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The history of study, the taxonomic composition and the origin of the sea anemone fauna of the Kara Sea (Actiniaria, Anthozoa, Cnidaria)

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ABSTRACT

Based on the study of new collection material and literature data, the composition of the sea anemone fauna of the Kara Sea is described. It includes 13 species of 7 families. Among them are 10 species that have previously been known for this region: *Urticina crassicornis* (O.F. Müller, 1776), *Aulactinia stella* (Verrill, 1864), *Hormathia digitata* (O.F. Müller, 1776), *Allantactis parasitica* Danielssen, 1890, *Actinostola callosa* (Verrill, 1882), *A. spetsbergensis* (Carlgren, 1893), *Anthosactis janmayeni* Danielssen, 1890, *Halcampa arctica* Carlgren, 1893, *Edwardsia arctica* Carlgren, 1921, *Ptychodactis patula* Appellöf, 1893, and 3 species reported for the Kara Sea for the first time: *Cactosoma abyssorum* Danielssen, 1890, *Haliactis arctica* Carlgren, 1921, and *Edwardsia vitrea* Danielssen, 1890. The ranges of the species are described. A detailed consideration of the species' geographical distribution, determined by the temperature, depth and salinity, allows the anemones to be subdivided into 3 groups: a) inhabiting the shelf and associated with high salinity; b) eurybathic, associated with the high latitudes, high salinity and a narrow interval of low temperatures; c) the most widespread, withstanding desalination and low temperatures. The geographic ranges of epibenthic polyps of the infraorder Thenaria have now been thoroughly studied, but the distribution of the representatives of the infraorder Athenaria in Arctic is known only from several finds. The distribution of the only Arctic representative of the suborder Ptychodacteae, *Ptychodactis patula*, is known from a fairly large number of finds, but its habitat requirements are little known. Therefore, our reasoning about the sources of the formation of the Kara Sea fauna is based mainly on the data derived from the thenarians. Our analysis has confirmed the participation of the species of Atlantic origin, most resistant to low temperatures, in the formation of the Kara Sea fauna, but no convincing evidence has been found for the participation of Pacific elements in the settlement of this region.

Key words: Actiniaria, Arctic, depth, geographical distribution, Kara Sea, salinity, sea anemones, systematics, temperature

История изучения, таксономический состав и происхождение фауны актиний Карского моря (Actiniaria, Anthozoa, Cnidaria)

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РЕЗЮМЕ

На основании обработки новых коллекционных материалов и литературных данных описан состав фауны актиний Карского моря. Она включает 13 видов из 7 семейств. Среди них ранее известные для этого региона ***Urticina crassicornis*** (O.F. Müller, 1776), ***Aulactinia stella*** (Verrill, 1864), ***Hormathia digitata*** (O.F. Müller, 1776), ***Allantactis parasitica*** Danielssen, 1890, ***Actinostola callosa*** (Verrill, 1882), ***A. spetsbergensis*** (Carlgren, 1893), ***Anthosactis janmayeni*** Danielssen, 1890, ***Halcampa arctica*** Carlgren, 1893, ***Edwardsia arctica*** Carlgren, 1921 и ***Ptychodactis patula*** Appellöf, 1893, и впервые найденные нами ***Cactosoma abyssorum*** Danielssen, 1890, ***Haliactis arctica*** Carlgren, 1921 и ***Edwardsia vitrea*** Danielssen, 1890. Подробно описаны ареалы видов. Детальное рассмотрение географического распространения видов, определяемого температурой, глубиной и соленостью вод, позволяет нам разделить актиний на три группы: а) населяющие шельф и приуроченные к высокой солености; б) эврибатные, высокоширотные, обитающие только при высокой солености и узком интервале низких температур; в) наиболее широко распространенные, выдерживающие опреснение и низкие температуры. К настоящему времени наиболее подробно изучены ареалы эпибентосных полипов инфраотряда Thenaria, а о распространении в Арктике представителей инфраотряда Athenaria известно лишь по небольшому числу находок. Распространение единственного арктического представителя подотряда Ptychodacteae, ***Ptychodactis patula***, 1893, представлено довольно большим числом находок, но его требования к факторам среды остаются малоизвестными. Поэтому наши рассуждения об источниках формирования фауны Карского моря опираются в основном на данные, относящиеся к тенарным полипам. В результате проведенного анализа доказано участие атлантических по происхождению видов, наиболее выносливых к низким температурам, в формировании фауны Карского моря. Однако не удалось получить убедительные свидетельства участия тихоокеанских элементов в заселении этого региона.

Ключевые слова: Actiniaria, Арктика, глубина, географическое распространение, Карское море, соленость, морские анемоны, систематика, температура

INTRODUCTION

At present, the fauna of anemones of the Kara Sea remains poorly studied. The first data on its species composition were obtained owing to several European expeditions. Among them are voyages of the Swedish scientist and navigator Baron A.E. Nordenskiöld (1832–1901) on sailing ships “Pröven” and “Ymer” to Novaya Zemlya and the Kara Sea in 1875–1876, as well as his world-famous passage through the Northern Sea Route on the sailing-steam ship “Vega” in 1878–1879 (Holm 1973; Goncharov 2014; Nordenskiöld 2018). Rich material on the fauna and flora of the Kara Sea was also obtained during the Danish and Dutch expeditions on the ships “Dimfna” and “Varna” (Vize 2016). The materials of these expeditions were processed by the Swedish zoologist O. Carlgren (1865–1954), widely known for his work on northern sea anemones. His detailed morphological descriptions of Actiniaria representatives were published in his two-volume monograph, issued in the reports “Danish Ingolf-Expedition” (1921, 1942). Materials from the Kara Sea allowed him to expand the ranges of 8 species of sea anemones known for this region at that time: *Urticina crassicornis* (O.F. Müller, 1776), *Aulactinia stella* (Verrill, 1864), *Hormathia digitata* (O.F. Müller, 1776), *Allantactis parasitica* Danielssen, 1890, *Actinostola callosa* (Verrill, 1882), *A. spetsbergensis* (Carlgren, 1893), *Anthosactis janmayeni* Danielssen, 1890, and *Halcampa arctica* Carlgren, 1893, and also to describe the new species: *Edwardsia arctica* Carlgren, 1921. After the works of Carlgren (1921, 1942), the sea anemones of the Kara Sea did not attract attention for a long time. Only in the 1980s, the material from the Kara Sea accumulated in the collection of the Zoological Institute of the Russian Academy of Sciences (ZIN RAS) was processed by Grebelnyi (1980a, 1980b). His articles, however, are devoted to the study of only large epibenthic polyps belonging to the infraorder Thenaria. These papers include taxonomic notes on certain species (see Grebelnyi 1980a) and a detailed analysis of thenarian distribution in the Arctic (see Grebelnyi 1980b). In addition, Riemann-Zürneck (1997) carried out a detailed study of the high-arctic thenarian sea anemone *Anthosactis janmayeni* Danielssen, 1890, collected during the Swedish YMER expedition in 1980 and ARK VII/2 of the German R/V “Polarstern” in 1990. It should be noted that when describing the macrobenthos communities of the Kara Sea, large representatives of this infraorder are often included in their composition (e.g. Galkin and Vedenin 2015; Vedenin et al. 2015). Furthermore, *Ptychodactis patula* Appellöf, 1893 was studied in detail by Cappola and Fautin (2000) and by Grebelnyi (2007). Representatives of the infraorder Athenaria, however, remained completely untreated at that time.

Our article is dedicated to the processing of new data, clarification of the species composition of the Kara Sea fauna, and analysis of the distribution of sea anemones in the Arctic seas.

MATERIALS AND METHODS

The material for this work is samples of anemones from the Kara Sea collected by a number of Russian and Soviet expeditions: Russian Polar Expedition (1900–1902) on the schooner "Zarya" under the leadership of Baron E.V. Toll; 2 expeditions of the Floating Marine Scientific Institute (Plavmornin) on the R/V "Perseus" (1927, 1932); as well as numerous expeditions of the Arctic and Antarctic Research Institute (AARI) on the icebreaking ships "Rusanov" (1931), "Sedov" (1934), "Sadko" (1936), "Malygin" (1937), "Multanovsky" (2019), etc.

The examined specimens during collection were fixed in 4% seawater formaldehyde and transferred to 70% ethanol for long-term storage. Ethanol-fixed specimens were examined whole, dissected and used to prepare serial sections. The histological sections, 3–7 µm thick, of a few individuals were prepared based on isopropanol-mineral oil method (see Sanamyan et al. 2013).

SYSTEMATICS

Class Anthozoa Ehrenberg, 1834

Order Actiniaria Hertwig, 1882

Suborder Nynantheae Carlgren, 1899

Infraorder Thenaria Carlgren, 1899

Family Actiniidae Rafinesque, 1815

Genus *Urticina* Ehrenberg, 1834

***Urticina crassicornis* (O.F. Müller, 1776)**
(Figs 1, 2A, B)

Actinia crassicornis sp. n. — Müller 1776: 231; Fabricius 1780: 348; 1797: 52; Lütken 1875: 186 (original description).
Rhodactinia daevisii sp. n. — Agassiz 1847: 677 (original description); Verrill 1863: 57; 1864: 18, pl. I, fig. 9 (pro parte); Agassiz 1865; 1871: 13, fig. 10; Packard 1865: 263; Pax 1915: 167, 172.
Actinia obtruncata sp. n. — Stimpson 1853: 7.
Urticina crassicornis Müller — Carlgren 1893: 58 (pro parte); 1901: 470, fig. 2a–b.
Urticina felina crassicornis — Carlgren 1921: 162, 170.
Tealia felina var. *crassicornis* — Stephenson 1935: 150.

Material. No. 12204 (8 ad. sp. and 5 juv. sp.): Novaya Zemlya, Zhelaniya Cape, Pospelova Bay, 13.09.1935; No. 12203 (1 sp.): Novaya Zemlya, Zhelaniya cape, Pospelova Bay, 09.09.1935; No. 12205 (1 sp.): R/V "Ya. Smirnizky", Kara Sea, Nordenskjold archipelago, 76°26´3″N 96°41´7″E, 09.09.1995, St. 80, 32 m depth, gravel, sand, silt.

Description. The body is dome-shaped or cylindrical. The height of the studied specimens varies from 0.6 to 4.5 cm, the diameter of the proximal end from 1 cm to 8.5 cm. Juveniles found in the gastric cavity reach 0.5 cm in height. The surface of the column is smooth, devoid of any specialized structures, but covered with fine wrinkles and rather large annular furrows (Figs 1A, 2B). The pedal disc is well developed, oval in shape, its edge is usually bent towards the center. The oral disc in some individuals is retracted, in others is expanded (Figs 1A, B, 2B). The perioral space does not have tentacles that sit along the edge of the oral disc. Their number is 70–80, 140 in a large specimen. Tentacles are conical, with longitudinal furrows. The pharynx is of the usual length, furrowed longitudinally, sometimes it can be everted (Figs 1A, 2B). Two siphonoglyphs (Fig. 1C), their aboral extensions descend below the proximal end of the pharynx. Mesenteries are arranged in 3 incomplete (10+10+15) or complete (10+10+20) cycles. In a large specimen, 4 cycles were found with some abnormality of symmetry (Fig. 1C). There are 2 cycles of perfect mesenteries. Gonads only on mesenteries of the third cycle. Longitudinal retractor muscles are distinct, diffuse, and restricted (Fig. 1C). The parieto-basilar and basilar muscles are well developed. Juvenile individuals with developed tentacles, pedal disc, pharynx, and mesenteries were found in the gastric cavity of some polyps (Fig. 2A).

Distribution. Georges Bank, Newfoundland, Baffin Bay, Greenland, Iceland, Norwegian Sea, Spitsbergen, Franz Joseph Land, White Sea, Barents Sea, Kara Sea, Laptev Sea, Chukchi Sea, Bering Strait, Beaufort Sea. Depth 0–600 m, temperature from −0.69° to +3°C.

Genus *Aulactinia* Agassiz in Verrill, 1864

Aulactinia stella (Verrill, 1864)

(Fig. 2C)

Bunodes stella sp. n. — Verrill 1864: 16, pl. I, figs 1–8.
Bunodes stella — Verrill 1868: 258; Andres 1883: 447; Parker 1900: 752.
Bunodactis spectabilis — Verrill 1879: 15; 1879: 152.
Bunodactis stella — Verrill 1899: 43; Carlgren 1942: 74, fig. 89.
Cribrina stella sp. n. — McMurrich 1910: 76, pl. III, figs 6, 7; Carlgren 1921: 148, textfig. 159.
Tealiopsis stella sp. n. — Verrill 1922: 112, pl. XX, figs 4–12; pl. XXVI, figs 1–6, Pl. XXXI, fig. 3.

Material. No. 12193 (1 sp.): R/V "Rusanov", 17.09.1931, Kara Sea, 73°36´N 78°22´E, St. 35, 17 m depth, silt and sand, coll. G. Gorbunov; No. 12194 (3 sp.): R/V "Perseus", 02.10.1932, Kara Sea, 74°17´N 70°00´E, St. 2202, 18 m depth, yellowish gray silty sand; No. 12195 (1 sp.): Kara expedition, Yugorsky Shar, Chabarovo, 69°38´N 60°25´E, 1945, St. 26.

Description. The body is cylindrical or conical (Fig. 2C). Height up to 2 cm. The column is not divided into regions, but bears transverse folds. Its wall is covered with longitudinal rows of verrucae, to which foreign particles are often attached. The pedal disc is well developed (Fig. 2C). The oral disc is small. Tentacles up to 48, conical or cylindrical, about the same size. In well-preserved specimens, transverse wrinkles are visible on the tentacles. The pharynx is of the usual length and has longitudinal burrows. Two distinct siphonoglyphs. The sphincter is pinnate or finger-like. There are 4 incomplete mesenteric cycles. Two cycles of perfect mesenteries are present. The retractors are distinct and diffuse. The parietobasilar and basilar muscles are well developed. This species is characterized by brooding. From May to October, juveniles can be found inside large individuals. Young polyps float freely in the gastric cavity, and the smallest of them can be seen inside the transparent tentacles of a living, expanded parent polyp.

Distribution. Newfoundland, Hudson Bay, Greenland, Iceland, Norway, Spitsbergen, Franz Josef Land, Barents Sea, White Sea, Kara Sea, Laptev Sea and Chukchi Sea, Bering Strait, Bering Sea, Pacific Ocean along West Kamchatka, the Commander Islands, the Aleutian and the Kuril Islands. Depth from nearly the point of the highest tide down to 178 m, temperature from +1.66° to +9.2°C, salinity from 22‰ to 32.61‰.

Family Hormathiidae Carlgren, 1932

Genus *Hormathia* Gosse, 1859

Hormathia digitata (O.F. Müller, 1776)

Remarks. The wide morphological variability of the polymorphic species *Hormathia digitata* abundantly present in the Arctic was the subject of detailed discussion in the works of Carlgren (1902, 1942) and Grebelnyi (1980a, 1980b). The polyps described under this name by Müller (1776), having a squat, short column, usually (almost without exception) are attached to the shells of live gastropods (*Neptunea*; Fig. 3 in Grebelnyi 1980a) or shells inhabited by hermit crabs (Fig. 2 in Grebelnyi 1980a). Sometimes they are found even on the crab carapace (*Hyas araneus*; see Carlgren 1942, pl. 1, fig. 3). The individuals of this species settling on a more stable substrate, on rocks or stones, usually acquire a more elongated shape. Fabricius (1780) described them under a new species name—*Hormathia nodosa*. Both Müller (1776) and Fabricius (1780) originally assigned these species to the genus *Actinia*. In both species, the mesogloeal tubercles on the column are well developed, but towards the base they gradually decrease in size. The tall, cylindrical column *Hormathia nodosa* is covered with tubercles, like a maize ear (see Carlgren 1942, pl. III, fig. 3, pl. IV, figs 6, 10; Grebelnyi 1980b). In the largest *nodosa* individuals, not very regular and not very straight vertical rows may consist of 6–7 tubercles. In *Hormathia digitata*, due to the shortened shape of the body, the largest tubercles cover only the upper part of the body, forming a ring of 12 "coronal" tubercles. Below them are less developed mesogloeal tubercles, decreasing in size towards the base. The third representative of the genus living in the northern seas

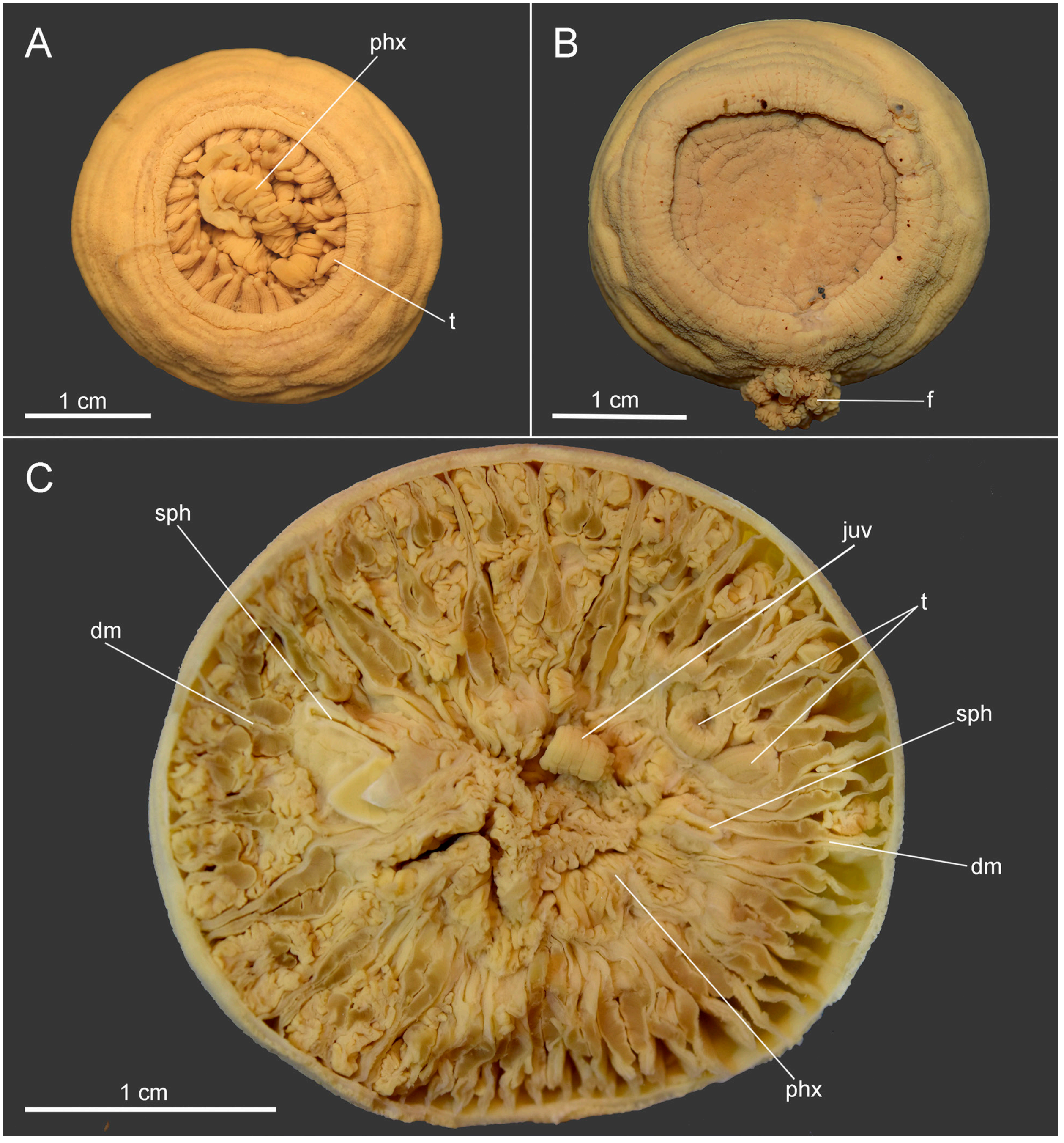

Fig. 1. *Urticina crassicornis* (ZIN No 12204): A – view of the oral side; B – view of the aboral side; C – transverse section at the pharynx level. Abbreviations: *dm* – directive mesenteries; *f* – filaments; *juv* – juvenile polyp; *phx* – pharynx; *sph* – siphonoglyph; *t* – tentacles.

was described much later by Zhiubikas (1977) under the name *Hormathia josefi* Zhiubikas, 1977. It is similar in body shape and settlement on the rocky bottom to *H. nodosa*. As the main argument for its separation from *H. nodosa*, this author drew on the statement that the thickness of the mesogloeal layer in the column wall of individuals of the same species cannot differ by 10 or more times (Zhiubikas,

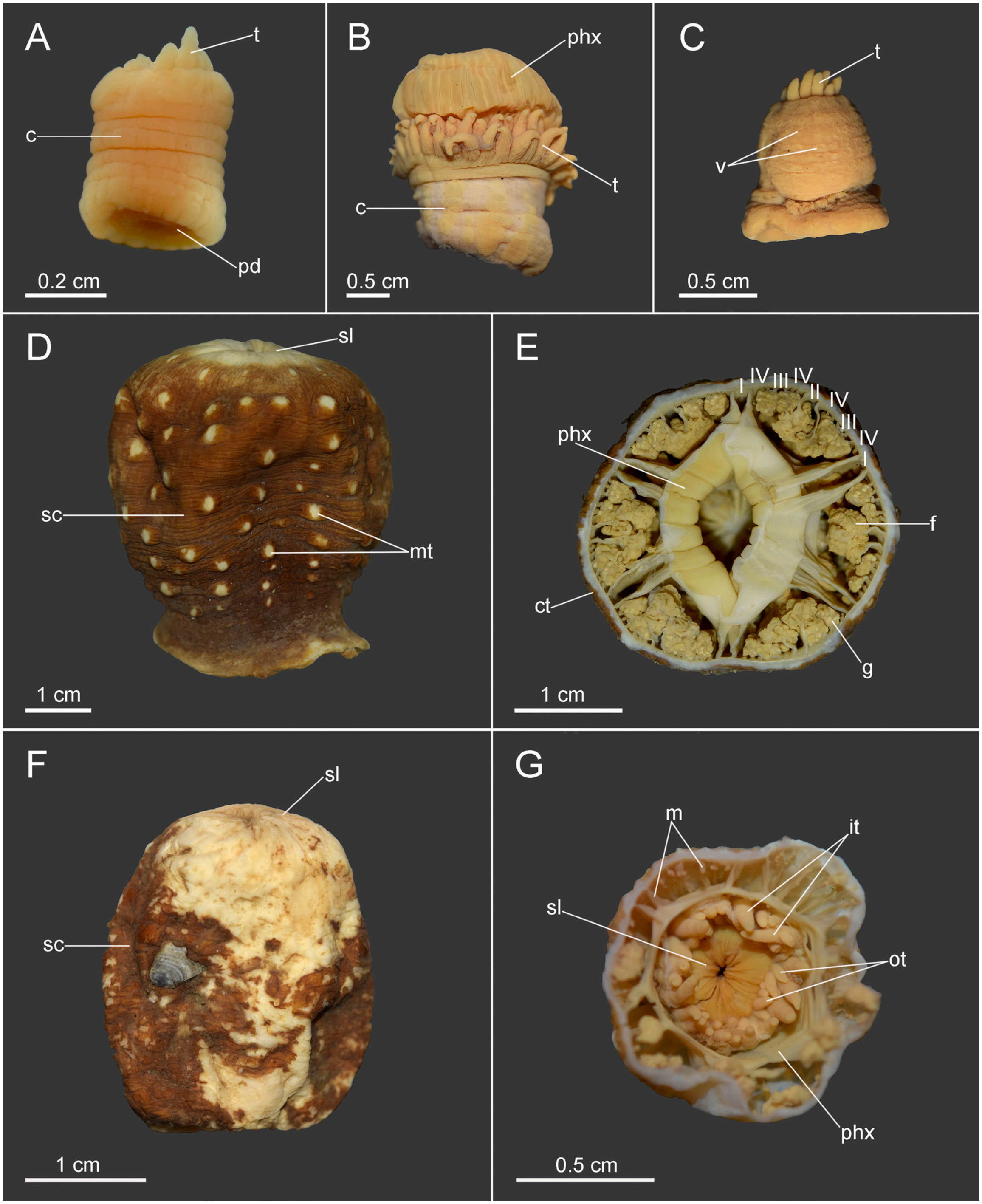

Fig. 2. External view and internal structure of sea anemones of different species: A – juvenile polyp of *Urticina crassicornis* (ZIN No 12204); B – specimen of *U. crassicornis* (ZIN No 12204) with an everted pharynx; C – longitudinal row of the verrucae on the column of *Aulactinia stella* (ZIN No 12195); D – mesogloeal tubercles on the scapus of *Hormathia digitata* morpha *nodosa* (ZIN No 12200); E – transverse section at the pharynx level of *Hormathia digitata* morpha *nodosa* (ZIN No 12201); F – *Hormathia digitata* morpha *josefi* (ZIN No 12197); G – differences in length of tentacles in *Hormathia digitata* morpha *josefi* (ZIN No 12199). Abbreviations: *c* – column; *ct* – cuticule; *f* – filaments; *g* – gonads; *it* – internal tentacles; *m* – mesenteries; *mt* – mesogloeal tubercles; *ot* – outer tentacles; *pd* – pedal disc; *phx* – pharynx; *sc* – scapus; *sl* – scapulus; *t* – tentacles; *v* – verrucae; *I–IV* – cycles of the mesenteries.

personal communication). When comparing "typical" specimens of *Hormathia digitata*, *nodosa*, and *josefi*, it is easy to come to the conclusion that we are dealing with species that well differ in morphological characters. However, the examination of a very rich collection (in the ZIN RAS funds, samples containing *Hormathia* individuals make up almost half of our entire northern collection), the statistical processing of data on their depth distribution (see in Grebelnyi 1980a), and the analysis of data on temperature and salinity do not allow these forms to be divided into 3 distinct species (Grebelnyi 1980a, 1980b). Apparently, in this case we are dealing with the variability of one species, manifested under the influence of the substrate (settlement conditions) and temperature. Such morphologically discrete forms, to which we do not give taxonomic significance, according to the terminology of Semenov-Tyan-Shansky (1910), should be distinguished as "morphs".

Hormathia digitata **morpha** ***nodosa*** **Fabricius, 1780**

(Fig. 2D, E)

Actinia nodosa — Fabricius 1780: 350.
Actinoloba nodosa — Blainville 1830: 288; 1834: 322.
Chondractinia nodosa (Fabr.) — Lütken 1861: 190; Haddon 1889: 308, pl. XXXIII, fig. 13, pl. XXXV, fig. 4; Carlgren 1893: 115, pl. VI, fig. 9; Grieg 1925: 29; 1926: 26.
Urticina nodosa — Verrill 1874: 413, pl. VII, fig. 7; 1885: 5, pl. VI, figs 6–8, 8a.
Actinauge nodosa var. *tuberculosa* — Verrill 1883: 53, pl. VI, fig. 7; 1885: 612, pl. V, fig. 20a.
Actinauge nodosa (Fabr.) — Danielssen 1890: 42, pl. III, fig. 4.
Hormathia nodosa — Haddon 1898: 459; Stephenson 1920: 535; Carlgren 1930: 3; 1932: 262; 1933: 26, fig. 14; 1934: 352; 1939: 9; 1942: 46, pl. III, figs 2, 3, pl. IV, figs 6, 10; Zhiubikas 1977: 114–117, figs 16–21.
Hormathia digitata morpha *nodosa* Fabricius — Grebelnyi 1980a: 12–26, map 3, figs 14–19; 1980b: 22, fig. 1 (map), 3; 2012: table 5, fig. 8.
H. [*Hormathia*] *digitata* morpha *nodosa* Fabricius — Grebelnyi 2012: 159, table 5, fig. 8.

Material. No. 12200 (1 sp.): 26.04.1982, Kara Sea, Severnaya Zemlya, Golomyaniy Island, 7–12 m depth, pebbles, gravel, stones; No. 12201 (2 sp.): 27.04.1982, Kara Sea, Severnaya Zemlya, Golomyaniy Island, 12–15 m depth, pebbles, stones; No. 12202 (3 sp.): 28.04.1982, Kara Sea, Severnaya Zemlya, Golomyaniy Island, 10–12 m depth, stones, pebbles.

Description. The height of the smallest specimen is about 2 cm, the largest is about 6 cm. The column is high, cylindrical, sometimes widened in the middle and distal part, gradually tapering towards the pedal disc. The column is divided into scapulus and scapus. Scapulus smooth, covered with longitudinal wrinkles. The scapus has a well-developed dark brown cuticle and well-developed large mesogloeal tubercles (Fig. 2D). As a rule, they are organized into more or less distinct vertical rows throughout the scapus and are sometimes confined to its distal part. The surface of the column is covered with numerous small longitudinal and transverse wrinkles. The pedal disc is distinct and round in shape, often its edge is bent towards the bottom. The oral disc is fully retracted in all studied specimens (Fig. 2D). Tentacles are 96. The pharynx is long and reaches almost to the base. It is wide open, has a longitudinal striation and 2 wide siphonoglyphs that do not continue aborally (Fig. 2E). The sphincter is mesogloeal. There are 4 mesenteric cycles. Of these, only the first is composed of perfect mesenteries. Gonads develop on the mesenteries of the second and third cycle (Fig. 2E). The mesenteric musculature is poorly developed.

Distribution. Hudson Bay, Baffin Sea, Greenland, Iceland, Faroe Islands, Norway, Spitsbergen, Franz Josef Land, Barents Sea, Kara Sea, Laptev and East Siberian Sea. Depth 5–650 m, temperature from −1.6° to +5.8°C.

Hormathia digitata **morpha** ***josefi*** **Zhiubikas, 1977**

(Figs 2F, G, 3)

Hormathia josefi Zhiubikas sp. n. — Zhiubikas 1977: 120–122, figs 27–31.
Hormathia digitata morpha *josefi* — Grebenyi 1980a: 12–26, map 1, figs 23 (holotype of *Hormathia josefi*), 24–27; 1980b: 24–26, fig. 1 (map), 15–17.
H. [*Hormathia*] *digitata* morpha *josefi* Zhiubikas, 1977 — Grebelnyi 2012: 159, table 5, fig. 6.

Material. No. 12197 (2 sp.): R/V "Sedov", 18.08.1934, Kara Sea, 80°15´N 75°02´E, St. 27, 41 m depth, dead shell; No. 12198 (1 sp.): R/V "Sedov", 18.08.1934, Kara Sea, 80°15´N 75°02´E, St. 27, 41 m depth, sand and shell; No. 12199 (1 sp.): R/V "Pr. Multanovsky", 02.09.2019, Kara Sea, 71°59´N 62°24´E, St. 51, 125 m depth, silt.

Description. The shape of the body is changeable. The column can be more or less hemispherical, cylindrical or have a widened distal part, but a narrower proximal part (Fig. 2F). Its height ranges from 1.1 cm to 3.8 cm. The column is divided into scapulus and scapus. The scapulus has longitudinal wrinkles. The scapus bears a well-developed but sometimes peeling cuticle (Fig. 2F). Its surface is covered with numerous transverse folds, developed to varying degrees in some specimens. Mesogloeal tubercles are poorly developed and arranged irregularly. The pedal disc is well developed, oval or round in shape. The oral disc is fully retracted (Fig. 2F, G). The tentacles are numerous (about 96), smooth, the inner ones are much longer than the outer ones (Fig. 2G). The pharynx is long and descends almost to the base, smooth or with a weak longitudinal striation. There are 2 wide siphonoglyphs. The sphincter is mesogloeal. Four mesenteric cycles are present. The first cycle consists of perfect and sterile mesenteries. The mesenteries of the second and third cycle carry the gonads. Numerous acontia develop on the mesenteries of the first and second cycle (Fig. 3). The mesenteric musculature is weak.

Distribution. Barents Sea, Kara Sea, Laptev Sea. Depth 1.5–262 m.

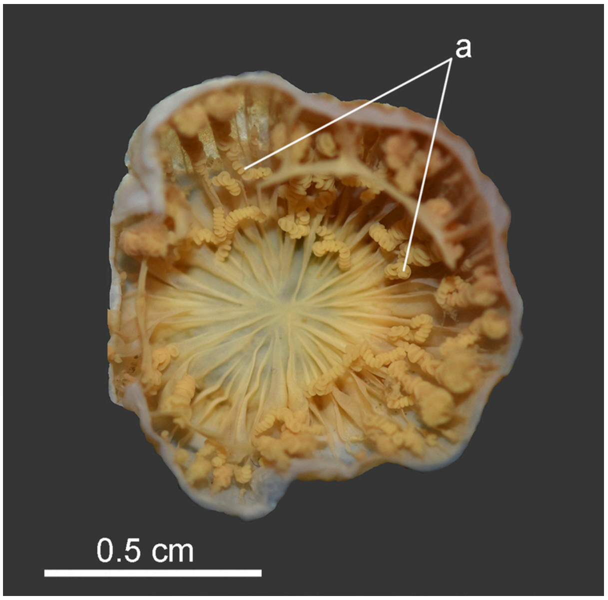

Fig. 3. Numerous acontia in *Hormathia digitata* morpha *josefi* (ZIN No 12199). Abbreviations: *a* – acontia.

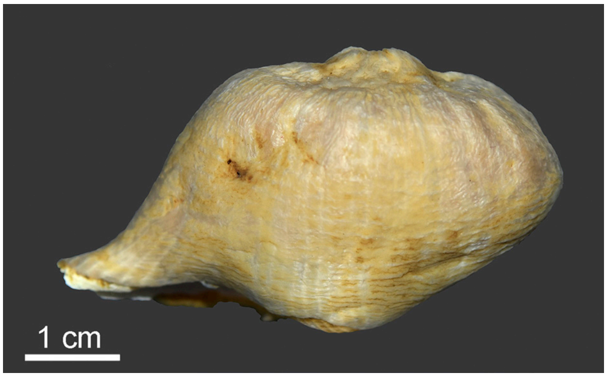

Fig. 4. *Allantactis parasitica* (ZIN No 12233) sitting on a gastropod mollusk, side view.

Genus *Allantactis* Danielssen, 1890

Allantactis parasitica Danielssen, 1890
(Figs 4, 5A, B)

Allantactis parasitica sp. n. — Danielssen 1890: 20, pl. II, fig. 3, pl. IX, figs 1–4.
Calliactis Kröyeri n. g. et. sp. — Danielssen 1890: 36, pl. II, fig. 2, pl. VIII, figs 6, 13, 14.
H. [*Hormathia*] *digitata* morpha *parasitica* Danielssen 1890 — Grebelnyi 1980b: 22, fig. 1 (map), figs 1, 4–9; 2012: 157, 159, table 5, fig. 4.

Material. No. 12213 (9 sp.): R/V "Sedov", 21.09.1936, Kara Sea, Nordenskjold archipelago, 76°25´N 95°30´E, 20 m depth, fine granite with silt; No. 12214 (1 sp.): R/V "Sedov", 22.09.1934, Kara Sea, 76°44´N 71°05´E, St. 89, 368 m depth, gray sandy silt with stones, −0.5°C, 34.92‰; No. 12215 (1 sp.): R/V "Zarnitsa", 02.09.1925, Kara Sea, 74°59´N 60°11´E, St. 13, 14–17 m depth, gravel, silt; No. 12216 (2 sp.): R/V "Pakhtusov", Kara Sea, 70°N 61°16´5″E, 13.08.1914, St. 5, 122 m depth, silt, −2.5°C; No. 12217 (4 sp.): R/V "Sadko", Kara Sea, 75°13´7″N 87°18´E, 21.08.1936, St. 4/5, 42 m depth; No. 12218 (~20 sp.): R/V "Belukha", Kara Sea, 75°01´N 86°50´E, 30.08.1931, St. 28, 16 m depth; No. 12219 (6 sp.): R/V "Sadko", Kara Sea, 75°45´N 86°05´E, 20.08.1936, St. 3/4, 29 m depth, silt; No. 12220 (6 sp.): R/V "Perseus", Kara Sea, 72°17´N 64°44´E, 11.09.1927, St. 839, 85 m depth, brown silt;

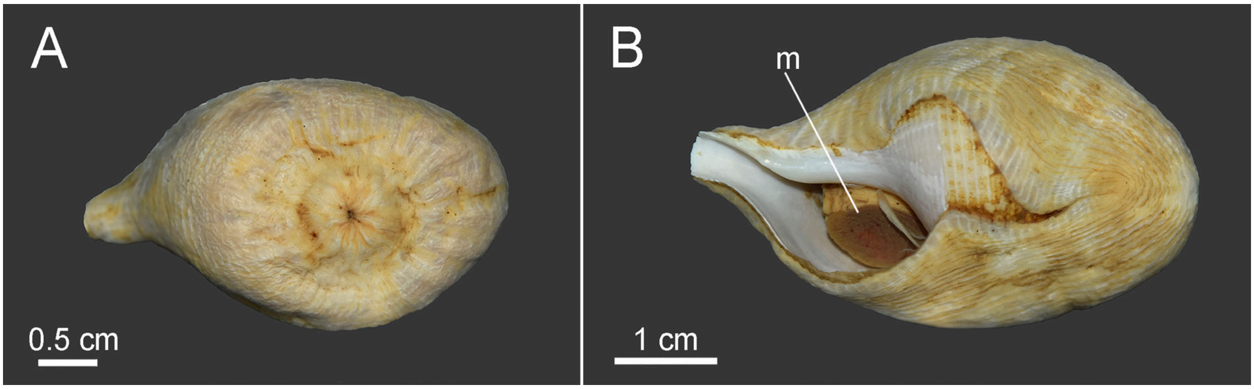

Fig. 5. *Allantactis parasitica* (ZIN No 12233) sitting on a gastropod mollusk: A – view of the oral side; B – view of the aboral side. Abbreviations: *m* – gastropod mollusk.

No. 12221 (2 sp.): R/V "Sadko", Kara Sea, 75°07´4″N 88°16´E, 26.08.1936, St. 5, 40 m depth, silt; No. 12222 (2 sp.): R/V "Perseus", Kara Sea, 71°56´N 63°34´E, 10.09.1927, St. 838, 128 m depth, brown silt with concretions; No. 12223 (2 sp.): R/V "Zarya", Kara Sea, 75°49´N 89°35´E, 26.08.1900, St. 14, 38 m depth, silt; No. 12224 (2 sp.): R/V "Zarya", Kara Sea, 76°8´N 93°30´E, 22.09.1900, St. 25, 22 m depth, pebbles; No. 12225 (8 sp.): R/V "Zarya", Kara Sea, 76°8´N 95°6´30″E, 06.08.1901, St. 36, 18 m depth, sand; No. 12226 (5 sp.): R/V "Litke", Kara Sea, 80°40´N 66°34´E, 06.10.1948, St. 196, 385 m depth, brown silt; No. 12227 (2 sp.): R/V "Zarya", Kara Sea, 76°8´N 95°6´30″E, 21.07.1901, St. 35, 18–20 m depth, pebbles with concretions; No. 12228 (>10 sp.): Kara expedition of I.D. Strelnikov, Kara Sea, 69°57´N 61°07´E, 01.09.1921, St. 8; No. 12229 (1 sp.): R/V "Malygin", Kara Sea, 75°30´6″N 88°44´5″E, 04.08.1937, St. 7, 38 m depth, green clay with ferromanganese with concretions, −1.82°C, 33.47‰; No. 12230 (1 sp.): Kara Sea, 73°27´N 80°10´E, 13.09.1929, St. 29, 27 m depth; No. 12231 (6 sp.): R/V "Zarya", Kara Sea, 75°54´N 92°59´E, 31.08.1900, St. 17, 11 m depth, silt and sand; No. 12233 (3 sp.): R/V "Zarya", Kara Sea, 76°8´N 95°07´E, 16.07.1901, 19–20 m, pebbles with concretions.

Description. The shape of the body is changeable. Individuals sitting on stones have a cylindrical column, those that settle on the shells of gastropod mollusks have a squat pyramid-shaped column (Figs 4, 5A, B) or often flattened. The height varies considerably in the studied specimens: from a few millimeters to 6 cm. The column is divided into scapulus and scapus. The scapulus is covered with more or less distinct longitudinal wrinkles (Fig. 5A). The scapus does not have mesogloeal tubercles, it has a gray or brown cuticle that easily falls off. The surface of the scapus is often covered with numerous longitudinal and transverse or multidirectional folds, developed to varying degrees. In a number of individuals, mesenteric insertions are visible through the column wall (Figs 4, 5A, B). The pedal disc is highly developed, it is wide and almost completely covers the shell of the gastropod mollusk (Figs 4, 5B). In most of the studied sea anemones, the oral disc is retracted; if extended, it is completely occupied by the tentacles. The tentacles are conical, smooth or irregularly wrinkled, numerous (about 96), the inner ones are much longer than the outer ones. The pharynx is long, has a weak longitudinal striation, and reaches the base. Two wide siphonoglyphs. The sphincter is strong, mesogloeal. There are 4 mesenteric cycles. Only the first cycle is composed of perfect and sterile mesenteries. The gonads lie on all other mesenteries. The longitudinal retractor muscles of the mesenteries are diffuse. Acontia are numerous.

Distribution. Newfoundland, Labrador Sea, Baffin Sea, Greenland, Iceland, Norwegian Sea, Spitsbergen, Franz Josef Land, Barents Sea, Kara Sea, Laptev and East Siberian Sea and Chukchi Sea. Depth from a few meters to 1150 m, temperature from −1.9° to +3.9°C, salinity from 33.47‰ to 34.92‰.

Remarks. One of the authors of this publication (Grebelnyi 1980a) has been studying the variability of northern Hormathiidae for a number of years and synonymized *Allantactis parasitica* with *Hormathia digitata*. I referred *Allantactis* to *Hormathia* *digitata* as an intraspecific form—*H. digitata* morpha *allantactis* (Grebelnyi 1980a, 2012). During my participation in the Russian-American expedition to the shores of the Franz Josef Land in summer 2013, I had the opportunity to observe the discussed forms of Hormathiidae in a living state at sea and on board. These recent observations have somewhat shaken my conviction that these forms are indeed conspecific. The polyps without coarse cuticles and tubercles, described by Danielssen (1890) as *Allantactis parasitica*, in life were distinguished by a brighter pink color (many of them are identical in color to the polyp shown in the watercolor in Danielssen's publication: pl. II, fig. 2). They seemed absolutely unclothed, perhaps perfectly incapable to secrete cuticle. So far, I have not been able to find other characters that distinguish *Allantactis* from *Hormathia*, the polyps of which undoubtedly can also be completely devoid of mesogloeal tubercles. All these forms, namely, the typical *Hormathia nodosa* equipped with large tubercles, the intermediate *Hormathia josefi* and the completely naked *Allantactis parasitica* are found in the neighborhood, in one place on the rock. I have collected samples for their molecular-genetic comparison, but this analysis has not yet been carried out.

Family Actinostolidae Carlgren, 1932

Genus *Actinostola* Verrill, 1883

***Actinostola callosa* (Verrill, 1882)**
[Fig. 6 (Map)]

Urticina callosa sp. n. — Verrill 1882: 224, 315.
Actinostola callosa — Verrill 1883: 57, pl. VII, fig. 2; Carlgren 1893: 71, pl. I, figs 17, 19, pl. IV, fig. 1, pl. VIII, fig. 3, pl. IX, figs 5, 6, textfigs 18, 19; 1921: 227; 1928: 284; 1933: 14; Riemann-Zürneck 1971; Zhiubikas 1977: 112, figs 11–15.
Bunodes abyssorum sp. n. — Danielssen 1890: 39, pl. III, fig. 3, pl. X, fig. 89.
Actinostola abyssorum sp. n. — Carlgren 1893: 66, pl. I, figs 5, 10, pl. VIII, figs 1, 2, 7, 8, 11, pl. X, fig. 4, textfigs 14–17; 1921: 229.
Actinostola groenlandica sp. n. — Carlgren 1899: 33; 1921: 230, pl. II, fig. 10.
Actinostola sibirica sp. n. — Carlgren 1901: 481.
Catadiomene artrosoma sp. n. — Stephenson 1918: 118, pl. XIV, figs 5, 7, 8, pl. XV, fig. 7, pl. XVI, fig. 11, 12, 16–20, pl. XVII, figs 1–4.

Material. No. 12206 (1 sp.): R/V "Pr. Multanovsky", 14.08.1994, Kara Sea, 73°49´8″N 73°19´6″E, St. 2/K07, 29 m depth, clayey silt; No. 12210 (1): R/V "Taimyr", 16.09.1921, Kara Sea, 76°N 70°30´E, St. 21, 110 m depth, stones; No. 12211 (1): R/V "Rusanov", 1931, Kara Sea, 73°50´N 75°52´E, St. 36(34), 27 m depth, silt; No. 12212 (1): R/V "Shtorm", 1960, Kara Sea, 74°26´N 72°38´E, St. 8, 26–27 m depth, silt, sand.

Description. The column is cylindrical or cup-shaped, the proportions and shape of the body vary markedly, usually the body height does not exceed 15 cm, but its diameter is 10 cm. The column is covered with mesogloeal tubercles, which are more distinct in its distal part. They are arranged in longitudinal rows or scattered randomly. Strong development of tubercles is observed in large individuals; in small ones, mesogloeal thickenings of the column wall are completely absent or very weakly developed. The pedal disc is well developed, oval or irregularly rounded. The oral disc is retracted or remains expanded. The central part of the disc is devoid of tentacles; they are located along its edge and form up to 7 hexamerous cycles. The tentacles are numerous (up to about 380), short, strongly wrinkled, with blunt tips, the inner ones are much longer than the outer ones. The outer side of all tentacles, or only the outer ones, can bear a mesogloeal thickening, which is devoid of nematocyst batteries. The sphincter is mesogloeal, reticular or alveolar, small in relation to body size. There are 5–7 cycles of hexamerously arranged mesenteries. The first 3 cycles are composed of perfect mesenteries. The third and subsequent cycles of mesenteries are arranged according to the *Actinostola* rule. The first 2 cycles are sterile, the gonads lie on the mesenteries of the third and younger cycles; filaments are present on all mesenteries. Retractor muscles are diffuse. Juvenile polyps, known in the literature as "giant larvae", are often found in the gastral cavity, at a stage with 3 to 4 cycles of mesenteries, pharynx, pedal disc, and developing tentacles.

Distribution. Newfoundland, Greenland, Iceland, Skagerrak, Kattegat, Spitsbergen, Barents Sea, Kara Sea, Laptev Sea, East Siberian Sea, Chukchi Sea, Beaufort Sea, Bering Sea, Sea of Okhotsk, Japan (Mikawa Bay) and the eastern part of the North Pacific (Fig. 6). Depth 14–2635 m, temperature from −1.9° to +2.8°C, salinity from 29.99‰ to 35.01‰.

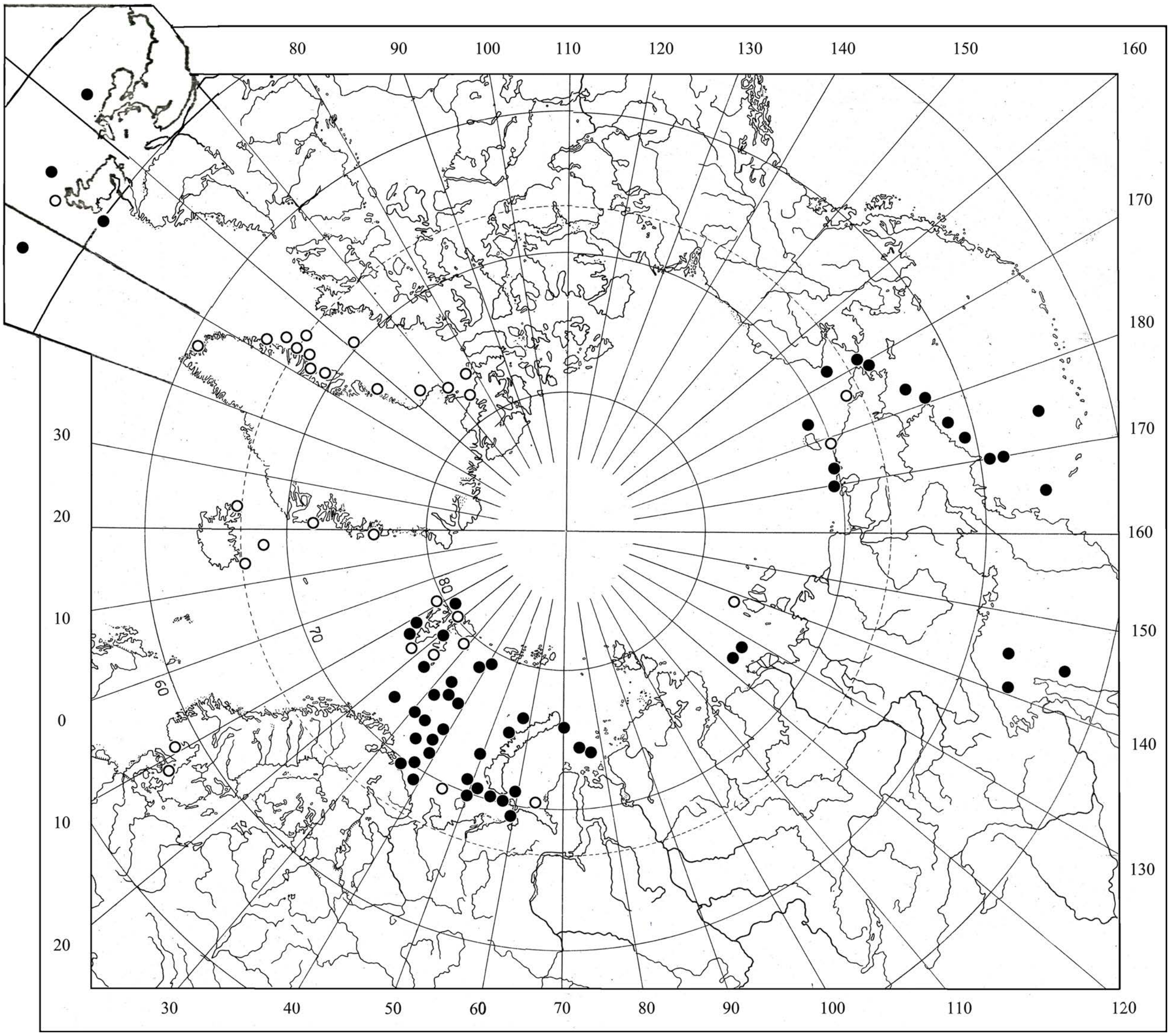

Fig. 6. Distribution of *Actinostola callosa* according to the collection of the ZIN RAS (black circles) and to the literature data (white circles). Finds in Japan (Mikawa Bay) and the eastern part of the North Pacific are not shown.

Actinostola spetsbergensis Carlgren, 1893

Actinostola spetsbergensis sp. n. — Carlgren 1893: 76–80, taf. I, fig. 15; taf. VIII, figs 9, 10; taf. IX, fig. 1.

A. [*Actinostola*] *spetsbergensis* Carlgren, 1893 — Grebelnyi 2012: 161, table 9, figs 8a–b.

Glandulactis spetsbergensis (Carlgren, 1893) — Riemann-Zürneck 1978.

Actinostola spetsbergensis sp. n. — Carlgren 1893: 76, taf. I, fig. 15, taf. VIII, figs 9, 10, taf. IX, fig. 1; 1921: 222, pl. II, figs 3, 4, pl. III, figs 13–15; 1935: 15.

Actinostola walteri sp. n. — Kwietniewski 1898: 130, pl. XIV, figs 4–6.

Remarks. As noted earlier (Grebelnyi 2012, p. 161), the 2 *Actinostola* species found in our northern seas, *Actinostola callosa* and *A. spetsbergensis*, differ primarily in the fact that in large individuals of the first species, the column is covered with well-developed mesogloeal tubercles, and in the second, they are absent. But young individuals do not have such a difference, therefore they cannot be distinguished. Another feature that Carlgren

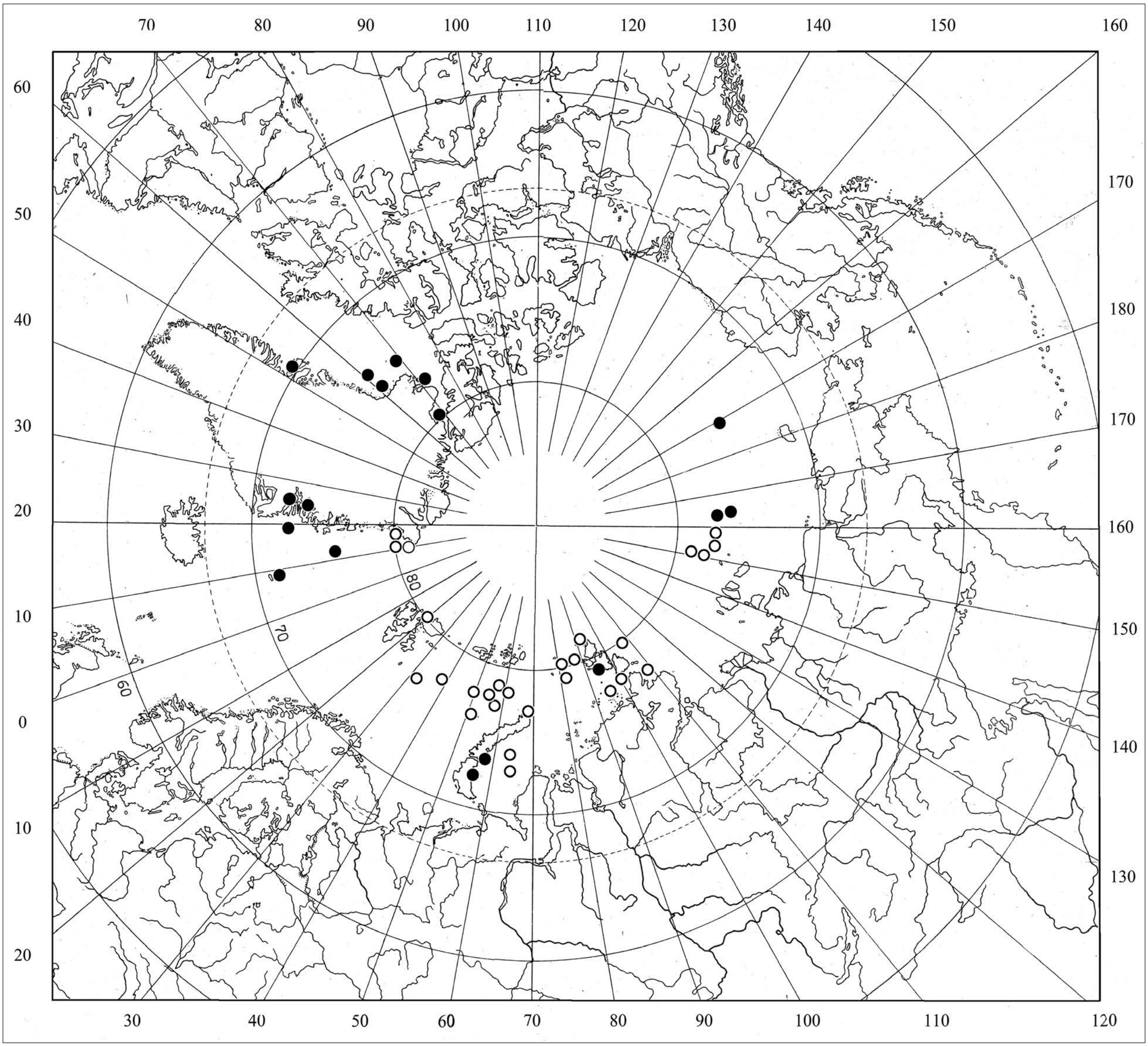

Fig. 7. Distribution of *Anthosactis janmayeni* according to the collection of the ZIN RAS (black circles) and to the literature data (white circles).

(1893) emphasizes in his description is the softness of the body and the accompanying wrinkling of the individuals that attracts attention. During the gathering of material from fishing trawls in the Sea of Okhotsk, where some species of *Actinostola*, very similar to the animals from the North Atlantic, constitute a characteristic, massive element of the bathyal community, we noted that the look of polyps that underwent freezing changes greatly. Large polyps with coarser mesoglea, covered with large tubercles, retained their appearance, familiar to us from observations on the deck. But small animals, frozen in jars with formalin, if they had not been transferred to alcohol before being transported by the Siberian Railway, became flabby and wrinkled, showing exactly the same external view as depicted in the drawings in Carlgren's (1893, taf. I, fig. 15) work. However, a detailed study of the anatomy of this material, unfortunately, has not yet been carried out, and at the present time we do not dare to classify *A. spetsbergensis* among the synonyms of *Actinostola callosa*.

Genus *Anthosactis* Danielssen, 1890

***Anthosactis janmayeni* Danielssen, 1890**
[Fig. 7 (Map)]

Anthosactis Jan Mayeni n. g. et sp. — Danielssen 1890: 24–26, table II. fig. 1; table X, fig. 1.
Anthosactis jan mayeni Dan. — Carlgren 1912: 21; 1916: 1.
Anthosactis jan mayeni Dan. — Carlgren 1921: 191–194, figs 184–186.
Anthosactis janmayeni Dan. — Carlgren 1928: 282; 1932: 261; 1933: 13–14; 1936: 4–5.
A. [*Anthosactis*] *janmayeni* Danielssen, 1890 — Grebelnyi 1980b: 163, table 5, fig. 2.
Anthosactis janmayeni Danielssen, 1890 — Riemann-Zürneck 1997: 487–491, figs 1, 2.

Material. No. 9635 (1 sp.): R/V "Malygin", 05.08.1937, Kara Sea, to W from Russky Island, 77°14´N 95°33´E, St. 8; 72–74 m depth, brown clayey silt with small and large concretions.

Description. The largest specimens reach a height of 3 cm and a diameter of 5–6 cm. Fixed specimens often have a hemispherical or irregular body shape if the tentacles are fully retracted. The column is completely smooth, devoid of any specialized formations. Due to contraction, it is covered with a network of transverse and longitudinal wrinkles that converge in the sphincter region. The pedal disc is distinct, usually covered with an easily falling off cuticle. The oral disc is very wide; when fully retracted, it forms a large cavity with a cup-shaped bottom. It contains 50–70 rather large, longitudinally furrowed, octomerously located tentacles organized in 4 incomplete cycles. The inner tentacles are usually much longer than the outer ones; however, when strongly contracted, they may not differ in length, but in this case the inner ones are much thicker. The outer tentacles have a mesogloeal thickening and an aggregation of large nematocysts (holotrichs from 90 μm) at the base on the outer (abaxial) side. The pharynx is short and bears 2 wide siphonoglyphs. The sphincter is alveolar, powerful and elongated, or short and thick, depending on the degree of contraction. The longitudinal musculature of the tentacles on the outer (abaxial) side is predominantly ectodermal, on the inner side is meso-ectodermal. The radial muscles of the oral disc are meso-ectodermal. The mesenteries are arranged octomerously in 3 cycles; however, failure of strict symmetry is possible. Only the first cycle is represented by perfect mesenteries. All mesenteries carry filaments and gonads, but sometimes the mesenteries of the third cycle lack these organs. Longitudinal retractor muscles are diffuse.

Distribution. Baffin Bay, Greenland, Jan Mayen, North Spitsbergen, Barents Sea, Kara Sea, Laptev Sea, East Siberian Sea, North of Wrangel Island, Arctic Ocean (Fig. 7). Depth 20–1710 m, narrow temperature range from −1.78°to +1.3°C, high salinity 34.28–34.97‰.

Infraorder Athenaria Carlgren, 1899

Family Halcampidae Andres, 1883

Genus *Cactosoma* Danielssen, 1890

***Cactosoma abyssorum* Danielssen, 1890**
[Figs 8A, B, 9 (Map)]

Phellia crassa sp. n. — Danielssen 1890: 60, pl. IV, fig. 9, pl. XIII, figs 5, 6, Pl. XIV, figs 1–5.
Cactosoma abyssorum sp. n. — Danielssen 1890: 82: pl. VI, fig. 5, pl. XXIII, figs 5–8; Sanamyan et al. 2016: 3, tables 1, 2, figs 1–4.
Phellia crossa [sic] — Kwietniewski 1897.
Phelliomorpha crassa sp. n. — Carlgren 1902: 44.

Material. No. 12186 (1 sp.): R/V "Perseus", 20.09.1927, Kara Sea, 73°21´N 58°22´E, St. 859, 270 m depth, brown silt.

Description. The body is elongated, with an extended middle part. The height is 3.5 cm, the width of the widest part is 1.8 cm. The column is divided into physa, scapus and scapulus (Fig. 8A). The scapus bears a cuticle encrusted with grains of sand. In the only individual studied by us, however, the cuticle is lost in the middle, well-spread part and the small tenaculi scattered along the wall are therefore clearly visible; also insertions of the mesenteries and gonads are visible through the body wall (Fig. 8A). The scapulus is very distinct, about 1.5 cm long. It is devoid of cuticle and bears 6 strong, large mesogloeal ridges extending slightly into the distal part of the scapus (Fig. 8B). The physa is clearly distinguished from the scapus. It is rounded, its central part is slightly retracted.

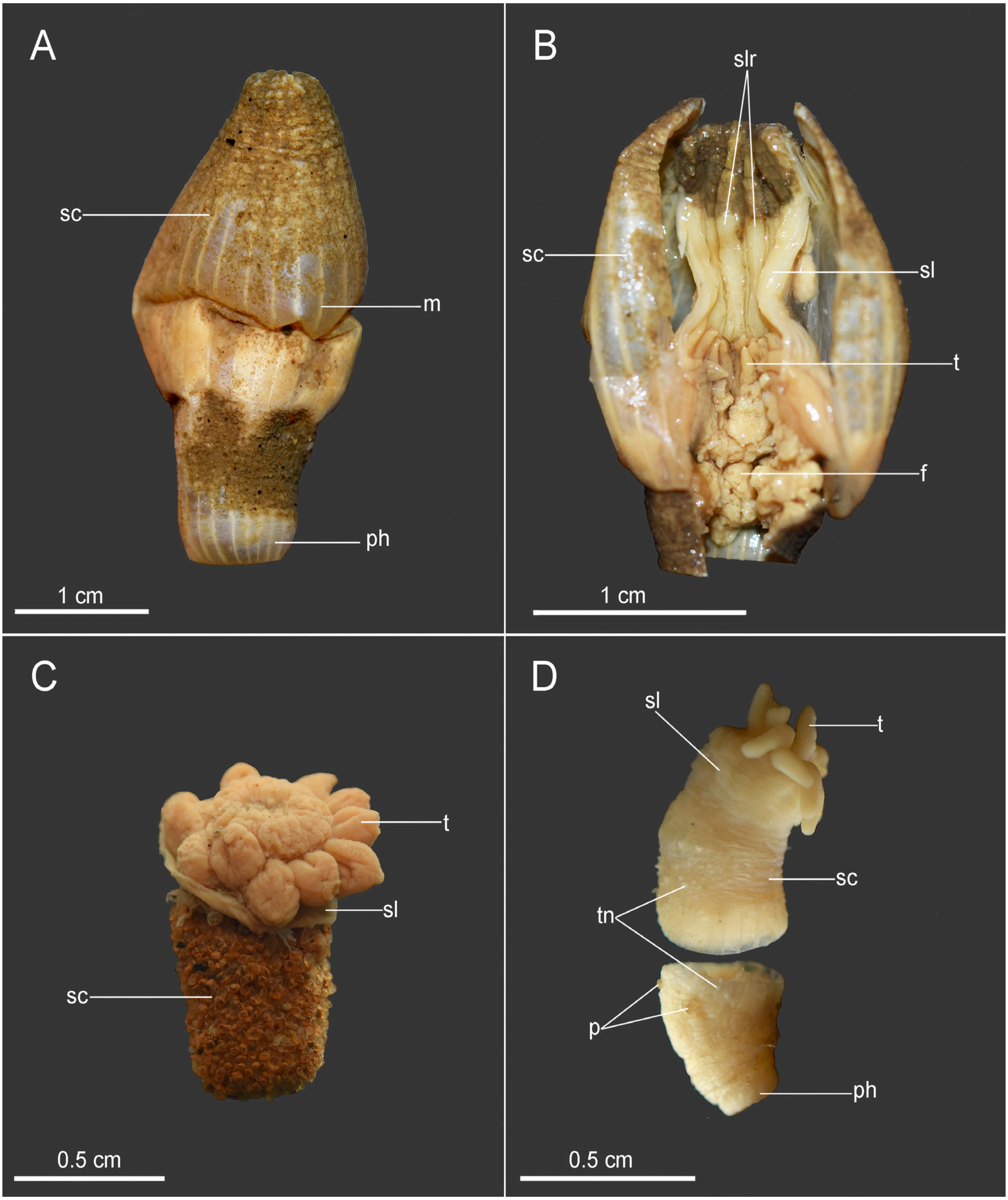

Fig. 8. External view and internal structure of sea anemones of different species: A – *Cactosoma abyssorum* (ZIN No 12186), general form; B – *Cactosoma abyssorum* (ZIN No 12186), longitudinal section; C – specimen of *Halcampa arctica* (ZIN No 12208) completely covered with the incrusted cuticle; D – specimen of *Halcampa arctica* (ZIN No 12188) with no cuticle. Abbreviations: *f* – filaments; *m* – mesenteries; *p* – particles of sand; *ph* – physa; *sc* – scapus; *sl* – scapulus; *slr* – scapular ridges; *t* – tentacles; *tn* – tenaculi.

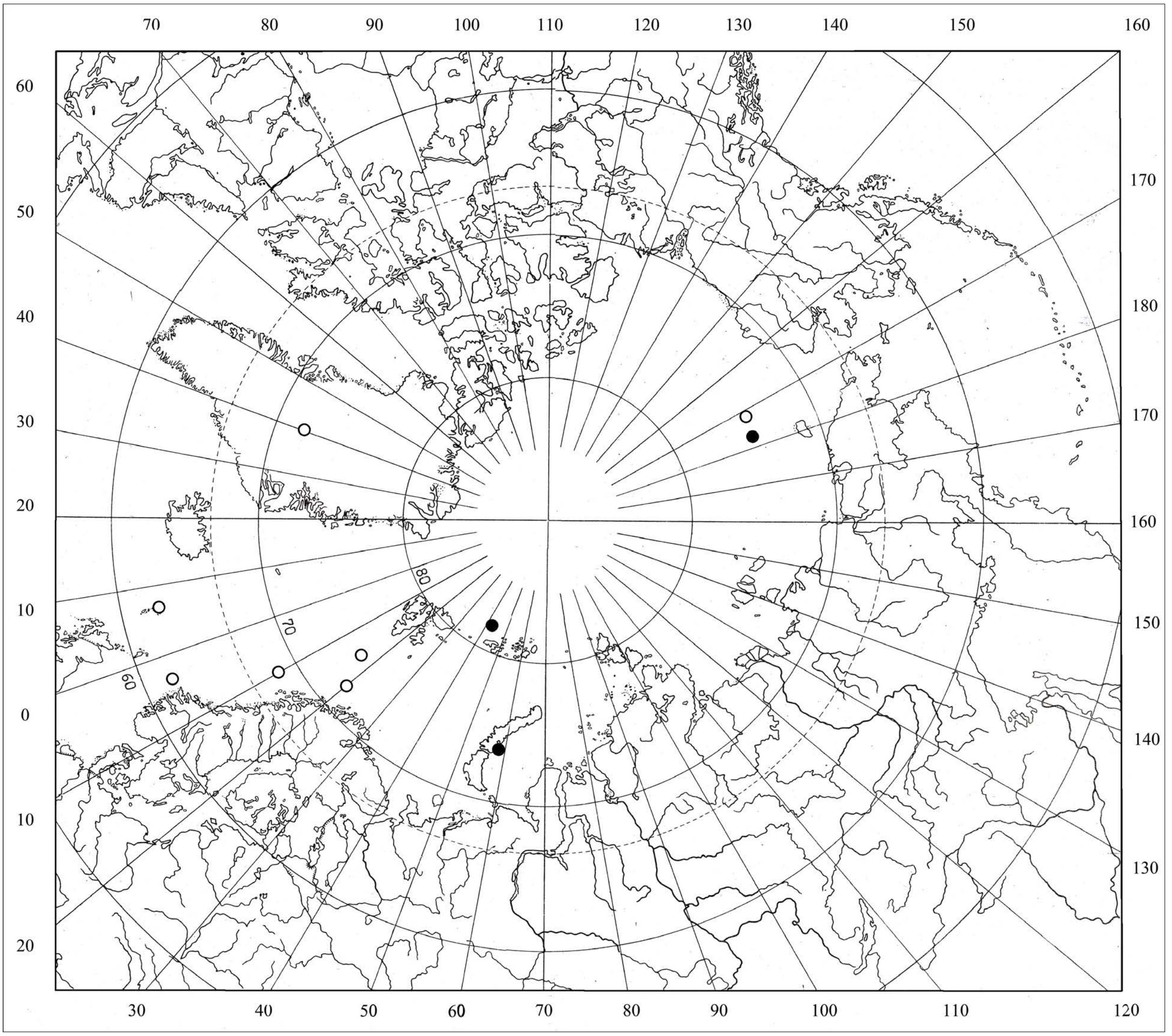

Fig. 9. Distribution of *Cactosoma abyssorum* according to the collection of the ZIN RAS (black circles) and to the literature data (white circles).

Insertions of mesenteries are visible through its transparent wall that is devoid of any specialized structures (Fig. 8A). The oral disc is small, the distance between the mouth opening and the bases of the tentacles is insignificant. Twenty four tentacles are hexamerously arranged in 3 cycles. They are short, conical, with a weak, barely discernible transverse striation. The inner and outer ones are approximately equal in length, about 0.4 cm, their diameter is about 0.1 cm. The pharynx is strongly contracted and very short. Due to poor preservation, it is difficult to judge about its structure and the presence of siphonoglyphs. The mesenteries are arranged in 2 cycles (6+6) along the entire length of the column. They are divided into macro- and microcnemes. Macrocnemes have longitudinal retractor muscles, parietal muscles, gonads and filaments. Microcnemes have only parietal muscles. The retractor muscles are strong, kidney-shaped and restricted. The parietal muscles of all mesenteries are well developed.

Distribution. Greenland, Norwegian Sea, Arctic Ocean, Kara Sea, Chukchi Sea (Fig. 9). Depths 270–836 m, temperature from −0.7° to +3.5°C.

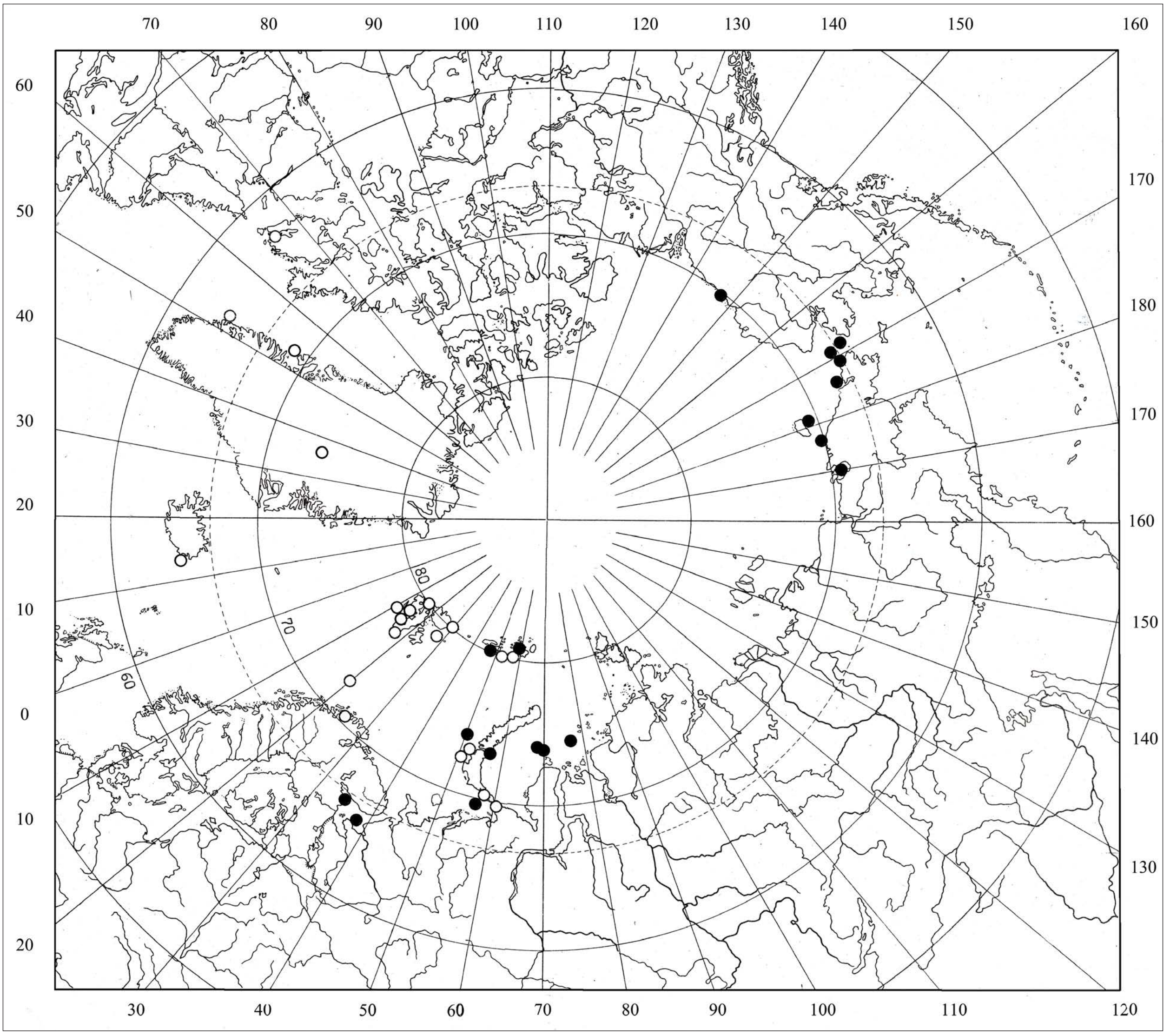

Fig. 10. Distribution of *Halcampa arctica* according to the collection of the ZIN RAS (black circles) and to the literature data (white circles).

Genus *Halcampa* Gosse, 1858

Halcampa arctica Carlgren, 1893

[Figs 8C, D, 10 (Map)]

Halcampa arctica sp. n. — Carlgren 1893: 45, pl. I, figs 1, 2, pl. V, figs 6–12; 1921: 120; Sanamyan et al. 2016: 9, table 3; figs 5–7.

Material. No. 12187 (3 sp.): 14.10.1926, Novaya Zemlya, Matochkin Strait, coll. P. Ushakov; No. 12209 (8 sp.): 18.09.1931, R/V “Rusanov”, Kara Sea, 73°49´N 70°32´E, St. 38, 17 m depth, sand and stone; No. 12208 (1 sp.): 1896, Kara Sea, 73°37´N 69°23´E, St. 5, coll. A.S. Botkin; No. 12188 (1 sp.): R/V “Pr. Multanovsky”, 30.08.2019, Kara Sea, 74°59´N 77°18´E, St. 42, 32 m depth, silt and sand.

Description. The body is elongated. Its height varies from a few millimeters to 1.5 cm, and its width is up to 0.6 cm. The column is divided into physa, scapus and scapulus. In many studied specimens, the scapus is covered with a cuticle that is heavily encrusted with foreign particles (Fig. 8C). In some individuals, it is devoid of cuticle and bears only single grains of sand (Fig. 8D). In this case, numerous tenaculi and insertions of mesenteries are clearly visible (Fig. 8D). The scapulus has noticeable transverse striation; longitudinal ridges are indistinct. The physa is naked, small, often completely retracted or only its central part is retracted (Fig. 8C, D). The oral disc is small; an everted pharynx sometimes rises above its central part. There are few tentacles, 12, less often 11. They are hexamerously located in 2 cycles. The tentacles are, as a rule, short (1.5–3 mm long), thick, conical in shape, pointed at the tips. Their surface is covered with small transverse wrinkles, sometimes rare large longitudinal furrows are visible (Fig. 8C). The pharynx is transversely furrowed. One well-preserved specimen has 2 rather deep siphonoglyphs, which differ from the rest of the pharynx by smooth walls and a lighter coloration. There are 2 mesenteric cycles (6+6). The first cycle is composed of perfect mesenteries with retractor muscles, parietal muscles, and filaments. The second cycle is represented by microcnemes only, it may not be complete. It is difficult to describe in detail the location of the gonads in our material, since the available specimens are young or in poor condition.

Distribution. Baffin Island, Greenland, Norwegian Sea, Barents Sea, Franz Josef Land, White Sea, Kara Sea, East Siberian Sea, Wrangel Island, Chukchi Sea, Bering Strait, Beaufort Sea and Baffin Island (Fig. 10). Depth 3–450 m; temperature from −1.9° to +7°C, salinity 32.70‰.

Family Halcampactinidae Carlgren, 1921

Genus *Haliactis* Carlgren, 1921

Haliactis arctica Carlgren, 1921

[Figs 11A, B, 12 (Map)]

Acthelmis schaudinnii sp. n. — Carlgren 1921: 95, textfigs 122–124; 1949: 36.

Haliactis arctica sp. n. — Carlgren 1921: 128, pl. I, fig. 31, textfigs 153, 154.

Material. No. 12196 (3 sp.): R/V “Pr. Multanovsky”, 30.08.2019, Kara Sea, 74°59´N 77°18´E, St. 42, 32 m depth, silt and sand.

Description. The body is elongated with a widened distal part or cylindrical. The largest specimen reaches 1.4 cm in height (Fig. 11A, B). The smallest specimen reaches a height of 0.2 cm and a diameter of 0.15 cm. The column is not divided into regions.

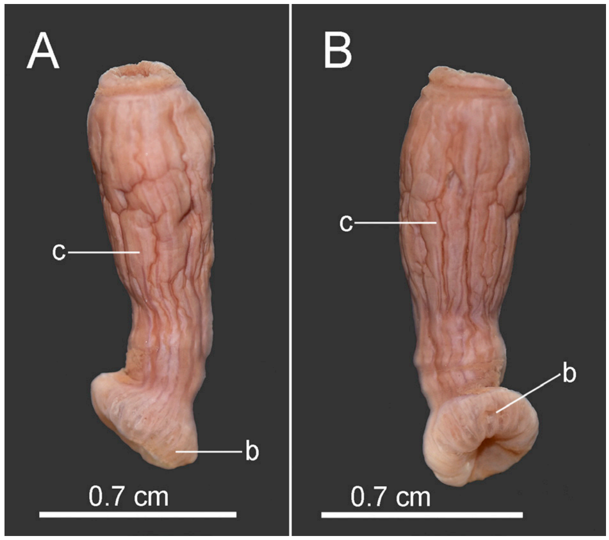

Fig. 11. *Haliactis arctica* (ZIN No 12196): A – general form; B – swollen base with central invagination. Abbreviations: *b* – base; *c* – column.

Its surface is smooth and does not bear any specialized structures. Due to contraction, it is covered with large longitudinal furrows (Fig. 11A, B). The proximal end is swollen, rounded, with retracted central part (Fig. 11A, B) or equipped with a flat pedal disc. Well-developed fossa. The oral disc is small, rounded, often retracted. Tentacles are numerous, up to 90 in adults. They are hexamerously arranged, smooth, and conical. The pharynx is of regular length, longitudinally furrowed. Siphonoglyphs are indistinct. The marginal sphincter is absent. The longitudinal musculature of the tentacles and the radial musculature of the oral disc are ectodermal. Along the entire length of the column, there are only 3 cycles of mesenteries (6+6+12); in the distal part, an incomplete fourth cycle develops. The mesenteries of the first cycle are perfect, supplied with filaments, gonads, and acontia. The mesenteries of the second cycle can carry these organs only in the middle or in the more distal part of the column. Mesenteries of the third and fourth cycles are microcnemes. The longitudinal retractor muscles are strong, restricted. Parietal muscles are elongated, occupy an extended area on the mesenteric mesogloeal plate.

Distribution. Greenland, Spitsbergen, Franz Josef Land, Barents Sea, White Sea, Novaya Zemlya, Kara Sea, East Siberian Sea, Chukchi Sea (Fig. 12). Depth 7–380 m, temperature from −1.6° to +1.66°C, salinity 30–33.06‰.

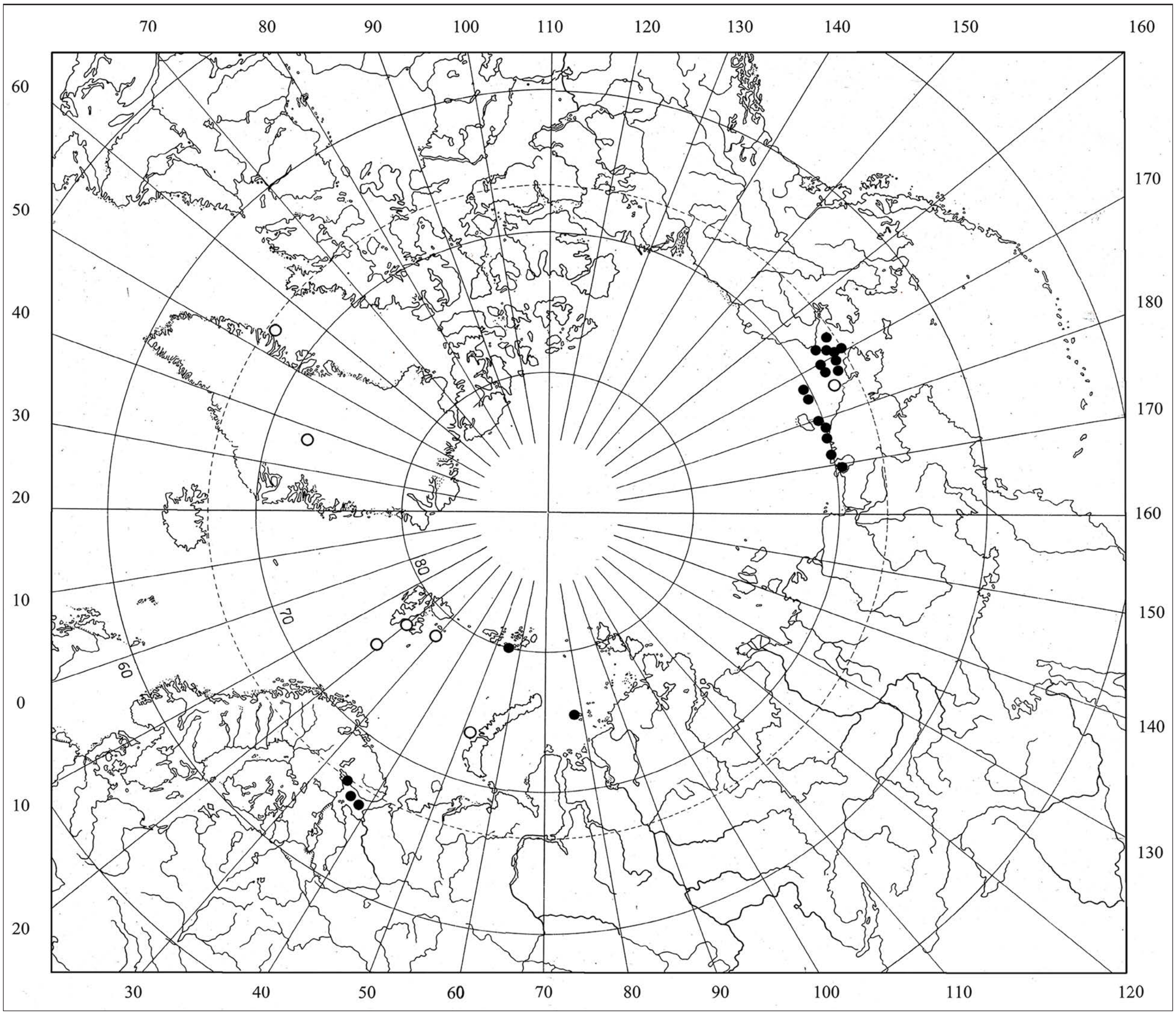

Fig. 12. Distribution of *Haliactis arctica* according to the collection of the ZIN RAS (black circles) and to the literature data (white circles).

Family Edwardsiidae Andres, 1881

Genus *Edwardsia* Quatrefages, 1842

***Edwardsia arctica* Carlgren, 1921**
[Fig. 13 (Map)]

Edwardsia arctica sp. n. — Carlgren 1921: 39, textfigs 33–38.

Material. No. 12207 (5 sp.): 1896, Kara Sea, 73°37´N 69°23´E, St. 5, coll. A.S. Botkin.

Description. The body is elongated, cylindrical, often widened in the proximal part. The height ranges from 0.4 cm to 0.9 cm. The scapus has a well-developed cuticle to which foreign particles can adhere. The nemathybomes are rather large, located between the mesenteries in 8 longitudinal rows that are most distinct in the distal part. The scapulus is polygonal. The physa is well-defined, sometimes foreign particles are attached to it. There are 16 tentacles. The pharynx is short. The longitudinal retractor muscles are weak and have 10–15 folds branched only in the outer part. The parietal muscles are relatively strong, fan-shaped or elongated. They spread considerably over the column wall.

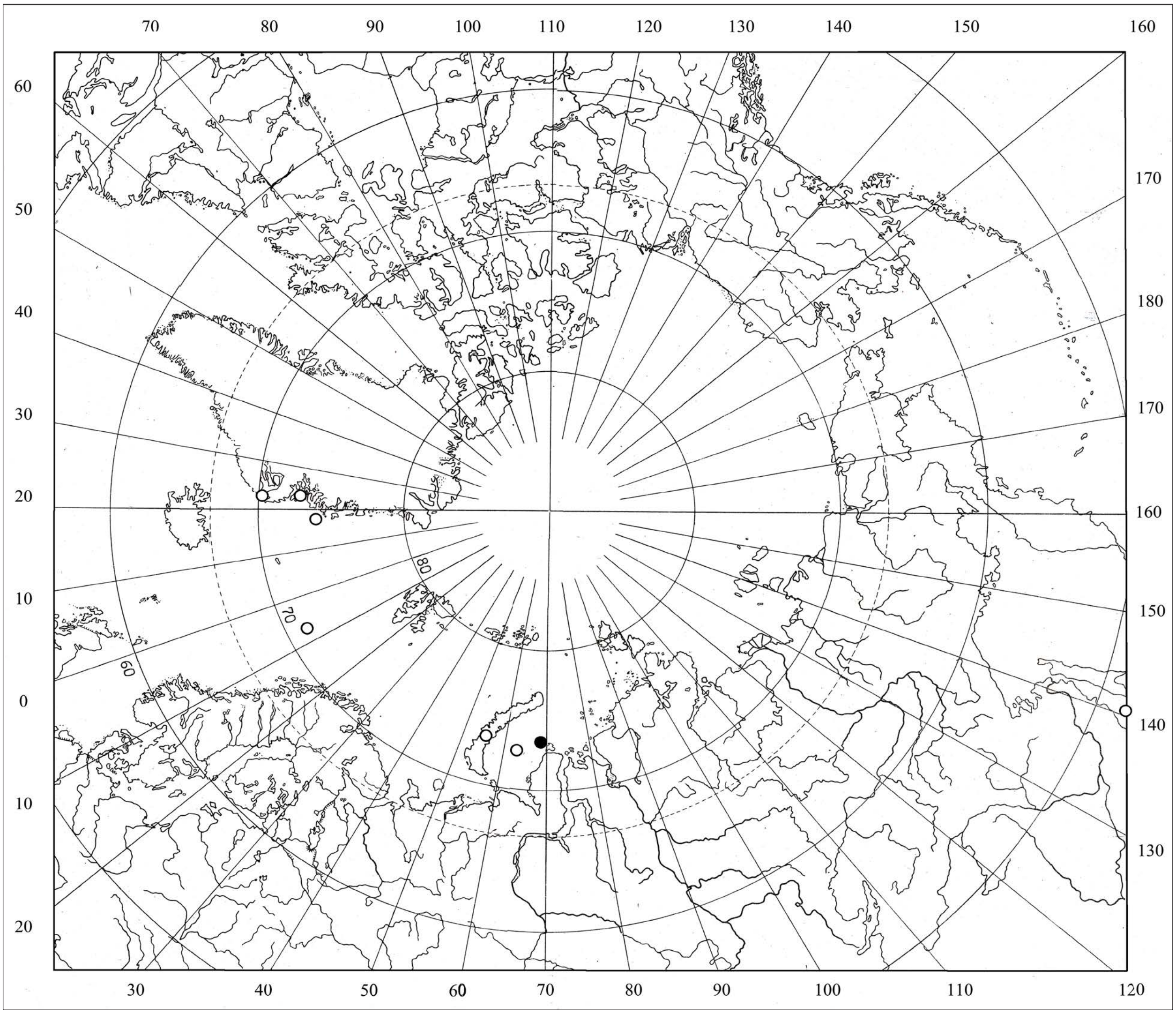

Fig. 13. Distribution of *Edwardsia arctica* according to the collection of the ZIN RAS (black circles) and to the literature data (white circles).

Distribution. East Greenland, Jan Mayen, Barents Sea, Matochkin Strait, Kara Sea, Sea of Japan (Fig. 13). Depth 3–2300 m; temperature +0.18ºC.

Edwardsia vitrea (Danielssen, 1890)

[Figs 14A, B, 15, 16, 17 (Map)]

Edwardsioides vitrea sp. n. — Danielssen 1890: 100, pl. V, fig. 3, pl. 16, figs 4–10.

Edwardsia vitrea — Carlgren 1921: 49, pl. I, figs 5, 11, textfigs 50–56.

Material. No. 12232 (2 sp.): R/V “Pr. Multanovsky”, 30.08.2019, Kara Sea, 74°59′N 77°18′E, St. 42, 32 m depth, silt and sand.

Description. The column is elongated, widens towards the proximal part. The height is 2.7 cm, the largest diameter (proximal part) is 0.8 cm, and the smallest diameter (distal part) is 0.45 cm. The column is divided into scapus, capitulum and physa. The scapus is covered with numerous transverse folds, especially strong in the distal part. It also bears a thin, easily falling off and weakly encrusted cuticle, which is most developed in the distal part of the column; it weakens significantly from about the

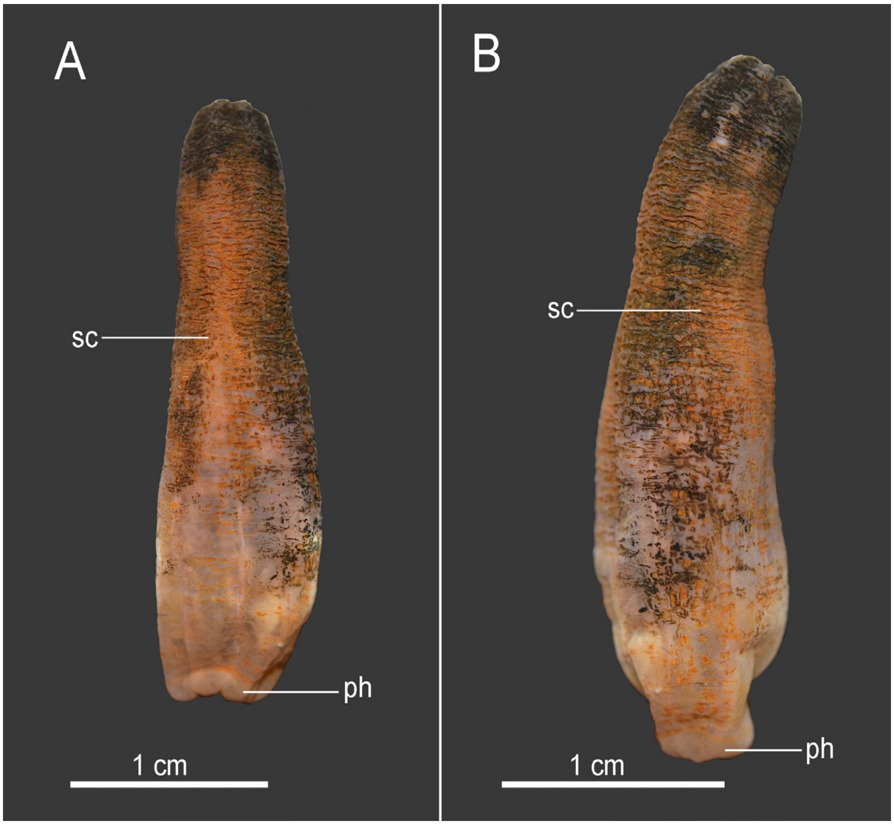

Fig. 14. *Edwardsia vitrea* (ZIN No 12232): A – proximal part of the column with no cuticle on one side and a small physa; B – significant cuticle development on the other side of the column, a small physa. Abbreviations: *ph* – physa; *sc* – scapus.

Fig. 15. Distal part of the scapus with numerous transverse wrinkles and 8 longitudinal ridges of *Edwardsia vitrea* (ZIN No 12232).

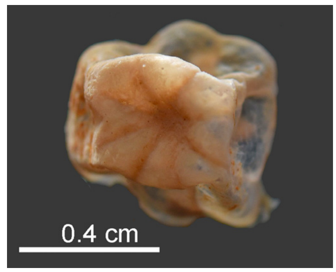

Fig. 16. Small physa of *Edwardsia vitrea* (ZIN No 12232), view of the aboral side.

middle (Fig. 14A, B). The scapus has 8 longitudinal ridges that are distinct in the distal, retracted part of the body (Figs 14B, 15). Nemathybomes are also confined to the distal part of the column, they are scattered and do not form regular vertical rows. The capitulum is short, with longitudinal and transverse wrinkles. The physa is small (Figs 14A, B, 16) and has a central pore. The oral disc is small, surrounded by 16 tentacles. They are conical and transversely striated. The pharynx is short, covered with transverse folds. The siphonoglyphs are missing. The longitudinal retractor muscles are strong. They have 20–30 folds, the most branched on the outer side; the central part of the retractor is often occupied by the folds that are completely unbranched. Closer to the proximal part of the column, the retractors are significantly reduced in size. The parietal muscles are strong, round or triangular in shape, depending on the degree of contraction. Distribution on the column wall is common.

Distribution. East Greenland, Norwegian Sea, Spitsbergen, Kara Sea (Fig. 17). Depth 9–836 m, temperature −0.7°C.

Suborder Ptychodacteae Stephenson, 1922

Family Ptychodactiidae Appellöf, 1893

Genus *Ptychodactis* Appellöf, 1893

Ptychodactis patula Appellöf, 1893

[Fig. 18 (Map)]

Ptychodactis patula sp. n. — Appellöf 1893: 1–22, pl. 1–3 (original description); Carlgren 1921: 11–13, pl. 3, fig. 6; Carlgren 1934: 348; Carlgren 1939: 2; Grebelnyi 1986: 91; Grebelnyi 2001: 37; Grebelnyi 2007: 54–57, figs 1, 2.

Material. No. 12282 (1 sp.): R/V “Taymyr”, Kara Sea, 69°57´N 61°07´E, 01.09.1921, St. 8,

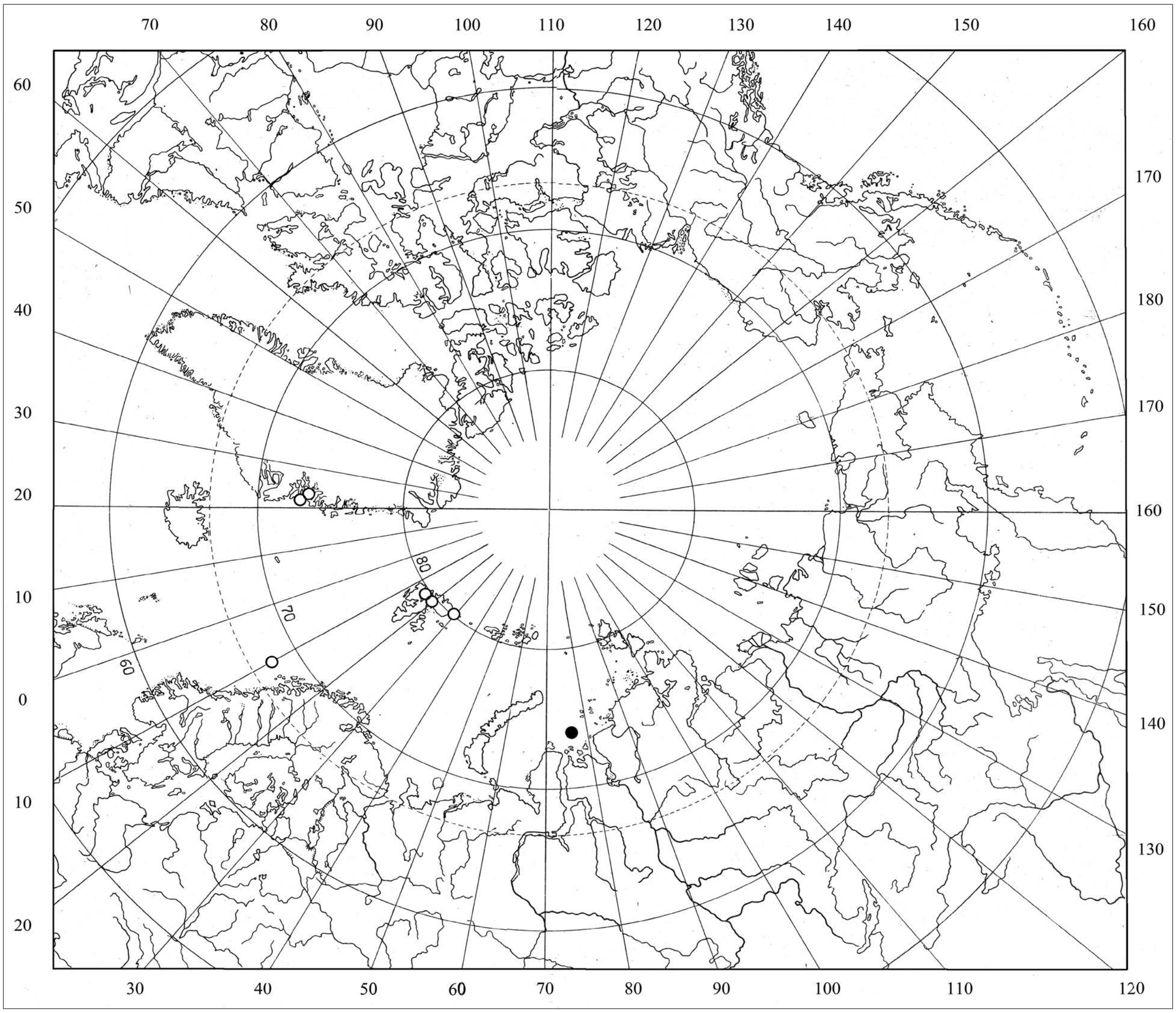

Fig. 17. Distribution of *Edwardsia vitrea* according to the collection of the ZIN RAS (black circles) and to the literature data (white circles).

155 m depth, silt and algae; No. 12283 (1 sp.): R/V "Shtorm", Kara Sea, 76°55´5″N 68°48´E, 25.08.1960, St. 16/99, 79 m depth, stones; No. 11680 (1 sp.): R/V "Vilnius", Kara Sea, 72°86´N 67°53´E, 12.07.2014, St. 7, 78 m depth, silt and clay.

Description. The body is often low with a wide proximal part. The height is up to 12 cm. The surface of the column does not bear specialized structures, but in the fixed state, it is covered with characteristic circular rough wrinkles. The body of the polyps is soft and fragile; the mesoglea is very thin, but with pronounced longitudinal muscles. The oral disc is covered with shallow radial furrows and has weak radial muscles. The tentacles are numerous, about 120. They are conical, longitudinally furrowed, short, and have weak ectodermal muscles. The actinopharynx devoid of siphonoglyphs; it is short, grading into peculiar folded lobes, which are located on large mesenteries of the first and second cycles. The marginal sphincter is absent. The mesenteries are organized in 4–5 cycles, which often are irregular. The mesenteries of the first and second cycle are perfect, at the base they can grow together. Longitudinal retractor muscles are poorly developed. The parieto-basilar muscles are indistinct.

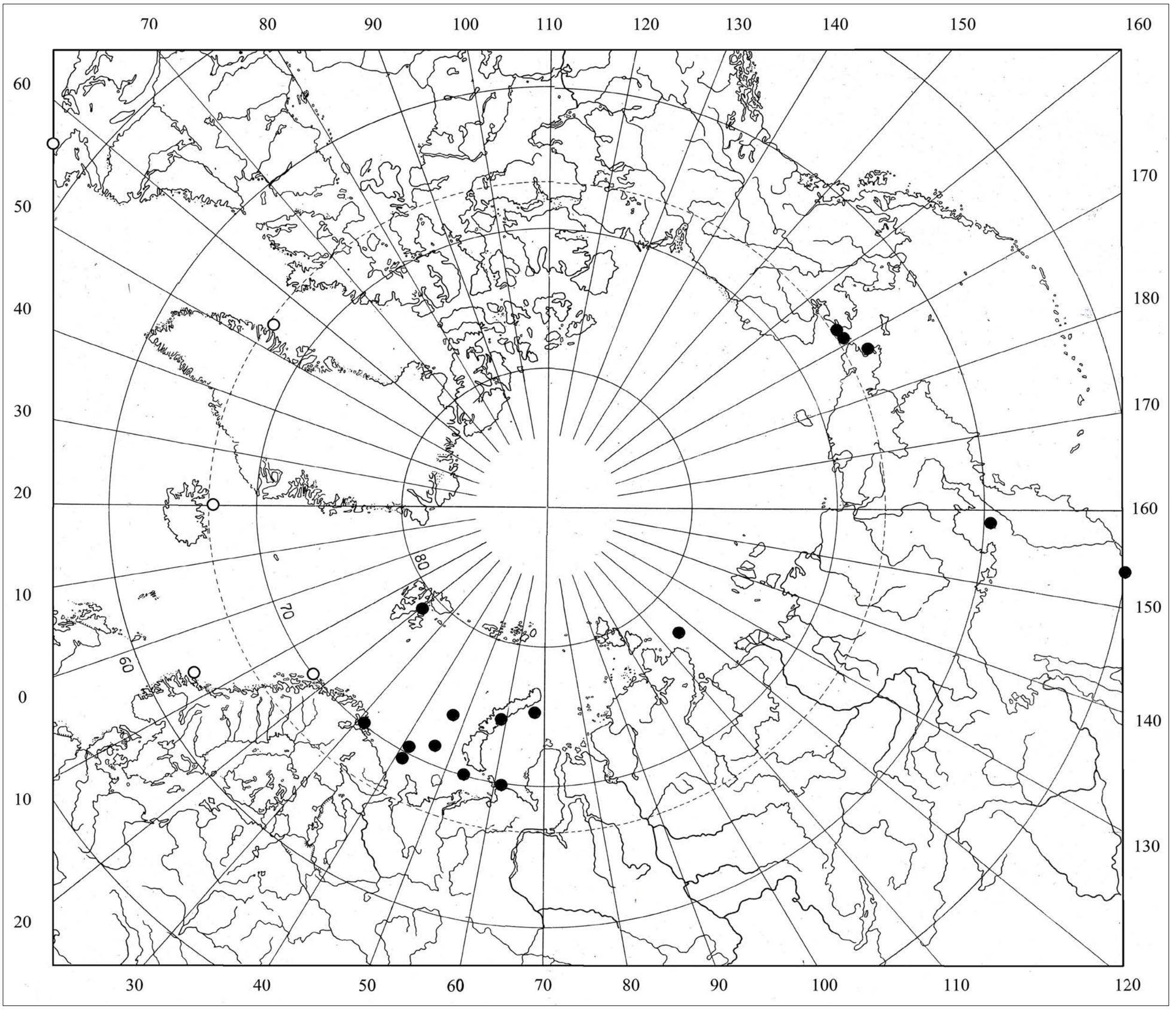

Fig. 18. Distribution of *Ptychodactis patula* according to the collection of the ZIN RAS (black circles) and to the literature data (white circles).

Distribution. Newfoundland, West Greenland, Iceland, Norway, Spitsbergen, Barents Sea, Kara Sea, Laptev Sea, East Siberian Sea, Chukchi Sea, Bering Strait, Kotzebue Sound, Bering Sea, Sea of Okhotsk and the Kuril Islands (Fig. 18). Depth from 47 to 502–499 m, temperature from −0.64° to +5.6°C, salinity 34.52–34.57‰.

DISCUSSION

The Kara Sea should be recognized as the poorest in species composition among the sea anemones of the northern seas of Eurasia. Its poverty can be explained by a small number of stations sampled in its waters. Despite the richness of benthic collections gathered in the seas of Russia, in the Kara Sea Actiniaria have been found and identified in only 45 samples. In total, 10 species of Actiniaria are currently known for the Kara Sea. We have discovered 3 species in newly studied collections.

With respect to the characterization of the region's fauna, it should be remarked that in addition to the scarcity of available collection materials, the small species number of anemones living here can be associated with the undoubted severity of the environmental conditions prevailing here. In the west, the Kara Sea is isolated from the Barents Sea and the warmer waters of the North Atlantic by the glacier-covered archipelago of Novaya Zemlya. In the east, it is separated from the remote temperate waters of the Pacific Ocean not only by the narrow Bering Strait, but also by the vast distance of Siberian Arctic coast. The second important factor influencing the population of this sea is undoubtedly the penetration of warm Atlantic waters flowing along the St. Anne Trench from the north, from the Central Arctic Basin.

An immense literature is devoted to the influence of Quaternary climate changes on the inhabitants of the Arctic shelf (for references, see Petrov 1982; Makarov et al. 2020). As a striking example of the study of climatic changes with the use of geographical distribution of animals, we would like to point to a couple of remarkable articles by Nesis (1983a, 1983b). Not being able to dwell in detail on the past changes in the hydrological regime of the Siberian seas, let us dwell on what reasonable assumptions can be drawn about the origin of the Kara Sea fauna by studying the ranges of species living here.

As it was shown in the reviews on other animals, the Arctic Region lacks the regional endemism (Toonen et al. 2016). We do not find autochthonous endemics in the Kara Sea. All the species living in this sea have certainly migrated here quite recently, after the shelf had been freed from the ice. Among the obvious aliens from the Atlantic, one can first of all name the most abundant polymorphic species *Hormathia digitata* present in all the seas of Siberia. It is widespread in the adjacent waters of the European coast, in Iceland, eastern and western Greenland, up to Hudson Bay. The limit of its distribution along the Asian coast to the east is the western half of the Chukchi Sea. The most complete map of its distribution was compiled by Grebelnyi (1980b, p. 22, fig. 1).

Hormathia digitata occurs mainly at depths from 50 to 200 m, occasionally rising to 11 m or dropping to the upper part of the slope, although under unusual conditions it can reach a depth of 1000 m (at a temperature of +1°C), as is the case in the fjords of Norway. At the southern border of the range, it tolerates an increase in temperature up to +7.9°C, but negative temperatures obviously do not restrict its normal existence.

Thus, in the Arctic, the main factor limiting the distribution of this species is depth. Salinity plays an important role in coastal areas. In the overwhelming majority of cases, when *Hormathia* was found, its values ranged from 34 to 35‰ (more than 250 measurements). Only in the East Siberian Sea, between 170° and 175°E, individuals of this species were found at 5 stations at a salinity of 28.8–31‰. Significant desalination recorded in this area at a depth of 30–40 m is probably due to the penetration of Pacific waters, which have a salinity lower than Atlantic waters. Their penetration here from the Bering Sea was shown by studying zooplankton (Virketis 1952).

In the Chukchi Sea, *Hormathia digitata* was found only at the edge of shelf at a depth of 152–153 m, at high salinity (34.2‰) and a temperature of −0.5°C, i.e. in the waters of Atlantic origin. Thus, salinity below 34‰, according to all available information, is unfavorable for this species and limits its distribution. This is evidenced by its absence in the White Sea, in Cheshskaya Bay (Cheshskaya Guba) and in the coastal, desalinated part of the Pechersk Sea. The widespread opinion about the strong desalination of the estuarine areas of the Siberian seas should in fact be attributed only to the upper 10–15 m layer. Fresh and warm river waters, spreading over heavy sea waters, create a large density gradient and do not lend themselves to wind mixing (for more details see Khmyznikov 1932; Grebelnyi 1980b). Consequently, the occurrence of *Hormathia digitata* near river mouths does not prevent this species from being classified as a highly stenohaline species. It does not reach the Bering Strait, where the salinity in all layers is less than 34‰ and was not found in rich collections from the Bering Sea and Sea of Okhotsk.

The next, less stenohaline and more eurybathic species inhabiting the Kara Sea is *Actinostola callosa*. According to the available observations, it was recorded at a salinity of 29.99–35.01‰ and temperatures from −1.9° to + 2.8°C at depths from 14 to 2047 m. Due to its ability to settle at greater depths and withstand reduced salinity, it is very widespread and is found from Newfoundland and Greenland to Iceland, Skagerrak, Kattegat, Spitsbergen, the Barents Sea, the Kara Sea, the Laptev Sea, the East Siberian Sea, and the Chukchi Sea. Some tolerance to low salinity, which drops to 33–31‰ in the North Pacific, allows it to inhabit the Bering Sea and the Sea of Okhotsk, where this species is very common everywhere (Fig. 6); this species was also recorded in the waters of Japan and the eastern part of the Northern Pacific. However, shallow desalinated areas of the Barents and Pechersk Seas are unsuitable for its settlement. The White Sea, which at the bottom has a temperature of about −1.4°C and salinity of 28–30.0‰, is also not inhabited by this species. Although its range covers the seas of both the Atlantic and the Pacific Oceans, in the seas of the Arctic Ocean it is present only at certain locations, which is apparently due to its weaker adaptability to Arctic conditions. *Ptychodactis patula* is similarly widespread (Fig. 18).

Another species present in the Kara Sea, *Anthosactis janmayeni*, is even more associated with the high latitudes of the Arctic than both previous ones (Fig. 7). It is eurybathic (20–1710 m), but is confined to a narrow temperature range, from +1.3° to −1.78°C, and to high salinity, namely, 34.28–34.97‰. In Baffin Bay and the Greenland Sea, it occurs only north of 60°N, is absent off the coast of Norway, Spitsbergen (except North Spitsbergen) and Franz Josef Land, and appears only in the central and northeastern, i.e. in the coldest part, of the Barents Sea. It was found at the bathyal depths in the Laptev Sea (79°26´N 107°48´E, 1073 m, −0.38°C), i.e. below the layer of Atlantic water[1]. This undoubtedly proves the ability of the species to exist throughout the year at negative temperatures. *Anthosactis janmayeni* is absent in the Pacific and the reason for this should certainly be sought in its need for high salinity, since the temperature regime of the Bering Strait does not isolate it from the Asian Far Eastern seas.

In the Kara Sea two more euryhaline and more widely spread species of anemones were noted, slightly differing from each other in their preferred depths. *Aulactinia stella* mainly settles in the intertidal zone, under stones or in the sand between them; however, it was also reported from considerable depths, up to 178 m. *Urticina crassicornis*, although it can also be found on the underside of stones exposed at low tide, is more common in the sublittoral, sinking to a depth of 600 m. Both species are common in the waters of the Atlantic coast of America and western Greenland from the Gulf of Maine (41°40´N) to the southern part of Baffin Bay, and have been recorded off the coast of Iceland. In addition, *Aulactinia stella* is found in Hudson Bay, Cumberland Sound (65°N 65°W) and off the east coast of Greenland (72°20´N 65°53´N), while *Urticina crassicornis* is found in northern Baffin Bay up to Smith Strait (78°25´N 74°W) and off Jan Mayen Island. Further to the east, both species live off the coast of Spitsbergen, Franz Josef Land, in the Barents Sea, northern Norway, near the Kola Peninsula and in the White Sea. In the White and Pechersk Seas, *Urticina crassicornis* inhabits the upper layer, warmed up to +9.9°C by the summer sun, and in the Barents Sea it penetrates to the Kara Gates and beyond along the trench that borders the southern coast of Novaya Zemlya and is filled with water having a positive temperature. *Aulactinia stella* is very common in the White Sea and inhabits here only the tidal zone and the uppermost sublittoral, the regions most heated by the sun, which is ensured by its resistance to strong desalination (up to 22‰). In the Siberian seas, where the tidal zone is essentially lifeless, it is found only in the sublittoral, but all 8 of its finds in the Kara Sea, the Laptev Sea and the Chukchi Sea belong to the uppermost, desalinated, but also the most heated layer of 3–22 m. Further to the east, both species were recorded in the Bering Strait; from here, *Aulactinia stella* goes down to the western coast of Kamchatka, the Commander, Aleutian and the Kuril Islands.

The rest of sea anemone species found in the Kara Sea are either known to date from a few finds, or they are similar in the ranges to the species we have already considered. The geographic distribution of *Edwardsia arctica* and *E. vitrea* is poorly known (Figs 13, 17). The distribution area of *Allantactis parasitica* broadly overlaps with that of *Hormathia digitata* in its northern part. *Actinostola spetsbergensis* is morphologically close to *Actinostola callosa* and, possibly, is not a separate species. Therefore, our considerations concerning the composition and supposed sources of formation of the Kara Sea anemone fauna in the current state of its study are based mainly on the ranges of the species considered in detail above. Naturally, the most widespread and best studied species provide us with the most detailed information and subject for discussion. The first of them, *Hormathia digitata*, is the most abundant in the sea and the most plentiful in the collections. It could undoubtedly penetrate into the region from the west, from the coldest northern parts of the Atlantic Ocean. This inference can be argued primarily by the fact that it is decidedly stenohaline. In addition, it is absent in the seas of the North Pacific, and under the current hydrological conditions, nothing, except for the lower salinity

[1] The term *Atlantic water* in the Arctic Ocean is used conventionally to designate a layer with a positive temperature.

of the Bering Strait and the adjacent parts of the North Pacific, prevents further spread of *Hormathia digitata* (and *Allantactis parasitica*) southward into boreal waters. The penetration of both Hormathiidae species into the Siberian seas could have proceeded along shallow coasts as they were freed from ice, but only following the salty Atlantic waters making their way to the east.

Another stenohaline species, *Anthosactis janmayeni*, no less resistant to low temperatures, reaching deeper depths, but more adhering to high latitudes, could also have appeared in the Kara Sea only from the Atlantic. But the path of its penetration, apparently, was different.

Given the current climatic situation, even the waters of western Spitsbergen, where some common European invertebrate species are now found (in particular, *Metridium senile* (L., 1761), common off the coast of Germany), are obviously too warm for it. It is pertinent to note that in earlier times, at the end of the last glacial period, the climatic situation could have been different, the water temperature off the coast of Spitsbergen could have been lower. But whatever the results of accurate paleoclimatic reconstructions, the Barents Sea shelf could not serve as a migration route, since it was certainly freed from ice later than the more northern deep-sea parts of the ocean. The penetration of deep-water bathyal forms on the Siberian shelf probably occurred by a roundabout route from the north around Spitsbergen and Franz Josef Land. These considerations are quite consistent with the hypothesis put forward by Gorbunov (1946) about the enrichment of the benthic fauna of the Siberian seas by means of introduction of bathyal species from the deep-water parts of the Central Arctic basin to the shelf[2].

The distribution of other widely spread anemones, *Actinostola callosa*, *Urticina crassicornis*, *Aulactinia stella* and *Ptychodactis patula*, existing in the Kara Sea, was not so strongly influenced by the restrictions associated with low salinity. They tolerate desalination better and are present in the cold seas of both the Atlantic and Pacific oceans. So they cannot be unequivocally attributed to aliens from the west or east. In fact, their ranges can hardly be considered a continuous chain of populations connecting the species of two oceans. Sea anemones of all three of these species require higher temperatures, so they develop in the Arctic only in few, the most favorable places where the influx of Atlantic waters or summer solar warming allows them to maintain their populations. Similar wide distribution and habitat requirements (temperature and salinity) are intrinsic to the athenarian sea anemones *Haliactis arctica* and *Halcampa arctica* (Figs 13, 17), but their area is somewhat less studied.

CONCLUSIONS

The not very rich set of samples, sorted out during the preparation of this paper, as well as all the available information on sea anemones of the Kara Sea published by now, give grounds to assert that the enrichment of the fauna of this region, and probably also of the other Siberian seas, went through colonization of the shelf areas vacated after the last glaciation by representatives of the North Atlantic fauna that are most resistant to low temperatures. Migration from the east, from the northern Pacific through the Bering Strait, of course, is also not excluded, but the data we have collected do not provide convincing evidence for this.

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[2] *Cactosoma abyssorum* also has a distribution pattern similar to *Anthosactis janmayeni*, but its area has not yet been adequately described.

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