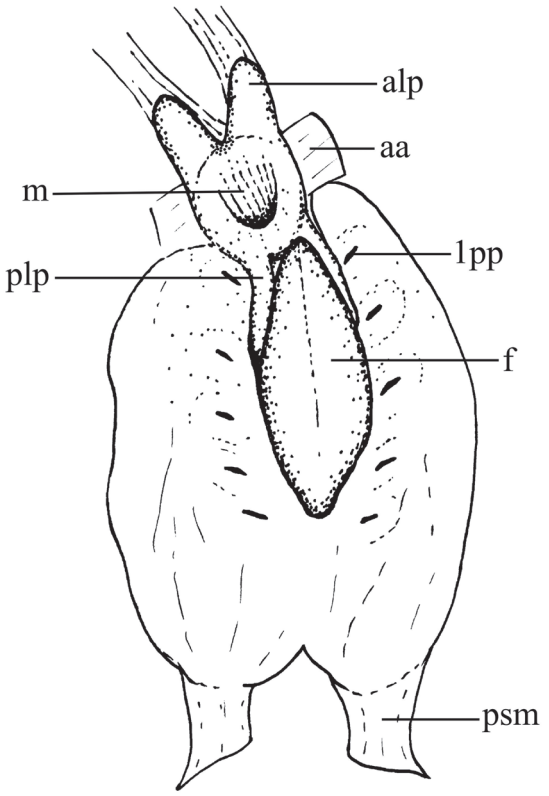

FIG. 3. *Cuspidaria trosaetes* Dall, 1925: ventral view of the septum with five pairs of septal pores; RV "*Buhoro*", Stn. 109, L=32.1 mm, IORAS. Abbreviations: 1pp, first pair of septal pores; aa, anterior adductor; alp, anterior labial palp; f, foot; m, mouth; plp, posterior labial palp; psm, posterior septal muscle.

РИС. 3. *Cuspidaria trosaetes* Dall, 1925: вентральный вид септы с пятью парами пор; НИС «Бухоро», ст. 109, L=32,1 мм, ИОРАН. Сокращения: 1pp, первая пара септальных пор; aa, передний аддуктор; alp, передняя лабиальная пальпа; f, нога; m, рот; plp, задняя лабиальная пальпа; psm, задняя септальная мышца

РИС. 2 (на пред. стр.). *Cuspidaria trosaetes* Dall, 1925: **A–E**, голотип, Японское море, глубина 594 м, L = 25,0 мм, USNM 110770; A, правая створка изнутри; B, правая створка снаружи; C, замковый край правой створки; D, левая створка изнутри; E, левая створка снаружи; **F–J**, Татарский пролив, Японское море, глубина 531 м, L= 27,7 мм, ZMFU № XII 53068/Bv-8533 (периостракум удален); F, правая створка изнутри; G, правая створка снаружи; H, замковый край правой створки; I, левая створка изнутри; J, левая створка снаружи.

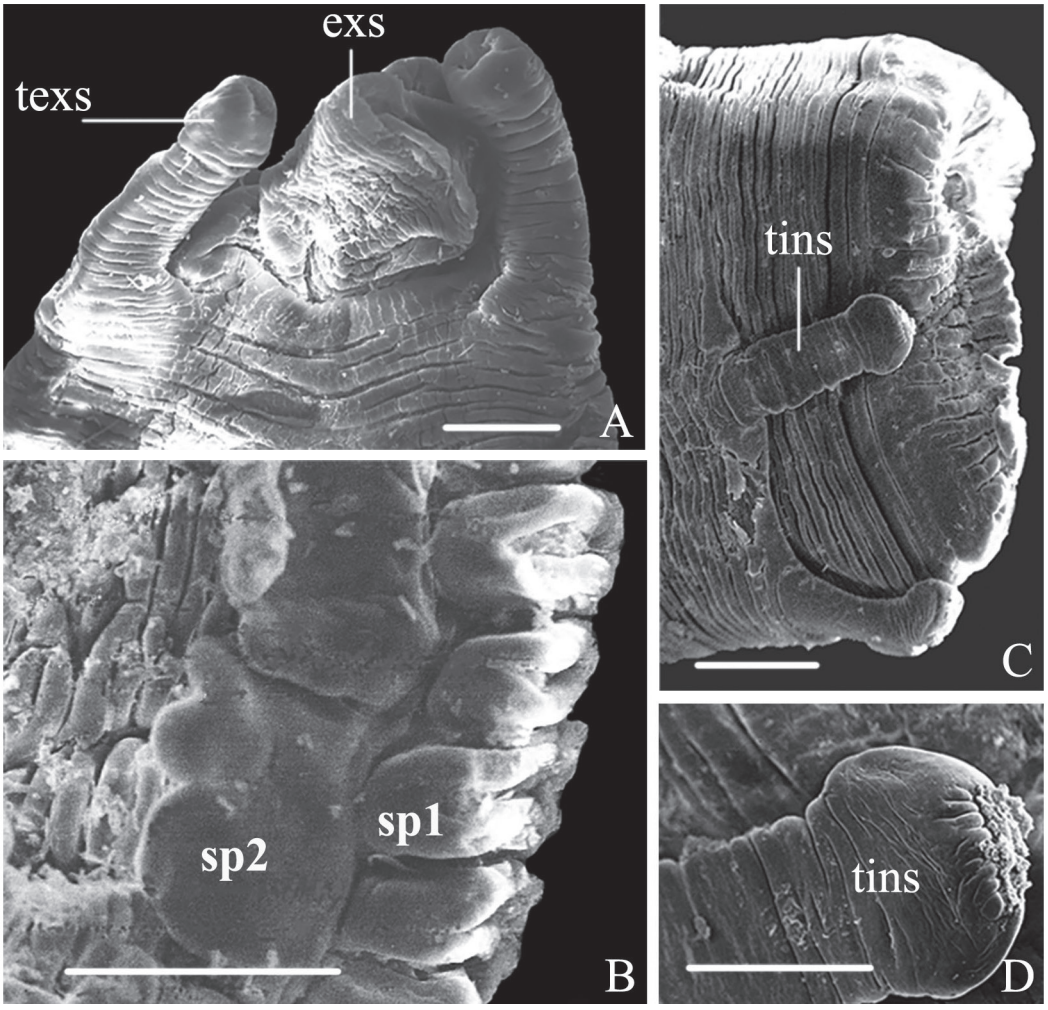

FIG. 4. *Cuspidaria trosaetes* Dall, 1925, scanning electron micrographs of anatomical details, RV "*Buhoro*", Stn. 109, L=32.1 mm, IORAS. **A.** Exhalant siphon, ventral view. **B.** Margin of siphonal sheath with two rows of papillae. **C.** Inhalant siphon, lateral view. **D.** Tentacle of inhalant siphon. Abbreviations: exs, exhalant siphon; sp1, outer papillae of siphonal sheath; sp2, inner papillae of siphonal sheath; texs, tentacles of exhalant siphon; tins, tentacles of inhalant siphon. Scale: A–C, 200 mkm; D, 100 mkm.

РИС. 4. *Cuspidaria trosaetes* Dall, 1925, фотографии анатомических деталей, полученные с помощью электронного сканирующего микроскопа, НИС «*Бухоро*», ст. 109, L = 32,1 мм, ИОРАН. **A.** Выводной сифон, вентральный вид. **B.** Край сифонального чехла с двумя рядами папилл. **C.** Вводной сифон, латеральный вид. **D.** Щупальце вводного сифона; exs, выводной сифон. Сокращения: sp1, наружный ряд папилл сифонального чехла; sp2, внутренний ряд папилл сифонального чехла; texs, щупальца выводного сифона; tins, щупальца вводного сифона. Шкала: A–C, 200 мкм; D, 100 мкм.

Discussion

The specimens studied well correspond to the images and the description of the holotype of *C. trosaetes* [Dall, 1925]. The finding of *C. trosaetes* in the Tatarsky Strait is the northernmost record of this species.

Examination of stomachs of *C. trosaetes* confirmed the predatory mode of life of the species. Foraminifers and copepods were most commonly found in stomachs; besides, among preys of *C. trosaetes* we discovered rissoid gastropods *Frigidoalvania asura*. Before, this type of prey was recorded for cuspidadriids only once for *C. glacialis* [Machado *et al*., 2019; Morton, Machado, 2019], however gastropods were reported as prey for four species of short-rostrumed *Cetomya* (Poromyiidae) [Krylova, 2001]. Both these species, *C. trosaetes* and *C. glacialis*, have not very long rostrums and obviously are able to feed on not only near-bottom plankton but are also preying on benthic animals.

C. trosaetes typified a monotypic subgenus *Cuspidaria* (*Nordoneaera*), which was established on the basis of the conchological features such as a thick-walled shell, thick periostracum, the absence of the concentric ribs and the presence of a very short rostrum which is not clearly delimited from the body of the shell [Okutani, 1985].

Status of *Nordoneaera* is still confusing. In the WoRMS database (accessed on 17.01.2024) this

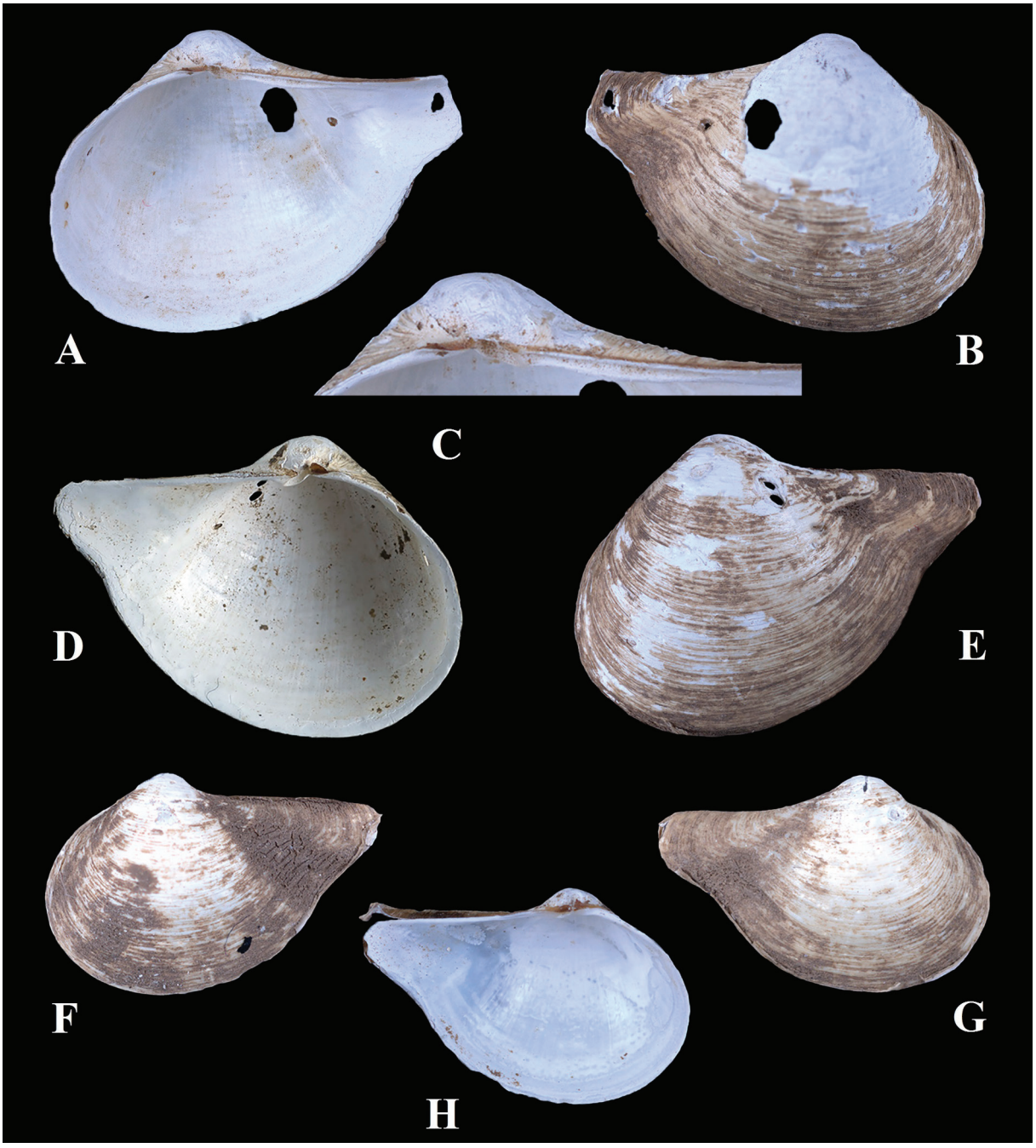

FIG. 5. *Cuspidaria glacialis* (Sars, 1878), RV "*Dmitry Mendeleev*", cruise 49, Stn. 4383; **A–E**, L=23.0 mm, IORAS; A, right valve, interior view; B, right valve, exterior view; C, right hinge margin; D, left valve, interior view; E, left valve, exterior view; **F–H**, L=12.0 mm, IORAS; F, left valve, exterior view; G, right valve, exterior view; H, left valve, interior view.

РИС. 5. *Cuspidaria glacialis* (Sars, 1878), НИС «*Дмитрий Менделеев*», рейс 49, ст. 4383; **A–E**, L=23,0 мм, ИОРАН; A, правая створка изнутри; B, правая створка снаружи; C, замковый край правой створки; D, левая створка изнутри; E, левая створка снаружи; **F–H**, L=12,0 мм, ИОРАН; F, левая створка снаружи; G, правая створка снаружи; H, левая створка изнутри.

taxon is used as a separate genus. In the absence of molecular data, information on anatomy of the type species of *Nordoneaera* could be especially important for clarification of its taxonomical position.

The firstly obtained data on anatomy *C. trosaetes* suggest its close affinity with the type species of the genus *Cuspidaria*, *C. cuspidata* [Allen, Morgan, 1981; Krylova, 2006], and *C. glacialis*. These species share such common features as the presence of 5 pairs of septal pores, continuous lateral septal muscles, longer and narrower posterior labial palps (type II of [Allen, Morgan, 1981]) and the presence of an additional ring of small irregular transparent processes below the ring of papillae on the rim of the

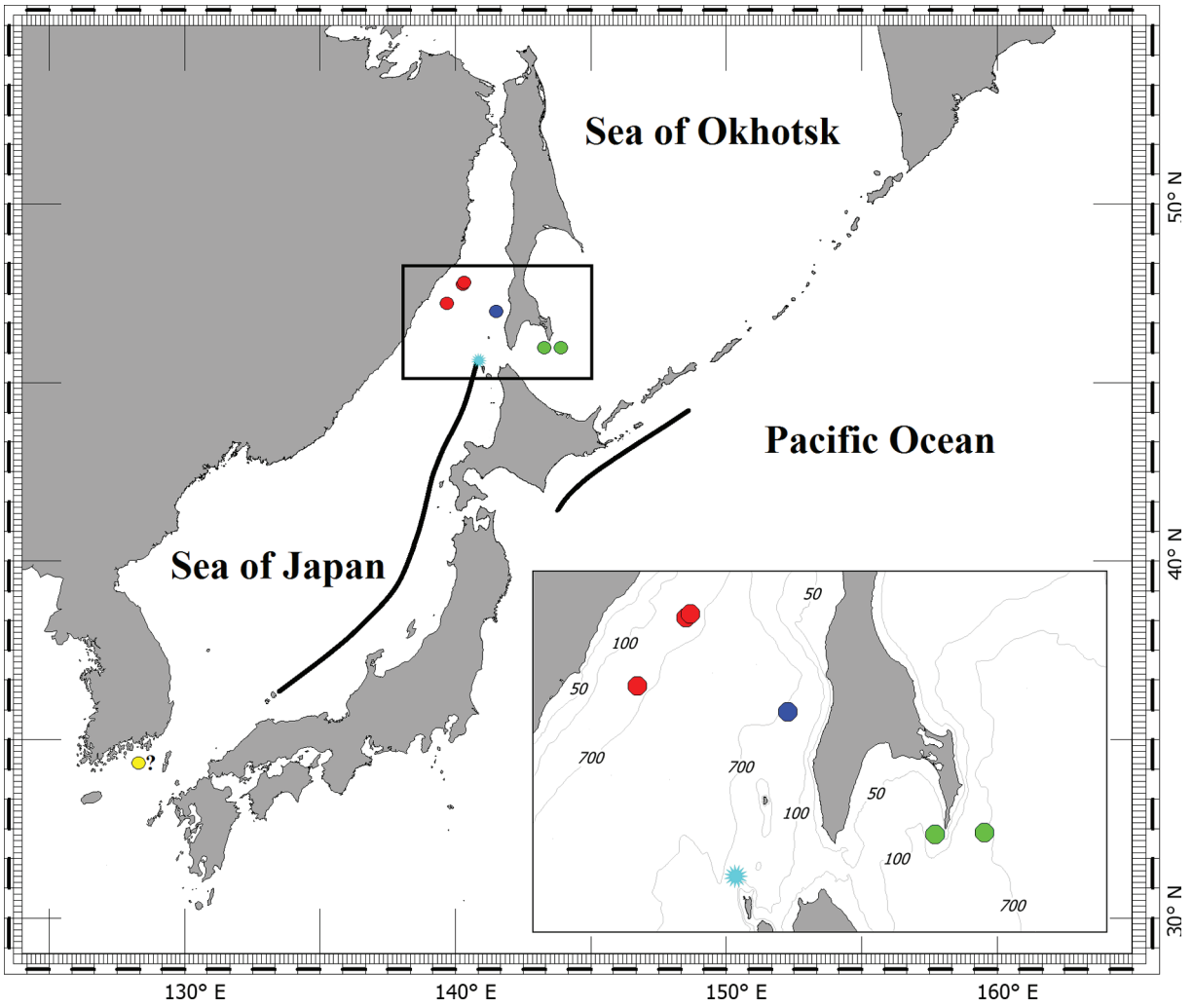

FIG. 6. Distribution of *Cuspidaria trosaetes* Dall, 1925 (dark lines), with some records marked by symbols of different colours: light blue, type locality [Dall, 1925]; red, alive specimens (our data); dark blue, alive specimen [Belan, Belan, 2008, as "*C. glacialis*"]; green, empty valves [Lutaenko, 2009], yellow, dubious record [Lee, Kim, 2002, as *C.* (*C.*) *obtusirostris*].

РИС. 6. Распространение *Cuspidaria trosaetes* Dall, 1925 (черные линии), отдельные находки отмечены символами разных цветов: голубой, типовое местонахождение [Dall, 1925]; красный, живые экземпляры (наши данные); синий, живой экземпляр [Belan, Belan, 2008, как "*C. glacialis*"]; зеленый, пустые раковины [Lutaenko, 2009]; желтый, находка под вопросом [Lee, Kim, 2002, как *C.* (*C.*) *obtusirostris*].

common siphonal sheath. The majority of species, presently assigned to the genus *Cuspidaria*, have four pairs of septal pores, short posterior labial palps (that is type I) and the only rim of siphonal sheath papillae. Taking into account the absence of anatomical differences between *C. trosaetes* and *C. cuspidata*, the type species of *Nordoneaera* and *Cuspidaria*, and the superficial character of conchological differences, we propose to synonymize these genera. The genus *Cuspidaria* obviously needs revision which cannot be conducted without using anatomical data.

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