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RESEARCH ARTICLE

A remarkable pogonophoran from a desalted shallow near the mouth of the Yenisey River in the Kara Sea, with the description of a new species of the genus *Galathealinum* (Annelida: Pogonophora: Frenulata)

Удивительная находка погонофоры на распресненном мелководье около устья Енисея в Карском море, с описанием нового вида рода *Galathealinum* (Annelida: Pogonophora: Frenulata)

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Abstract. A new species of Pogonophora obtained from one station at a depth of 25 m from near the Dikson Island in the Kara Sea is described. *Galathealinum karaense* **sp. nov.** is one of the largest pogonophorans, the first known representative of the rare genus *Galathealinum* Kirkegaard, 1956 in the Eurasian part of the Arctic Ocean and a highly unusual finding for the desalted shallow of the Yenisey Gulf. Several characters occurring in the new species are rare or unique among the congeners: under-developed, hardly discernible frills on the tube segments, extremely thin felted fibres in the external layer of the tube, and very faintly separated papillae in the anterior part of the trunk. Morphological characters useful in distinguishing species within the genus *Galathealinum* are defined and summarised in a table. Diagnosis of the genus *Galathealinum* is emended and supplemented by new characters. Additionally, three taxonomic keys are provided to the species of *Galathealinum* and to the known species of the Arctic pogonophorans using either animals or their empty tubes only, with the brief zoogeographical information on each Arctic species.

Резюме. Дано описание нового вида погонофор, найденного на одной станции на глубине 25 м близ о. Диксон в Карском море. *Galathealinum karaense* **sp. nov.** – первый представитель этого редкого рода в евроазиатской части Северного Ледовитого океана и крайне необычная для распресненного мелководья Енисейского залива находка одного из крупнейших видов погонофор. Новый вид отличается от других видов рода рядом необычных или даже уникальных морфологических признаков, в частности, неразвитыми, едва заметными воротничками на сегментах трубки, исключительно тонкими волокнами в наружном войлокообразном слое трубки и крайне слабо обособленными папиллами в передней части туловища. Диагностические признаки всех видов рода *Galathealinum* Kirkegaard, 1956 подвергнуты сравнительному анализу и объединены в таблице. Изменен и дополнен новыми признаками диагноз рода *Galathealinum*. Кроме того, представлены три определительных ключа для видов рода *Galathealinum*, а также для всех известных в Арктике видов погонофор, включая определитель по пустым трубкам, с краткой зоогеографической информацией по каждому арктическому виду.

Key words: morphology, taxonomy, Yenisey Gulf, Arctic Ocean, Siboglinidae, new species

Ключевые слова: морфология, таксономия, Енисейский залив, Северный Ледовитый океан, Siboglinidae, новый вид

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Introduction

The collection gathered during the expedition of the Russian Research Vessel "Akademik Mstislav Keldysh" in the Arctic Ocean in 2011 contained the second pogonophoran specimen to be reported from the Kara Sea. A few fragments of the tube and one incomplete worm were obtained from a desalted shallow at 25 m depth near the mouth of the Yenisey River off western Dikson Island. In the present paper, the specimen is described as *Galathealinum karaense* **sp. nov.**, a new species of the frenulate pogonophorans. Only four species of the genus *Galathealinum* Kirkegaard, 1956 were hitherto known, and the last paper on the genus was published more than half a century ago, when Adegoke (1967) described *G. mexicanum* Adegoke, 1967 from the Gulf of Tehuantepec off the Pacific Mexican coast. The other three species are *G. bruuni* Kirkegaard, 1956 from the Celebes Sea in the Indonesian archipelago, *G. brachiosum* Ivanov, 1961 from the northeastern Pacific off Oregon and Canada, and *G. arcticum* Southward, 1962 from the Beaufort Sea in the Canadian Arctic (Kirkegaard, 1956; Ivanov, 1961; Southward, 1962). Among these species only *G. arcticum* was found living in shallow and probably freshened water, 36 m depth, in the Mackenzie River Delta region, while three other species are known from deeper ocean waters at the depths ranging from 1233 to 5110 m. *Galathealinum arcticum* was the fourth extremely shallow-water record of Pogonophora, the first three being the findings of *Oligobrachia mashikoi* Imajima, 1973 in the Tsukumo Bay (the Japan Sea, 20 m depth), *Siboglinum* (*Nereilinoides*) *caulleryi* Ivanov, 1957 in the Sakhalin Gulf (the Sea of Okhotsk, 22 m depth), and one undescribed species in the Yenisey Gulf (the Kara Sea, 28 m depth) (Ivanov, 1957; Southward, 1962; Kubota et al., 2007; Rimskaya-Korsakova et al., 2020).

Ten species of Pogonophora were until now found in the Arctic Ocean, including nine frenulates: *Polybrachia gorbunovi* (Ivanov, 1949); *Siboglinum* (*Ekmanifilum*) *ekmani* Jägersten, 1956; *Siboglinum* (*Siboglinum*) *norvegicum* Ivanov, 1960; *S.* (*S.*) *hyperboreum* Ivanov, 1960; *Nereilinum murmanicum* Ivanov, 1961; *N. squamosum* Smirnov, 1999; *Galathealinum arcticum*; *Polarsternium rugellosum* Smirnov, 1999; *Oligobrachia haakonmosbiensis* Smirnov, 2000, and one moniliferan sclerolinid *Archeolinum contortum* (Smirnov, 2000) (Ivanov, 1963; Smirnov, 1999, 2000a, 2011, 2014a; for taxonomic revisions see Smirnov, 2008a, 2014b). Other species will probably be discovered there in the future. Two species from the Northern Atlantic are likely to occur in the European Arctic: *Oligobrachia webbi* Brattegard, 1966 known from near Tromsø in northern Norway (69°57′N 18°34′E), and *Siboglinum* (*Ekmanifilum*) *brevicephalum* Flügel, 1990 known from 67°46′N 06°01′E in the Norwegian Sea (Brattegard, 1966; Flügel, 1990; Smirnov, 2000a, 2014a). In addition, the Bering Sea is rich in pogonophoran species (Ivanov, 1963), some of which might occur north of the Bering Strait, in the American, Canadian or Russian Asian Arctic.

The first member of the pogonophoran clade to be recorded from the Russian Asian Arctic was collected in 1938 by the Soviet arctic expedition onboard the icebreaker "Sadko" in the Laptev Sea at a depth of about 3700 m in the Sadko Trench. One badly preserved incomplete specimen with a few tube fragments was described as a new species of the genus *Lamellisabella* Ushakov, 1933, *L. gorbunovi*, later transferred to the genus *Polybrachia* Ivanov, 1952 (Ivanov, 1949, 1957). This was the third representative of Pogonophora, that became known to science. Subsequently, all Arctic Asian findings of pogonophorans were confined to the Laptev Sea. Two new species, *Polarsternium rugellosum* and *Nereilinum squamosum* were described from there in 1999, and *Siboglinum* (*Siboglinum*) *hyperboreum*, previously known from the Greenland Sea, was also found in this region

(Ivanov, 1963; Smirnov, 1999). Then in the Laptev Sea, two other European species were found, *Archeolinum contortum* and *Oligobrachia haakonmosbiensis*, described from the Norwegian Haakon Mosby mud volcano (Smirnov, 2000a, 2011, 2014a). The former species widely known as *Sclerolinum contortum* is now proved to be a bipolar, possibly cosmopolitan one (Georgieva et al., 2015); and the latter species was shown by some recent molecular evidence to be possibly replaced in the Laptev Sea by a cryptic one (Sen et al., 2018). *Galathealinum karaense* **sp. nov.** is the first representative of the genus *Galathealinum* in the Eurasian Arctic and the second pogonophoran found in the Kara Sea. Recently, one specimen of a probably new genus and new species of the frenulate pogonophorans was found in approximately the same area, in the southern part of the Kara Sea (Rimskaya-Korsakova et al., 2020).

The present paper provides additional evidence concerning the taxonomic position of the genus *Galathealinum* and further elucidates its diagnostic characters. Three taxonomic keys are also provided to the species of *Galathealinum* and to the known species of the Arctic pogonophorans using either animals or their empty tubes only, with the brief zoogeographical information on each Arctic species.

Material and metods

The single specimen of the new species described below was obtained from the depth of 25 m during the 59th cruise of the Russian Research Vessel Akademik Mstislav Keldysh (2011) in the Kara Sea. Five samples were taken by an Ocean 0.1 grab, but only one contained a pogonophoran. The sediment was a pellite silt. Water temperature near the bottom was −0.62°C, salinity 31.7‰. The material was fixed in 4% buffered formalin and then transferred to 70% ethanol. The specimens were studied using both light microscopy and scanning electron microscopy (SEM). SEM micrographs were taken by a Quanta 250 after the specimens had been critical-point dried and coated with platinum. The observations, measurements and drawings of the specimen and the tube fragments were carried out by means of stereoscopic and standard light microscopes with drawing attachments. The type material is deposited at the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg (catalogue number ZIN No. HN77).

In the present paper the following designations for morphometric parameters are used: D_f, maximum diameter of the forepart (usually near the bridle); L_f, length of the forepart; L_f/D_f, forepart length to diameter ratio; L_{cl}, length of the cephalic lobe; L_{cl}/D_f, ratio of cephalic lobe length to forepart diameter; L_{tn}/D_f, ratio of tentacle(s) length to forepart diameter; Q_{tn}, number of tentacles; D_{tb}, tube diameter at the anterior end; L_s, length of tube segments; L_s/D_{tb}, ratio of tube segment length to tube diameter; L_r/D_{tb}, ratio of tube ring length to tube diameter; D_{fn}, diameter of tube segment funnels; D_{fn}/D_{tb}, ratio of tube funnel diameter to tube diameter. Qualitative adjectives used in the descriptions below reflect relative, not absolute, dimensions of various body parts.

The images in Fig. 5 illustrate not the new species, but only some morphological characters mentioned in this paper. For explanations of all features not illustrated here, see Ivanov (1963) and Smirnov (2000b, 2008a).

Results

Classification. The inclusion of the pogonophorans in the phylum Annelida now does not raise any doubts and is supported by abundant molecular and morphological evidence (e.g., McHugh, 1997; Rouse & Fauchald, 1997; Halanych et al., 2001; Halanych, 2005; Weigert et al., 2014; Andrade et al., 2015; Struck et al., 2015; Weigert & Bleidorn, 2016). However, reducing the whole taxonomic diversity of Pogonophora to one annelid family Siboglinidae Caullery, 1914 proposed by McHugh (1997) and Rouse (2001) appears impractical in our view. Pogonophora has complex multilevel taxonomic structure with at least two (but more likely four) main subsidiary clades, Frenulata and Vestimentifera, and these can still be considered to contain several other subclades of different taxonomic value each (Southward et al., 2005; Smirnov, 2008b). In addition, Rousset et al. (2007), Zrzavý et al. (2009), Kvist & Siddall (2013) and Weigert et al. (2014) showed that the rooting of the Siboglinidae clade within Annelida is uncertain and their sister-group relationships with the other annelids cannot be unambiguously established. The new system of Vestimentifera recently proposed by Karaseva et al. (2016) requires introduction of fractional taxa (infrafamilies), but it is hardly applicable for the frenulates with their great diversity and complex taxonomic hierarchy. It would be necessary to establish even more uncommon and fractional taxa to give the phylogenetic definition for the frenulate orders, in particular. Thus, it is currently inadvisable to renounce the multilevel taxonomic system hitherto existing within Pogonophora, and therefore the older classification and family names are used here (Ivanov, 1963; Southward et al., 2002, 2005, 2011; note comments by Bartolomaeus et al., 2005).

Family **Polybrachiidae** Ivanov, 1952

Genus ***Galathealinum*** Kirkegaard, 1956

Diagnosis. Very large polybrachiids (D_f 1.0–1.5 mm, in average ~1.42 mm). Tentacles numerous (Q_{tn} ~78–268, in average ~162), very short (L_{tn}/D_f ~15), arranged in multirowed horseshoe. Segmental groove on forepart. Cephalic lobe comparatively small (L_{cl}/D_f ~0.95). Bridle keels homogenous. Wing-like epidermal folds on forepart. Papillae in anterior (metameric) part of trunk usually well-developed, with one or several cuticular plaques and numerous multicellular glands in each papilla. Nonmetameric papillae tranversely elongated, arranged alternately on right and left sides of mid-dorsal groove. Spermatophores wide, leaf-like, with one asymmetrical wing. Tube rigid, opaque, segmented and sometimes ringed. Segments with funnel-like rigid frills. Anterior end of tube rigid, funnel-like. Funnel simple.

The genus comprises five species: *G. bruuni*, *G. brachiosum*, *G. arcticum*, *G. mexicanum*, and *G. karaense*. Type species: *G. bruuni*.

Galathealinum karaense **sp. nov.**
(Figs 1–4)

Holotype. Female (ZIN No. HN77), **Arctic Ocean**, *Kara Sea*, Yenisey Gulf, near mouth of Yenisey River off western Dikson I., 25 m depth, grab, station 5019, 73°10′13″N 79°51′48″E; 20 Sept. 2011; R/V Akademik Mstislav Keldysh (coll. A.A. Vedenin).

Description. Tube represented by 12 fragments, of which longest one measures 40 mm, and estimated overall length of incomplete tube about 200 mm. Diameter near tube front end reaches 2.25 mm, diminishing backwards to 1.75–2.1 mm. Tube red-brown in colour, opaque and very stiff. Fragments from anterior part of tube segmented and ringed, segments furnished with narrow and barely noticeable frills (D_{fn} 2.4–2.5 mm, D_{fn}/D_{tb} 1.1–1.2) (Fig. 2e, 2f). These frills consist of felted fibres, which also comprise external layer in very thick and multilayered tube wall (Fig. 4a). In general, fibrous layer very thin and weekly developed, with individual fibres 0.05–0.08 mm in diameter, being only visible under scanning electron microscope, and no aggregations of these detected (Fig. 4b). Segments vary in length from 1 to 2 mm (L_s/D_{tb} 0.5–0.9), each with two–four rings, except for a few anterior-most segments having numerous coarse fibres or wrinkles. Rings slightly irregular, with anastomotic uneven edges, and very narrow, varying in length from 0.25 to 0.95 mm (L_r/D_{tb} 0.14–0.45), usually 0.35–0.45 mm (L_r/D_{tb} 0.2–0.22) (Fig. 2f).

Tentacular crown up to 15 mm long, consists of numerous (about 150) free tentacles joined to forepart in many horseshoe-shaped rows with opening on dorsal side (Figs 1, 2a). Majority of tentacles slightly shorter than several tentacles on ventral side, possibly due to some damage during collection. Each tentacle with double or triple dense row of pinnules along one side flanked by two bands of long cilia, but no glandular epidermis (Fig. 3d, 3e). Pinnules as short (8–10 mm) buds near the head, becoming ten times longer distally, up to 75–100 mm (Fig. 3e, 3f). Cephalic lobe long (1.75 mm, L_{cl}/D_f 1.25) shaped like narrow, slightly flattened triangle with separated apex, with obscure whitish glandular patches on ventral side (Fig. 2c). Four distinct grooves on forepart; longitudinal one runs dorsally from behind tentacles to bridle, and three transverse grooves, one curved groove demarcates cephalic lobe on ventral side near bases of tentacles, another one near boundary of trunk, and last groove encircles body in front of bridle (Figs 1, 2a, 2c). Region between bridle and bases of tentacles occupied by pair of low epidermal folds, most prominent on dorsal and lateral sides (Figs 1, 2a, 2c). These folds with some indistinct patches of light glandular epidermis. Bridle with thin, greyish-brown keels close together both dorsally and ventrally, but not joined. D_f 1.35–1.45 mm, L_f 7.5 mm, L_f/D_f 5.2–5.5. Papillae in anterior (so-called

Fig. 1. *Galathealinum karaense* **sp. nov.**, tentacular crown, forepart and anterior part of trunk, lateral view. Photo taken immediately after sampling. Scale bar: 2 mm.

metameric) part of trunk actually absent, instead of them strong epidermal-muscular ridges, slightly divided into low irregular papillae-like areas containing numerous light multicellular glands (Figs 1, 2a, 2b). Ridges separated by wide and deep dorsal furrow. Tiny (20–29 µm) greyish-brown cuticular plaques with thickened anterior rims arranged in barely discernible line along dorsal surface of each ridge, starting some distance from trunk-forepart boundary (Figs 2a, 3c). Some of largest papillae-like areas with several (two or three) cuticular plaques, but most areas with only one plaque each, and cushions (pulvilli) absent (Fig. 2b). Wide ciliated band on ventral side of anterior part of trunk arising little behind trunk-forepart boundary and extending backwards all along ridges, for about 40 mm (Fig. 2c). In posterior part of this region, dorsal furrow flattens out gradually and papillae in ridges become smaller, but more pronounced and less scattered, with still numerous multicellular glands in each (Fig. 2d). Posterior (nonmetameric) region of trunk with very regular arrangement of papillae. These papillae look like transversely elongated ridges lying alternately on either side of body at intervals of 0.5–2.0 mm (Fig. 2d). Most ridges lie in pairs, distance between them in pairs much smaller than between pairs. Each papilla with a few multicellular glands and 6–16 cuticular plaques 25–29 µm across (Fig. 3a, 3b). Length of nonmetameric region exceeds 100 mm. Thus, total body fragment not less than 163 mm long, but since all other body parts, including zone of enlarged papillae, girdles, postannular region and opisthosoma missing, intact animal should be at least twice as long. Gametes found neither in tube nor in sexual ducts.

Comparison. *Galathealinum karaense* **sp. nov.** is a typical representative of the genus *Galathealinum*, all members of which are distinguished by four peculiar characters, unknown in the other frenulate pogonophorans: the alternative arrangement of papillae in the nonmetameric part of the trunk, wing-like epidermal folds on the forepart, the felt-like fibrous external layer of the tube, and asymmetrical spermatophores with a single wing. The latter feature is known in only one species, *G. arcticum*, but there is no reason to suppose that the congeners may have a different structure of spermatophores (see below). Felted fibres are

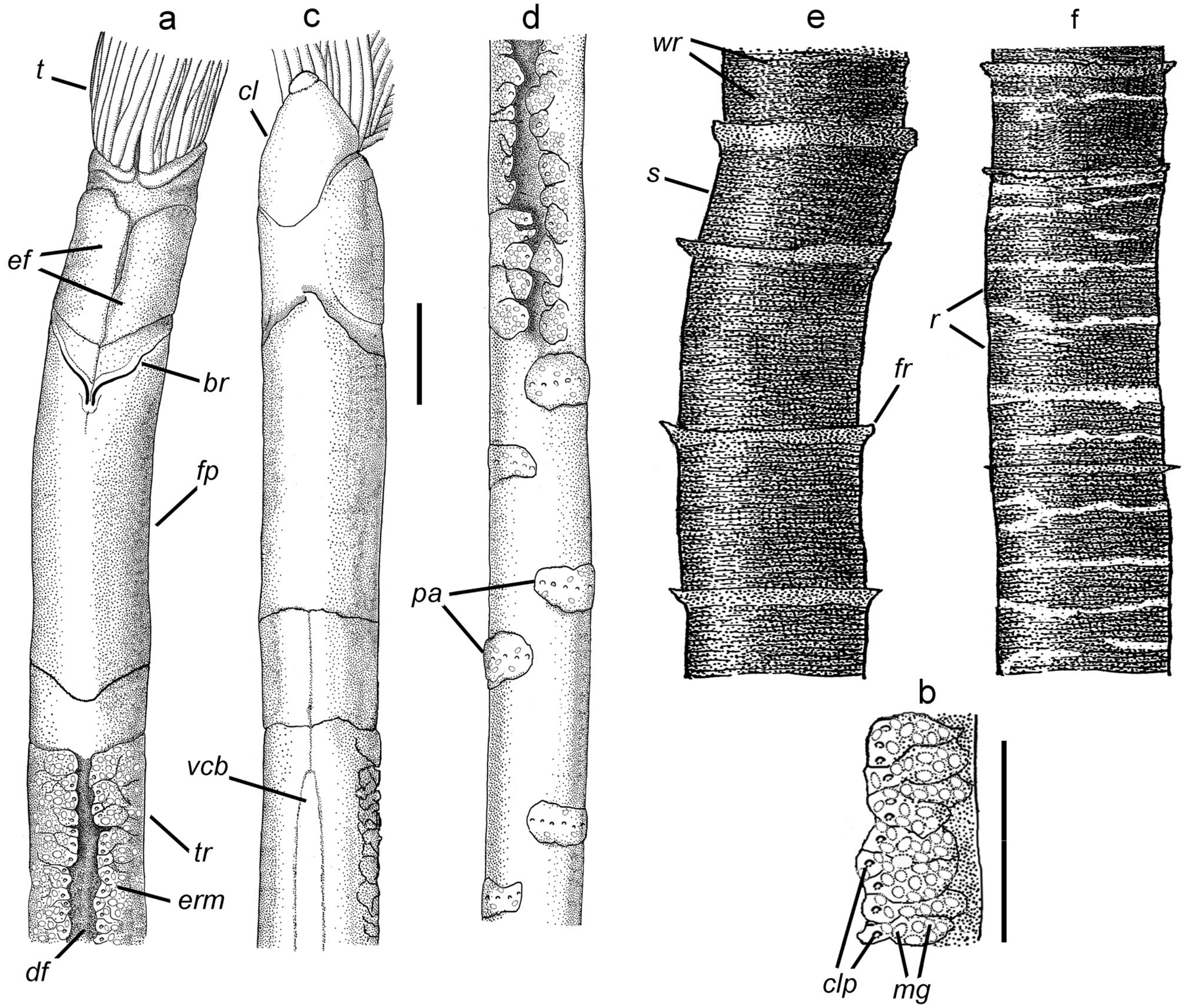


Fig. 2. *Galathealinum karaense* **sp. nov.** **a**, forepart and anterior part of trunk, dorsal view; **b**, enlarged part of trunk dorsal ridge; **c**, forepart and anterior trunk, ventral view; **d**, posterior part of trunk metameric region and beginning of nonmetameric region, dorsal view; **e**, tube, anterior part with segments; **f**, tube, middle part with segments and rings. *br* – bridle; *cl* – cephalic lobe; *cpl* – cuticular plaques; *df* – dorsal furrow; *ef* – epidermal folds; *emr* – epidermal-muscular ridge; *fp* – forepart; *fr* – frill; *mg* – multicellular glands; *pa* – papillae; *r* – rings; *s* – segment; *t* – tentacles; *tr* – trunk; *vcb* – ventral ciliary band; *wr* – wrinkles. Scale bar: 2 mm.

hitherto unknown in any other pogonophoran tubes, but more detailed studies are required to validate this feature. One more character is shared by all *Galathealinum* species, and very rarely occurs among the other frenulates, namely the presence of numerous multicellular glands in each papilla in the metameric part of the trunk (Figs 2a, 2b, 5i). In size and number of tentacles, *G. karaense* **sp. nov.** resembles *G. brachiosum* and possibly *G. mexicanum*, both described from the Pacific. These are very large and multitentacular species (this is expected in the case of *G. mexicanum* due to the size of its tube), but they differ from the new species in lacking rings on the tube, and *G. brachiosum* is markedly different in many other morphological characters (see Table 1) (Ivanov, 1961; Adegoke, 1967). The new species is likely most closely related to the geographically nearest *G. arcticum* from the Canadian Arctic, sharing many significant morphological features: the

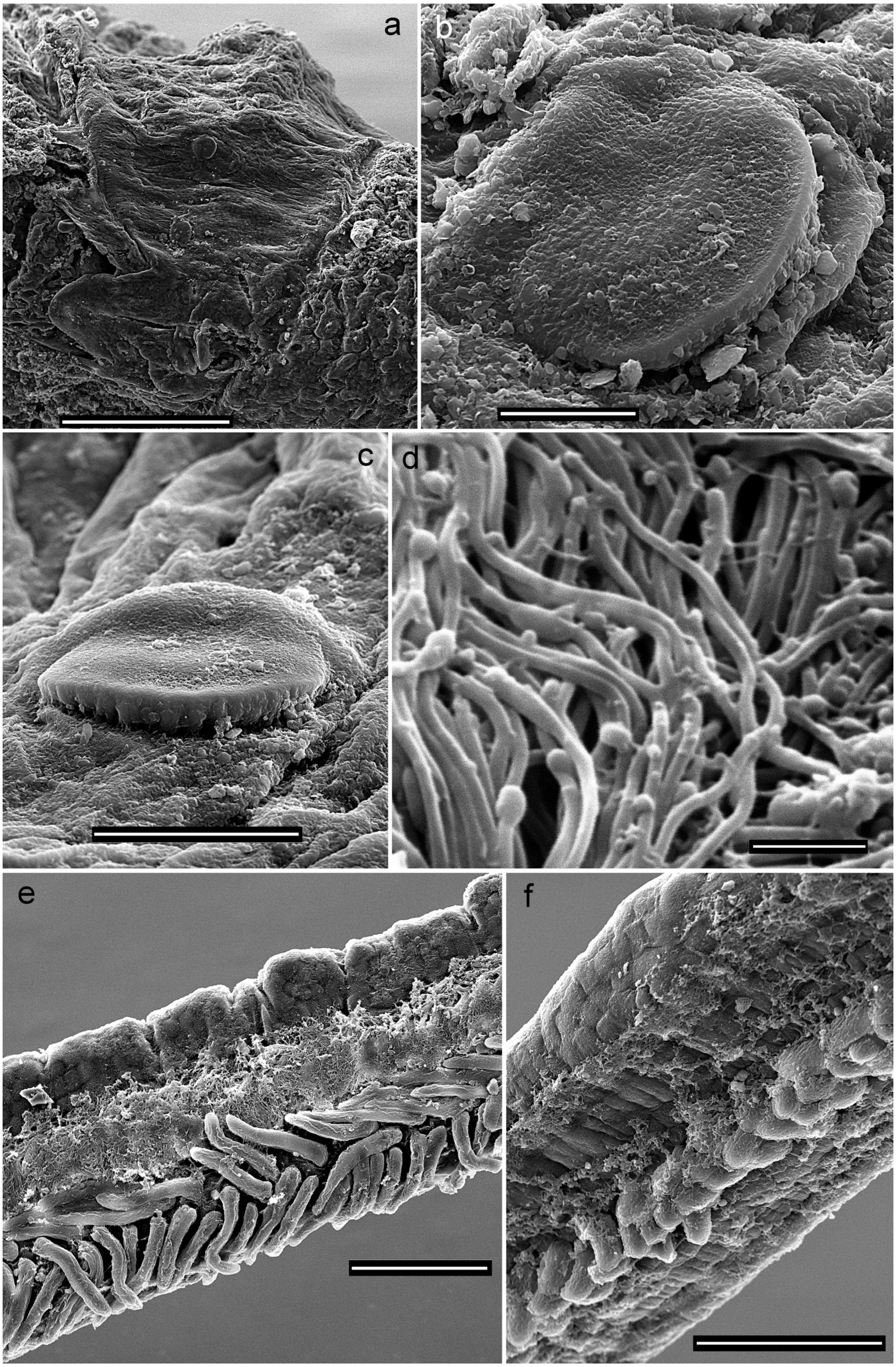


Fig. 3. *Galathealinum karaense* **sp. nov. a**, papilla from trunk nonmetameric region; **b**, cuticular plaque from nonmetameric papilla; **c**, cuticular plaque from trunk metameric region; **d**, cilia from tentacle; **e**, pinnulae and ciliary band on distal part of tentacle; **f**, pinnulae and ciliary bands on basal part of tentacle. *ci* – cilia; *cpl* – cuticular plaques; *me* – membrane; *pa* – papilla; *pi* – pinnulae; *ri* – rim; *ro* – rods. SEM micrographs. Scale bars: 200 mm (a), 10 mm (b), 20 mm (c), 1 mm (d), 50 mm (e), 40 mm (f).

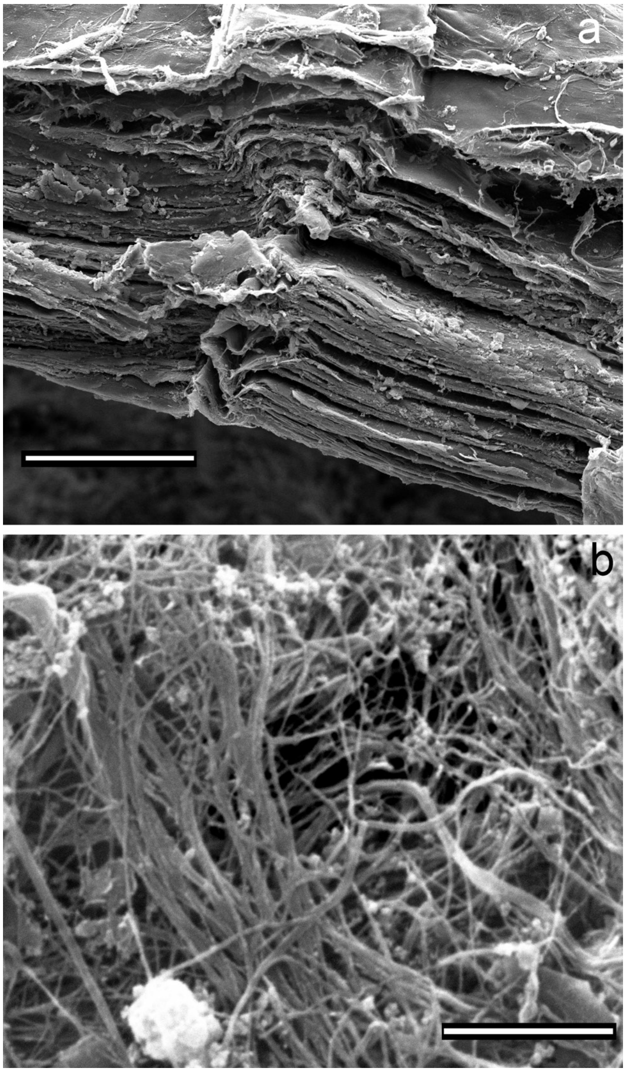
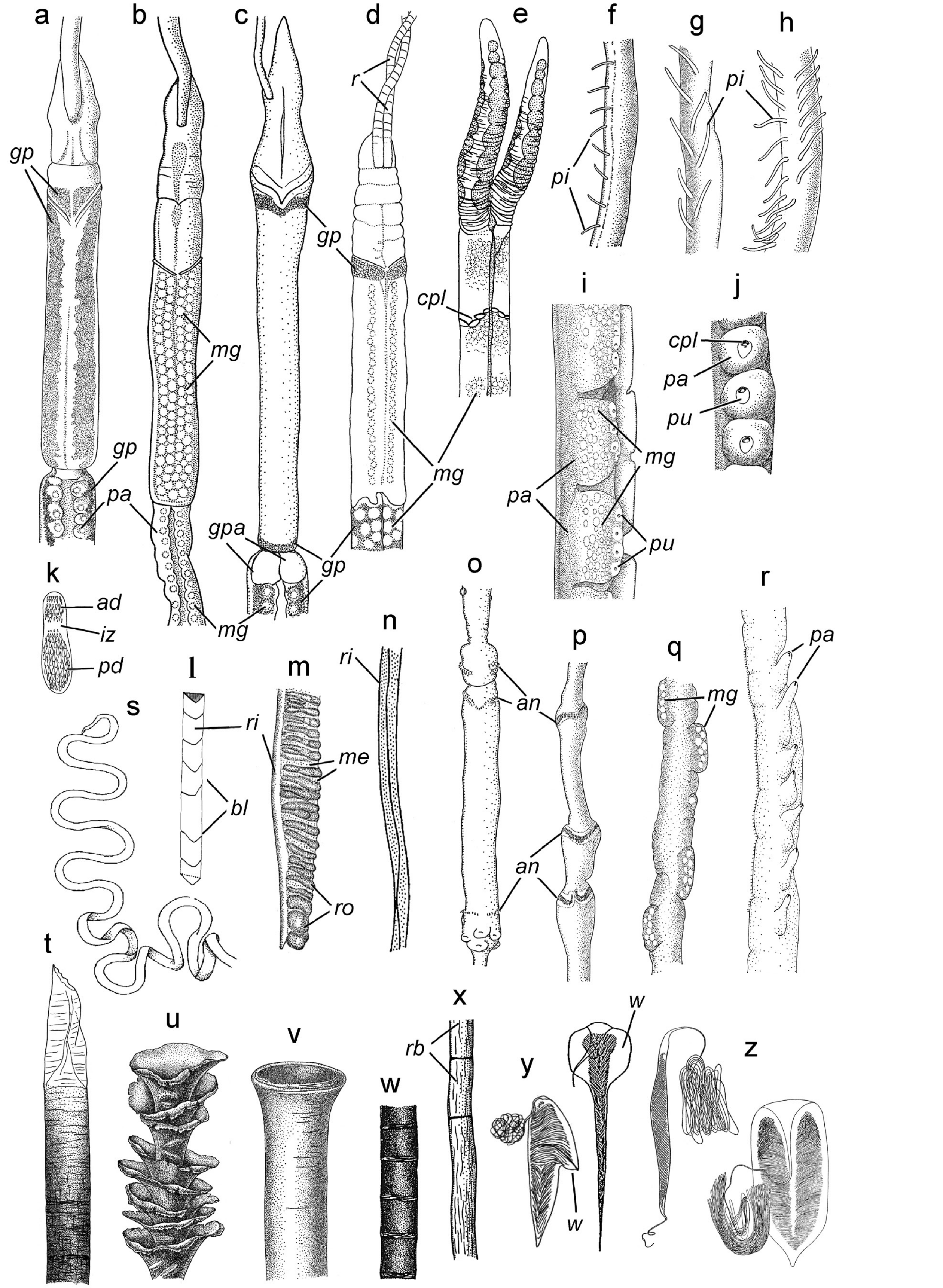


Fig. 4. *Galathealinum karaense* **sp. nov. a**, multilayered tube wall; **b**, felted fibres of external tube layer. SEM micrographs. Scale bars: 100 mm (a), 2 mm (b).

bridle pattern, cilia on the tentacles, a long cephalic lobe, uniformly shaped nonmetameric papillae, which are very regularly arranged in transverse ridges, very small cuticular plaques in the metameric region of the trunk, very regularly arranged cuticular plaques in the nonmetameric region, and the tube is very similar, with rings and small frills. *Galathealinum karaense* **sp. nov.** differs from *G. arcticum* in having shorter but more numerous tentacles with shorter pinnules, more prominent wings on the forepart, smaller cuticular plaques on the nonmetameric papillae, slightly irregular rings on the tube, and it also lacks any patches of glandular epidermis on the forepart posterior to the bridle (Fig. 5a, 5c). The new species differs from all congeners in having more or less continuous lateral ridges instead of well-separated papillae in the anterior part of the trunk and extremely fine felted fibres in the tube, two orders finer than the thinnest described so far in *G. arcticum*. The different length of the tentacles in *G. karaense* **sp. nov.**, in our view, is an artifact, resulted from their partial damage during the collection of the material. This is typical for any pogonophorans, including representatives of the genus *Galathealinum*, with free (not united by the cuticle into a rigid cylinder or a plate) tentacles. In addition, the structural features of the tentacular apparatus in the pogonophorans are very conservative and specific within various taxa, including genera. If the presence of tentacles of different length was an actual trait in *G. karaense* **sp. nov.**, other species of the genus would exhibit the similar structure of the tentacular apparatus, but this is not observed. The diagnostic characters of the species of *Galathealinum* are summarised in the Table 1.

Etymology. The specific name refers to the occurrence of *G. karaense* **sp. nov.** in the Kara Sea.

Remarks. The genus *Galathealinum* to which the new species undoubtedly belongs is rare and very poorly studied. Until now, four species have been known in this genus, none of which has been described from more than one or two extremely incomplete specimens, and one species, *G. mexicanum*, is known only from empty tubes. Our knowledge of their morphology is replete with gaps; suffice it to say that no postannular region or girdles are known in any species. Of *Galathealinum* sexual products, only spermatophores in *G. arcticum* are hitherto known. These are flattened as in the other polybrachiids, but their asymmetrical single-winged outline and curved superficial ridge are unique among the pogonophorans (Fig. 5y) (Southward, 1962). Despite this, we consider it necessary and quite valid to include this character in the diagnosis of the genus, because the structural features of spermatophores in the frenulates are very conservative and specific within all genera and subgenera; polymorphism of spermatophores is minimal. Significant differences in the structure of spermatophores can be the basis for the erection of a new genus, as happened, for example, with the genus *Volvobrachia* Smirnov, 2000 (Smirnov, 2000b). Judging by the absence of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genital papillae in a large and obviously mature specimen of the new species, it is likely a female. The arrangement of nonmetameric papillae in *Galathealinum* represents a rare type of metamerism in the pogonophorans, namely, the complex one, caused by a combination of translational symmetry with reflective (i.e., the presence of a plane of sliding reflection) (Beklemishev, 1964). In these large pogonophorans, papillae having such features form groups (or transverse rows, as in the postannular region of the other pogonophorans), alternately located on the right and left of the mid-dorsal groove. This metamerism is especially developed in *G. arcticum* (Southward, 1962; Ivanov, 1963) and in the new species. In *Oligobrachia kernohanae* Batham, 1973, the same case of metamerism is also described in the nonmetameric region, but concerning the multicellular (pyriform) glands. In this species, the glands form compact groups, regularly alternating on the right and left side of the body and never located opposite each other (Fig. 5q) (Batham, 1973). The same type of metamerism can also be traced in the arrangement of the pinnules on the tentacles of many pogonophoran species in a half-double row, which is transitional from a double row to a single one (Fig. 5f–h) (Ivanov, 1963). The wing-like folds between the cephalic lobe and the bridle on the dorso-lateral sides of the forepart of the species of *Galathealinum* have a different degree of development, from very strong lappets in *G. bruuni* to weakly pronounced lobes in *G. arcticum*. Although it is likely that the dorso-lateral ridges on the anterior part of the moniliferan (sclerolinid) body should be recognised as the initial structure for the origin and further evolution of the so-called vestimental wings of the vestimentiferans (Bright et al., 2012; Eichinger et al., 2013), no one has yet paid attention to how similar the wings on the forepart of *Galathealinum* are to the vestimental wings of the vestimentiferans. Indeed, these structures are in fact epidermal or epidermal-muscular folds located both on the anterior part of the body, fusing ventrally and being divided dorsally. On the dorsal and lateral sides, these structures are most strongly developed. No matter how the problem of homology of the anterior body part of different pogonophoran clades is resolved (Rouse, 2001; Rousset et al., 2004; Southward et al., 2005; Nussbaumer et al., 2006; Hilário et al., 2011; Eichinger et al., 2013; Worsaae et al., 2016), it is obvious that at least the region anterior to the bridle in the frenulates is homologous to the anterior part of the vestimental region of the vestimentiferans and to the anterior part of the body of the moniliferans. According to Bright et al. (2012), the forepart in the frenulates and the vestimentum in the vestimentiferans each contain the prostomium, peristomium and some portion of the anterior (first) chaetiger, while Worsaae et al. (2016) assumes that both forepart and vestimentum comprise only the anterior chaetiger. Thus, the forepart wings of *Galathealinum* and the vestimental wings of the vestimentiferans can be considered homoplasic in the sence of Beklemishev (1964), since they develop in closely related taxa as a

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Fig. 5. Infographic explaining characters mentioned in the paper. **a**, various glandular patches, regular well-developed uniform papillae, median position of tentacle base; **b**, multicellular glands multirowed in forepart and unirowed in trunk, faintly separated papillae; **c**, leftward shift of tentacle base, genital papillae; **d**, multicellular glands multirowed in trunk and unirowed in forepart, rings of thickened cuticle; **e**, cuticular plaques of bridle; **f**, unirowed pinnulae; **g**, semi-double row of pinnulae; **h**, double row of pinnulae; **i**, regular well-developed uniform papillae with numerous cuticular plaques, pulvilli and multicellular glands; **j**, papillae with cuticular plaques on pulvilli; **k**, setal head with anterior and posterior groups of denticles, separated by intermediate zone; **l**, ridge of bridle with rim and blocks; **m**, ridge of bridle with rim, mebrane and rods; **n**, homogenous bridle ridge; **o**, girdles pattern of two+one; **p**, girdles pattern of one+two; **q**, alternating arrangement of multicellular glands; **r**, enlarged papillae; **s**, twisted tube; **t**, membranous anterior part of tube; **u**, tube with simple terminal funnel; **v**, tube with complex terminal funnel; **w**, tube with regular rings; **x**, tube with longitudinal ribs; **y**, winged spermatophores with one or two wings; **z**, wingless spindle-shaped and leaf-shaped spermatophores. *ad* – anterior group of denticles; *an* – girdles; *bl* – blocks; *cpl* – cuticular plaques; *gp* – glandular patches; *gpa* – genital papillae; *iz* – intermediate zone; *me* – membrane; *mg* – multicellular glands; *pa* – papillae; *pd* – posterior group of denticles; *pi* – pinnulae; *pu* – pulvilli; *r* – rings; *rb* – ribs; *ri* – rim; *ro* – rods; *w* – wing. Schematic drawings (after Southward, 1962, 1963; Ivanov, 1963; Ivanov & Gureeva, 1973, 1980; Smirnov, 1999, 2000a, 2000c, 2005, 2008a, 2015).

result of a similar differentiation (parallel evolution) of the original homologous structures, although they are not inherited from a common ancestor. The tube of all *Galathealinum* species has a peculiar external layer consisting of dense interlacing fibres that look like a felt under the microscope (Ivanov, 1963). This layer entirely forms the funnel-like frills of the tube segments. The individual fibres of this layer differ very much in diameter, from very thick 22 mm (in *G. mexicanum*) to very thin 1 mm (in *G. arcticum*). The new species has remarkably thin felted fibres, only 0.05–0.08 mm in diameter, which are hardly detectable even by the SEM. However, since the determination of the validity of this feature requires huge comparative studies of the pogonophoran tube by the SEM, which should be the subject of a separate article, we do not further include this character in the diagnosis of the genus.

The representatives of the genus *Galathealinum* are the most specialised pogonophorans of the Polybrachiidae stem. The emergence of this genus is associated, in addition to the four above-mentioned synapomorphies, with the powerful polymerisation of the tentacles (up to ~ 270, the maximum number known for the frenulate pogonophorans), a significant increase in body and tube diameter (and a corresponding decrease in the relative length of the cephalic lobe, the forepart and the tentacles), the multiplication of multicellular glands in each papilla of the anterior (metameric) region of the trunk in parallel with an increase in the number of its cuticular plaques and pulvilli (Fig. 5i, 5j), the disappearance of all derivates of cuticular plaques (except for the rim) from the bridle (Fig. 5l–n).

Such finding of a large pogonophoran is highly unusual for freshened shallow waters at the mouth of the Yenisey River. Only twice were pogonophorans found at a shallower depth of 20–22 m (Ivanov, 1957; Kubota et al., 2007), and never before these were found at salinity less than 32‰. Recently, one specimen of a so far undescribed species of the frenulates was obtained from approximately the same area, in the Yenisey Gulf of the Kara Sea, at a depth of 28 m (Rimskaya-Korsakova et al., 2020). The area of these findings is characterised by high methane concentrations caused by degradation of permafrost under the influence of river flow (Shakhova et al., 2007; Rimskaya-Korsakova et al., 2020). It should be noted that *G. arcticum*, which is morphologically closest to the new species also inhabits the similar environmental conditions, in the freshened shallow waters of the Mackenzie River Delta off the Arctic coast of Canada. In the description of *G. arcticum*, salinity and temperature were not provided, but according to the environmental conditions of the studied area, the salinity should be about 30‰, or even less, and the water temperature is slightly below zero (Macdonald & Yu, 2005). In any case, it is obvious that these three species, including the undescribed one from the Kara Sea, are ecological counterparts. Characterising the vertical distribution of the pogonophorans in the Arctic, it is worth noting that almost all species are restricted to relatively shallow waters with depths not exceeding 2000 m. Only *Polybrachia gorbunovi* was found at a depth of more than 3.5 km, in the Sadko Trench (Laptev Sea) (Ivanov, 1963). The most eurybathic species is *Siboglinum* (*Siboglinum*) *hyperboreum*, found at one of the stations in the Laptev Sea at a depth of 55 m (one of the shallowest pogonophoran findings in history) and recorded at a depth of 2166 m northwest of Spitsbergen (Smirnov, 1999). *Nereilinum murmanicum* has the smallest depth range (75–341 m) (Ivanov, 1963; Kanafina, 2019). The pogonophorans have traditionally been viewed as deep-sea organisms. Later, the distribution of the pogonophorans began to be considered as being predominantly affected by water temperature, rather than by depth (Southward, 1962, 1971a, 1971b). However, there is growing evidence now that the distribution of the pogonophorans in the World Ocean is affected primarily by the chemical composition of the substrate and bottom water, namely the concentration of methane and hydrogen sulfide, which are extremely important for nutrition of the pogonophorans (Malakhov et al., 1992; Karaseva et al., 2019; Rimskaya-Korsakova et al., 2020; Sen et al., 2020). The new record from 25 m in the area of high methane concentrations adds further support to this idea. Thus we can certainly assert that the estuaries of great Arctic rivers are very favourable for the settlement of the pogonophorans in upper bathyal or even sublittoral locations.

Key to the species of the genus *Galathealinum*

1a. D_{tb} >2 mm. D_f>1.4 mm. Q_{tn} ≥150 (up to ~270) . . . 2
1b. D_{tb} ≤2 mm. D_f≤1.4 mm. Q_{tn} <150 (~80–130) 4
2a. Segments of tube long (>3.5 mm, L_s/D_{tb}≥1.5). Felted fibres of external tube layer 15–22 mm thick. . . . . ***G. mexicanum***
2b. Segments of tube short (<3 mm, L_s/D_{tb} ≤1). Felted fibres of external tube layer thinner than 15 mm. . . 3
3a. Q_{tn} ~268. Cephalic lobe short (~1 mm, L_{cl}/D_f ~0.68). Bridle keels separated widely on ventral side. Metameric papillae well-developed, regular, uniform (Fig. 5i). Nonmetameric papillae irregular in shape, alternating pattern in arrangement somewhat unclear. Each metameric papillae with two–ten cuticular plaques 80–90 mm across. Cuticular plaques on nonmetameric papillae ~80 mm across, irregularly arranged. Felted fibres of external tube layer 7–12 mm thick . . . . ***G. brachiosum***
3b. Q_{tn} ~150. Cephalic lobe very long (~1.75 mm, L_{cl}/D_f ~1.25). Bridle keels meet ventrally. Metameric papillae not clearly separated, irregularly arranged and variable in shape. Nonmetameric papillae uniform and arranged very regularly in alternating pattern. Each papillae in anterior (metameric) part of trunk with single cuticular plaque, rarely two–three, 20–29 mm across. Cuticular plaques on nonmetameric papillae 25–29 mm across, arranged in one row. Felted fibres of external tube layer 0.05–0.08 mm thick. . . . . ***G. karaense* sp. nov.**
4a. Cephalic lobe long (~1.58 mm, L_{cl}/D_f ~1.18). Forepart short (L_f/D_f ~4.5). Bridle keels touch both dorsally and ventrally. Wing-like epidermal folds on forepart not very clear. Funnels on tube narrow and weakly developed (D_{fn} 2–2.1 mm, D_{fn}/D_{tb}1–1.1) . . . . ***G. arcticum***
4b. Cephalic lobe short (~0.95 mm, L_{cl}/D_f ~0.69). Forepart long (L_f/D_f ~7). Bridle split on both sides of body. Wing-like epidermal folds on forepart prominent. Funnels on tube wide and strongly developed (D_{fn} 2.4–2.75 mm, D_{fn}/D_{tb} 1.2–1.4). . . . . . ***G. bruuni***

Key to the species of the Arctic pogonophorans (complete animals)

1a. One tentacle 2
1b. More than one tentacle. 5
2a. Multicellular glands form three to five rows (Fig. 5d) bordered with glandular strips on each side of dorsal furrow in anterior part of trunk (Fig. 5a). Ten to twelve enlarged papillae (Fig. 5r). D_f 0.3–0.37 mm . . . . ***Polarsternium rugellosum***
Laptev Sea. Depth 100–566 m.
2b. One or two rows of multicellular glands on each side of dorsal furrow in anterior part of trunk (Fig. 5a–c). No glandular patches on trunk. Zone of enlarged papillae absent. D_f0.1–0.22 mm 3
3a. Tentacle with pinnules. Cephalic lobe long (L_{cl}/D_f ~1.81). Multicellular glands in forepart distributed in numerous rows (Fig. 5b). First setal girdle interrupted on ventral side only. Setae in girdles arranged in single rows. Tube segmented in anterior and mid regions, with five–nine rings per segment . . . . . ***Siboglinum* (*Ekmanifilum*) *ekmani***
Northeast and northwest Atlantic. Depth 350–>2000 m. Arctic Basin to northeast of Spitsbergen. Depth 2090–2166 m.
3b. Pinnules absent. Cephalic lobe short (L_{cl}/D_f ~1). Multicellular glands in forepart distributed in two rows (Fig. 5d). First girdle of setae interrupted only dorsally. Setae in girdles form two to four rows. Tube not segmented 4
4a. Tentacle attached to left of body medial line (Fig. 5c). L_f/D_f 4.5–5, D_f 0.13–0.16 mm. Post-tentacular furrow present. Setal girdles distributed in pattern of two+one (Fig. 5o); third girdle separated from two anterior girdles by 0.60–0.64 mm; second girdle interrupted only ventrally. Intermediate zone on heads of setae very broad (12–21% of head length); area of anterior group of denticles about the same as area of posterior group (Fig. 5k). Tube rings brown or yellow . . . . ***Siboglinum* (*Siboglinum*) *hyperboreum***
Greenland Sea, Laptev Sea and Arctic Basin to southeast of Spitsbergen. Depth 55–2166 m.
4b. Tentacle attached medially (Fig. 5a, 5b). L_f/D_f 7, D_f 0.2–0.22 mm. Post-tentacular furrow absent. Setal girdles distributed in pattern of one+two (Fig. 5p); first girdle ~0.5 mm distance from group of two posterior girdles; second girdle interrupted only dorsally. Intermediate zone on head of setae narrow (~ 3% of head length); anterior group of denticles occupies about one-third of head length. Tube rings colourless . . . . ***Siboglinum* (*Siboglinum*) *norvegicum***
Northeast Atlantic. Depth 120–1165 m. Arctic Basin to northeast of Spitsbergen. Depth 2090–2166 m.
5a. Tentacles always two. 6
5b. From five to nearly 150 tentacles. 8
6a. Tentacles and cephalic lobe very short (L_{tn}/D_f ~10, L_{cl}/D_f ~0.3). Bridle consists of separate cuticular plaques in anterior region of forepart. Multicellular glands in whole forepart distributed in numerous rows (Fig. 5e). Ventral ciliary band on forepart. No external furrow between forepart and trunk. Trunk lacks postannular region. Spermatophores absent. Tube rigid, thick-walled, more or less twisted,

without rings and segments . . . . ***Archeolinum contortum***
Widespread in Atlantic Ocean, including Atlantic Sector of Antarctic. Depth 721–2700 m. Laptev Sea and Arctic Basin to northeast of Spitsbergen. Depth 311–2166 m.

6b. Tentacles and cephalic lobe very long (L_{tn}/D_f >85, L_{cl}/D_f ≥0.9). Bridle consists of two cuticular ridges encircling forepart. Multicellular glands in forepart distributed in two rows, but absent from pre-frenular part (Fig. 5d). Ventral ciliary band on trunk. External furrow between forepart and trunk present. Trunk has postannular region. Spermatophores present in males. Tube straight, flexible, thin-walled and ringed 7

7a. Bridle and glandular band beneath it interrupted on dorsal and ventral sides of body. Tentacles with rings of thickened cuticle (Fig. 5d). Three girdles of setae. Spermatophores ~140 μm long. Tube segmented in posterior region, D_{tb} 0.35–0.45 mm. . . . . ***Nereilinum squamosum***
Laptev Sea and Arctic Basin to northeast of Spitsbergen. Depth 243–603 m.

7b. Bridle and glandular band beneath, interrupted only ventrally. Tentacles lack areas with thickened cuticle. Two girdles of setae. Spermatophores ~100 μm long. Tube not segmented, D_{tb} 0.21–0.28 mm . . . . ***Nereilinum murmanicum***
Barents Sea. Depth 75–341 m.

8a. Spermatophores flattened leaf-shaped, wingless or with one asymmetrical wing (Fig. 5y, 5z). Q_{tn} from18 to ~150. L_f/D_f 3–5.5. Papillae in anterior part of trunk present and usually well-developed (Fig. 5a). Anterior part of tube with funnel-like segments (Fig. 5u) 9

8b. Spermatophores spindle-shaped, with two symmetrical wings (Fig. 5y). Q_{tn} 5–12. L_f/D_f ~7. Papillae in anterior part of trunk absent (Fig. 5d). Tube segmented in posterior part, segments lacking frills (Fig. 5x) . . . . . . ***Oligobrachia haakonmosbiensis***
Northeast Atlantic. Depth 350–745 m. Laptev Sea and Arctic Basin to northeast and northwest of Spitsbergen. Depth 63–2166 m.

9a. Q_{tn} ~18. Cephalic lobe very short (0.14–0.15 mm, L_{cl}/D_f ~0.52). Forepart lacks patches of glandular epidermis and wing-like epidermal folds. D_f 0.27–0.29 mm. Bridle keels separated widely on ventral side. Metameric papillae uniform. Nonmetameric papillae scattered. Segments on tube short (L_s 0.12–0.67 mm), with prominent frills (D_{fn}/D_{tb} 1.66–2.16). No rings in anterior part of tube. External felted layer on tube absent. D_{tb} ~0.5 . . . . ***Polybrachia gorbunovi***
Arctic Basin, Sadko Trench. Depth 3700–3800 m.

9b. Q_{tn} >70. Cephalic lobe very long (>1.5 mm, L_{cl}/D_f ~1.2). Forepart with various patches of glandular epidermis and wing-like epidermal folds. D_f ≥1 mm. Bridle keels touch on ventral side. Metameric papillae variable in shape. Nonmetameric papillae arranged regularly alternating on left and right side of trunk. Segments on tube long (L_s ≥1 mm). Frills weakly developed and narrow (D_{fn}/D_{tb} 1–1.2). Anterior part of tube ringed. Felted fibres in external tube layer. D_{tb} ≥1.9 10

10a. Tentacles long (20–29 mm, L_{tn}/D_f ~21), with long pinnules (125–163 mm). Q_{tn} ~80–130. Glandular patches on forepart in post-frenular and diaphragm areas. Metameric papillae of two types (small and large), well-developed and regularly arranged in alternating pattern. Cuticular plaques on nonmetameric papillae 50–65 mm across. Felted fibres of external tube layer 1–2 mm thick. . . . . ***Galathealinum arcticum***
Beaufort Sea. Depth 36 m.

10b. Tentacles short (~15 mm, L_{tn}/D_f ~11), with short pinnules (75–100 mm). Q_{tn} ~150. Glandular patches on forepart in pre-frenular area. Papillae in anterior part of trunk not clearly separated, irregularly arranged and variable in shape. Cuticular plaques on nonmetameric papillae 25–29 mm across. Felted fibres of external tube layer 0.05–0.08 mm thick. . . . . ***Galathealinum karaense* sp. nov.**
Kara Sea. Depth 25 m.

Key to the species of the Arctic pogonophorans (empty tubes)

1a. Anterior portion of tube segmented. 2

1b. Tube segmented only in most posterior region, or unsegmented 5

2a. Most part of tube very rigid and opaque. Walls of tube thick, with multiple layers. Segmented part of tube dark brown-red or black, rings, if present, brown; segments with frills. D_{tb} ≥0.5 mm. 3

2b. Tube flexible, transparent. Walls of tube thin, looking like a single layer. Segmented portion of tube with yellowish-brown rings; segments lacking frills. D_{tb} 0.11–0.17 mm . . . . ***Siboglinum* (*Ekmanifilum*) *ekmani***

3a. D_{tb} ~0.5. Segments short (L_s 0.12–0.67 mm). Frills well-developed, wide (D_{fn}/D_{tb} 1.66–2.16). No rings in anterior part of tube. No external felted layer on tube . . . . ***Polybrachia gorbunovi***

3b. D_{tb} ≥1.9. Segments long (L_s ≥1 mm). Frills weakly developed and narrow (D_{fn}/D_{tb} 1–1.2). Anterior part of tube ringed. Felted fibres in external tube layer 4

4a. D_{tb} 2.1–2.25 mm. D_{fn} 2.4–2.5 mm. Rings irregular (anastomotic). Felted fibres of external tube layer 0.05–0.08 mm thick. . . . . ***Galathealinum karaense* sp. nov.**

4b. D_{tb} 1.9–1.95 mm. D_{fn} 2–2.1 mm. Rings regular, with even edges (Fig. 5w). Felted fibres of external tube layer 1–2 mm thick. . . . . ***Galathealinum arcticum***

5a. Tube straight; at least posterior part is ringed. 6

5b. Tube without rings; anterior part twisted (Fig. 5s) . . . . ***Archeolinum contortum***

6a. Rings colourless. D_{tb} ≤0.25 mm . . . . ***Siboglinum* (*Siboglinum*) *norvegicum***

6b. Rings in mid-part of tube yellow to almost black. D_{tb} 0.13–1 mm. 7

7a. Rings more or less regular, with even edges, long (L_r/D_{tb} ≥0.67), nearly lacking in fibres. D_{tb} ≥0.24 mm 8

7b. Rings over most of tube irregular (anastomotic with uneven edges), very fibrous. L_r/D_{tb} 0.5–0.67. D_{tb} ≤0.32 mm. . . . . ***Siboglinum* (*Siboglinum*) *hyperboreum***

8a. Rings in mid-part of tube dark brown or black, almost opaque. Anterior membranous, unringed part of tube 2–5 mm long (Fig. 5t). Posterior part of tube with longitudinal ribs on surface (Fig. 5x). D_{tb} ≥0.45 mm. . . ***Oligobrachia haakonmosbiensis***

8b. Rings in mid-part of tube yellow or brown, transparent. Anterior membranous, unringed portion no less than 15 mm long. Tube surface without longitudinal ribs. D_{tb} ≤0.5 mm 9

9a. Tube thin-walled. Rings yellow, elongate (L_r/D_{tb} ~1), very regular. Intervals between rings concave on substantial portion of tube. D_{tb} 0.21–0.45 mm 10

9b. Tube thick-walled. Rings yellow to brown, short (L_r/D_{tb} ~0.67). Rings in posterior part of tube somewhat irregular (anastomotic), intervals between rings convex. D_{tb} 0.3–0.5 mm. . . . . ***Polarsternium rugellosum***

10a. Tube segmented in posterior section. D_{tb} 0.32–0.45 mm . . . . ***Nereilinum squamosum***

10b. Tube lacking segments. D_{tb} 0.21–0.28 mm . . . . ***Nereilinum murmanicum***

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