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RESEARCH ARTICLE

Revision of the genus *Amicula* (Mollusca: Polyplacophora: Mopaliidae)

Ревизия рода *Amicula* (Mollusca: Polyplacophora: Mopaliidae)

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Abstract. In recent years, three of the six described species of the genus *Amicula* Gray, 1847 have been retained in its composition: *A. amiculata* (Pallas, 1788), *A. gurjanovae* Jakovleva, 1952, and *A. vestita* (Broderip et Sowerby, 1829). This article presents a morphological analysis of the species of this genus, based on extensive collection material. The validity of the name *A. gurjanovae*, which had been questioned in recent years, is confirmed. *Amicula vestita*, **syn. nov.** placed in synonymy with *A. amiculata*. It is shown that the reversal of precedence cannot be applied to these two names (according to Article 23.9 of the Code), despite the extensive usage of *A. vestita*. Illustrated redescriptions of *A. amiculata* and *A. gurjanovae* are provided.

Резюме. В последние годы из описанных шести видов рода *Amicula* Gray, 1847 в его составе остались три: *A. amiculata* (Pallas, 1788), *A. gurjanovae* Jakovleva, 1952 и *A. vestita* (Broderip et Sowerby, 1829). В настоящей статье проведен морфологический анализ видов рода на основе обширного коллекционного материала. Для *A. gurjanovae* подтверждена валидность названия, которая в последние годы подвергалась сомнению. Название *A. vestita*, **syn. nov.** признано младшим субъективным синонимом *A. amiculata*. Показано, что принцип приоритета не может быть приостановлен относительно этих двух названий (согласно статье 23.9 Кодекса), несмотря на широкое употребление *A. vestita*. Приведены иллюстрированные переописания *A. amiculata* и *A. gurjanovae*.

Key words: chitons, north-west Pacific, taxonomy, nomenclature, new synonymy

Ключевые слова: хитоны, северо-западная Пацифика, таксономия, номенклатура, новый синоним

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Introduction

The first species of the genus *Amicula* Gray, 1847, *Chiton amiculatus* Pallas, 1788, was described by P.S. Pallas from the Kuril Islands at the end of the 18th century. Three other species of this genus were described in the 19th century: *Ch. vestitus* Broderip et Sowerby, 1829 from the Arctic Ocean, *Ch. emersonii* Couthouy, 1838, from Massachusetts Bay, and *Ch. pallasii* Middendorff, 1847 from the Sea of Okhotsk. In 1841, Gould (1841) changed the name *Ch. emersonii* to *Ch. emersonianus* Gould, 1841. Two more species, *Amicula rosea* Jakovleva, 1952 from the Sea of Okhotsk, and *A. gurjanovae* Jakovleva, 1952 from the Sea of Japan and the southern Kuril Islands, were described in the 20th century. By the 21st century, only three species remained distinct: *A. amiculata* (Pallas, 1788), *A. vestita* (Broderip et Sowerby, 1829), and *A. gurjanovae* (Kaas & Van

Belle, 1994; Sirenko, 2013; Saito, 2017; WoRMS, 2024), with various papers considering both *A. amiculata* and *A. gurjanovae* as valid names or as synonyms (Okutani & Saito, 1987; Kaas & Van Belle, 1994, 1998; Sirenko, 2013; Saito, 2017; WoRMS, 2024).

The present paper aims to analyse the morphological characters of the chiton valves of three species: *A. amiculata*, *A. vestita*, and *A. gurjanovae*. Additionally, it evaluates the differences in certain characters of the perinotum armament and shell shape of *A. vestita* in comparison to A. *pallasii* and *A. rosea*, the names of which have been placed into synonymy.

Material and methods

Available type specimens of *A. pallasii* and *A. rosea*, along with the description and images of *Chiton amiculatus* Pallas, 1787, were used for analysis. All the material examined is stored in the collection of the Zoological Institute of the Russian Academy of Sciences (St Petersburg, Russia). Preparations of *A. amiculata* and *A. gurjanovae* for scanning electron microscopy were conducted following the established method (Sirenko, 2023).

The following abbreviations are used: *BL* – body length; BMNH – The Natural History Museum, London; R/V –research vessel; USNM – United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; SCUBA – self-contained underwater breathing apparatus; ZIN – Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia.

Taxonomy

Class **Polyplacophora** Gray, 1821

Subclass **Neoloricata** Bergenhayn, 1955

Order **Chitonida** Thiele, 1909

Suborder **Acanthochitonina** Bergenhayn, 1930

Superfamily **Mopalioidea** Dall, 1889

Family **Mopaliidae** Dall, 1889

Genus ***Amicula*** Gray, 1847

Type species: *Chiton vestitus* Broderip et Sowerby, 1829, by subsequent designation (Gray, 1847: 66).

Diagnosis. Oval, medium-sized to large; tegmentum reduced to very small, heart-shaped or round areas; slit formula 7–12/1/sinus +2, rare +3–4; girdle wide, thick, covered with small, smooth sharp-tipped spicules and single or clustered bristles.

Distribution. North Pacific Ocean from Japan to Alaska, Chukchi, East-Siberian and Beaufort seas, Northwest Atlantic Ocean.

Composition. In publications from 1921 to 2023, *A. amiculata* and *A. vestita* were considered as separate species. However, from 1994 to 2023, *A. amiculata* has been recognised as the senior subjective synonym of *A. gurjanovae*. Until now, *A. vestita* has never been considered a synonym of *A. amiculata*. In this paper, based on the aforementioned considerations, two species are recognised within the genus *Amicula*: *A. amiculata* and *A. gurjanovae*. *Amicula amiculata* is recognised as the senior subjective synonym of *A. vestita*, **syn. nov.**

Note. According to the Principle of Priority (Article 23, ICZN, 1999), "The valid name of a taxon is the oldest available name applied to it, unless that name has been invalidated or another name is given precedence by any provision of the Code or by any ruling of the Commission". *Amicula amiculata* (Pallas, 1788) is the oldest name, and *A. vestita* (Broderip et Sowerby, 1829) must be considered its junior subjective synonym. The reversal of precedence (under Article 23.9) cannot be applied in this case as the conditions outlined in both Articles 23.9.1.1 and 23.9.1.2 are not met. According to Article 23.9.1, "prevailing usage must be maintained when the following conditions are both met: 23.9.1.1. the senior synonym or homonym has not been used as a valid name after 1899, and 23.9.1.2. the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years". In fact, the name *A. amiculata* has been used as a valid name in 13 publications since 1899 (Dall, 1921; Taki, 1938; Leloup, 1942; La Rocque, 1953; Burghardt & Burghardt, 1969; Abbott, 1974; Kaas & Van Belle, 1980, 1994, 1998; Putman, 1980; Higo et al., 1999; Saito, 2000; Granpoder et al., 2023). The name *A. vestita* has been used as a valid name in only 15 publications by

twelve authors over the preceding 50 years (Abbott, 1974; Kaas & Van Belle, 1980, 1994, 1998; Putman, 1980; Clark, 1982; Hanselman, 1983; Sirenko & Scarlato, 1983; Mayhew & Cole, 1993; Sirenko & Agapova, 1997; Slieker, 2000; Sirenko, 2001, 2013; Gagaev, 2005; Sirenko & Ivanov, 2005).

Amicula amiculata (Pallas, 1788)
(Figs 1B, C, 2B–E, 3–5, 6A–C, 7, 11)

Chiton amiculatus Pallas, 1788: 241, pl. 7, figs 26–30; Wood, 1815: pl. l, fig. 12; Reeve, 1847: pl. 11, sp. and fig. 59 (syntypes: Curilis insulis; lost).

Amicula amiculata (Pallas, 1788): Pilsbry, 1893: 46, pl. 5, figs 15, 16; Leloup, 1942: 6, fig. 2, pl. 1, figs 3, 7, 9 (bibliography); La Rocque, 1953: 17; Burghardt & Burghardt, 1969: 9; Putman, 1980: 35; Kaas & Van Belle, 1998: 19.

Chiton vestitus Broderip et Sowerby, 1829: 368; Crosse, 1877: 117 (syntypes: Oceano Arctico; BMNH), **syn. nov.**

Amicula vestita (Broderip et Sowerby, 1829): Pilsbry, 1893: 43, pl. 8, figs 23–26; Leloup, 1942: 4, fig. 1, pl. 1, figs 2, 6, pl. 2, fig. 1 (bibliography and synonymy); Jakovleva, 1952: 83, fig. 38, pl. 6, fig. 2; La Rocque, 1953: 17; Burghardt & Burghardt, 1969: 10; Burghardt, 1971: 66, fig.; Abbott, 1974: 404, fig. 4744; Putman, 1980: 36; Clark, 1982: 153; Hanselman, 1983: 30; Sirenko & Scarlato, 1983: 3, 4, fig.; Mayhew & Cole, 1993:11; Kaas & Van Belle, 1994: 346, fig. 140, maps 56, 57, 1998: 198; Sirenko & Agapova, 1997; Slieker, 2000: 90; Sirenko, 2001: 103, 2013: 149; Gagaev, 2005.

Chiton emersonii Couthouy, 1838: 83, pl. 3: fig. 10 (syntypes: Massachusetts Bay; USNM). Synonymysed by Pilsbry, 1893: 44.

Chiton emersonianus Gould, 1841: 151, fig. 19 (new name for *Chiton emersonii* Couthouy, 1838).

Chiton pallasii Middendorff, 1847: 117 (lectotype: Sea of Okhotsk; ZIN). Synonymised by Sirenko & Scarlato, 1983: 4.

Amicula pallasii (Middendorff, 1847): Pilsbry, 1893:45, pl. 5, figs 1–11; Jakovleva, 1952: 84, fig. 39, pl. 6, fig. 3; Talmadge, 1977: 139.

Amicula rosea Jakovleva, 1952: 86, fig. 41, pl. 6, fig. 4 (lectotype: Sea of Okhotsk, Northern Sakhalin; ZIN). Synonymised by Sirenko & Scarlato, 1983: 4.

Material examined. **Russia**: *Khabarovsk Terr., Sea of Okhotsk*: Academy Bay, 55 m, R/V "Poseydon", station 250, 24.VIII.1978, collector unknown, 1 specimen, *BL* 50 mm; Tugur Peninsula, 9 m, R/V "Poseydon", SCUBA, station 206, 17.VII.1978, collector unknown, 1 specimen, *BL* 42 mm; Tugur Bay: 1844, Middendorff leg., *lectotype* (ZIN No. 947) and 5 *paralectotypes* (ZIN No. 943) of *Chiton pallasii*, 4 specimens (ZIN Nos. 941 & 942); 2.5 m, R/V "Poseydon", SCUBA, station 204, 17.VIII.1978, collector unknown, 1 specimen, *BL* 55 mm; 21 m, R/V "Poseydon", SCUBA, station 209, 17.VIII.1978, collector unknown, 2 specimens, *BL* 43–48 mm; Mamga Bay: 11 m, R/V "Poseydon", SCUBA, station 207, 17.VIII.1978, collector unknown, 1 specimen, *BL* 54 mm; 17 m, R/V "Poseydon", SCUBA, station 208, 17.VIII.1978, collector unknown, 1 specimen, *BL* 3,5 mm; Shantara Is., 20–30 m, rocks, 16.VIII.1899, collector unknown, 2 specimens, *BL* 50–52 mm (ZIN No. 945); Bolshoy Shantar I., Jakshina Bay, intertidal zone, 25.VIII.1966, collector unknown, 10 specimens, *BL* 42–70 mm; Ulban Bay: 54°46′45″N, 137°27′00″E, 14–20 m, rocks, R/V "Lieutenant Dydymov", station 33, 30.VII.1911, collector unknown, 2 specimens, *BL* 45–51 mm; 54°53′45″N, 136°56′00″E, 30 m, rocks, R/V "Lieutenant Dydymov", station 36, 24.VII.1911, 1 specimen, *BL* 64 mm; 56°55′00″N, 139°14′00″E, 80 m, 04.IX.1932, collector unknown, *lectotype* of *Amicula rosea*, *BL* 63 mm (ZIN No. 953); 56°24′00″N, 143°12′00″E, 80 m, 06.IX.1932, collector unknown, *paralectotype* of *Amicula rosea*, *BL* 54 mm (ZIN No. 954); 5 m, R/V "Poseydon", SCUBA, station 235, 21.VIII.1978, collector unknown, 3 specimens, *BL* 42–45 mm; 52 m, R/V "Poseydon", station 267, 27.VIII.1978, collector unknown, 4 specimens, *BL* 23–37 mm; between Okhotsk Settlm. and Iona I., 58°17′N, 143°15′E, 70 m, 27.VIII.1908, collector unknown, 7 specimens, *BL* 52–78 mm; 54°35′45″N, 137°07′00″E, 80 m, rocks, R/V "Lieutenant Dydymov", station 32, 03.VIII.1911, collector unknown, 1 specimen, *BL* 52 mm; Yakshina Bay, 21 m, R/V "Poseydon", SCUBA, station 226, 20.VIII.1978, collector unknown, 4 specimens, *BL* 40–58 mm; Sakharnaya Golova I., 20 m, R/V "Poseydon", SCUBA, station 186, 14.VIII.1978, collector unknown, 1 specimen, *BL* 9.5 mm, 1 specimen, *BL* 12.5 mm;

Sakhalin Prov., Sea of Okhotsk: Sakhalin Bay, 62 m, R/V "Poseydon", station 268, 27.VIII.1978, collector unknown, 1 specimen, *BL* 36 mm; Cape Elizabeth: 5 m, R/V "Poseydon", SCUBA, station 72, 19.VII. 1978, collector unknown, 1 specimen, *BL* 42 mm; 9 m, R/V "Poseydon", SCUBA, station 73, 19.VII.1978, collector unknown, 2 specimens, *BL* 15–52 mm; 8 m, R/V "Poseydon", SCUBA, station 73, 19.VII.1978, collector unknown, 1 specimen, *BL* 21 mm; *Pacific Ocean*, Northern Kuril Is.: Paramushir I.: 50°06′N, 155°34′E, 37 m, rocks, boulders, R/V "Vityaz'", station 2764, 22.V.1954, collector unknown, 1 specimen, *BL* 40 mm (ZIN No. 971); Okeanskiy Cape, 41 m, rocks, R/V "Lebed'", station 147, 22.05.1954, collector unknown, 1 specimen (ZIN No. 971), *BL* 40 mm; Onekotan I.,

Gorelyy Cape, 10 m, R/V "Krylatka", SCUBA, station 315, sample 816, rock, 08.IX.1971, collector unknown, 1 specimen, *BL* 3.5 mm;

Magadan Prov., *Sea of Okhotsk*, near Magadan, 57 m, station 83, 04.VII.1974, 4 specimens, collector unknown, *BL* 40–58 mm;

Kamchatka Terr.: *Sea of Okhotsk*: Shelikhov Bay, 106 m, 27.VIII.1964, collector unknown, *BL* 51 mm; Penzhina Bay, intertidal zone, 15.VII.1973, collector unknown, 16 specimens, *BL* 57–86 mm; *Bering Sea*, Karaginsky Gulf, Litke Strait, 52 m, sand, shell, stones, 01.VIII.1975, collector unknown, 3 specimens, *BL* 35–43; 56°08′N, 163°31′E, 105 m, sand with pebbles, R/V "Vityaz'", station 523, 16.VIII.1950, collector unknown, 6 specimens, *BL* 25–38 mm; Shelikhov Bay, R/V "Babushkin", 106 m, 03.VIII.1986, collector unknown, 1 specimen, *BL* 51 mm;

Chukotka Autonomous Prov.: *East Siberian Sea*, Chaunskaya Bay: Shelagskiy Cape, 6 m, rocks, pebbles, silty sand, 10.VIII.1986, collector unknown, 1 specimen, *BL* 23 mm; Pevek, 4–12 m, rocks, pebbles, silty sand, 15.VIII.1986, Sirenko B.I. leg., 77 specimens, *BL* 6.5–59 mm; *Chukchi Sea*: 71°01.2′N, 175°59′W, 60 m, rocks, station NS3, 07.IX.2012, collector unknown, 22 specimens, *BL* 15–35 mm; Wrangel I., Rogers Bay, 2–4 m, silted pebbles, 22.VIII.1976, Sirenko B.I. leg., 19 specimens, *BL* 6–41 mm; 71°23′N, 174°52′W, 69 m, R/V "Professor Khromov", station 62B, 19.VIII.2004, B.I. Sirenko leg., 13 specimens, *BL* 18–61 mm; *Berng Strait*: 65°52′N, 169°00′W, 47 m, rocks, R/V "Dal'nevostochnik", station 22, 13.VIII.1932, collector unknown, 1 specimen, *BL* 12 mm; 66°00′N, 169°25′W, 47 m, rocks, R/V "Dal'nevostochnik", station 24, 14.VIII.1932, collector unknown, 3 specimens, *BL* 36–70 mm; 65°58′N, 169°52′W, 37 m, rocks, R/V "Dal'nevostochnik", station 33, 10.VIII.1933, collector unknown, 2 specimens, *BL* 53–55 mm; 66°00′N, 169°37′W, 51 m, R/V "Professor Khromov", station 10, 11.VIII.2004, B.I. Sirenko leg., 2 specimens, *BL* 25–30 mm; *Bering Sea*: Between St Lawrence I. and Chukchi Peninsula, 64°05′N, 172°02′W, 56 m, rocks, R/V "Dal'nevostochnik", station 40, 26.VIII.1932, collector unknown, 1 specimen, *BL* 21 mm; Providence Bay: 64°16′7″N, 173°50′00″W, 53 m, rocks, R/V "Dal'nevostochnik", station 14, 30.VII.1932, collector unknown, 1 specimen, *BL* 41 mm; Gulf of Anadyr: 64°22′7″N, 179°46′00″E, 46 m, rocks, R/V "Dal'nevostochnik", station 46, 29.VIII.1932, collector unknown, 3 specimens, *BL* 47–76 mm; 62°42′N, 179°53′E, 48 m, rocks, R/V "Dal'nevostochnik", station 17, 31.VII.1933, collector unknown, 2 specimens, *BL* 40–48 mm; 64°27′N, 175°18′W, 69 m, clay with sand, R/V "Krasnoarmeets", station 21, 01.VIII.1933, collector unknown, 5 specimens, *BL* 20–50 mm (ZIN No. 969).

USA, *Alaska*: *Bering Sea,* 65°16′7″N, 168°33′00″W, 50 m, rocks, R/V "Dal'nevostochnik", 06.VIII.1932, collector unknown, 1 specimen, *BL* 20 mm; *Chukchi Sea*, 70°40′20″N, 160°04′60″W, 10.3 m, sandy bottom, 08.VIII.1954, R/V "Dallas Hanna", cruise II, station 10, collector unknown, 2 specimens, *BL* 50–51 mm (ZIN No. 973); *Beaufort Sea*, Boulder Patch, SCUBA, 8 m, date unknown, K. Dunton leg., 1 specimen, *BL* 34 mm. **Canada**, *Newfoundland and Labrador Prov.*, *Atlantic Ocean*, Newfoundland Bank, 45°60′N, 51°15′W, 75–81 m, R/V "Sevastopol'", station 3098, 12.VIII.1960, collector unknown, 1 specimen, *BL* 79 mm.

Redescription. Body large, up to 86 mm, usually 40–45 mm in length. Shell rounded or slightly carinated. White colour of tegmentum often obscured by a layer of dirty gray coating. Articulamentum white. Perinotum light sandy in colour, less frequently in ivory or yellowish green hues. Ratio of width of head valve (together with articulamentum) to width of tail valve ranging from 1.10 to 1.22 (Table 1). Ratio of area of tegmentum to articulamentum varying significantly. Generally, in large intertidal specimens, tegmentum less developed, more severely abraded. Tegmentum equal in width to, or 0.25–0.50 times as wide as articulamentum on one side of valves. Apex not protruding. Mucro located posteriorly. Tegmentum with fine-grained sculpture. Small specimens measuring approximately 10 mm in length occasionally with six to eight weakly developed, short longitudinal ribs on central area (Fig. 3). In vast majority of specimens larger than 50 mm, tegmentum destroyed to varying degrees (Fig. 7).

Articulamentum strongly developed, head valve with seven to ten slits, intermediate valves with one slit on each side, tail valve featuring a sinus with one or, occasionally, two slits on its sides.

During ontogenesis, ratio of perinotum area to tegmentum area increasing. Ratio of width of perinotum at valve V to width of tegmentum ranging from 1.3 (specimens measuring 12 mm in length) to 4.5 (in specimens measuring 50 mm in length). Perinotum covered with colourless or white pointed spicules varying in length from 50 to 150 μm among different individuals (Fig. 4C). Dorsal spicules almost completely immersed in cuticle. Entire surface of cuticle covered with numerous short, simple bristles, and bearing longer, more complex bristles grouped into bundles or tufts, with each tuft containing between two to

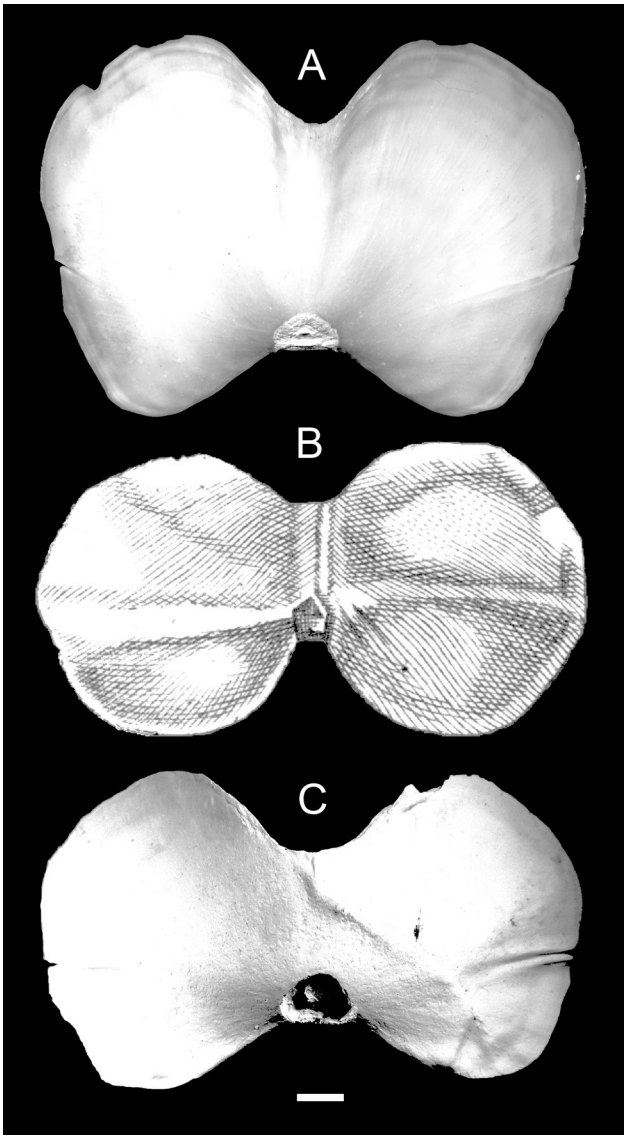


Fig. 1. Intermediate valves of *Amicula* Gray, 1847 spp. **A**, *A. gurjanovae* Jakovleva, 1952, Iturup Island, *BL* 90 mm (ZIN No. 2586), valve V, width 30 mm; **B**, *A. amiculata* (Pallas, 1788), intermediate valve of syntype (after Pallas, 1787, pl. VII, fig. 29); **C**, *A. vestita* (Broderip et Sowerby, 1829), Shantar Islands, Jakshina Bay, *BL* 70 mm, valve V, width 25 mm. Scale bar: 2 mm (A, C).

30 bristles (Fig. 4A). Bristles within a bundle sometimes diverging from extreme base, often glued together at their basal ends, creating appearance of branching bristles, as described by Jakovleva (1952). In fact, branching bristles absent. All bristles formed in bundles, not as a result of branching, but independently of one another [it is more accurate to refer to them as glued bristles rather than branching, as each bristle appears to be inserted into the body of a glued bundle of bristles]. Perinotum of almost every specimen with tufts of bristles diverging from base and tufts of glued together bristles (Fig. 5C). In specimens inhabiting deeper waters, number of glued tufts greater that of tufts with bristles diverging from the base. Generally, total number of tufts in these specimens smaller than that in littoral specimens. Length of tufts of glued bristles reaching 6–7 mm. At tegmentum exit site, bristles and bristle tufts often more densely arranged than in rest perinotum. Special marginal spicules absent. Spicules of hyponotum similar to those of perinotum, with lengths varying from 40 to 80 μm across different specimens. Ventral spicules inserted into chitinous stem cups (Fig. 6A–C). In vast majority of large specimens examined, cups empty, probably because of destruction of spicules caused by acidic medium in which hyponotum of these chitons consistently located.

In specimens measuring 55 mm and 80 mm in length, radula 14 mm and 16 mm in length, respectively; number of transverse rows of plates in radula 42 and 45, respectively. Margins of all marginal plates of radula without serrations. During ontogenesis, shape of blade of major lateral tooth of the radula changing only slightly.

Number of gills increasing with age from 17 (in specimens measuring 9 mm in length) to 30 (in specimens measuring 86 m in length) on each side of body, with gills located from valve V in young specimens and from 3rd to 7th valve in larger specimens.

Comparison. This species differs from *A. gurjanovae* in having the more broad head valve (with a ratio of the width of the head valve to the width of the tail valve of 1.1–1.2 *vs.* 0.9–1.0 in *A. gurjanovae*), the more broad intermediate valve (with a ratio of the width of the intermediate valve to its length of 1.75–2.10 *vs.* 1.42–1.43 in *A. gurjanovae*), the absent of serrations on the marginal tooth of the radula, the rounded or slightly carinated valves (*vs.* always carinated in *A. gurjanovae*), the pale yellowish girdle (*vs.* pink brown in *A. gurjanovae*), and a smaller body size.

Note. Morphological analysis of chitons previously classified as three distinct species, *A. pallasii*, *A. rosea*, and *A. vestita*, has led to the conclusion that all their specimens belong to the same species.

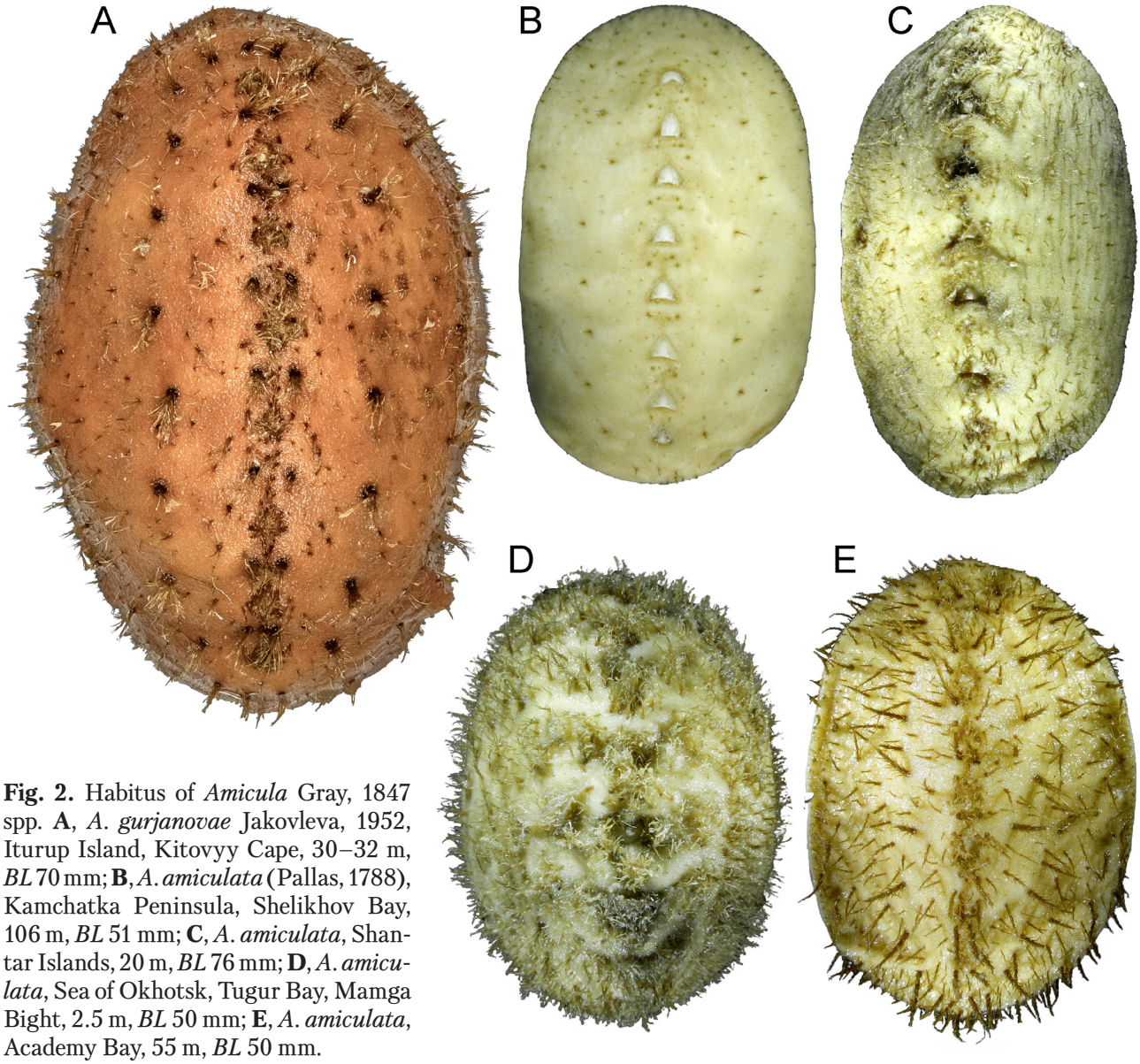


Fig. 2. Habitus of *Amicula* Gray, 1847 spp. **A**, *A. gurjanovae* Jakovleva, 1952, Iturup Island, Kitovyy Cape, 30–32 m, *BL* 70 mm; **B**, *A. amiculata* (Pallas, 1788), Kamchatka Peninsula, Shelikhov Bay, 106 m, *BL* 51 mm; **C**, *A. amiculata*, Shantar Islands, 20 m, *BL* 76 mm; **D**, *A. amiculata*, Sea of Okhotsk, Tugur Bay, Mamga Bight, 2.5 m, *BL* 50 mm; **E**, *A. amiculata*, Academy Bay, 55 m, *BL* 50 mm.

The differences among these species were reduced to varying degrees of density in the arrangement of bristle tufts on the perinotum. No branched bristles, as described by Jakovleva (1952), were found; the pink coloration of the perinotum in specimens attributed to *A. rosea* (Jakovleva, 1952) was a result of fixation in formalin. The body shape of the *Amicula* species is not a reliable character, as it is influenced by fixation conditions and the state of the specimens, which are typically compressed during the fixation process. At depths of 60–100 m, specimens with long, thin, and sparse tufts of bristles are more prevalent, distinguishing them from those previously attributed to *A. pallasii*, an intertidal form characterised by numerous bristle tufts. However, there is a significant number of specimens that represent a gradual transition in the density of bristle tuft arrangement between these two forms.

The study of the shape of intermediate valves revealed that the ratio of the width of the valves to their length in all examined specimens identified as *A. vestita* ranges from 1.75 to 2.10. This range includes the ratio of the syntype of *A. amiculata*, which is 1.87, thereby providing clear confirmation of the identity of these two species (Table 2).

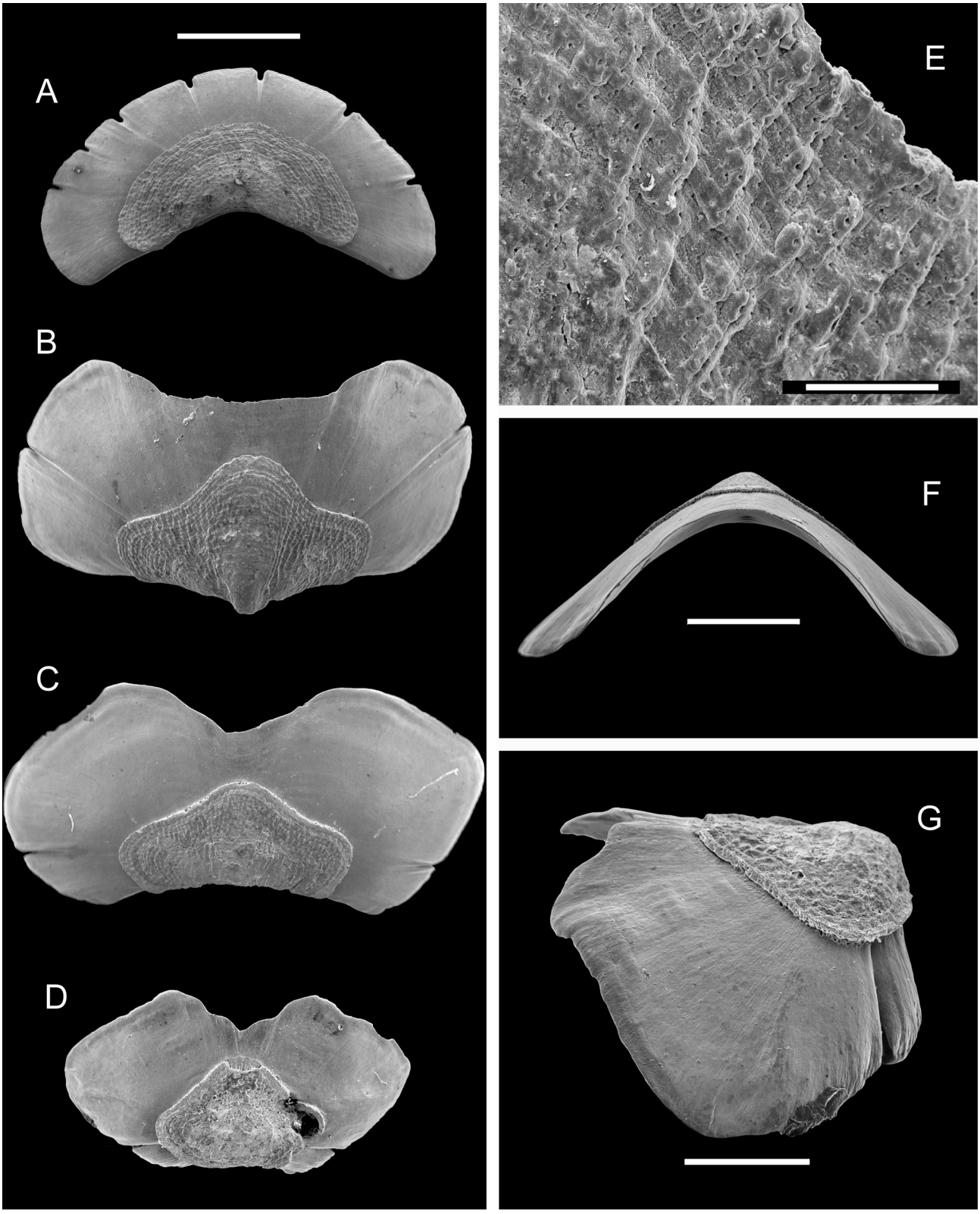


Fig. 3. *Amicula amiculata* (Pallas, 1788), Chukchi Sea, R/V "Professor Khromov", station NC–3, 60 m. **A**, valve I, dorsal view; **B**, valve II, dorsal view; **C**, valve V, dorsal view; **D**, valve VIII, dorsal view; **E**, sculpture of tegmentum in jugal and pleurolateral areas; **F**, valve V, rostral view; **G**, valve VIII, lateral view. Scale bars: 2 mm (A–D, F), 200 μm (E), 1 mm (G).

Table 1. The ratios of the height to width of the intermediate valves (dorsal elevation), the ratio of the width of the head valve to the width of the tail valve, and a slit formula for several specimens of *Amicula vestita* (Pallas, 1788).

Species	Locality	Dorsal elevation	Ratio of width of head valve to width of tail valve	Slit formula
Amicula vestita	Sea of Okhotsk, Magadan	0.36	1.20	8/1/sinus+1–2
A. vestita	Sea of Okhotsk, Iona Island	0.44	1.22	8/1/sinus+1–1
A. vestita	Sea of Okhotsk, Shantar Islands	0.28	1.20	9/1/sinus+1–2
A. vestita	Sea of Okhotsk, Shantar Islands	0.39	1.10	10/1/sinus+1–1
A. vestita	Chukchi Sea	0.50	1.12	10/1/sinus+1–2
A. vestita	Chukchi Sea, Wrangel Island	0.42	1.14	8/1/sinus+1–1
A. vestita	Bering Strait	0.40	1.13	8/1/sinus+1–1
A. vestita	East Siberian Sea, Chaun Bay	0.47	1.20	7/1/sinus+2–2
A. vestita	Bering Sea, Kamchatka	0.30	1.10	8/1/sinus+1–1

Table 2. The ratios of the width of the intermediate valve to its length in species of the genus *Amicula* Gray, 1847.

Species	Locality	Body length (mm)	Ratio
Amicula vestita	Chukchi Sea	28	2.1
A. vestita	Chukchi Sea	35	1.75
A. vestita	Sea of Okhotsk, Shantar Islands	54	1.9
A. vestita	Sea of Okhotsk, Shantar Islands	65	1.92
A. vestita	Bering Sea	51	1.81
A. amiculata (syntype)	Kuril Islands	—	1.87
A. gurjanovae	Iturup Island	90	1.43
A. gurjanovae	Iturup Island	67	1.42

Distribution. Boreal-arctic species. Widespread in the Beaufort, Chukchi, East Siberian, Bering, and Okhotsk seas, as well as around Kamchatka and off the Commander and Northern Kuril Islands. In the Atlantic Ocean, this species inhabits the waters off the coast of North America, extending southward to the Cape Cod Peninsula (Oldroyd, 1927). These species are most commonly found in the southern Chukchi Sea, northern Bering Sea, and the northern and western parts of the Sea of Okhotsk.

According to the distribution of *A. amiculata* (Fig. 11), it can be inferred that the migration of this species from the northern Pacific to the northwestern Atlantic occurred during the Pliocene, through the Canadian Arctic Archipelago. This pattern is similar to that observed in many other species (Dixon, 1979; Golikov, 1980), including *Tonicella marmorea* (Fabricius, 1780) (Sirenko & Dell Angelo, 2023). However, unlike the latter species, *A. amiculata* was unable to cross the Atlantic and remained confined to its western region. It is possible that a connection between the northern Pacific and northern Atlantic populations still exists today.

Ecology. *Amicula amiculata* inhabits the intertidal zone (Shantar Islands and Penzhina Bay) to a depth of 150 m in the western part of the Sea of

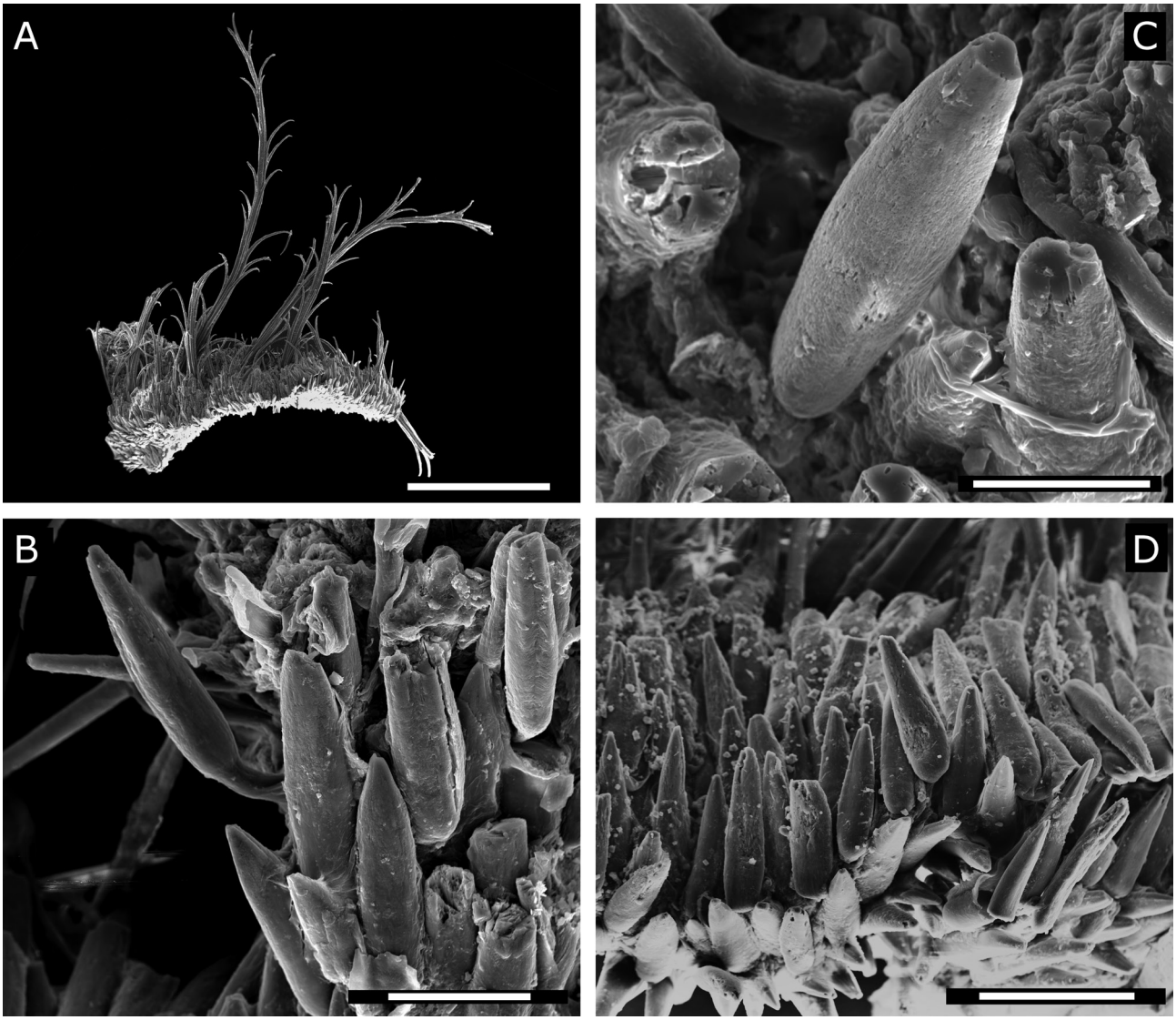


Fig. 4. *Amicula amiculata* (Pallas, 1788), Chukchi Sea, R/V "Professor Khromov", station NC–3, 60 m. **A**, single and glued, complete bristles in perinotum; **B**, ventral spicules in stem cups and single bristles on margin of girdle; **C**, dorsal spicules; **D**, ventral spicules. Scale bars: 1 mm (A), 50 μm (B), 30 μm (C), 100 μm (D).

Okhotsk. This species is typically found on stony, sandy-pebble, and gravel-pebble substrates, often with an admixture of clay and silt, in temperatures ranging from −1.8 to +12 °C and salinity levels of 28.5–33.0 ‰. This species prefers to inhabit intertidal pools and depths of 4–90 m in the Sea of Okhotsk, 10–100 m off eastern Kamchatka, and 3–50 m in the Chukchi Sea. Average settlement densities and biomass of chitons across different parts of the range are approximately similar: in the Chukchi Sea near Wrangel Island (2 specimens/m² and 3.2 g/m²), in the northern part of the Bering Sea (2 specimens/m² and 6.0 g/m²), and in the area of the Shantar Islands (1.5 specimens/m² and 8.0 g/m²). The highest recorded settlement density was off northeastern Sakhalin, with 8 specimens/m² and a biomass of 40 g/m². Females with mature oocytes were observed off Wrangel Island and in the Bering Strait in September. The diameter of mature eggs without an egg hull measures 300–350 μm, while those with an egg hull can reach up to 400 μm. The translucent egg hull features appendages with a broadened base, from which the body of each appendage splits at the distal end into four to six short, hook-like processes. Juveniles of the smallest size, measuring

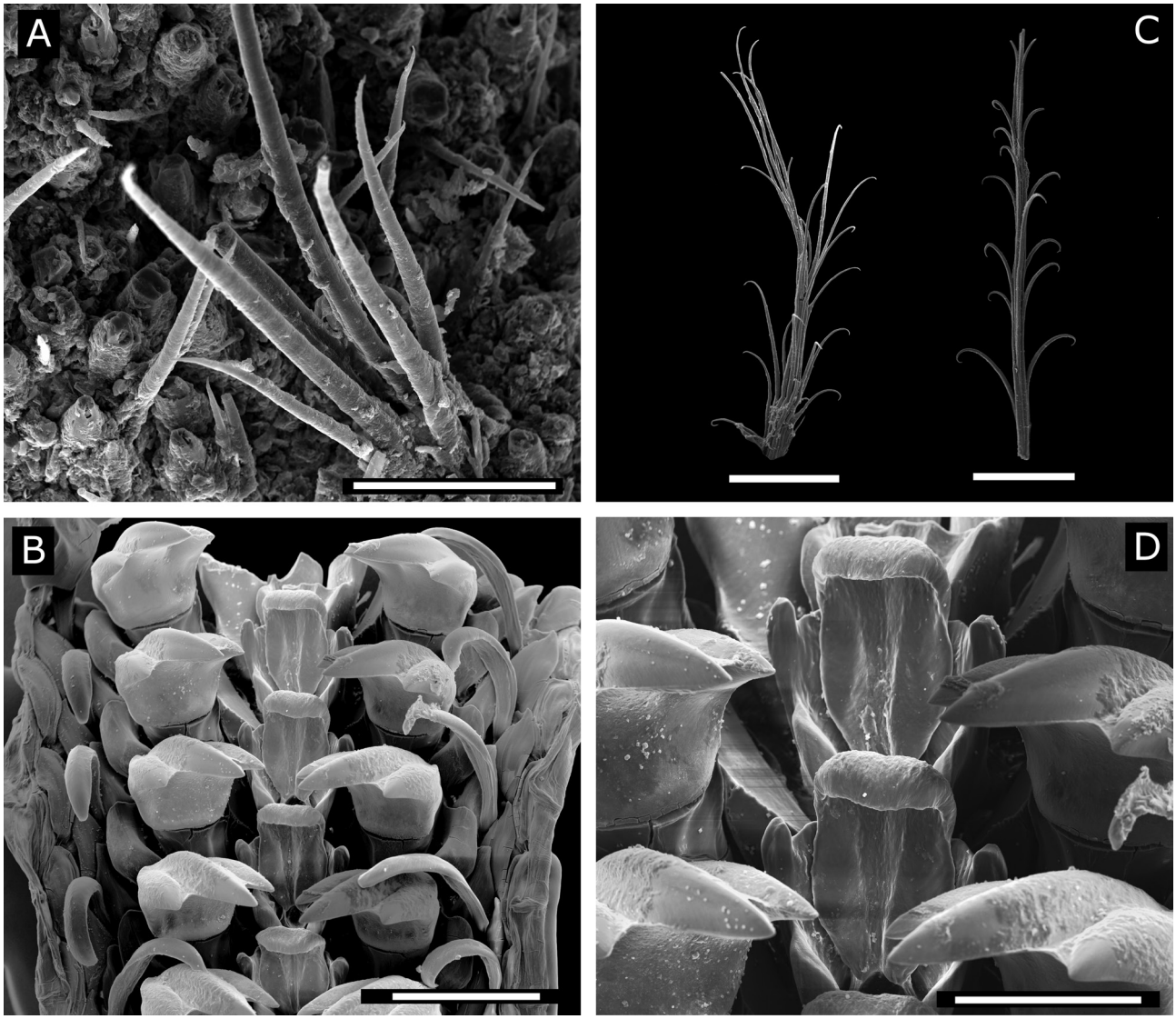


Fig. 5. *Amicula amiculata* (Pallas, 1788), Chukchi Sea, R/V "Professor Khromov", station NC–3, 60 m (A–C), Sea of Okhotsk, North Sakhalin, 42 m (D). **A**, dorsal spicules, simple bristles and tuft with bristles diverging from the base; **B**, radula; **C**, tuft with glued bristles; **D**, central, first lateral and major lateral teeth of radula. Scale bars: 100 μm (A), 500 μm (B), 1 mm (C), 300 μm (D).

3–4 mm, were collected in the western part of the Sea of Okhotsk and off the northern Kuril Islands between July and September. In the Chukchi Sea, the species appears to breed at temperatures ranging from 0 to +2 °C during September and October. The maximum lifespan exceeds ten years, with populations predominantly consisting of specimens aged six to seven years. The largest specimens, measuring 80–86 mm in length, were collected from intertidal pools in Penzhina Bay and at depths of 40–65 m in the Bering Strait. According to my observations, adult molluscs primarily feed on animal matter and detritus. The digestive tract contains a diverse array of organisms, including bryozoans, colonial ascidians, barnacles, sponges, spirorbis, and small quantities of hydroids, foraminifera, and other small invertebrates. The detritus consumed by chitons is primarily of plant origin, consisting mainly of remnants of brown algae and sand. Dunton et al. (2006) consider this species as herbivorous, noting that it primarily feeds on kelp tissues in the

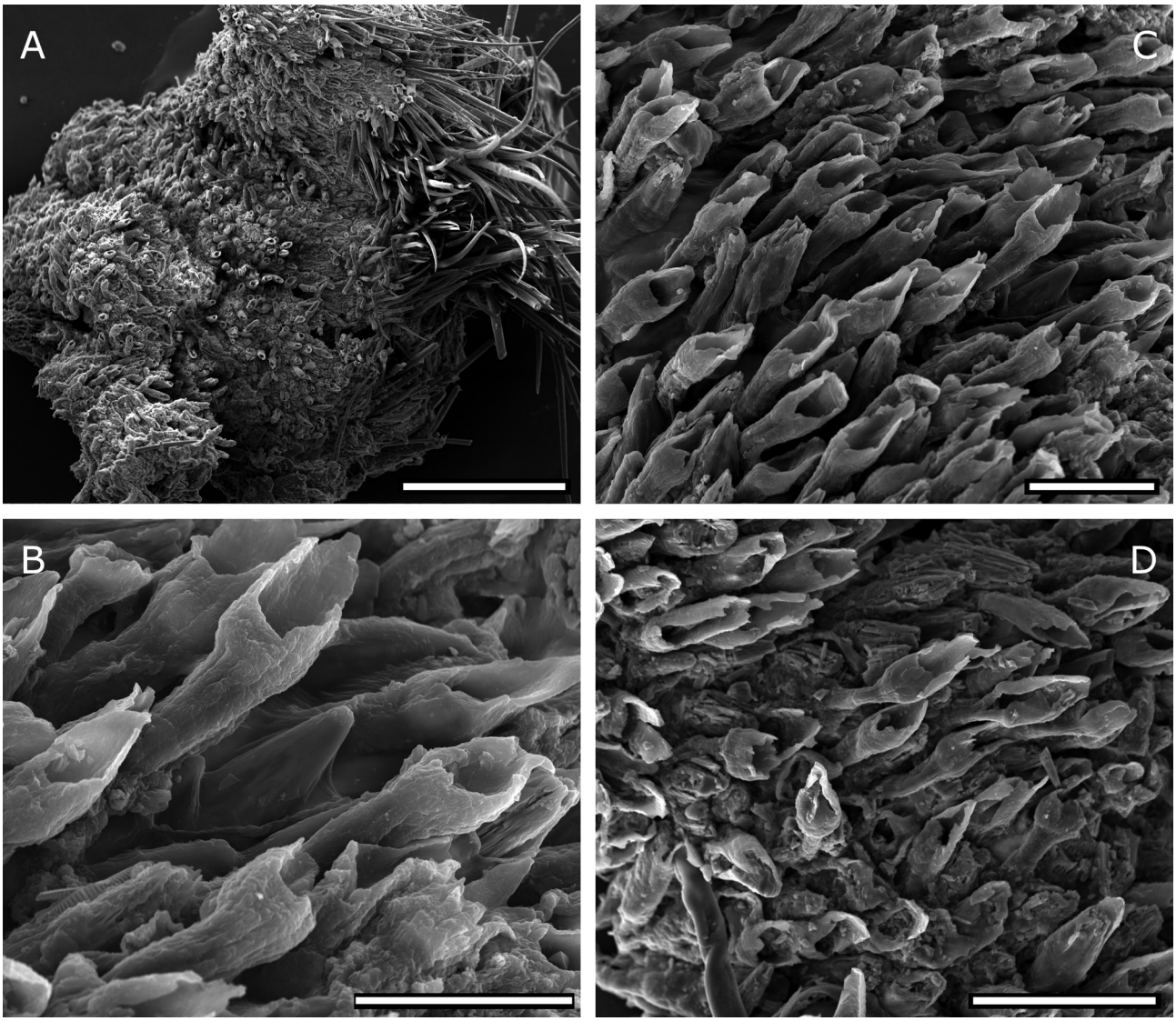


Fig. 6. *Amicula amiculata* (Pallas, 1788) (A–C) and *A. gurjanovae* Jakovleva, 1952 (D). **A**, Atlantic Ocean, Newfoundland Bank, 75–81 m, dorsal single and complete bristles and stem cups, most of them without ventral spicules; **B**, **C**, Sea of Okhotsk, near Magadan, 57 m, stem cups on hyponotum near its margin and several ventral spicules; **D**, Iturup Island, Kitovyy Cape, 30–32 m, stem cups and remains of ventral spicules. Scale bars: 500 μm (A), 50 μm (B), 40 μm (C), 100 μm (D).

Beaufort Sea off the coast of Alaska. However, I believe that this species does not directly consume kelp tissues in this region; rather, it primarily feeds on detritus of plant origin, predominantly derived from kelp, which is the dominant algal species in the area. In addition to detritus, which constitutes 60% of the contents of the digestive tract, the analysis revealed the presence of bryozoans, spirorbis, foraminifera, and juvenile gastropod molluscs (17%), small amounts of kelp scraps (15%), and sand (8%) in the chitons from the Beaufort Sea. It appears that kelp fragments enter the digestive tract of chitons when they ingest damaged algal parts that have been colonised by fungi, bacteria, and protozoa.

The varying degrees of destruction observed in the tegmentum of most individuals larger than 50 mm (see above) may suggest that chitons of this species inhabit an aggressive environment, resulting in the corrosion of their calcareous shells.

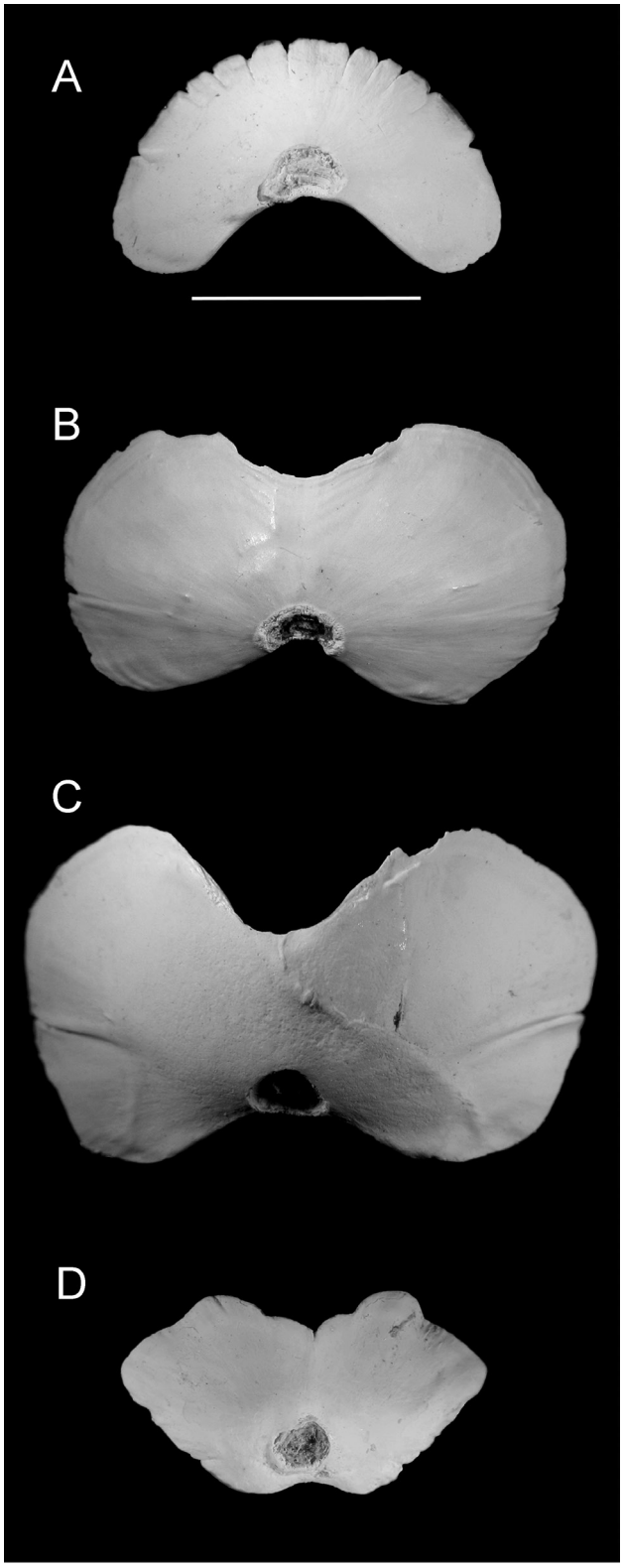


Fig. 7. *Amicula amiculata* (Pallas, 1788), valves in dorsal view, Sea of Okhotsk, Bolshoy Shantar Island, Jakshina Bay, intertidal zone, *BL* 70 mm. **A**, valve I; **B**, valve II; **C**, valve V; **D**, valve VIII. Scale bar: 1 cm (A–D).

Amicula gurjanovae Jakovleva, 1952
(Figs 1A, 2A, 6B, 8–10, 12)

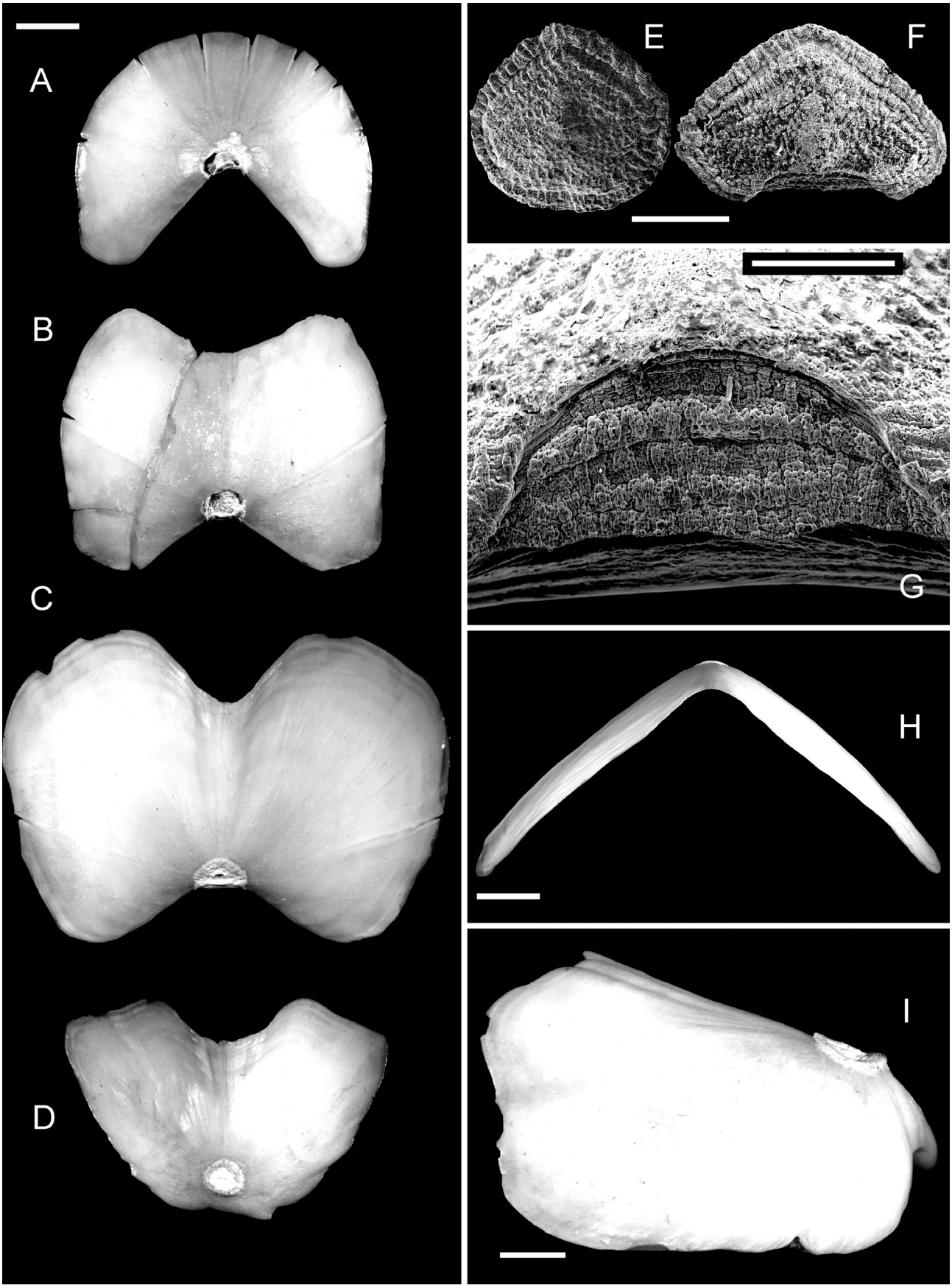
Amicula gurjanovae Jakovleva, 1952: 85, fig. 40, pl. 7, fig. 1; Sirenko & Scarlato, 1953: 3; Taki, 1964: 411; Burghardt, 1971: 66; Sirenko, 1985: 358, fig. 10, tab. 2; Okutani & Saito, 1987: 166, figs 1–11, pl. 1; Matsukuma et al., 1991: 80; Saito, 1994: 101.

Amicula amiculata sensu Kaas & Van Belle, 1994: 344, fig. 139, map 50, 1998: 19; Higo et. al., 1999: P85; Saito, 2000: 17, pl. 8, fig. 10 (non *Chiton amiculatus* Pallas, 1788).

Type material examined. *Lectotype* (ZIN No. 940/1), Sea of Okhotsk, southeastern coast of Sakhalin I., Gulf of Patience, 48°53.8′N, 143°05.3′E, 18–27 m, R/V "Toporok", 12 IX.1947, collector unknown, *BL* 86 mm.

Non-type material examined. **Russia**: *Sakhalin Prov.*: *Sea of Okhotsk*: Sakhalin I., Gulf of Patience, 48°33.0′N, 144°32.5′E, 36–39 m, R/V "Toporok", 11.IX.1947, collector unknown, 1 specimen, *BL* 83 mm; Iturup I.: Kitovyy Cape, 30–32 m, rocks, 30.VII.1969, collector unknown, 1 specimen, *BL* 96 mm; L'vinaya Past' Bay: 5–10 m, rocks, 30.VII.1969, collector unknown, 1 specimen, *BL* 90 mm (ZIN No. 2586); 5–50 m, rocks, SCUBA, 13.VII.1972, collector unknown, 1 specimen, *BL* 80 mm (ZIN No. 2579); 6 m, rocks, SCUBA, 25.VIII.1976, collector unknown, 1 specimen, *BL* 100 mm; 10–20 m, stones, SCUBA, 30.VII.1969, collector unknown, 1 specimen, *BL* 120 mm; Konservnyy Cape, 20–25 m, rocks, stones, SCUBA, 31.VIII.1971, collector unknown, 1 specimen, *BL* 123 mm; *Sea of Japan*, Moneron I.: 40–60 m, rocks, SCUBA, 29.VII.1976, collector unknown, 1 specimen, *BL* 23 mm (ZIN No. 2582); 40 m, pebble, SCUBA, 30.VII.1976, collector unknown, 1 specimen, *BL* 21 mm (ZIN No. 2585); *Pacific Ocean*: Iturup I., 50 m, Dobroe Nachalo Bay, 44°31.0′N, 147°06.5′E, rocks, 1972, collector unknown, 1 specimen, *BL* 80 mm (ZIN No. 2582); Shikotan I.: 15 m, stones, SCUBA, 07.X.1971, collector unknown, 1 specimen, *BL* 85 mm (ZIN No. 2581); 25 m, stones, SCUBA, 29.IX.1972, collector unknown, 1 specimen, *BL* 80 mm (ZIN No. 2580); South Kuril Strait: 30 m, 43°40.1′N, 146°14.5′E, rocks, 16.VII.1987, collector unknown, 1 specimen (ZIN No

Fig. 8. *Amicula gurjanovae* Jakovleva, 1952, valves in dorsal view, Iturup Island, L'vinaya Past' Bay: 10–20 m, *BL* 90 mm (ZIN No. 2586) (A–D, H, I), 5–50 m, *BL* 80 mm (ZIN No. 2579) (E–G). **A**, valve I; **B**, valve II; **C**, valve V; **D**, valve VIII; **E**, tegmentum of tail valve; **F**, tegmentum of valve V; **G**, apical area of valve V. Scale bars: 4 mm (A–D, H), 1 mm (E, F), 500 μm (G), 2 mm (I).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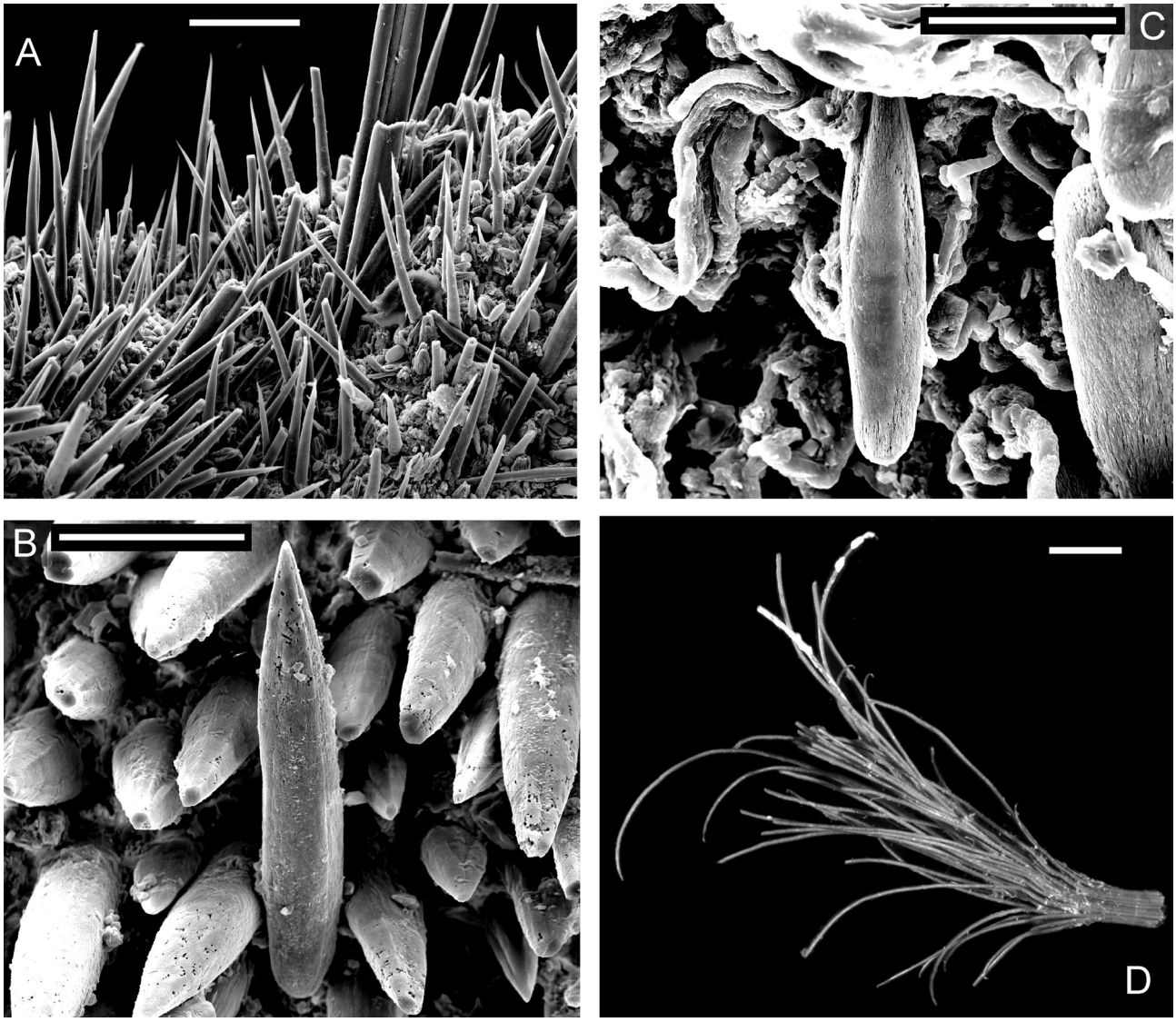

Fig. 9. *Amicula gurjanovae* Jakovleva, 1952, Sea of Japan, Moneron Island, 40 m (ZIN No. 2582), *BL* 23 mm. **A**, dorsal simple and complete bristles; **B**, ventral spicules; **C**, dorsal spicule; **D**, complete bristle. Scale bars: 100 μm (A, D), 50 μm (B), 40 μm (C).

2584); 100–110 m, rocks, 08.IX.1987, collector unknown, 1 specimen, *BL* 112 mm (ZIN No 2583).

Redescription. Large chiton, second only to *Cryptochiton stelleri* (Middendorff, 1847) in size; body length usually 80–100 mm. Shell carinated. Colour of perinotum from pink-brown to brown. Separate tufts of bristles, arranged in rows along sides of shell protrusions, clearly defined. All shell valves long, narrow, especially at tail valve. Head valve narrower or equal in width to tail valve. Tegmentum of valve V less than 0.25 times as wide as articulamentum on one side of valve. Apex not protruding. Mucro located slightly posteriorly.

Tegmentum yellowish white. Area of articulamentum adjacent to tegmentum pink, gradually transitioning to white toward margins. Sometimes, articulamentum in posterior part of valve light brown. Ventrally, central part of valve pink, remaining areas are white. Coloration of perinotum from pink-brown to brown.

Head valve of articulamentum with seven to eight slits, intermediate valves with one slit on each side, tail valve bearing a sinus with a slit on each side.

Perinotum of valve V nine to ten times as wide as tegmentum of this valve. Spicules of perinotum

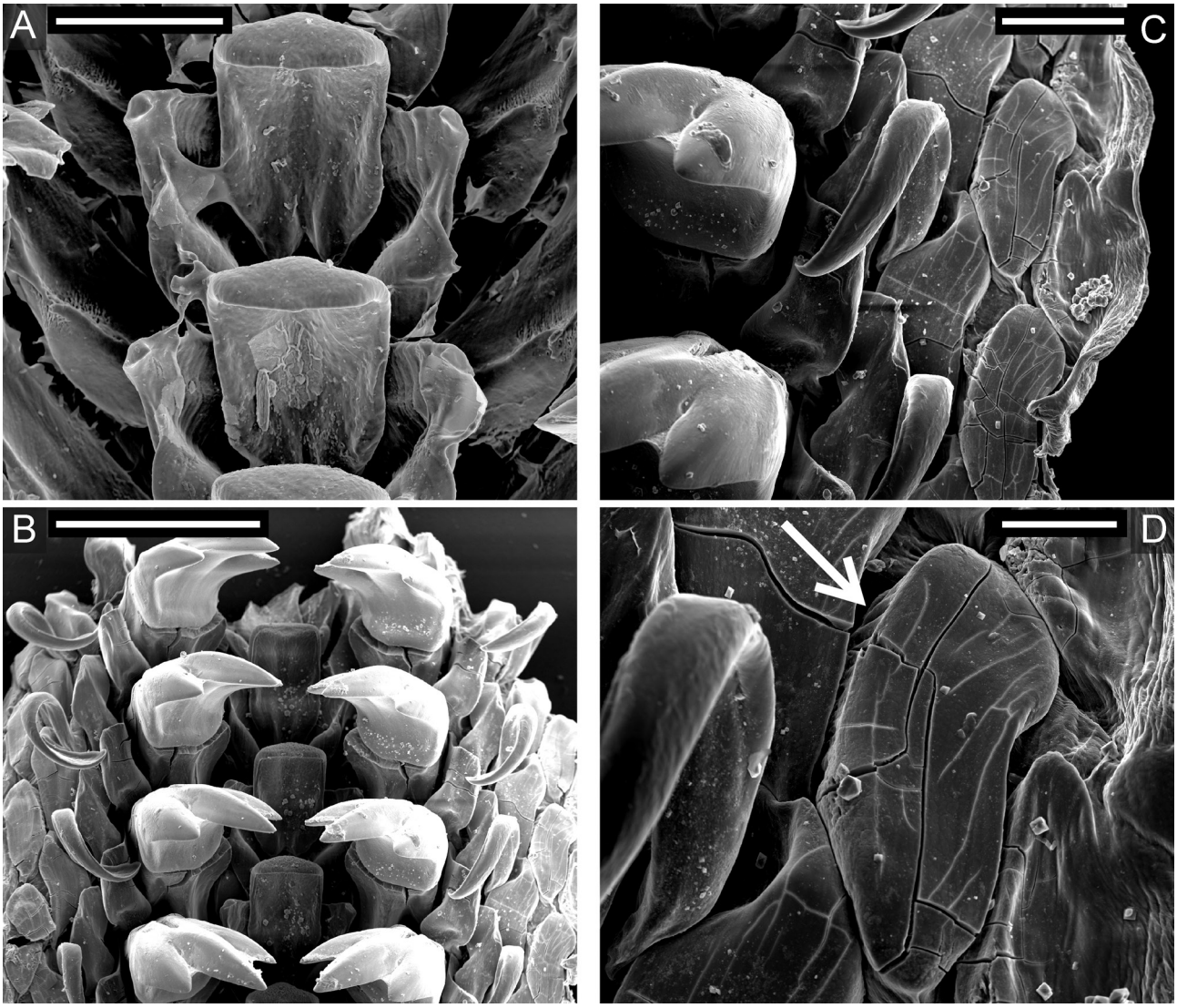

Fig. 10. *Amicula gurjanovae* Jakovleva, 1952, Sea of Japan, Moneron Island, 40 m (ZIN No. 2582), *BL* 23 mm. **A**, central, first lateral and major lateral teeth of radula; **B**, radula; **C**, major lateral, uncinal and marginal teeth of radula; **D**, major uncinal, second marginal and third marginal teeth of radula. Arrow shows serration in second marginal tooth. Scale bars: 300 μm (A), 400 μm (B), 500 μm (C), 100 μm (D).

red, narrow, pointed, 70 to 120 μm in length (Fig. 9C). Perinotum densely covered with single bristles measuring up to 500 μm in length (Fig. 9A), and bearing small and very large tufts of long, usually free bristles, ranging from two to 60 or more bristles in each tuft (Fig. 9D). Length of bristles in tufts reaching up to 7 mm. Each side of body with a row of larger bristle tufts located opposite tegmentum. Due to presence of bristles, silt particles accumulating on perinotum, enhancing camouflage of molluscs. Special marginal spicules absent. White spicules of hyponotum slightly larger than those of perinotum, measuring up to 100–150 μm in length. Ventral spicules inserted into chitinous cups with stem; in large specimens examined, cups appeared empty (Fig. 6D), likely due to destruction of spicules by acidic environment in which hyponotum of these chitons consistently situated.

In specimens measuring 80 mm and 120 mm in length, lengths of radula 18 mm and 27 mm, respectively, with number of transverse rows of plates being 49 and 53. Inner margins of last two marginal teeth of radula serrated (Fig. 10D).

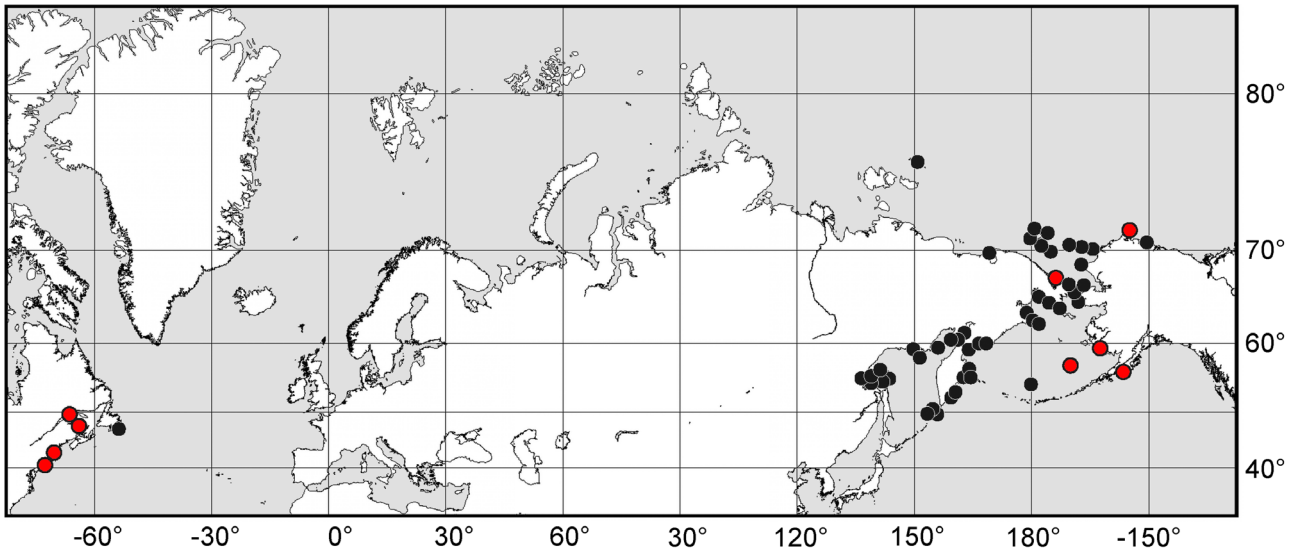

Fig. 11. Distribution of *Amicula amiculata* (Pallas, 1788). Black circles – specimens examined, red circles – by literature data.

Number of gills changing in ontogeny, starting from 24 on each side of body in individuals measuring 21 mm in length, increasing to 34 in those measuring 85 mm, and reaching 38 in individuals measuring 123 mm in length. Smaller specimens with rows of gills ranging from four, while larger ones with three to seven rows on each side of body.

Comparison. This species differs from *A. amiculata* in having the less broad head valve (with a ratio of the width of the head valve to the width of the tail valve of 0.9–1.0 *vs.* 1.1–1.2 in *A. amiculata*), the less broad intermediate valve (with a ratio of the width of the intermediate valve to its length of 1.42–1.43 *vs.* 1.75–2.10 in *A. amiculata*), the presence of serrations on the marginal tooth of the radula, red-coloured spicules on the perinotum, the narrower carinated shell, pink spots on the articulamentum, and a larger body size.

Distribution. West-Pacific low-boreal species. Widespread in the southern part of the Sea of Okhotsk (Gulf of Patience, Iturup Island) and off the coasts of Shikotan, Moneron (Sea of Japan), and Hokkaido islands.

Ecology. Chitons of this species have been found at depths ranging from six metres (Iturup Island) to 100–110 m (South Kuril Strait) on stony and pebbly substrates, including bedrock and shell outcrops. Their habitats are characterised by temperatures ranging from 0 °C in winter to +15 °C in summer, with salinities of 32.5–33‰. Although the entire range of this species falls within the boundaries of the low-boreal subregion, their vertical distribution indicates a preference for relatively cold-water habitats. In the Gulf of Patience, these molluscs are found at depths of 27–36 m, 6–32 m off Iturup Island, 15–25 m off Shikotan Island, 40–60 m off Moneron Island, and 100–110 m in the South Kuril Strait. In most of these areas, summer temperatures do not exceed 12 °C at the specified depths. Only in the L'vinaya Past' Bay (Iturup Island), at a depth of six meters, can summer water temperatures reach 15°C. This species is quite rare. The collection at ZIN contains several adult specimens measuring over 65 mm in length and one juvenile specimen measuring 21 mm. The largest number of chitons was collected near Iturup Island, where the largest specimen, measuring 123 mm in length and 72 mm in width, was found at a depth of 25 m. Chitons primarily feed on colonial ascidians and bryozoans, with foraminiferans, oligochaetes, and spirorbis present in small quantities in their digestive tracts.

Discussion

Six species of the genus *Amicula* were initially described. Following the description of the species *Chiton emersonii*, the name of which was later replaced by *Ch. emersonianus*, both names were

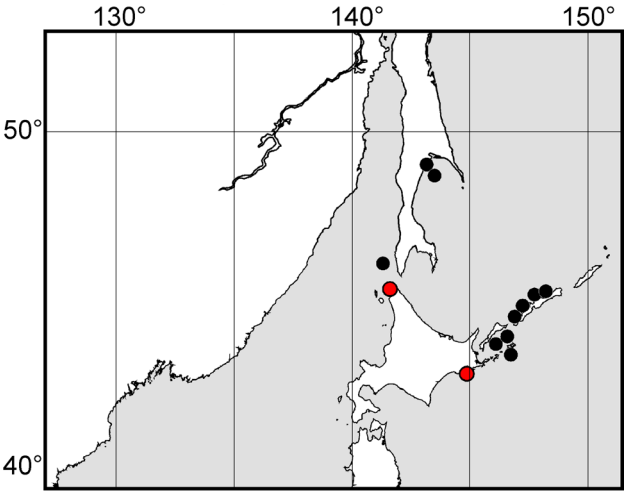

Fig. 12. Distribution of *A. gurjanovae* Jakovleva, 1952. Black circles – specimens examined, red circles – by literature data.

considered junior synonyms of *A. vestita* (Kaas & Van Belle, 1994). *Amicula pallasii* and *A. rosea*, which primarily differ in the density of bristle tufts on the perinotum, have also been found to be conspecific with *A. vestita* (Sirenko & Scarlato, 1983).

The main distinguishing characters of *Amicula pallasii*, according to Middendorff (1847) and Jakovleva (1952), are: the short and rounded body, the tegmentum covered only with granules and lacking ribs, a large number of bristle tufts on the perinotum, and the gills that extend to half the length of the foot. It should be noted that the shape of the body can be influenced by the fixation of specimens; during fixation, they may bend to varying degrees, causing both the anterior and posterior ends of the body to curve toward the foot. As a result, this character is unstable and may not be reliable for classification purposes. In specimens identified as *A. pallasii*, the tegmentum is covered with grains and occasionally features weakly expressed ribs. Furthermore, in the majority of chitons belonging to the genus *Amicula*, the tegmentum deteriorates with age (Figs. 1C, 7), rendering this character unreliable for identification purposes. The number of simple bristles in tufts, as well as the number of tufts on the perinotum, are also highly variable characters, exhibiting continuous transitions from dense tufts of bristles to nearly bare surfaces, as illustrated in Fig. 2B–E. Additionally, in some specimens, the tufts of bristles are partially removed during feeding by their conspecifics (Fig. 2B). The length of the gill arrangement in all chitons of the genus *Amicula* examined in this study exceeds half the length of the foot.

The original description of *Amicula rosea* by Jakovleva (1952) includes several main characters: an almost round body shape; the greyish pink perinotum that is sparsely covered with long, stiff, single bristles; bristles do not form tufts (although Jakovleva notes that each bristle is a rod from which smaller and finer bristles branch in various directions), and the shell valves are nearly flat. No species in the genus has branching setae, including *A. rosea* and its type specimens. There are two types of bristle tufts: loose tufts that diverge at the base and dense tufts composed of glued bristles, the tips of which are slightly bent away from the main mass. The shape of the body and the density of bristle coverage on the perinotum have been mentioned above. The colour of the perinotum in some paralectotypes of *A. rosea* is not greyish pink, but rather pale sandy, similar to that of most specimens of *A. vestita*. The shell valves of *A. rosea* collected from the Sea of Okhotsk, Magadan, and Iona Island are similar to those of all other species in the genus examined in this study; they are neither flat nor low but rather of medium height (Schwabe, 2010) (dorsal elevation is 0.36–0.44) (Table 1).

The characters of the intermediate valves of the shells of *Amicula amiculata*, *A. vestita* and *A. gurjanovae*, which are now recognised within the genus, are presented in Fig. 1 and Table 1.

The ratio of the width to the length of intermediate valves in all studied specimens of *A. vestita* ranges from 1.75 to 2.10, which is significantly closer to the corresponding ratio in the syntype of *A. amiculata* (1.87) (Fig. 1, Table 2). In contrast, specimens of *A. gurjanovae* exhibit a much smaller ratio, ranging from 1.42 to 1.43. Furthermore, *A. gurjanovae* is a rare species listed in the Red Book (Sirenko, 2021), with only 15 specimens in the collections of ZIN. This species inhabits depths of six meters or greater. It was first found off the southern coast of Sakhalin only in 1947, highlighting both its rarity and inaccessibility. In contrast, *A. vestita* is widespread and, in some regions, abundant in the North Pacific and Arctic

oceans. The species often inhabits the intertidal zone, which makes it more accessible for collection. Consequently, the likelihood of collecting a specimen of *A. amiculata* from the southern Kuril Islands, where *A. gurjanovae* is present and *A. vestita* is absent, is extremely low. In contrast, the probability of collecting *A. amiculata* from the northern Kuril Islands, where *A. vestita* is present, is significantly higher. This observation further supports the hypothesis that *A. amiculata* and *A. vestita* are conspecific. Pilsbry (1893: 47) also asserts that he has no doubt that *A. pallasii* (synonymous with *A. vestita*) is the same species as *A. amiculata*.

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