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Redescription of the Arctic burrowing sea anemone *Halcampa arctica* Carlgren, 1893 (Actiniaria: Halcampidae), with discussion on the taxonomic status of *H. vegae* Carlgren, 1921

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ABSTRACT: An investigation of numerous specimens of the sea anemone *Halcampa arctica* Carlgren, 1893, which are stored in the collection of the Zoological Institute of the Russian Academy of Sciences, revealed wide intraspecific variability in the morpho-anatomical features of this species. We synonymize here *Halcampa vegae* Carlgren, 1921 with *H. arctica* based on their high morphological similarity.

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KEY WORDS: burrowing sea anemones, Halcampidae, *Halcampa arctica*, *Halcampa vegae*, intraspecific variability, taxonomically significant characters, synonymy.

Переописание арктической зарывающейся актинии *Halcampa arctica* Carlgren, 1893 (Actiniaria: Halcampidae) с обсуждением таксономического статуса *H. vegae* Carlgren, 1921

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РЕЗЮМЕ: Изучение многочисленных экземпляров *Halcampa arctica* Carlgren, 1893, которые хранятся в коллекции Зоологического института, показало широкую внутривидовую изменчивость морфо-анатомических признаков этого вида актиний. Основываясь на высоком морфологическом сходстве, в настоящей работе мы считаем *Halcampa vegae* Carlgren, 1921 синонимом *Halcampa arctica*.

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КЛЮЧЕВЫЕ СЛОВА: зарывающиеся актинии, Halcampidae, *Halcampa arctica*, *Halcampa vegae*, внутривидовая изменчивость, таксономически значимые признаки, синонимия.

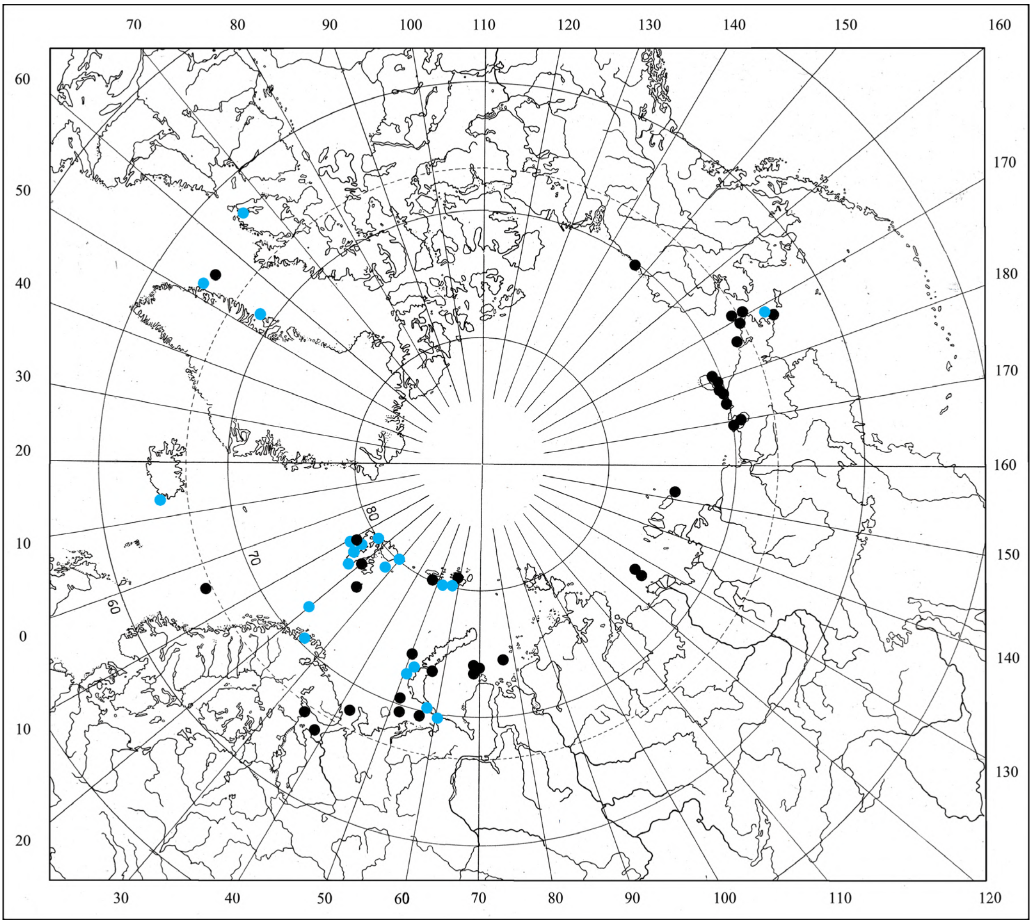


Fig. 1. Distribution of *Halcampa arctica* Carlgren, 1893 based on the collection of the ZIN RAS (black dots) and to the literature data (blue dots). Each dot represents one or more localities.

Рис. 1. Распространение *Halcampa arctica* Carlgren, 1893 по данным коллекции ЗИН РАН (чёрные кружки) и литературным данным (голубые кружки). Каждый кружок обозначает одну или больше станций.

Introduction

The genus *Halcampa* Gosse, 1858 contains ten species (see Fautin, 2016), five of which, *Halcampa medusophila* Graeffe, 1884, *H. vegae* Carlgren, 1921, *H. octocirrata* Carlgren, 1927, *H. capensis* Carlgren, 1938 and *H. abtaoensis* Carlgren, 1959, are known only from original often insufficient descriptions, or based on few poorly preserved specimens. Two oldest species of the genus, *H. chrysanthellum* (Peach in Johnston, 1847) and *H. duodecimcirrata* (Sars, 1851), require careful comparative analysis despite the large number of their descriptions (Peach in Johnston, 1847; Sars, 1851; Landsborough, 1852; Gosse, 1858, 1860; Wright, 1860; Keferstein, 1862; Verrill, 1869, 1922; Andres, 1883; Haddon, 1885, 1886, 1889; Carlgren, 1893; Walton, Rees, 1913, etc.). In contrast, the original descriptions of *H. decemtentaculata* Hand, 1955 and *H. crypta* Siebert et Hand, 1974, are quite detailed and based on many specimens (Hand, 1955; Siebert, Hand, 1974). Moreover, *H. decemtentaculata*, originally recorded in the intertidal zone, has been found at greater depths in subsequent studies (Fautin, 1998).

Halcampa arctica Carlgren, 1893 is the most studied species. Despite new information that has become available (Sanamyan *et al.*, 2016; Ivanova, Grebelnyi, 2021), the study of the extensive material from the collection of the Zoological Institute has shown that our knowledge on this Arctic burrowing sea anemone is still incomplete. A comparison of the characters of *H. arctica* and the little-known *H. vegae* suggests that they are synonyms.

In the present work we describe variability of *Halcampa arctica* basing on numerous specimens collected from different localities in the Arctic region and discuss the taxonomic position of *Halcampa vegae*.

Material and methods

The material (111 specimens in total) was collected during numerous Russian and Soviet expeditions in various locations within the Arctic region (see Table S1 and Fig. 1) and stored in the collection of the Zoological Institute RAS. The collected specimens were fixed in 4% seawater formaldehyde and then transferred to 70% ethanol for long-term storage. All ethanol-preserved specimens were examined whole, and then dissected. Seven specimens (ZIN 12474, 12927, 12488, 12476, 12465, 12466, 12480) from the Greenland, Barents, White, Laptev, Chukchi and Bering Seas were embedded in paraffin and cut into histological serial sections 3–7 μm thick, using the isopropanol-mineral oil method (Sanamyan *et al*., 2013). The cnidom was determined from small pieces of tissue from tentacles, column, pharynx and mesenterial filaments of 1–3 specimens from the each sea. For general cnidae terminology, we use a combination of classifications provided by Weill (1934a, b) and Carlgren (1940).

Taxonomy

Order Actiniaria
Family Halcampidae Andres, 1883
Halcampa Gosse, 1858
Halcampa arctica Carlgren, 1893
Figs 1–18, Tables 1, S1.

Halcampa arctica Carlgren, 1893: 45, 1921: 120, 118, 1928: 274, 1932: 259, 1933: 11, 1934: 348, 1939: 5; Gravier, 1922: 15, 94; Sanamyan *et al*., 2016: 9; Ivanova, Grebelnyi, 2021: 171.

Halcampa vegae Carlgren, 1921: 123.

DESCRIPTION. The specimen ZIN 12474 collected in the type locality of *Halcampa arctica* is elongated, 26 mm in height and 8 mm in largest diameter. The remaining specimens measure 3–52 mm in length and 1–30 mm in largest diameter.

The column is divided in scapulus, scapus and physa (Figs 2A–C, 4E, H). In expanded specimens, the scapulus is usually completely covered with strong or weaker annular wrinkles (Figs 3A, 4E, H). Sometimes the distal part is devoid of transverse folds and smooth, whereas the proximal part, in contrast, is covered with them – or vice versa (Fig. 3C). The longitudinal furrows were present in only a few specimens (Fig. 4B). In some specimens, the scapulus wall is very thin (Fig. 4C). If the scapulus is fully retracted, it forms longitudinal mesogloeal ridges, which have wrinkles on their surface (Figs 2B, 4A 5B) or may be completely smooth (Fig. 5A, red arrow). If only the distalmost part of the scapulus is retracted, then the remaining extended proximal part bears transverse folds, with or without longitudinal furrows (Fig. 4D).

The scapus of specimen ZIN 12474 and another 22 individuals is completely covered with sand particles and sediment (Figs 2A, D (arrow), 3A); only small areas of its surface may be naked. In the remaining specimens, the scapus is sheltered with sand to a lesser extent, sometimes entirely devoid of it (Fig. 4B, E, H). The scapus wall has tenaculi, which vary greatly in size and shape even within the same specimen (Figs 2D, 6). The tenaculi often resemble rather high, wide or narrow papillae that rise above the mesogloeal layer of the body wall (Figs 2D, 6A, C, 7A, B), but they can also be very low, flattened and saucer-shaped (Fig. 7C). Histological sections show that the ectoderm of the tenaculi is often located on a low rectangular or trapezoidal mesogloeal elevation that is slightly higher than the mesogloeal layer of the scapus wall; sometimes the mesogloeal elevation is completely absent (Figs 6B, 7D). The edges of the mesogloeal elevation often extend upward and to the side (Fig. 7E). The upper surface of the mesogloeal elevation can be flat or more often forms a depression, sometimes pronounced. The surface of the elevation is covered with a modified ectoderm composed of very small and low cells, in contrast to the tall columnar cells of the remaining ectodermal layer, and includes glandular cells. This modified tenaculi ectoderm secretes a cuticle (Fig. 7F, arrow) that promotes the attachment and retention of sand particles. The cuticle itself is easily lost along with sand grains when these are removed, and is typically visible only on histological sections (Fig. 7F). The distinct golden-brown cuticle was clearly visible under low magnification in only four specimens (Fig. 7G). Another variable tenaculi character is the varying degree of their development on the scapus of *H. arctica*. In most specimens, the tenaculi are very numerous and crowded (Figs 2D, 4B, 7G). In some specimens, however, they are few and spaced, so that they absent in many places (Fig. 8A). A few specimens had “hidden” tenaculi, so they appear as numerous small wrinkles or folds of varying sizes and irregular shapes. Only the presence of sand grains and sediment reveal these structures on the scapus wall to be tenaculi (Fig. 8B). In some specimens, the tenaculi are difficult to detect due to loss of ectoderm during collection or fixation: here, tenaculi were clearly visible on most of the scapus

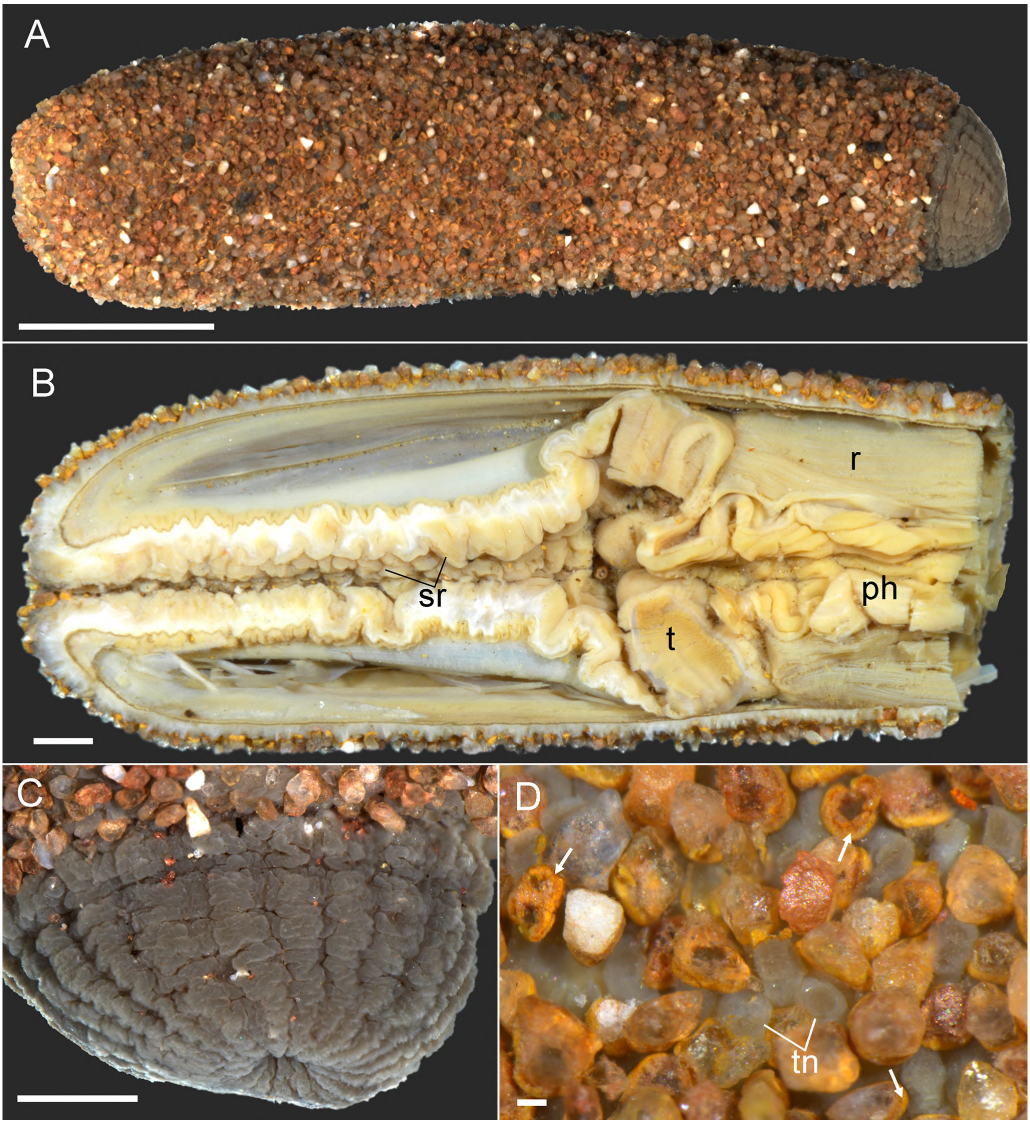


Fig. 2. *Halcampa arctica* Carlgren, 1893, specimen ZIN 12474 from the Greenland Sea. A — external view; B — longitudinal section, distal part; C — physa, enlarged; D — scapus surface with tenaculi (arrows indicate sand grains with sediment).

Abbreviations: ph — pharynx; r — longitudinal retractor muscle; sr — scapular ridges; t — tentacle; tn — tenaculi. Scale bar: A — 5 mm; B, C — 1 mm; D — 0.1 mm.

Рис. 2. *Halcampa arctica* Carlgren, 1893, экземпляр ZIN 12474 из Гренландского моря. A — внешний вид; B — продольный разрез, дистальная часть; C — физа, увеличено; D — поверхность скапуса с тенакулями (стрелки указывают на песчинки и осадок).

Обозначения: ph — глотка; r — продольный мускул-ретрактор; sr — скапулярные гребни; t — щупальце; tn — тенакули. Масштаб: A — 5 мм; B, C — 1 мм; D — 0,1 мм.

but lacking in areas with lost ectoderm (Fig. 8C). Tenaculi were not detected in one juvenile specimen completely devoid of ectoderm (Fig. 8D). Although histological sections show a wrinkled surface of the mesogloeal layer of the scapus, the complete absence of ectoderm makes it impossible to determine the presence of tenaculi (Fig. 8E). At the same time, there are many specimens completely or partially devoid of ectoderm but with well-developed tenaculi (Fig. 4H). Moreover, the modified ectoderm of tenaculi of such

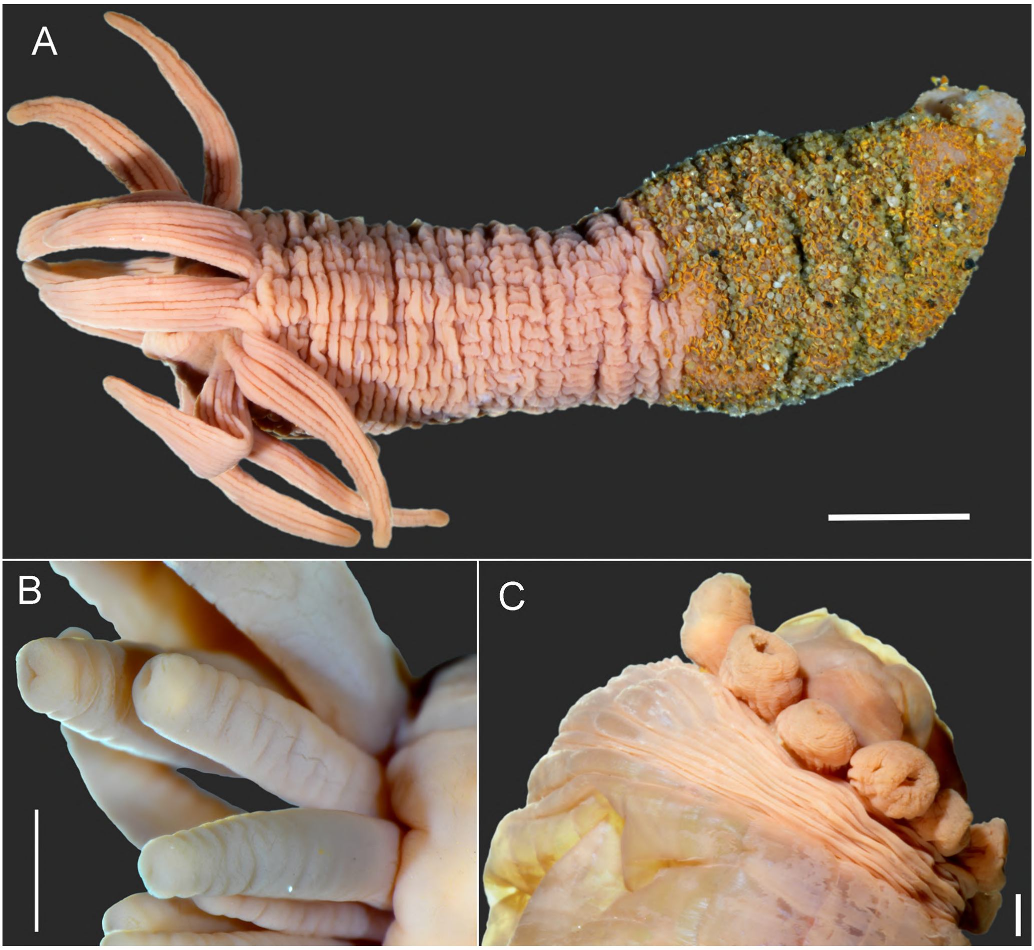


Fig. 3. Tentacles and scapulus structure of *Halcampa arctica* Carlgren, 1893. A — specimen with long tentacles ZIN 12458b from the Barents Sea; B — details of tentacle structure of specimen ZIN 12458a from the Barents Sea; C — retracted tips of tentacles of specimen ZIN 12927c from the Barents Sea. Scale bar: A — 5 mm; B, C — 1 mm.

Рис. 3. Щупальца и структура скапулюса *Halcampa arctica* Carlgren, 1893. A — экземпляр с длинными щупальцами ZIN 12458б из Баренцева моря; B — детали структуры щупалец экземпляра ZIN 12458а из Баренцева моря; C — втянутые кончики щупалец экземпляра ZIN 12927c из Баренцева моря. Масштаб: A — 5 мм; B, C — 1 мм.

specimens is not always lost along with the ectoderm of the scapus (Fig. 7D).

The physa is distinct and well developed in almost all studied specimens (the proximal part of a few specimens was torn off during collection (Fig. 3A)). In many individuals it is completely retracted, fewer specimens have a swollen physa, which has a central depression varying in size (Figs 2A, 4H). The physa wall is usually thick, but in some specimens it is thin and the mesenterial insertions are visible through it. The physa surface may be smooth or covered with numerous fine wavy, annular and radial wrinkles (Figs 8D, F). The physa of specimen ZIN 12474 is covered with 24 narrow, radially divergent grooves, between which there are wrinkled ridges (Fig. 2C). A series of longitudinal histological sections of some specimens shows that the physa wall, characterized by a rather thick mesogloea, lack any apertures (Fig. 8G, arrow indicates scapus–physa border). However, the physa of other specimens exhibits openings, but these are more likely to be accidental, fixation- or histology preparation-related ruptures than natural structures (Fig. 8H, arrow indicates mesentery).

The oral disc is small, rounded, edged by 12 tentacles. In specimen ZIN 12474 they are short, with rounded or more often with slightly retracted tips,

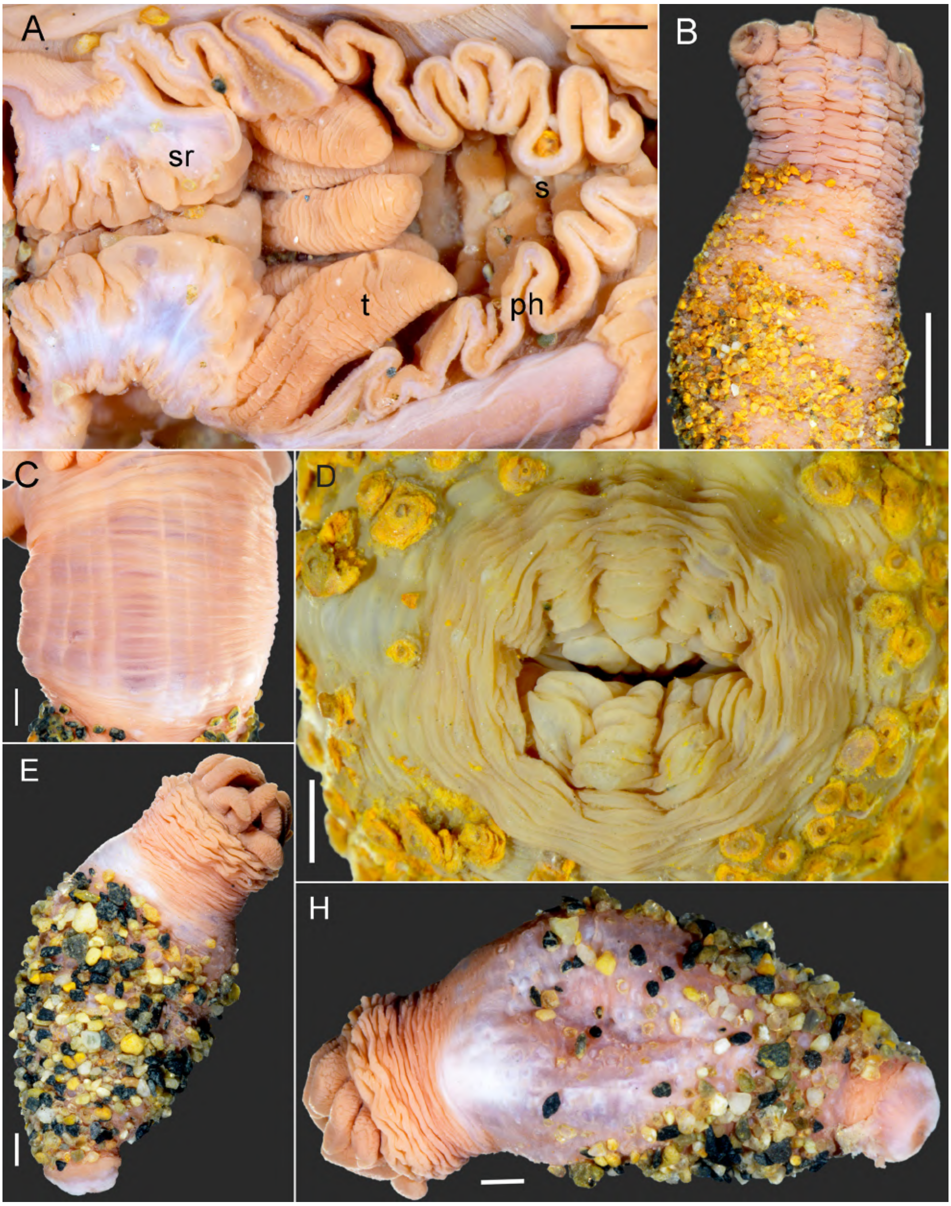


Fig. 4. Structure of scapulus and scapus of *Halcampa arctica* Carlgren, 1893. A — distal part of specimen ZIN 12927b from the Barents Sea, longitudinal section; B — distal part of specimen ZIN 12459d from the Barents Sea, lateral view; C — scapulus of specimen ZIN 12846 from the East Siberian Sea; D — scapular ridges of specimen ZIN 12455a, top view; E, H —specimen ZIN 12847d from the East Siberian Sea, lateral view from different side.

Abbreviations: ph — pharynx; s — siphonoglyph; sr — scapular ridges; t — tentacle. Scale bar: A, C–H — 1 mm; B — 5 mm.

Рис. 4. Структура скапулюса и скапуса *Halcampa arctica* Carlgren, 1893. A — дистальная часть экземпляра ZIN 12927b из Баренцева моря, продольный разрез; B — дистальная часть экземпляра ZIN 12459d из Баренцева моря, вид сбоку; C — скапулюс экземпляра ZIN 12846 из Восточно-Сибирского моря; D — скапулярные гребни экземпляра ZIN 12455a, вид сверху; E, H — экземпляр ZIN 12847d из Восточно-Сибирского моря, вид сбоку с разных сторон.

Обозначения: ph — глотка; s — сифоноглиф; sr — скапулярные гребни; t — щупальце. Масштаб: A, C–H — 1 мм; B — 5 мм.

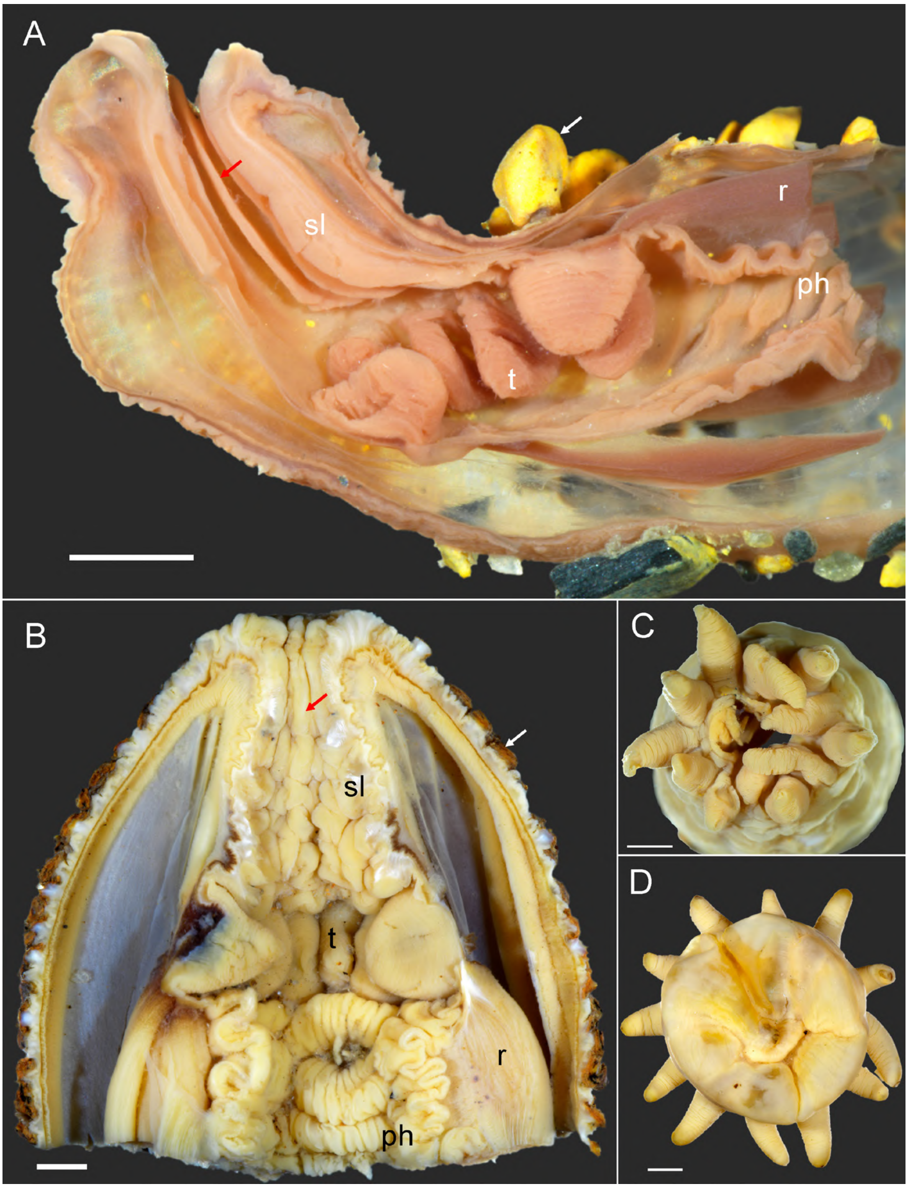


Fig. 5. Details of the external and internal structure of *Halcampa arctica* Carlgren, 1893. A — distal part of specimen ZIN 12481a from the Chukchi Sea, longitudinal section, red arrow points to scapular ridge, white arrow points to sediment; B — distal part of specimen ZIN 12485 from the East Siberian Sea, longitudinal section, arrow points to scapular ridge, white arrow points to sediment; C — oral disc and tentacles of specimen ZIN 12455b from the Barents Sea, top view; D — everted pharynx and tentacles of specimen ZIN 12478 from the White Sea, top view.

Abbreviations: ph — pharynx; r — longitudinal retractor-muscle; sl — scapulus; t — tentacle. Scale bar: A–D — 1 mm.

Рис. 5. Детали внешнего и внутреннего строения *Halcampa arctica* Carlgren, 1893. A — дистальная часть экземпляра ZIN 12481a из Чукотского моря, продольный разрез; B — дистальная часть экземпляра ZIN 12485 из Восточно-Сибирского моря, продольный разрез; C — ротовой диск и щупальца экземпляра ZIN 12455b из Баренцева моря, вид сверху; D — вывернутая глотка и щупальца экземпляра ZIN 12478 из Белого моря, вид сверху.

Обозначения: ph — глотка; r — продольный мускул-ретрактор; sl — скапулюс; t — щупальце. Масштаб: A–D — 1 мм.

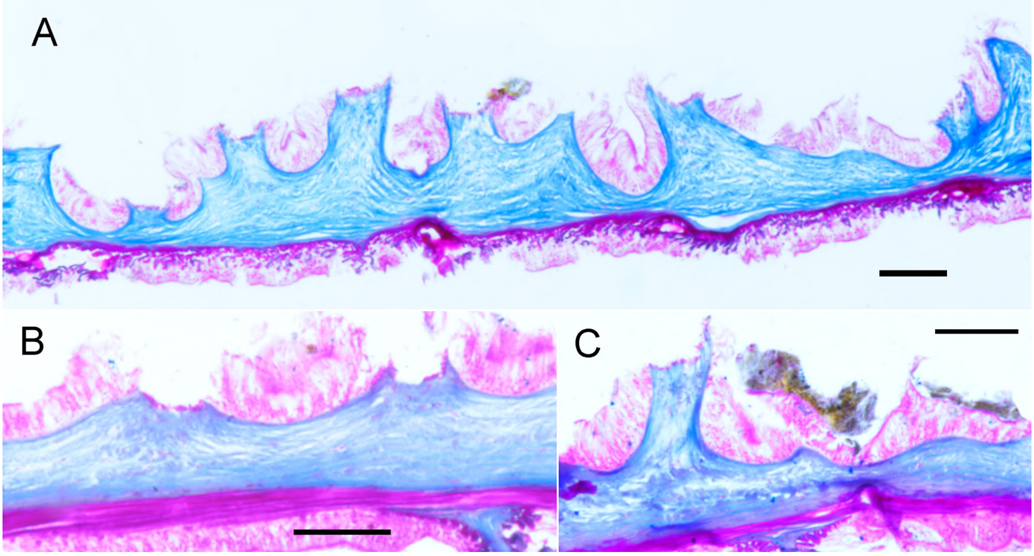


Fig. 6. *Halcampa arctica* Carlgren, 1893, specimen ZIN 12474 from the Greenland Sea. A–C — tenaculi, histological sections. Scale bar: 0.1 mm.

Рис. 6. *Halcampa arctica* Carlgren, 1893, экземпляр ZIN 12474 из Гренландского моря. A–C — тенакули, гистологические срезы. Масштаб: 0,1 мм.

thick, tightly pressed to each other; their surface is covered with numerous very small annular wrinkles (Fig. 9A). In the remaining specimens the tentacles vary from thick and short to long and narrow (Figs 3, 5). The surface of extended and retracted tentacles is covered with circular wrinkles, expressed to varying degrees (Figs 3B, 4E, 5, 8D). Deep longitudinal furrows cover the surface of only extended tentacles (Fig. 3A, C). Only a few specimens had longitudinal furrows in the most proximal part of retracted tentacles (Fig. 4A). The tentacle tips could be blunt or pointed (Fig. 5), sometimes even in one and the same specimen. In addition, the tips may be retracted, forming weak or strong depressions, or become damaged during fixation (Figs 3B, C, 4B).

The structure of the pharynx is rather stable. Its surface is typically covered with clearly defined longitudinal narrow ridges. Its wall also forms large transverse folds, which can either be very numerous and frequent or, on the contrary, rare (Figs 5A, B, 9A, 10, 11A). The ability to determine the presence and the number of siphonoglyphs depends in part on the development of the longitudinal ridges of the pharynx. The specimens with pronounced longitudinal folding have two very distinct siphonoglyphs that are rather wide, with a smooth surface, often somewhat lighter-colored than the remaining pharynx (Fig. 10). Sometimes the edges of siphonoglyphs were marked with high narrow ridges corresponding to mesentery insertions. In specimens with weak longitudinal or without striation of the pharynx, the siphonoglyphs appear to be weak or even absent (Fig. 5D).

The circular endodermal muscles of the column are well developed (Fig. 9B). The longitudinal muscles of the tentacles and the radial muscles of the oral disc are ectodermal (Fig. 11B). The general structure of the marginal sphincter (mesogloeal, reticular, and elongated) is characteristic of all studied specimens, but the details of the structure vary. In specimen ZIN 12474, the sphincter is small, narrow and slightly extends into the bases of the tentacles (Fig. 11C). In the tentacle region, the sphincter consists of a small number of individual small mesogloeal meshes, slightly closer to the ectoderm than to the endoderm (Fig. 11D, arrow). Between the tentacles, the sphincter consists of larger and denser mesogloeal meshes, which are also close to the ectoderm (Fig. 11E, arrow). In other specimens the sphincter is wider, can extend above the base of the tentacle (Fig. 12A–C, E), and may also have a different shape in the area of the tentacles and between them (Fig. 12C–E). Mesogloeal meshes may be barely visible (Fig. 12B) or very distinct (Fig. 12D, E).

Mesenteries are arranged hexamerously in two cycles (6+6), dividing into macrocnemes and microcnemes (Fig. 13A). In juveniles, however, the second cycle may be incomplete; the mesenteries of that cycle are better developed proximally (Fig. 8E) than distally (Fig. 13B, arrow). Accordingly, mesentery formation in *H. arctica* occurs in the proximal part of the column. We also noted one case of an intermittent course of the microcnemes (Fig. 13C, arrow). Another abnormality involved the development of mesenteries of the first cycle. Here, two adjacent mesenteries of

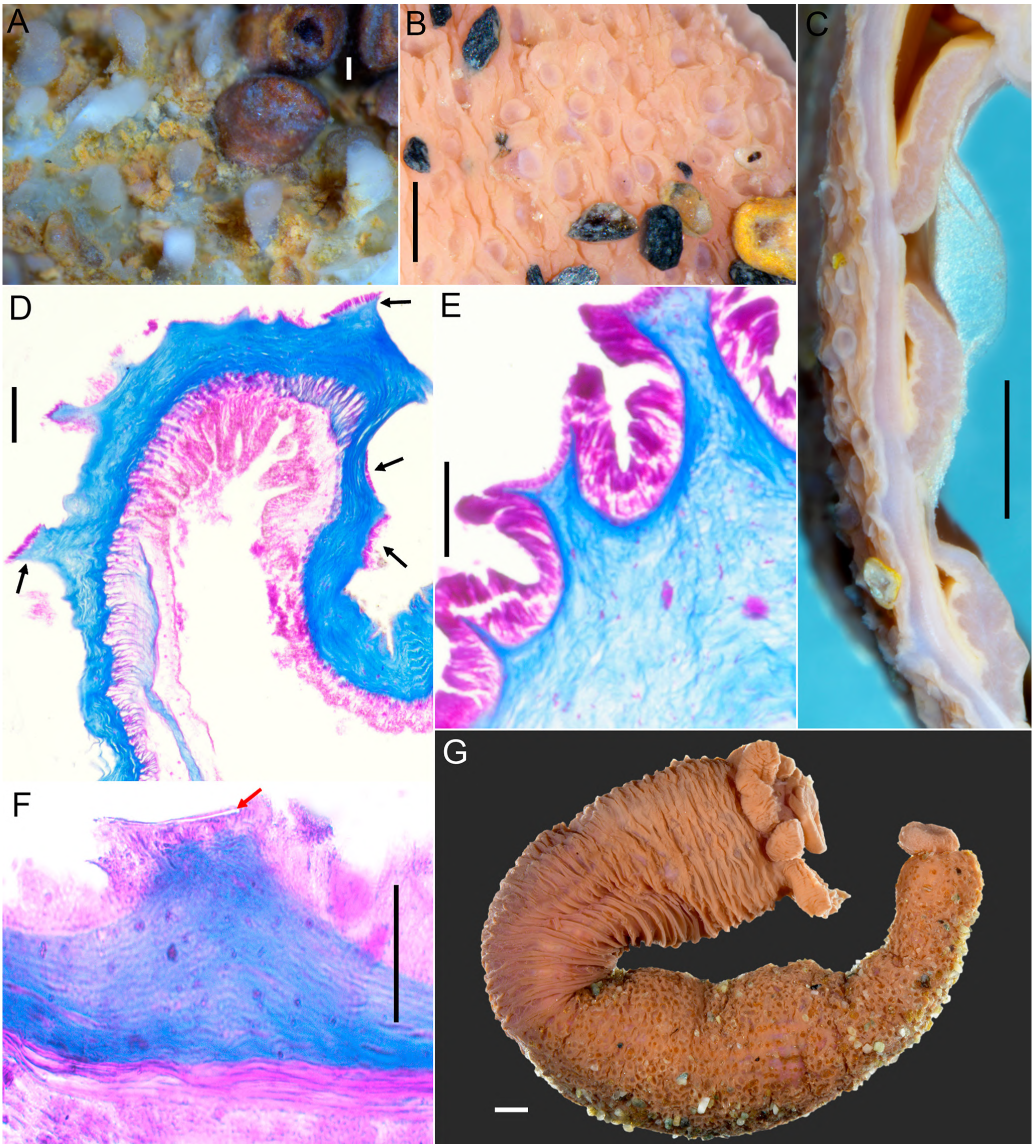


Fig. 7. Tenaculi of *Halcampa arctica* Carlgren, 1893. A — surface of the scapus of specimen ZIN 12472 from the Barents Sea; B — surface of scapus of specimen ZIN 12846 from the East Siberian Sea; C — transversal section of specimen ZIN 12927g from the Barents Sea; D — aboral part of column of specimen ZIN 12465 with tenaculi (arrows) from the Laptev Sea, longitudinal section; E — piece of scapus of specimen ZIN 12927g from the Barents Sea, longitudinal section; F — tenacula with cuticle (arrow) of specimen ZIN 12476b from the White Sea, transversal section; G — clearly defined cuticle of specimen ZIN 12480b from the Bering Sea. Scale bar: A, C–E — 0.1 mm; B — 0.5 mm; G — 0.1 mm; F — 0.05 mm.

Рис. 7. Тенакули *Halcampa arctica* Carlgren, 1893. A — поверхность скапуса экземпляра ZIN 12472 из Баренцева моря; B — поверхность скапуса экземпляра ZIN 12846 из Восточно-Сибирского моря; C — поперечный срез экземпляра ZIN 12927д из Баренцева моря; D — аборальная часть колюмна экземпляра ZIN 12465 с тенакулями (стрелки) из моря Лаптевых, продольный срез; E — кусочек скапуса экземпляра ZIN 12927g из Баренцева моря, продольный срез; F — тенакуля с кутикулой (стрелка) экземпляра ZIN 12476b из Белого моря, поперечный срез; G — четко выраженная кутикула экземпляра ЗИН 12480б из Берингова моря. Масштаб: A, C–E — 0,1 мм; B — 0,5 мм; G — 0,1 мм; F — 0,05 мм.

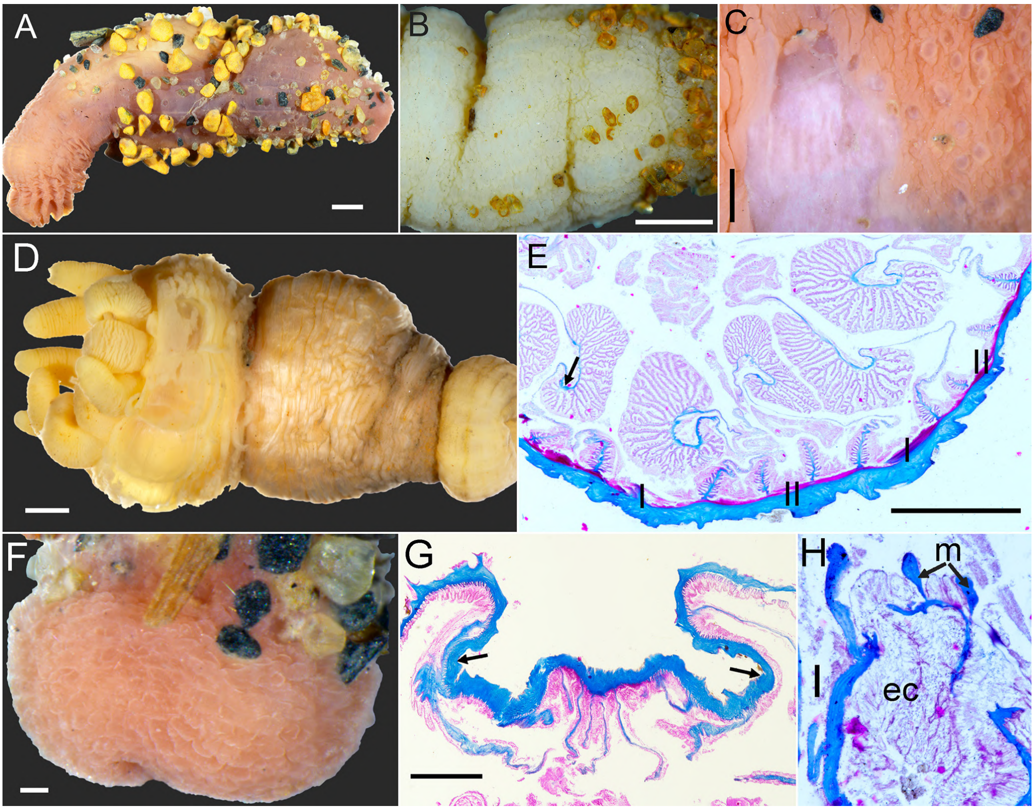


Fig. 8. Varying degrees of development of tenaculi, physa of *Halcampa arctica* Carlgren, 1893. A — specimen ZIN 12481a with rare tenaculi and sand grains, heavily overgrown by sediment, from the Chukchi Sea; B — specimen ZIN 12302b with "hidden" tenaculi from the Barents Sea; C — piece of the scapus of specimen ZIN 12846c from the East Siberian Sea; D — juvenile specimen ZIN 12488 without tenaculi from the Barents Sea; E — transversal section of same specimen, arrow indicates thickening of the mesoglea at the outer edge of the retractor muscle; F — physa of specimen ZIN 12844 from the East Siberian Sea; G — aboral part of specimen ZIN 12465 from the Laptev Sea, longitudinal section, arrows indicate the boundary between the lower scapus and the physa; H — central part of physa of specimen ZIN 12488 without tenaculi from the Barents Sea, longitudinal section.

Abbreviations: ec — ectoderm; m — mesentery; I, II — cycles of mesenteries. Scale bar: A, B, D, E — 1 mm; C, G — 0.5 mm; F, H — 0.1 mm.

Рис. 8. Различная степень развития тенакулей, физа *Halcampa arctica* Carlgren, 1893. A — экземпляр ЗИН 12481a с редкими тенакулями и сильно обросшими осадком песчинками из Чукотского моря; B — экземпляр ZIN 12302b со "спрятанными" тенакулями из Баренцева моря; C — участок скапуса экземпляра ZIN 12846c из Восточно-Сибирского моря; D — ювенильный экземпляр ZIN 12488 без тенакулей из Баренцева моря; E — поперечный срез того же экземпляра, стрелка указывает на утолщение мезоглеи на наружном крае мускула-ретрактора; F — физа экземпляра ZIN из Восточно-Сибирского моря; G — аборальная часть экземпляра ZIN 12465 из моря Лаптевых, продольный срез, стрелки показывают границу между нижним скапусом и физой; H — центральная часть физы экземпляра ZIN 12488 без тенакулей из Баренцева моря, продольный срез.

Обозначения: ec — эктодерма; m — мезентерий; I, II — циклы мезентериев. Масштаб: A, B, D, E — 1 мм; C, G — 0,5 мм; F, H — 0,1 мм.

two neighboring pairs (one of them formed by directives) did not form a whole plate and grew together in two places: in the region of the pharynx and in the region of the column wall (Fig. 13A, arrows). The mesenteries of the second cycle were thus inside a closed space. At the same time, both the parietal and retractor muscles of these fused perfect mesenteries developed normally (Fig. 13A).

Many specimens had very numerous stomata. They can be approximately the same size and located

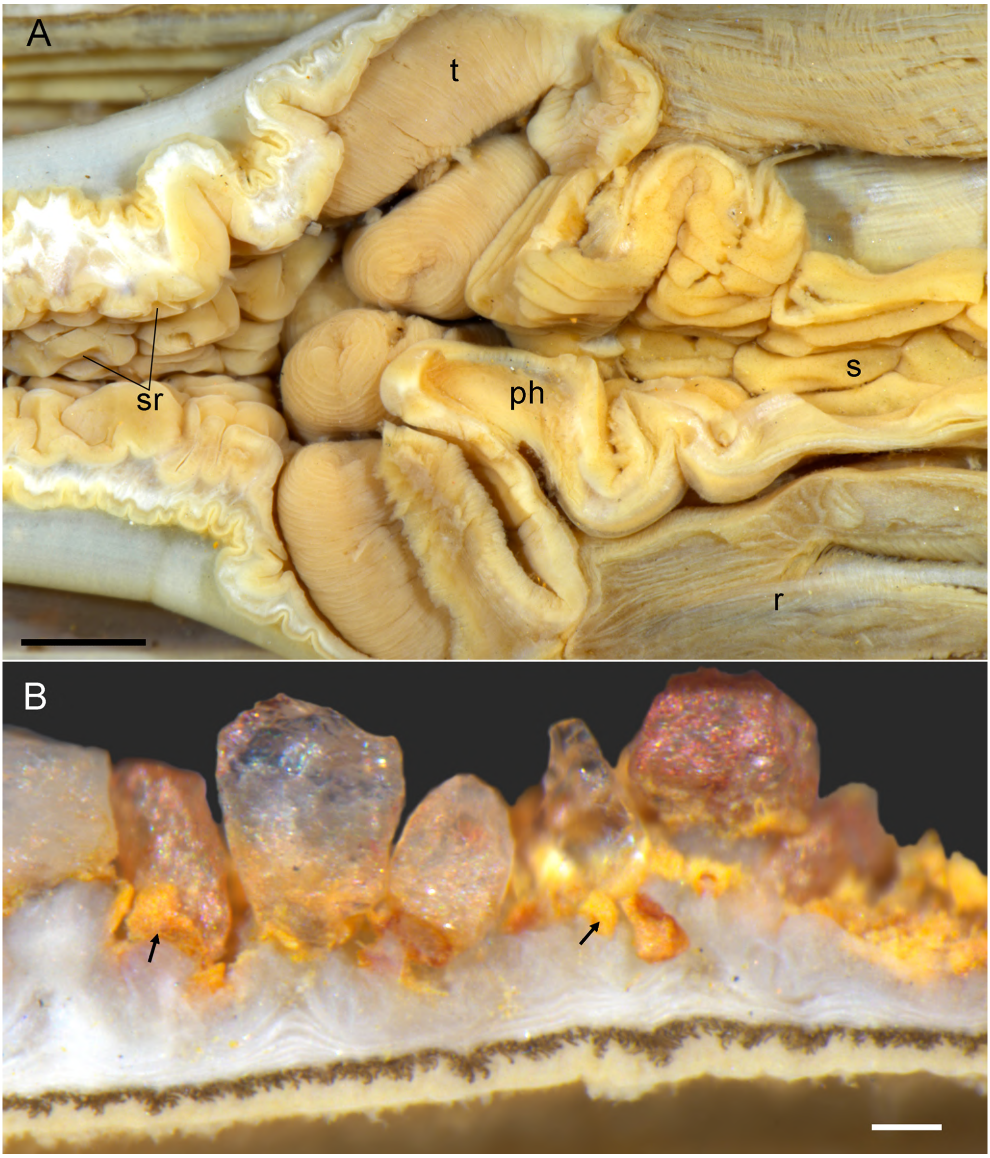


Fig. 9. *Halcampa arctica* Carlgren, 1893, specimen ZIN 12474 from the Greenland Sea. A — longitudinal section, distal part, enlarged; B — circular endodermal muscles of column wall, arrows point to sediment.
Abbreviations: ph — pharynx; r — longitudinal retractor muscle; s — siphonoglyph; sr — scapular ridges; t — tentacle. Scale bar: A — 1 mm; B — 0.1 mm.

Рис. 9. *Halcampa arctica* Carlgren, 1893, экземпляр ZIN 12474 из Гренландского моря. A — продольный разрез, дистальная часть, увеличено; B — кольцевая энтодермальная мускулатура стенки колюмна, стрелки указывают на осадок.
Обозначения: ph — глотка; r — продольный мускул-ретрактор; s — сифоноглиф; sr — скапулярные гребни; t — щупальце. Масштаб: A — 1 мм; B — 0,1 мм.

in one row in the central part of the mesenterial plate or slightly closer to the column wall. Only in the most distal part of the mesentery did a group of apertures disrupt the regularity of the row (Fig. 13D, arrow). The stomata of other specimens, however, vary in size and shape, often separated only by a very thin partition (Fig. 13E, arrow). In contrast, the stomata in some individuals are quite small and very sparse (Fig. 13F, arrow). The mesenteries of other specimens lack any stomata (Fig. 5B).

Fig. 10. Everted pharynx with two siphonoglyphs of specimen ZIN 12459e from the Barents Sea. Scale bar: 1 mm.

Рис. 10. Вывернутая глотка с двумя сифоноглифами экземпляра ZIN 12459e из Баренцева моря). Масштаб: 1 мм.

The longitudinal retractor muscles can be of three types. Some individuals have small (up to about 700 μm), restricted retractors with 20–25 folds especially branched in their outer part. The mesenteric plate is attached to the outer edge of the retractor (Fig. 14A, B). Retractors of other type are characterized by the development of a clearly defined mesogloeal outgrowth on the outer edge (Fig. 14C–F). This mesogloeal outgrowth may be elongated and narrow, or broad and short. Regardless of its shape, it produces

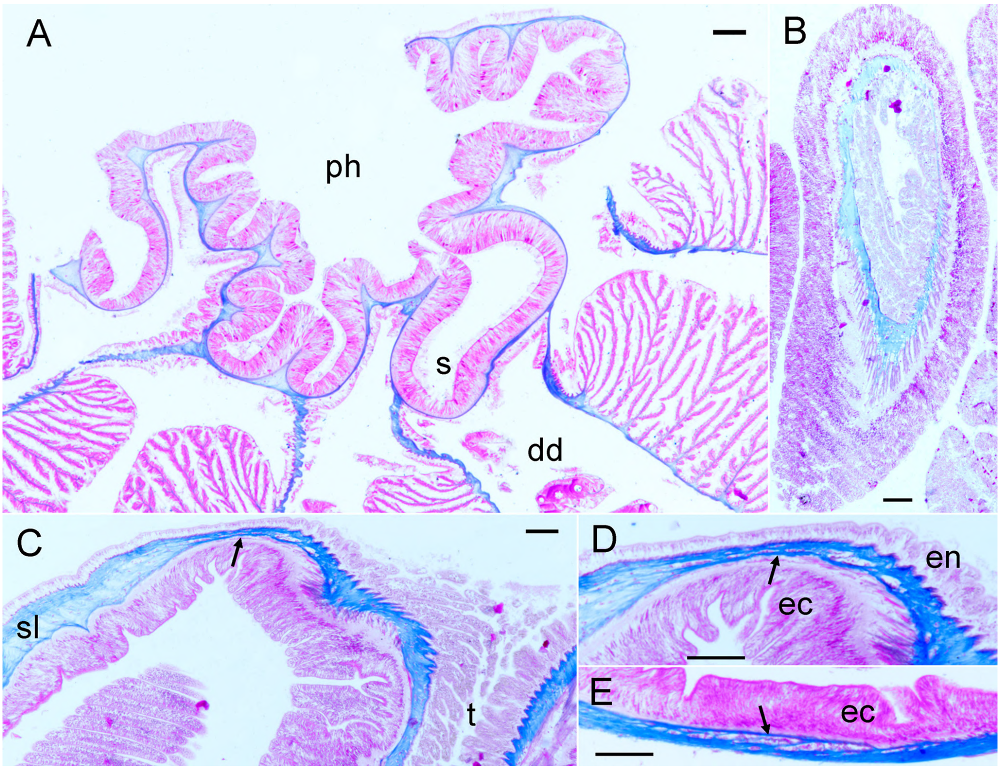


Fig. 11. *Halcampa arctica* Carlgren, 1893, specimen ZIN 12474 from the Greenland Sea. A — pharynx, transversal section; B — ectodermal muscles of tentacle, transversal section; C — marginal sphincter, longitudinal section; D — marginal sphincter, enlarged; E — marginal sphincter in area between tentacles. Abbreviations: dd — directive mesenteries; ph — pharynx; s — siphonoglyph; sl — scapulus; t — tentacle; arrows indicate sphincter. Scale bar: A–E — 0.1 mm.

Рис. 11. *Halcampa arctica* Carlgren, 1893, экземпляр ZIN 12474 из Гренландского моря. A — глотка, поперечный срез; B — энтодермальная мускулатура щупальца, поперечный срез; C — маргинальный сфинктер, продольный срез; D — маргинальный сфинктер, увеличено; E — маргинальный сфинктер в области между щупалец. Обозначения: dd — направляющие мезентерии; ph — глотка; s — сифоноглиф; sl — скапулюс; t — щупальце; стрелками показан сфинктер. Масштаб: A–E — 0,1 мм.

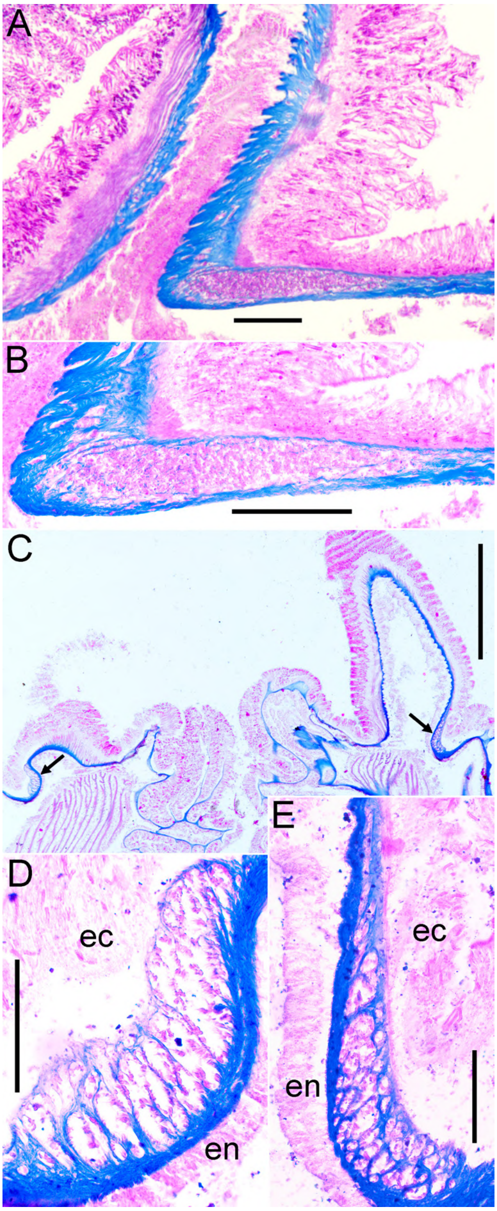


Fig. 12. Marginal sphincter of *Halcampa arctica* Carlgren, 1893. A — position of sphincter in scapulus wall of specimen ZIN 12465 from the Laptev Sea, longitudinal section; B — details of sphincter structure of same specimen, longitudinal section; C — longitudinal section showing different shapes of sphincter at base of tentacle (arrow) and in the area between tentacles (arrow), specimen ZIN 12488 from the Barents Sea; D — sphincter in the area between tentacles, enlarged; E — sphincter at base of tentacle, enlarged.
Abbreviations: ec — ectoderm; en — entoderm. Scale bar: A, B, D, E — 0.1 mm; C — 1 mm.

Рис. 12. Маргинальный сфинктер *Halcampa arctica* Carlgren, 1893. A — положение сфинктера в стенке скапулюса экземпляра ZIN 12465 из моря Лаптевых, продольный срез; B — детали строения сфинктера того же экземпляра, продольный срез; C — продольный срез, показывающий разную форму сфинктера в основании щупальца (стрелка) и в области между щупальцами (стрелка), экземпляр ZIN 12488 из Баренцева моря; D — сфинктер в области между щупалец, увеличено; E — сфинктер в основании щупальца, увеличено.
Обозначения: ec — эктодерма; en — энтодерма. Масштаб: A, B, D, E — 0,1 мм; C — 1 мм.

richly branched processes that are thicker than those formed on the inside of the retractor. In some specimens, the length of the part of the main mesentery plate bearing the folds is much greater than the length of this outer mesogloeal process; in such cases, the retractors are rather restricted (Fig. 14C, D). The retractors of many specimens become restricted to circumscribed because their mesogloeal outgrowth is approximately equal in size or larger than the main mesentery plate bearing folds (Fig. 14E, F). Retractors of the third type are very large (usually >1000 µm), very elongated and sometimes circumscribed rather than restricted (Fig. 15A, B). In addition to the outer, often very long mesogloeal outgrowth, these retractors have mesogloeal thickenings of the main mesentery plate, giving rise to a few strong, thick and highly branched processes, forming lobes (Fig. 15A, B). These processes may also be unstable, i.e. a single process does not continue through the entire length of the retractor. A single specimen can have retractors of different types, but we more often recorded the first and second or second and third types (Fig. 15C). Short muscular processes (narrow or wide) are very often present on the mesentery between the pharynx and the retractor muscle (Fig. 14D–F, arrow).

The parietal muscles of perfect mesenteries also exhibit variability. Some specimens have small (up to about 300 µm), oval or triangular parietal muscles (Fig. 15D–F). Their folds may be few in number, short, thickened, slightly branched, closely spaced or distant from each other. The main mesogloeal plate of the mesentery can sometimes be very thick (Fig. 15D, E). In contrast, the folds in other specimens are numerous, thin, and highly branched (Fig. 15F). In most specimens, however, the parietal muscles of macrocnemes are elongated (100–1200 µm). Their processes can be sparse or numerous, long or short, branched or not. Each parietal muscle can consist of processes that are approximately the same in size and shape or significantly different (compare Figs 8E and 15G). Sometimes the long processes are concentrated in the area of insertion of the mesentery into wall of column, but larger part of the mesenterial plate is occupied by the short processes (Fig. 15H). In the

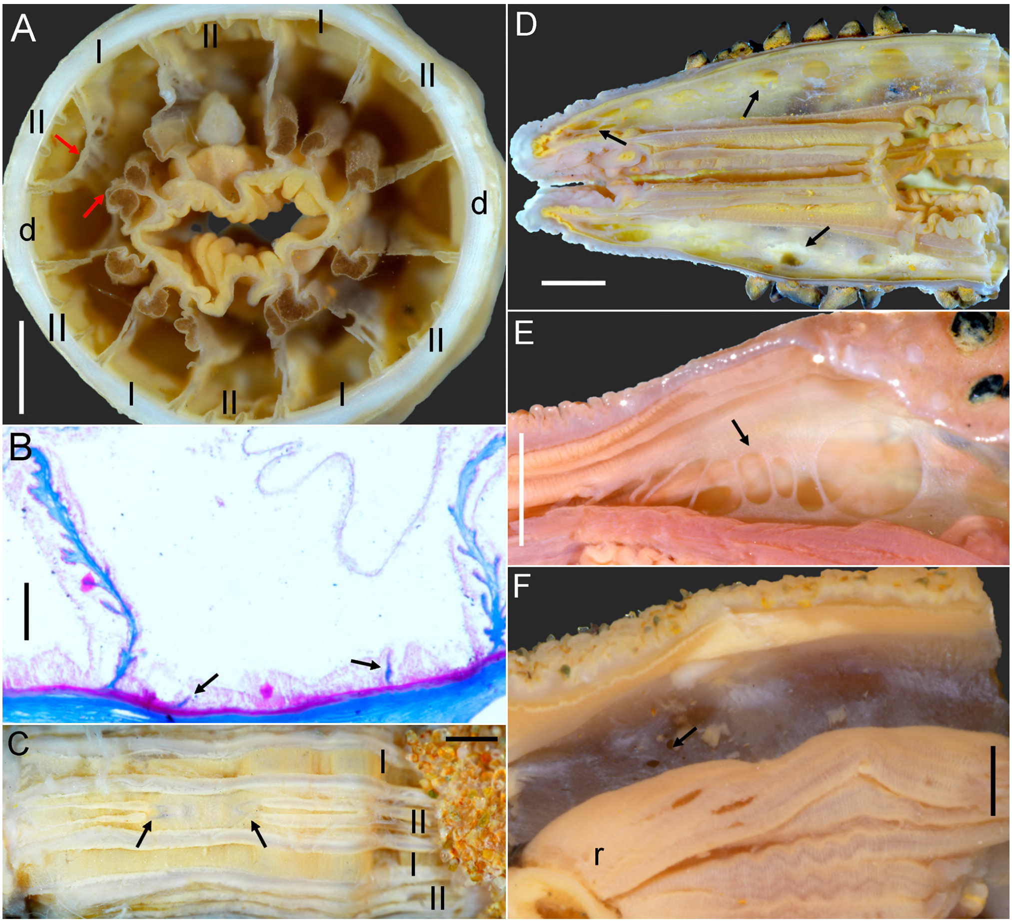


Fig. 13. Development of mesenteries and their aberrations, stomata of *Halcampa arctica* Carlgren, 1893. A — fusion of adjacent mesenteries (arrows) of first cycle from different pairs in specimen ZIN 12455b from the Barents Sea, transversal section; B — underdeveloped mesenteries of second cycle (arrows) in distal part of specimen ZIN 12488 from the Barents Sea, transversal section; C — intermittent course of the microcnemes (arrows) in the partially inverted specimen ZIN 12483 from the Barents Sea; D — rounded and approximately equal-sized stomata (arrows) arranged in an almost regular row along column wall in specimen ZIN 12460a from the East Siberian Sea; E — stomata (arrows) of different size and shape located in center of mesenterial plate in specimen ZIN 12847d from the East Siberian Sea; F — small and very few stomata (arrows) in specimen ZIN 13338 from the East Siberian Sea.

Abbreviations: d — pairs of directive mesenteries; r — longitudinal retractor muscle; I, II — cycles of mesenteries. Scale bar: A, C–F — 1 mm; B — 0.1 mm.

Рис. 13. Развитие мезентериев и их аберрации, стомы *Halcampa arctica* Carlgren, 1893. A — срастание прилежащих мезентериев (стрелки) первого цикла из разных пар у экземпляра ZIN 12455b из Баренцева моря, поперечный разрез; B — недоразвитые мезентерии второго цикла (стрелки) в дистальной части экземпляра ZIN 12488 из Баренцева моря, поперечный срез; C — прерванный ход микрокнем (стрелки) у частично вывернутого экземпляра ZIN 12483 из Баренцева моря; D — округлые и примерно равные по размеру стомы (стрелки), лежащие в почти правильном ряду вдоль стенки колюмна у экземпляра ZIN 12460a из Восточно-Сибирского моря; E — стомы (стрелки) разного размера и формы, расположенные по центру мезентериальной пластины у экземпляра ZIN 12847d из Восточно-Сибирского моря; F — мелкие и очень малочисленные стомы (стрелки) у экземпляра ZIN 13338 из Восточно-Сибирского моря.

Обозначения: d — пары направляющих мезентериев; r — продольный мускул-ретрактор; I, II — циклы мезентериев. Масштаб: A, C–F — 1 мм; B — 0,1 мм.

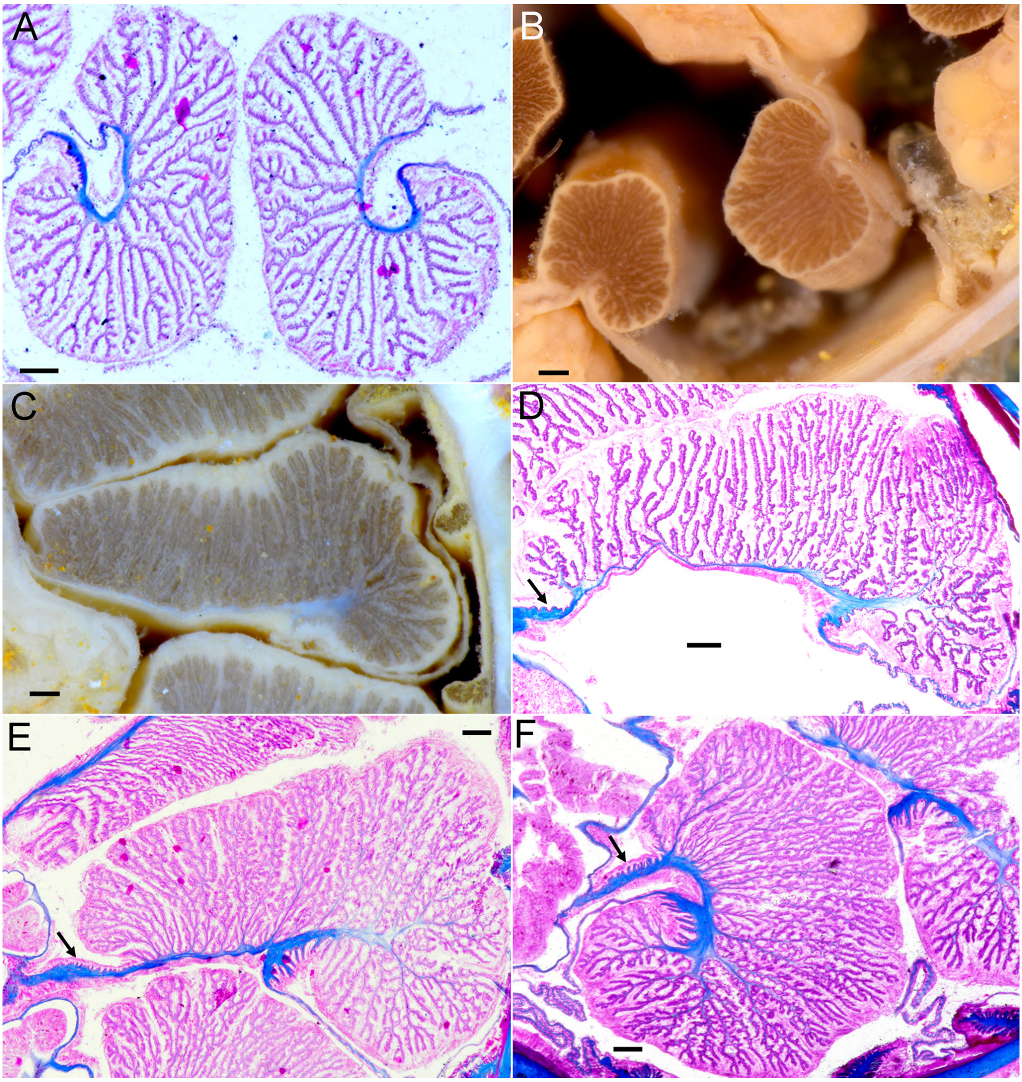
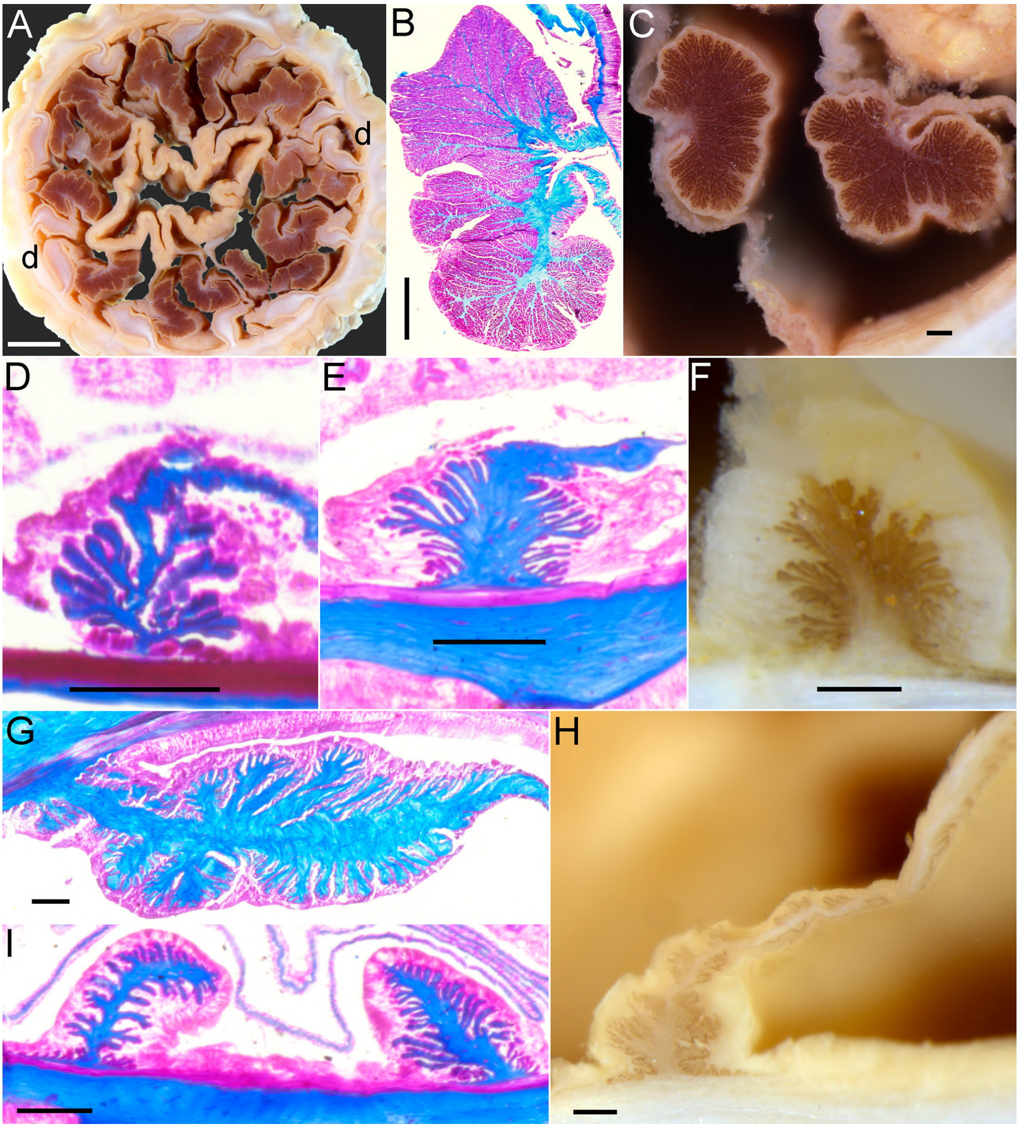


Fig. 14. Longitudinal retractor muscles of *Halcampa arctica* Carlgren, 1893. A — elongated restricted retractor muscles of specimen ZIN 12488 from the Barents Sea; B — elongated restricted retractor muscles of specimen ZIN 12307 from the Chukchi Sea; C — elongated restricted retractor muscle with a relatively short mesogloeal outer process in specimen ZIN 12472 from the Barents Sea; D — elongated restricted retractor muscle with a relatively short mesogloeal outer process of specimen ZIN 12465 from the Laptev Sea; E, F — restricted to circumscribed retractor muscle of specimen ZIN 12476 from the White Sea.

Abbreviations: arrows point to the short muscular processes between the retractor muscle and the pharynx. Scale bar: A–E — 0.1 mm.

Рис. 14. Продольные мускулы-ретракторы *Halcampa arctica* Carlgren, 1893. A — удлиненные ограниченные мускулы-ретракторы экземпляра ZIN 12488 из Баренцева моря; B — удлиненные ограниченные мускулы-ретракторы экземпляра ZIN 12307 из Чукотского моря; C — удлиненный ограниченный мускул-ретрактор с относительно коротким наружным мезоглеальным отростком экземпляра ZIN 12472 из Баренцева моря; D — удлиненный ограниченный мускул-ретрактор с относительно коротким наружным мезоглеальным отростком экземпляра ZIN 12465 из моря Лаптевых; E, F — ограниченно-циркумскриптический мускул-ретрактор экземпляра ZIN 12476 из Белого моря.

Обозначения: стрелки указывают на короткие мышечные отростки между мускулом-ретрактором и глоткой. Масштаб: A–E — 0,1 мм.



distal part of young specimens, the parietal muscles are very weakly developed or absent (compare Figs 8E and 13B). In the region of the scapulus, the parietal muscles may have a very thick mesogloea and very short folds resembling teeth (Fig. 15A). The parietal muscles of the microcnemes resemble only the elongated ones of the perfect mesenteries (Fig. 15I). We did not find oval or triangular forms, even if the parietal muscles of the perfect mesenteries have such shapes. Size varies from 50 µm in small specimens to 1200 µm in large adults. In some specimens, they may be slightly larger than the parietal muscles of the perfect mesenteries. Parietal muscle is considerably expanded in the column wall where they form short unbranched folds (Fig. 15H, I).

The species is dioecious.

Cnidom. The cnidom includes spirocysts, basitrichs, *p*-mastigophores. The sizes of nematocysts of different specimens vary slightly (see Table 1 and Fig. 16). In addition, the spirocysts in the ectoderm of the tentacles and scapulus in all studied specimens are always very numerous. The basitrichs of the tentacles are either common or numerous, and the basitrichs of the scapulus are either numerous or very numerous. *P*-mastigophores of the pharynx and filaments are usually numerous, basitrichs are either common or numerous.

HABITAT. Underwater observations of *Halcampa arctica* in the coastal waters of the Franz Josef Land archipelago by A.F. Pushkin (Heiss Island, 1982),

Fig. 15. Longitudinal retractor muscles and parietal muscles of *Halcampa arctica* Carlgren, 1893. A — very large retractor muscles of specimen ZIN 12458b from the Barents Sea; B — very large retractor muscle of specimen ZIN 12927g from the Barents Sea; C — retractor muscles of different structure in specimen ZIN 12459e from the Barents Sea; D — rounded parietal muscle of macrocnemes with few thickened branched processes in specimen ZIN 12465 from the Laptev Sea; E — rounded parietal muscle of macrocnemes with numerous thin and weakly branched processes and thick mesogloea of mesenterial plate in specimen ZIN 12476b from the White Sea; F — rounded parietal muscle of macrocnemes with numerous thin and highly branched processes of specimen ZIN 12485 from the East Siberian Sea; G — elongated parietal muscle of macrocnemes with numerous thick branched and unbranched processes and thick mesogloea of the mesenterial plate in specimen ZIN 12927g from the Barents Sea; H — parietal muscle of macrocnemes of the mixed type in specimen ZIN 12489 from the Chukchi Sea; I — elongated parietal muscles of microcnemes of specimen ZIN 12476 from the White Sea.

Abbreviations: d — pairs of directive mesenteries. Scale bar: A — 1 mm; B — 0.5 mm; C–I — 0.1 mm.

Рис. 15. Продольные мускулы-ретракторы и париетальные мускулы *Halcampa arctica* Carlgren, 1893. A — очень крупные мускулы-ретракторы экземпляра ZIN 12458b из Баренцева моря; B — очень крупный мускул-ретрактор экземпляра ZIN 12927g из Баренцева моря; C — мускулы-ретракторы разной структуры экземпляра ZIN 12459e из Баренцева моря; D — округлый париетальный мускул макрокнем с малочисленными утолщенными и разветвленными отростками экземпляра ZIN 12465 из моря Лаптевых; E — округлый париетальный мускул макрокнем с многочисленными тонкими и слабо разветвленными отростками и толстой мезоглеей мезентериальной пластины экземпляра ZIN 12476b из Белого моря; F — округлый париетальный мускул макрокнем с многочисленными тонкими и сильно разветвленными отростками экземпляра ZIN 12485 из Восточно-Сибирского моря; G — удлиненный париетальный мускул макрокнем с многочисленными толстыми разветвленными или нет отростками и толстой мезоглеей мезентериальной пластины экземпляра ZIN 12927g из Баренцева моря; H — париетальный мускул макрокнем смешанного типа экземпляра ZIN 12489 из Чукотского моря; I — удлиненные париетальные мускулы микрокнем экземпляра ZIN 12476 из Белого моря.

Обозначения: d — пары направляющих мезентериев. Масштаб: A — 1 мм; B — 0,5 мм; C–I — 0,1 мм.

Table 1. Size ranges (length × width, in microns) and distribution of cnidae of the specimen ZIN 12474 from the Greenland Sea, the last column includes the sizes of cnidae of other specimens. Letters in brackets correspond to letters in Fig. 16.

Таблица 1. Размеры (длина × ширина, в микронах) и распределение стрекательных капсул экземпляра ЗИН 12474 из Гренландского моря, последний столбец включает размеры стрекательных капсул других экземпляров. Буквы в скобках соответствуют буквам на рис. 16.

Body regions	**Cnidae**	**Size ranges**	**Size ranges**
Tentacles	(A) spirocysts (very numerous)	20–40 × 2–4	20–40 × 3–4
	(B) basitrichs (common)	14–16 × 2	14–17 × 2
Scapulus	(C) spirocysts (very numerous)	16–25 × 2–3	16–28 × 3–4
	(D) basitrichs (numerous)	12–15 × 2	12–16 × 2
Scapus and physa	(E) basitrichs (common)	12–13 × 2–3	13–15 × 2–3
Pharynx	(F) *p*-mastigophores (numerous)	27–38 × 4–6	27–42 × 4–6
	(G) basitrichs (common)	15–16 × 3	13–16 × 2–3
Filaments	(H) basitrichs (rare)	17 × 2	17–20 × 2–3
	(I) *p*-mastigophores (numerous)	25–34 × 5–7	25–36 × 5–7
	(J) *p*-mastigophores (numerous)	11–15 × 4–6	11–17 × 4–6

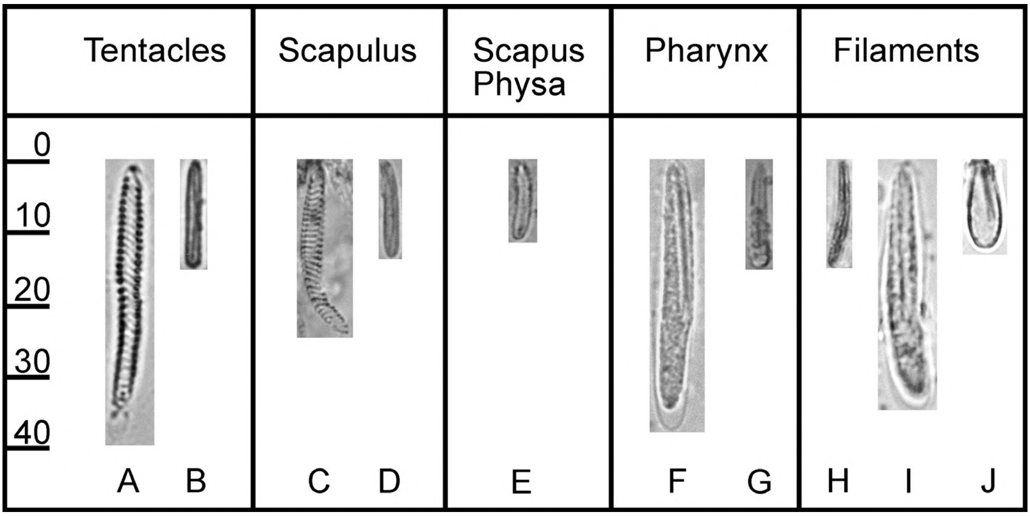


Fig. 16. *Halcampa arctica* Carlgren, 1893, specimen ZIN 12474 from the Greenland Sea. Distribution of cnidae (see Table 1 for size ranges).

Рис. 16. *Halcampa arctica* Carlgren, 1893, экземпляр ZIN 12474 из Гренландского моря. Распределение книд (размеры указаны в табл. 1).

S.D. Grebelnyi and O.V. Savinkin (Bliss Island, Luigi Island, Bell Island, and Wilton Island, 2013) showed that this species lives in large aggregations (see also Sanamyan *et al.*, 2016) often consisting of individuals of different ages. Specimens may be scattered or burrow into the sand in small groups (Fig. 17A, B). Interestingly, small, probably juvenile, individuals are positioned very close to a large adult specimen, sometimes almost in the same burrow (Fig. 17B–D, arrow). This may suggest a maternal individual with offspring, but the presence of brooding in *H. arctica* was not confirmed in the collected samples. The reproduction of *Halcampa arctica* is potentially similar to that of *H. duodecimcirrata*, which, according to Nyholm (1949), lacks the ability to disperse via pelagic larvae, and its offspring do not leave their birthplace. Underwater photos also reveal that the polyps of the studied species freely coexist with various invertebrates, namely with polychaetes (Fig. 17A), bivalves, gastropods (Fig. 17D), other species of Actiniaria (Fig. 18A), brittle stars (Fig. 18A), ceriantharians (Fig. 18B), etc., and also with fishes (Fig. 18A). Nevertheless, some of these animals serve as prey for *H. arctica*. Accordingly, the gastral cavity of one of the specimens contained chaetae of an annelid worm (Fig. 18C) belonging to the genus *Harmothoe* Kinberg, 1856.

DISTRIBUTION. Baffin Island (Carlgren, 1933; Ellis, Wilce, 1961), Greenland (Carlgren, 1921, 1928; 1933; our data), Iceland (Carlgren, 1921, 1933), Norwegian Sea (Carlgren, 1933; our data), Greenland Sea (Carlgren, 1921, 1933; our data), Barents Sea (Carlgren, 1893, 1921, 1933; Gravier, 1922; our data), Franz Josef Land (Carlgren, 1934; Sanamyan et al., 2016; our data), White Sea (our data), Kara Sea (Carlgren, 1921; our data), Laptev Sea (our data), East Siberian Sea (our data), Chukchi Sea (our data), Bering Strait (our data), Bering Sea (Carlgren, 1921; our data), Beaufort Sea (our data). Depth 2–802 m; temperature from −1.9° to +7°C, salinity 30.90–33.90‰ (Table S1, Fig. 1).

REMARKS. Our specimens agree well with the original description (Carlgren, 1893) both in external and internal features. Nevertheless, detailed study of numerous *Halcampa arctica* specimens underlines the wide variability of the morpho-anatomical characters. This variability does not seem to have geographical origins. Our specimens from all Arctic seas of Russia, as well as the Norwegian, Greenland and Beaufort Seas, did not reveal any relationship between character variability and habitat. Individuals even from the same station have different conditions of the same feature.

The variability of morpho-anatomical characteristics is mainly associated with serious deformation of the body during the fixation. This deformation occurs due to the extensible mesogloea and high contractility of muscle fibers (see Batham, Pantin, 1951). So, photographs of living specimens in the natural environment show that the tentacles of *Halcampa arctica* are quite long and thick, conical, with rounded tips and a smooth surface (Figs 17, 18A, B). In fixed specimens, their shape and surface structure changes significantly because strong contraction of the muscle layer leads to the formation of a folded structure of both itself and the wall as a whole (see Batham, Pantin, 1951). The holes at the tips of the tentacles noted by

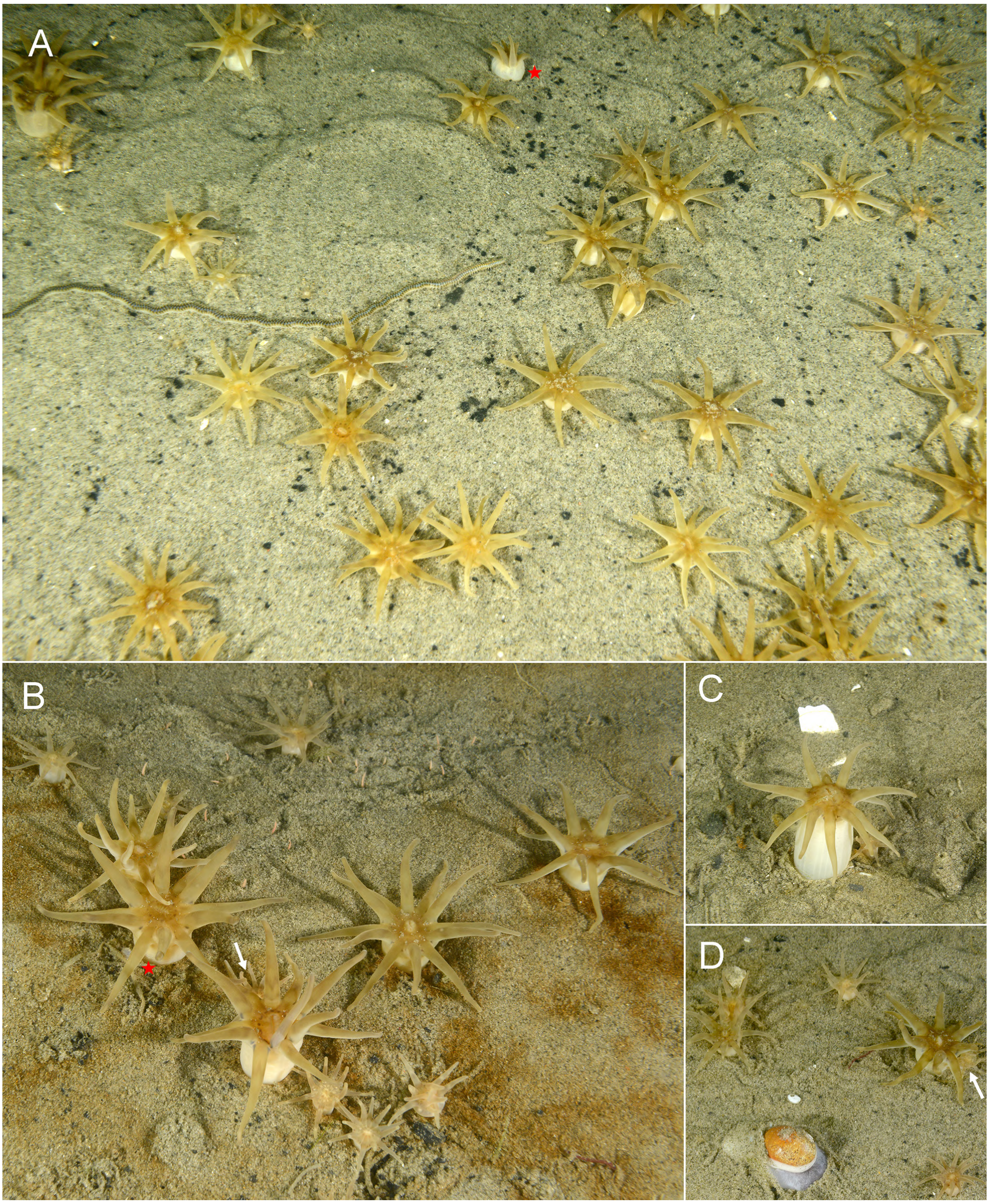


Fig. 17. *Halcampa arctica* Carlgren, 1893 in coastal waters of Aldger Island, Franz Josef Land (photographs: O.V Savinkin). A — a large group of individuals of different colors; annelids among them; B–D — adults with juveniles. Abbreviations: red stars show some specimens with clearly visible scapulus structure, white arrows indicate very closely spaced juveniles and adults.

Рис. 17. *Halcampa arctica* Carlgren, 1893 в прибрежных водах острова Алджер, Земля Франца-Иосифа (фотографии О.В. Савинкина). A — большая группа особей разной окраски; среди них многощетинковый червь; B–D — взрослые особи с молодью. Обозначения: красные звездочки указывают на некоторые экземпляры с хорошо заметной структурой скапулюса, белые стрелки указывают на очень близко расположенные ювенильные и взрослые особи.

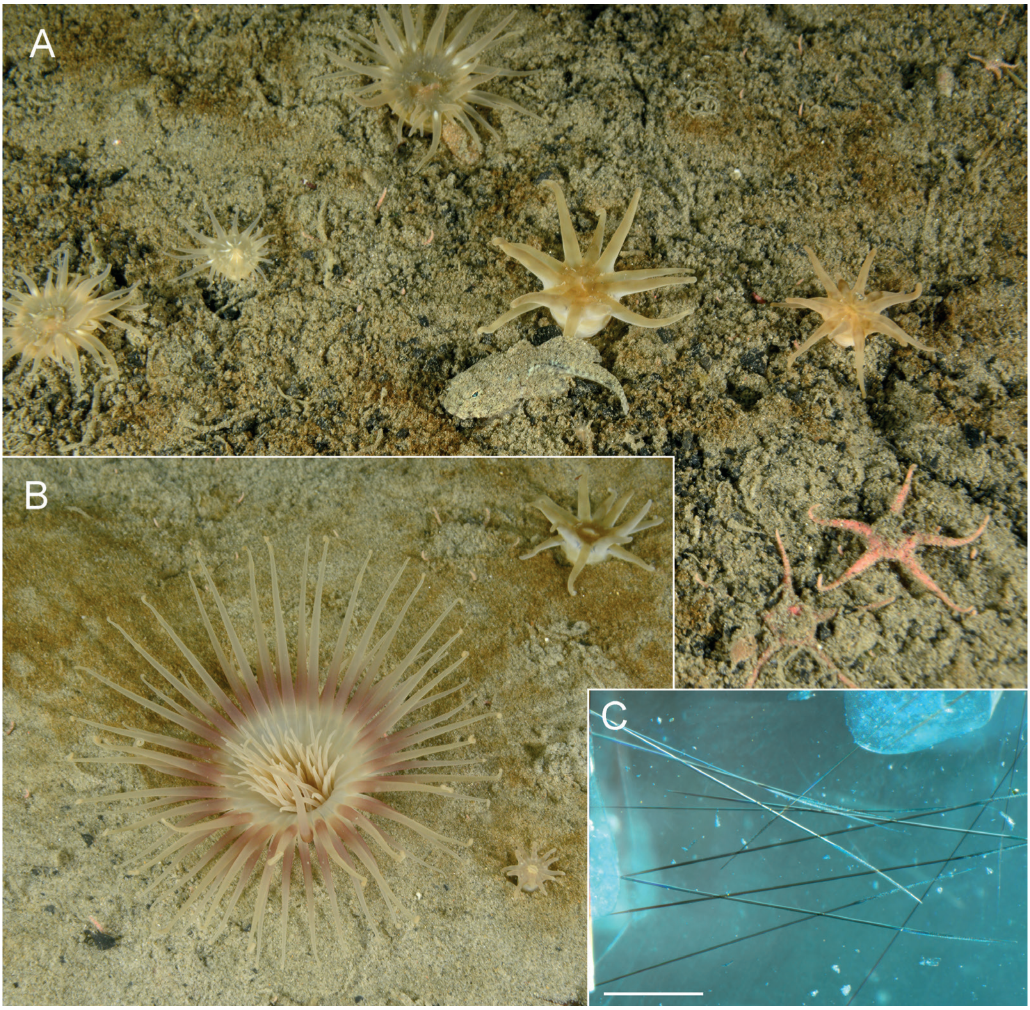


Fig. 18. Coexistence of *Halcampa arctica* Carlgren, 1893 with other benthic inhabitants. A — *Halcampa arctica* with other sea anemones, fish, and brittle stars (Aldger Island, Franz Josef Land, photograph: O.V Savinkin); B — *Halcampa arctica* with ceriantharians (Aldger Island, Franz Josef Land, photograph: O.V Savinkin); C — chaetae of annelid worm belonging to the genus *Harmothoe* Kinberg, 1856, from the gastric cavity of specimen ZIN 12927, Bell Island, Franz Josef Land. Scale bar: 1 mm.

Рис. 18. Сосуществование *Halcampa arctica* Carlgren, 1893 с другими обитателями бентоса. A — *Halcampa arctica* с другими актиниями, рыбой и офиурами (остров Алджер, Земля Франца-Иосифа, фотография О.В. Савинкина); B — *Halcampa arctica* с цериантусом (остров Алджер, Земля Франца-Иосифа, фотография О.В. Савинкина); C — щетинки многощетинкового червя, принадлежащего роду *Harmothoe* Kinberg, 1856, из гастральной полости экземпляра ZIN 12927, остров Белл, Земля Франца Иосифа. Масштаб: 1 мм.

Carlgren (1893) are also the result of weak or strong retractions or severe damage to the tentacles during fixation, but not natural ruptures of the tentacle wall. The different structure of the scapulus wall is also caused by contraction. Based again on underwater photographs, the scapulus of *H. arctica* has a rather thin wall through which mesentery insertions are clearly visible. The surface of the scapulus is covered with small ring wrinkles (Fig. 17A–C, red stars). The widely variable form of the tenaculi is probably also the result of contraction, so their key feature is the modified ectoderm secreting the cuticle. The form of mesogloeal thickening of the tenaculi is secondary.

Variations in the structure of the mesenterial musculature can also be explained by the contracted or relaxed state of the animals. Batham and Pantin

(1951) already noted the need to be careful when using muscle folding as a systematic feature. Nevertheless, the three types of retractor muscles discovered, in our opinion, are largely explained by the age of the specimens and their individual development rather than by different degrees of contraction. Our assumption may be supported by the report of Batham and Pantin (1951) that the strong folding of the retractors is quite constant, therefore it is similar in both the extended and contracted states of the individual. Under prolonged favorable conditions during ontogenesis retractor development from stage one to stage three probably occur. This assumption is supported by the presence of a small mesogloeal thickening on the outer edge of the retractor of juveniles, characterized by stage I retractors (Fig. 8E, arrow). This mesogloeal thickening eventually develops into a well-defined mesogloeal outgrowth of the second type. The development of large mesogloeal processes extending from the main plate of the mesentery probably occurs after the outer mesogloeal process is formed; none of the specimens we examined with strong mesogloeal processes of the main plate lacked an external outgrowth.

As noted above, most specimens have numerous tenaculi. It is not entirely clear why some individuals, on the contrary, have rather rare tenaculi. We found no relationship with soil type, depth or temperature. Interestingly, two specimens from the same station had different types of tenaculi arrangement. Perhaps the different number of tenaculi in different specimens are due to phenotypic plasticity within *Halcampa arctica* and/or individual development. Together they can also be the cause of an interesting phenomenon in that mesenteries of many of *Halcampa arctica* specimens are perforated by very numerous and large stomata, however, the stomata of other individuals are rare and small or absent. In *Exocoelactis actinostoloides* (Wassilieff, 1908) and *Sagartiogeton californicus* (Carlgren, 1940), for example, the center of some complete mesenteries is perforated by a stoma (Arellano, Fautin, 2001; Eash-Loucks, Fautin, 2012). According to Arellano, Fautin (2001), this "central stoma" is apparently an atypically positioned oral stoma, but according to Sanamyan *et al*. (2021: 398), "this is atypically positioned marginal (not oral) stoma".

The discovery of the variability of retractor and parietal muscle structure necessitates discussion on the taxonomic position of *Halcampa vegae*. The variability of these mesenterial muscles suggests that Carlgren's (1921) *Halcampa vegae* is conspecific with *H. arctica*. Carlgren (1921: 123–124) points out that the specimen he studied corresponds well in a number of characters to the genus *Halcampa,* the anatomy of the new species recalls that of *H. arctica* in many details. However, unlike the latter, *H. vegae* has very highly branched retractors (see Carlgren, 1921: 123, textfig. 146) and the parietal muscles of the perfect mesenteries are not elongated, more branched and transversally spread (see Carlgren, 1921: 123, textfig. 147); the muscles of the imperfect mesenteries (see Carlgren, 1921: 123, textfig. 148) are also more ramificated. According to Carlgren (1921: 124), this may reflect a different contraction of the muscles, so he was uncertain whether the specimens studied belong to two different species. Some of our specimens exhibited retractors and parietal muscles of a similar structure (compare Fig. 15A, B, F and textfigs 146, 147 in Carlgren, 1921). Nonetheless, our study underlines the instability of combination described by Carlgren. We found specimens whose perfect mesenteries were equipped with both very highly branched retractors (Fig. 15B) and elongated parietal muscles (Fig. 15G). In other specimens, in contrast, perfect mesenteries had retractors with structure typical for *H. arctica* (Fig. 14E, F), and the parietal muscles were branched, not elongated and transversally spread (Fig. 15E). Unfortunately, Carlgren (1921) did not provide a detailed description of other characters of *Halcampa vegae* due to the unsatisfactory condition of the single specimen, and the holotype was not available to us for research: we have only two photographs published earlier by Daphne Gail Fautin on a currently inaccessible website "Hexacorallians of the World". However, in addition to the similar structure of the mesenterial musculature, the general structure (three divisions of the column, 12 tentacles, 2 mesenterial cycles, tenaculi) and size of the nematocysts (basitrichs) of the scapus, scapulus and tentacles (about 13 × 1.5 μ) indicated by Carlgren (1921) also suggests the affinity of these two species. Additionally, Carlgren's specimen was collected in the Bering Sea (64˚52′N 172˚3′W) at a depth of about 33 m, and several of our specimens were collected nearby at a depth of 37.5 m. Thus, among the currently known characters of *H. vegae*, there is not a single one that supports the independence of this species. Therefore, in this paper we consider *H. vegae* to be a synonym of *H. arctica*.

Currently, taxonomists still face difficulties in identifying sea anemones. On the one hand, strong contraction of the sea anemones body during collection leads to the loss of some characters and prevents the indisputable division of the remaining features into taxonomically significant and those resulting from fixation. On the other hand, there are a large number of old poorly illustrated, brief, or excessively verbose, but not informative original descriptions, often based on the study of a single specimen (e.g, the verbose original description of *Halcampoides abyssorum* Danielssen, 1890 or very short original description of *Peachia carnea* Hutton, 1880). However, these problems have solutions. The native appearance of sea anemones, as well as their external significant features, which are lost during fixation, are successfully remained due to photographing animals in their natural environment or aquarium (Barragán *et al*., 2019; Sanamyan *et al*., 2019; Vassallo-Avalos *et al*., 2022; Yap *et al*., 2023 etc.). Moreover, our investigation of *Halcampa arctica* showed the need to study a large number of individuals, especially in the case of fixed specimens kept in museum collections. Such a study allows to trace changes in the state of morpho-anatomical features. Studying many specimens simplifies the detection of taxonomically significant characters that in turn will avoid dispensable descriptions of new species. For example, we found that in *H. arctica* the retractor muscles vary from restricted to circumscribed and the parietal muscles range from rounded to elongated. Therefore, we consider that *H. vegae* was described by Carlgren (1921) on the base of one of the variants of the state of these characters; it is only an adult sexually mature specimen of *H. arctica*, but not a separate species. In addition, the study of large material revealed a new feature of *H. arctica* – numerous stomata located in the center of the mesenterial plate. On the other hand, the physa apertures, located in two cycles around the central pore, are not a diagnostic character of *H. arctica*, as noted by Carlgren (1893).

Variability of morpho-anatomical characters has been noted in many species (González-Muñoz *et al*., 2015; Yap *et al*., 2020 etc.). For example, studies of *Lebrunia coralligens* (Wilson, 1890) showed the presence of two morphotypes in this species (Crowther, 2013; González-Muñoz *et al*., 2016; González-Muñoz *et al*., 2017). They differ in the structure of the pseudotentacles and the size of their cnidae, as well as variations in the size of the cnidae in other tissues. However, other mophro-anatomical features of the two morphotypes are similar. Comparison of *L. coralligens* with its congeners *L. neglecta* showed significantly greater differences between *L. neglecta* and the two morphotypes of *L. coralligens* than between the latter (González-Muñoz *et al*., 2017). The researchers note that these morphotypes are due to broad phenotypic plasticity within *L. coralligens*, which might be related to specific adaptations to the surrounding environment or to an early speciation process. Now there are many examples where morphological variations in species were originally described as separate species (Fautin, 1984; Excoffon *et al*., 1997; Arellano, Fautin, 2001; González-Muñoz *et al*., 2015; Spano, Häussermann, 2017 etc.).

Supplementary data. The following materials are available online.

Table S1. List of all examined and cataloged specimens of this study, also including the region, collection locality and coordinates, date of collection, and physical characteristics of stations (depth, soil, salinity, temperature).

Compliance with ethical standards

Conflicts of interest: The authors declare that they have no conflicts of interest.

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