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## NEW SPECIES OF *SIBOGLINUM* (ANNELIDA: POGONOPHORA) FROM THE ANTARCTIC OCEAN

R. V. Smirnov

Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia;  
e-mail: vsroman@inbox.ru

### ABSTRACT

Four new species of the genus *Siboglinum* Caullery, 1914, obtained from 12 stations at depths of 1265–6070 m in the Atlantic and Indian Ocean Sectors of the Antarctic Ocean are described. The material came from the following regions: Scotia Sea, Weddell Sea, Bransfield Strait, Orkney Trench, Laurie Trench and Davis Sea. The comparative characteristics of the new species are given in a table. Several characters occurring in various of the new species are rare or unique among the congeners: cuticular plaques on the metameric region of the trunk, four separate girdles of chaetae, an extremely long distance (up to 7 mm) between the girdles, occurrence of a transverse row of interannular papillae, a remarkable leftward shift of the tentacle base, and a combination of both main types of arrangement of postannular papillae (in rows and singly) within one species. The new species are assigned to two subgenera, *Siboglinum* Caullery, 1914 and *Ekmanifilum* Smirnov, 2014; the diagnostic characters of all *Siboglinum* subgenera are compared and summarized in a table. Two keys are provided to the *Siboglinum* subgenera and to the known species of Antarctic pogonophorans.

**Key words:** Antarctic, new species, Pogonophora, *Siboglinum*

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## НОВЫЕ ВИДЫ *SIBOGLINUM* (ANNELIDA: POGONOPHORA) ИЗ АНТАРКТИЧЕСКОГО ОКЕАНА

Р. В. Смирнов

Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт-Петербург, Россия;  
e-mail: vsroman@inbox.ru

### РЕЗЮМЕ

Описано 4 новых вида рода *Siboglinum* Caullery, 1914, добытых на 12 станциях в атлантическом и индийском секторах Антарктического океана на глубинах 1265–6070 м. Материал относится к следующим районам: море Скоша, море Уэдделла, пролив Брансфилда, Оркнейский желоб, желоб Лори и море Дэвиса. Сравнительные характеристики новых видов даны в виде таблицы. Несколько признаков новых видов являются редкими или уникальными среди видов рода, а именно: кутикулярные пластинки на метамерном отделе туловища, 4 отдельных пояса щетинок, очень большое расстояние между поясами (до 7 мм), поперечный ряд папилл между поясами, значительное смещение влево основания щупальца, а также сочетание обоих основных типов расположения постаннулярных папилл (в рядах или по одной) в пределах одного вида. Новые виды принадлежат 2 под родам, *Siboglinum* Caullery, 1914 и *Ekmanifilum* Smirnov, 2014; диагностические признаки всех под родов *Siboglinum* подвергнуты сравнительному анализу и суммированы в таблице. Представлены 2 определительных ключа под родов *Siboglinum* и всех известных в Антарктике видов погонофор.

**Ключевые слова:** Антарктика, новые виды, Pogonophora, *Siboglinum*

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## INTRODUCTION

This paper continues a series of publications (Smirnov 2000a, b) devoted to the study of a very large collection of Antarctic pogonophorans stored at the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia). The pogonophorans described here were found at 12 stations in the Atlantic and Indian Ocean Sectors of the Antarctic Ocean during four Russian expeditions carried out from 1957 to 1989. They are considered to be new species of the largest pogonophoran genus *Siboglinum* Caullery, 1914.

The author of the first scientific description of Pogonophora, Prof. M. Caullery, used the family name Siboglinidae and the generic name *Siboglinum* in two short notes in 1914, but did not name the species *Siboglinum weberi* until his 1944 paper, in which he remarked that there might be more than one species in his type material (Caullery 1914a, b, 1944). Another famous pogonophoran researcher, Acad. A.V. Ivanov, recognized *Siboglinum* as a pogonophoran in 1951, and distinguished the family Siboglinidae Caullery, 1914 (defined as Pogonophora with one tentacle and lacking plaques on the anterior paired papillae) from the Lamellisabellidae of Ushakov (1933) (Ivanov 1951). Jägersten (1956) described one new species (*Siboglinum ekmani*) without defining the genus. Ivanov (1957) published descriptions of five new species of *Siboglinum*, but did not define the genus. The Russian edition of Ivanov's monograph on Pogonophora (Ivanov 1960) provides the first formal definition of the genus *Siboglinum* Caullery, 1914, with the type species stated to be *S. weberi* Caullery, 1914, though the species was in fact named in 1944. Caullery's material of *Siboglinum weberi* was re-examined by Southward (1961), and 14 species of Pogonophora were found, belonging to at least to four genera. A lectotype was chosen to resemble Caullery's 1944 figures and description as closely as possible. *Siboglinum weberi* Caullery, 1944 was re-described from this lectotype. This became the description of the type species of *Siboglinum*. Ivanov's (1963) monograph translated and revised his 1960 definition of the genus and included the re-description of *S. weberi* by Southward (1961). Thus, *S. weberi* Caullery remains the type of *Siboglinum*.

The investigation of new species of *Siboglinum* from the Antarctic and a review of some other congeneric species (Smirnov 2014) allow me to clarify to some extent the taxonomic structure of the genus, which is still very complex and obscure.

**Institutional abbreviations.** ZIN, Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia).

## MATERIAL AND METHODS

Specimens of the four new species described below were obtained from depths between 1265 and 6070 m on cruises with the Russian Research Vessels Ob (1957) in the Davis Sea, Akademik Kurchatov (1971 and 1985) in the Laurie Trench and Scotia Sea, and Dmitry Mendeleev (1989) in the Weddell Sea, Bransfield Strait, Scotia Sea and Orkney Trench. In total, a few hundred animals and some empty tubes were collected from 12 stations (see Table 1 and Fig. 1). Samples were taken by Sigsbee trawl and Ocean 0.25 grab. Sediments varied, but clay silts prevailed. The material was fixed in 4% formalin and then transferred to 70% ethanol. The extraction of the animals from their fine tubes was a difficult problem. The tubes were usually removed in bits by chipping away with sharpened dissecting needles or fine scalpels. The observations, measurements and drawings of the specimens were carried out by means of binocular and standard light microscopes with drawing attachments. The type material is deposited at the Zoological Institute of the Russian Academy of Sciences (ZIN SN71, HN72, PN72, HN73, HN74, PN74), Saint Petersburg.

In the present paper the following designations for morphometric parameters are used:  $D_p$ , diameter of forepart;  $L_p$ , length of forepart;  $L_p/D_p$ , forepart length and diameter ratio;  $L_{cl}$ , length of cephalic lobe;  $L_{cl}/D_p$ , cephalic lobe length and forepart diameter ratio;  $D_t$ , diameter of tentacle;  $D_t/D_p$ , tentacle diameter and forepart diameter ratio;  $D_{tb}$ , diameter of tube. Qualitative adjectives used in the descriptions below reflect relative, not absolute, dimensions of various body parts.

## SYSTEMATICS

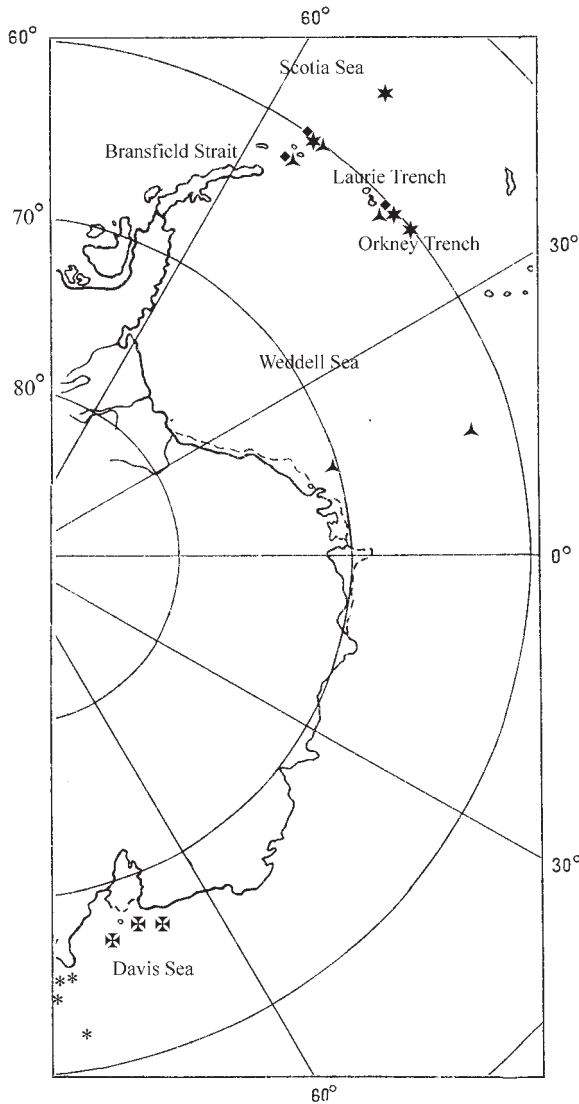
### Family Siboglinidae Caullery, 1914

#### Genus *Siboglinum* Caullery, 1914

#### Subgenus *Ekmanifilum* Smirnov, 2014

#### *Siboglinum Ekmanifilum davisiense* sp. nov. (Fig. 2)

**Material examined.** R.V. Ob, station 161: several dozen tube fragments, some with animals; st.



**Fig. 1.** Distribution of *Siboglinum* species in the Antarctic Ocean: ✖ *S. S. meridiale* Ivanov, three stations in Davis Sea; \* *S. E. davisense* sp. nov., four stations in Davis Sea; ★ *S. E. scotiense* sp. nov., one station in Laurie Trench, three stations in Scotia Sea, one station in Orkney Trench; ◆ *S. S. gureevae* sp. nov., one station in Laurie Trench, one station in Scotia Sea; ▲ *S. S. quadrannulatum* sp. nov., one station in Laurie Trench, two stations in Scotia Sea, one station in Bransfield Strait, two stations in Weddell Sea.

162: many tubes, partly occupied; st. 166: 15 tubes, including 2 occupied; st. 172: 10 empty tubes. Type material. St. 162, 5 syntypes (ZIN SN71).

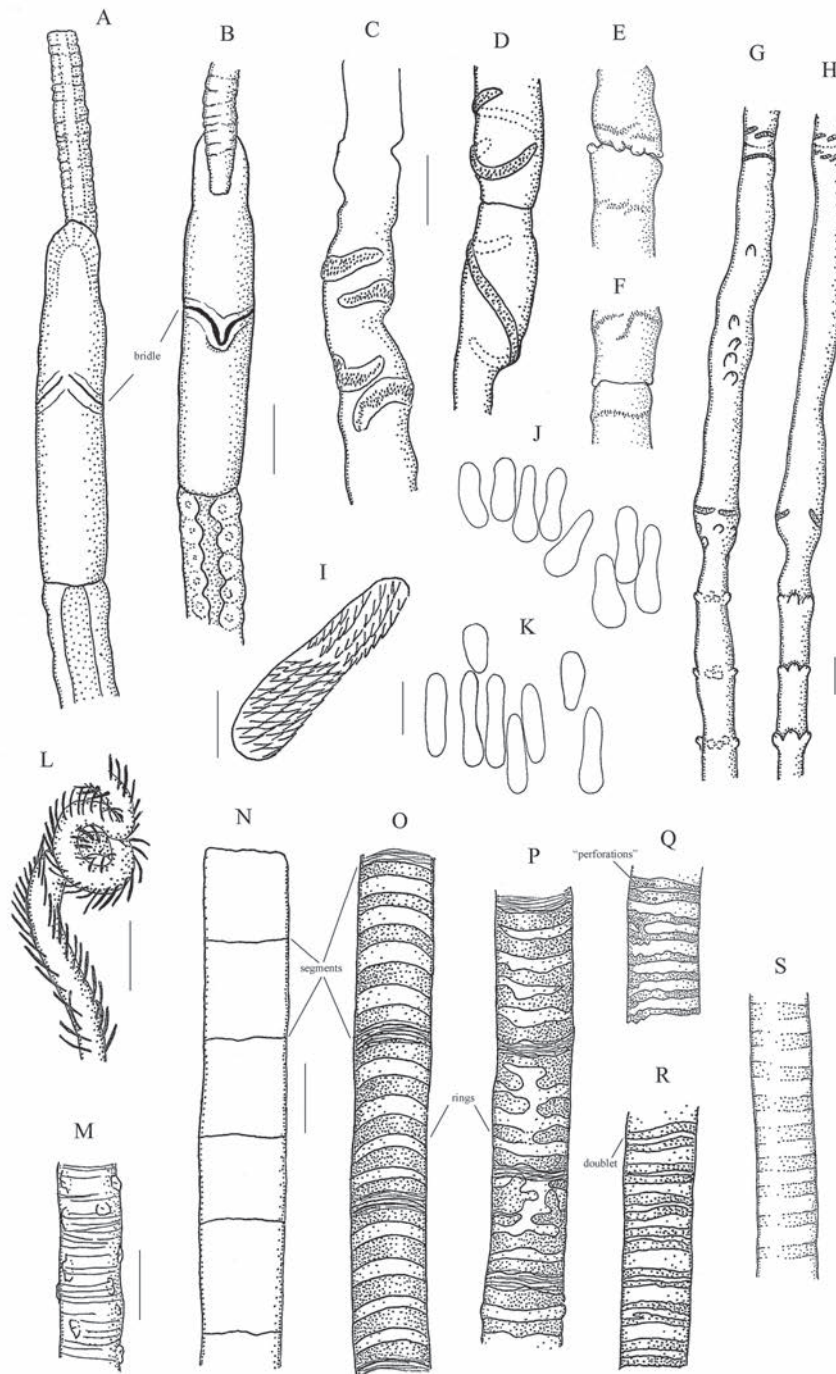
**Etymology.** The specific name came from the type locality of the species; *S. E. davisense* was found for the first time in the Davis Sea and is at present known only from this region of the Antarctic Ocean.

## Description

**Tube.** The tube is quite rigid, with segments and rings,  $D_{tb}$  0.19–0.27 mm. On the anterior filmy part, the segments are 1.5 times as long as the tube diameter (Fig. 2N) and become longer posteriorly, up to 2.5 times as long as  $D_{tb}$  (Fig. 2O). The segmental borders on the unringed part of the tube are narrow and clear, while the more posterior ones are wider and less distinct (Fig. 2N, O). Fibres in the tube wall are very few. The rings usually appear as separate spots, which then join together to form true rings. The latter are yellow with uneven edges and anastomoses (Fig. 2P), at first just a little wider than the intermediate spaces and then equal to them. There are four to six rings per segment (Fig. 2O). In the middle, unsegmented part of the tube, the rings become more distinct, darker, somewhat wider (up to a quarter of  $D_{tb}$ ), and are divided into doublets (Fig. 2Q, R). The doublets are formed by a paling of the central part of the ring without any “perforation” stage (Fig. 2P). In some specimens “perforations” may sometimes be observed in the doublets (Fig. 2Q). Farther back the rings appear to become single again and gradually become paler and almost invisible (Fig. 2S). The longest tube fragment is about 110 mm long.

**Forepart.** The forepart is rather short (0.9–1.1 mm,  $D_f$  0.18–0.2 mm,  $L_f/D_f$  5–6). The cephalic lobe is small ( $L_{cl}$  ~0.2 mm,  $L_{cl}/D_f$  ~1), somewhat narrower than the remaining forepart (Fig. 2A, B). The thick (90–100  $\mu$ m,  $D_t/D_f$  ~0.52) wrinkled tentacle, about 6 mm long, is attached medially. Pinnules are present only on the distal half of the tentacle, where they form two widely spaced rather sparse rows (Fig. 2L). The pinnules reach 150  $\mu$ m in length. The keels of the bridle are situated near the middle of the forepart and join together on the dorsal side of the body, while on the ventral side they are separated by a narrow space.

**Trunk.** The anterior (metameric) region possesses well-developed papillae, each with a large pyriform (multicellular) coelomic gland (Fig. 2B). Glandular patches of unicellular epidermal glands are absent from the trunk. The nonmetameric region is characterised by the presence of small papillae, furnished with cuticular plaques, on the dorso-lateral region of the body (Fig. 2M). The plaques are widely oval, 20–25  $\mu$ m across, with a medial ridge. A zone of enlarged papillae has not been seen. The girdle region has a particularly complicated structure

*Siboglinum Ekmanifilum davisiense*

**Fig. 2.** *Siboglinum Ekmanifilum davisiense* sp. nov.: A – forepart, ventral view; B – the same, dorsal view; C, E – two anterior girdles in different specimens, dorsal view; D – specimen shown in C, lateral view; F – specimen shown in E, ventral view; G – girdle region, ventral view; H – the same, dorsal view; I – toothed head of chaeta of girdles; J – part of third girdle; K – part of first girdle; L – tentacle with pinnules; M – nonmetameric region, dorsal view; N–S – parts of tube in anterior to posterior series. Scales: A–H, L–S – 0.2 mm; I – 5  $\mu$ m; J, K – 10  $\mu$ m.

**Table 1.** Samples containing the new *Siboglinum* species in the Antarctic.

Ship	Cruise	Station	Gear	Date	Location	Depth, m	Bottom
R.V. Ob	2	161	grab Ocean 0.25	16.01.1957	Davis Sea, 65°24.8'S, 89°35.2'E	2720	silty sand with gravel
R.V. Ob	2	162	Sigsbee trawl	16.01.1957	Davis Sea, 65°06.2'S, 90°33.0'E	2720–2750	silty sand with gravel
R.V. Ob	2	166	grab Ocean 0.25	17.01.1957	Davis Sea, 64°43.0'S, 91°20.0'E	3112	mud with gravel
R.V. Ob	2	172	grab Ocean 0.25	20.01.1957	Davis Sea, 62°34.2'S, 86°21.2'E	3782	mud with gravel
R.V. Akademik Kurchatov	11	909	Sigsbee trawl	10.12.1971	Laurie Trench, 60°12.9'S, 43°59.0'W	5450–5480	mud
R.V. Akademik Kurchatov	11	914	Sigsbee trawl	14.12.1971	Scotia Sea, 56°21.0'S, 50°48.0'W	5650–6070	mud with gravel
R.V. Akademik Kurchatov	48	4882	Sigsbee trawl	09.12.1985	Scotia Sea, 60°41.5'S, 54°48.2'W	3110	mud with gravel
R.V. Dmitry Mendeleev	48	4093	Sigsbee trawl	05.03.1989	Orkney Trench, 60°42.3'S, 41°14.4'W	3700–3970	mud with gravel
R.V. Dmitry Mendeleev	48	4097	Sigsbee trawl	09.03.1989	Scotia Sea, 60°40.7'S, 54°40.6'W	3060–3100	sandy silt with gravel
R.V. Dmitry Mendeleev	48	4100	Sigsbee trawl	11.03.1989	Bransfield Strait, 62°18.9'S, 56°59.3'W	1265–1376	clay silt with gravel
R.V. Dmitry Mendeleev	48	4103	Sigsbee trawl	29.03.1989	Weddell Sea, 70°42.4'S, 15°38.4'W	4485–4520	mud
R.V. Dmitry Mendeleev	48	4104	Sigsbee trawl	02.04.1989	Weddell Sea, 62°33.4'S, 15°28.1'W	5110–5120	mud

(Fig. 2C–H). There are three girdles, the third one situated 3.5–4 mm behind the two anterior ones. The first two girdles are usually separated by a groove and show a tendency to become spiral in some individuals (Fig. 2C–F). The first and third girdles consist of two halves each, the second girdle is broken once or twice dorsally, but is continuous ventrally. The chaetae form one to three rows and vary considerably in shape and size, even in the same individual (Fig. 2I–K). Most have an elongated head, 10–18 µm long, with a rather narrow anterior end and a toothless intermediate zone near the middle of the head. The anterior group of teeth usually occupies 50–60% of the length of the head. A longitudinal row of four to six papillae is sometimes seen on the ventral side between the two anterior and the third girdles (Fig. 2G). Papillae are also present as a transverse row on the dorsal side near the groove between the first and second girdles and form aggregations on the lateral sides of the body between the girdles (Fig. 2E, G). In all specimens, three or four small papillae are situated on the dorsal side immediately behind the third gir-

dle. All these papillae carry cuticular plaques, which are identical to those in the nonmetameric region. On the postannular region, groups of papillae occur rather close to each other, beginning almost immediately behind the girdles (Fig. 2G, H). Each group comprises a dorso-lateral row of three to four papillae furnished with cuticular plaques and is accompanied by a group of ventral multicellular glands. The papillae are well-separated and the plaques are 13–14 µm across. The opisthosoma is missing in all specimens. Spermatophores have not been found.

**Comparison.** *Siboglinum E. davisense* sp. nov. resembles the following species listed below in having double rings on the segmented tube: *Siboglinum E. fedotovi* Ivanov, 1957, *S. E. silone* Ivanov, 1963, *S. E. ordinatum* Southward, 1981, *S. E. macrobrachium* Southward, 1961, *S. E. sumatrense* Ivanov, 1963 and *S. Varifilum variabile* Ivanov, 1960. With the exception of the latter species, they also share the presence of three girdles of chaetae, well-developed anterior teeth on the chaetal heads and the thick tentacle with pinnules (Ivanov 1957, 1960, 1963; Southward 1961,

1969a, 1980; Ivanov and Gureeva 1973) (see Table 2). As compared with these species, the new species has a noticeably smaller cephalic lobe. Furthermore, *S. E. davisiense* sp. nov. is considerably larger than *S. E. sumatrense*, *S. E. ordinatum* and *S. E. macrobrachium*, and also differs from them in the length of pinnules and in the configuration of the bridle and girdles. The new species, unlike *S. E. macrobrachium*, does not have any zone of enlarged papillae, and, unlike *S. E. silone*, has a considerably smaller number of rings per segment on the tube and lacks glandular patches on the trunk. *Siboglinum E. davisiense* sp. nov. seems to be most similar to *S. E. fedotovi*, from which, however, it differs in the smaller number of rings per segment (four–six to nine–nineteen), the configuration of the girdles (and other structural details of the annular region) and the position of the bridle in the middle of a comparatively short forepart. The chief distinctions of *S. E. davisiense* sp. nov. from *S. Siboglinum meridiale* Ivanov, 1960, co-inhabiting the Davis Sea, lie in the presence of pinnules and also the presence of segments and double rings on the tube (Table 2). The presence of the interannular papillae is not rare, but their peculiar arrangement in *S. E. davisiense* sp. nov. is unknown among other pogonophoran species.

**Distribution.** Davis Sea, Indian Ocean Sector of the Antarctic Ocean (2720–3782 m depth).

***Siboglinum Ekmanifilum scotiense* sp. nov.**  
(Fig. 3)

**Material examined.** R.V. Akademik Kurchatov; station 909: plenty of tubes, partly with animals; st. 914: 22 tubes, including 7 tubes with animals; st. 4882: 30 specimens, 28 empty tubes. R.V. Dmitry Mendeleev; st. 4093: 1 empty tube; st. 4097: several dozen animals and tube fragments. Type material. R.V. Akademik Kurchatov; st. 909, holotype (ZIN HN72) and 3 paratypes (ZIN PN72).

**Etymology.** The specific name refers to the occurrence of *S. E. scotiense* in the Scotia Sea, where this species is widely distributed.

**Description**

**Tube.** The tube is rigid and mainly brown in colour. The anterior end and sometimes the middle parts of the tube are segmented (Fig. 3R–T). The segments are 0.2 to 0.94 mm long (more often 0.3–0.5 mm) and usually each segment has three to six rings

(rarely from two to eleven rings). The segmented part is 15 to 30 mm in length. Anterior rings are regular and narrow (Fig. 3R), and then become somewhat wider and less regular, forming anastomoses and “perforations” in the central zone of each segment (Fig. 3S, T). In the middle part of the tube there are many fibres, and the rings are extremely irregular (Fig. 3V). Posteriorly the rings are better delimited, and there are a few more or less regular “perforations” in the centre of each ring, which sometimes unite so that a doublet is formed (Fig. 3W). Fibres are aggregated mainly in very narrow interspaces between the primary rings and often stand out. The next zone of the tube is again characterised by increasing irregularity in the ring arrangement and structure; finally, in the most posterior part of the tube the rings become regular and much narrower, separated by wide interspaces (Fig. 3X).  $D_{tb}$  0.15–0.26 mm, the longest known fragment measures 150 mm.

**Forepart.** The rather short forepart ( $L_f$  0.7–1.05 mm) is only five to six times longer than its diameter ( $D_f$  0.13–0.2 mm). The large cephalic lobe ( $L_{cl}$  0.2–0.32 mm,  $L_{cl}/D_f \sim 1.65$ ) is wider than the rest of the forepart. There is a groove at the level of the tentacle base, which is more distinct on the dorsal side of the body (Fig. 3A, B). The tentacle is very thick (up to 150  $\mu$ m,  $D_t/D_f \sim 0.74$ ) and has a strongly flattened base that is slightly displaced to the left of the medial line. Small wrinkles and larger folds are frequent on the tentacle surface. Pinnules up to 200  $\mu$ m long form two very dense rows but are missing from the proximal (2–3 mm) part of the tentacle (Fig. 3C). The maximum length of the tentacle is 11.5 mm. The bridle, with brown keels lying on well-developed ridges, is near the middle of the forepart. The ventral keels of the bridle are very close or even touch each other and on the dorsal side of the body the keels are noticeably thicker and are always fused together. Large multicellular glands can be seen by transparency in the coelom behind the bridle (Fig. 3A).

**Trunk.** The main part of the metameric region of the trunk lacks clear papillae and each dorsal ridge carries a row of cuticular plaques on its surface; the plaques are 16.2–29.7  $\mu$ m across with a front rim (Fig. 3P) and they are present throughout the ridges, except on their anterior-most parts (Fig. 3A, D). On each side of the narrow dorsal furrow multicellular glands are arranged in one row, which is bordered by a dark band of glandular epidermis on the ventrolateral side (Fig. 3B). This epidermis also branches

**Table 2.** Main morphological characteristics of the new and some previously described species of *Siboglinum* (in order of appearance in the text).

Species	<i>S. fedotozi</i>	<i>S. silone</i>	<i>S. ordinatum</i>	<i>S. macro-brachium</i>	<i>S. sumatrense</i>	<i>S. variabile</i>	<i>S. davisiense</i>	<i>S. meridiale</i>	<i>S. gareetae</i>
Tube, D <sub>th</sub> (mm)	0.25	0.21–0.25	0.11–0.13	0.1–0.135	0.12–0.135	0.12–0.2	0.19–0.27	0.32–0.35	0.15–0.18
Tube, colour	brown	brown	brown	brown	brown	brown	yellow-brown	yellow-brown	yellow
Tube, character	thin-w, sm	thin-w, sm	thin-w, sm	thin-w, sm	thin-w, sm	thick-w, sm	thin-w, sm	thin-w, wr	thin-w, sm
Tube, segments	+	+	+	+	+	+	+	–	–
Tube, rings (character)	+(double)	+(double)	+(double)	+(double)	+(double)	+(double)	+(double)	+(single)	+(single)
Tube anterior ring/less part/longer than ringed part	–	–	–	–	–	–	–	–	–
Tube, rings regularity	perf	ana	perf, ana	ana	perf	ana	perf, ana	regular	regular
Tube, rings colour	brown	brown	brown	brown	brown	brown	yellow-brown	yellow-brown	yellow
Tube, rings per segment	9–19	16–40	5–8	6–7	7	3–9	4–6	–	–
Tube, ring interspaces concave	–	–	–	–	–	–	–	–	–
Tentacle, D <sub>i</sub> /D <sub>o</sub>	0.43	0.55	0.5–0.57	0.6–0.7	0.53	0.35	0.52	0.16	0.31
Pinnules (length, mm)	+(100)	+(150–350)	+(90)	+(80)	+(70)	–	+(150)	–	+(56)
Cephalic lobe, L <sub>ce</sub> /D <sub>i</sub>	1.29	1.66	1.8	1.56	1.33	1.08	1	0.84	1.45
Forepart, D <sub>i</sub> (mm)	0.17–0.21	0.2–0.25	0.07–0.095	0.09–0.11	0.09	0.13–0.16	0.18–0.2	0.15–0.26	0.15–0.16
Forepart, L <sub>o</sub> /D <sub>i</sub>	7–10	7–11	5.5–10	6–10	9	5–6	5–6	8–9	4–5
Forepart, glandular patches	br belt	br belt	–	–	–	br belt	–	–	–
Forepart multicellular glands visible by transparency (rows)	–	+(many)	–	–	+(3)	–	–	–	–
Forepart, segmental groove	circular	circular	–	–	circular	circular	–	–	–
Bridle, location on forepart	anterior	anterior	middle	anterior	anterior	middle	middle	anterior	middle
Bridle keels, structure	homogeneous	homogeneous	homogeneous	homogeneous	homogeneous	homogeneous	homogeneous	homogeneous	homogeneous
Bridle keels fused d	+	+	+	+	–	+	+	+	+
Bridle keels fused v	–	–	+	+, –	–	–	–	–	–
Trunk met reg, gl pat	–	–	–	–	–	–	–	–	bands
Trunk met reg, cut pl (Ø, mm)	–	–	–	–	–	–	–	–	+(24, 3–27)
Trunk anteriormost part, cut pl	–	–	–	–	–	–	–	–	+
Enlarged papillae	–?	–?	–	3	–?	–	–	?	–
Postannular papillae	?	1	?	–	1	?	3–4	?	–
Postannular cut pl (Ø, mm)	?	+(?)	?	?	+(?)	?	+(14–15)	?	3
Girdle region, papillae (number)	p <sup>3</sup> (1)	p <sup>3</sup> (1)	p <sup>3</sup> (1)	–?	p <sup>3</sup> (1)	–	p <sup>2</sup> (few), p <sup>3</sup> (3–4)	?	+(19–27)
Girdle region, cut pl (Ø, mm)	+(–18)	+(?)	+(?)	–	+(?)	–	+(20–25)	?	–
Girdles, arrangement (mm apart)	2+1 (?)	2+1 (0.7–2.2)	2+1 (0.5–1.7)	2+1 (1–1.5)	2+1 (3.25)	2	2+1 (3.5–4)	?	2+1 (0.9–2.75)
First girdle fused d	+	+	+	+	–	–	–	?	–
First girdle fused v	+	–	–	–?	–	–	–	?	+
Second girdle fused d	+	–	–	–?	–	–	–	?	+
Second girdle fused v	–	+	+	+	–	–	+	?	–
Third girdle fused d	–	–	?	–?	–	–	–	?	–
Third girdle fused v	–	–	?	–?	–	–	–	?	–
Fourth girdle fused d	–	–	–	–	–	–	–	?	–
Fourth girdle fused v	–	–	–	–	–	–	–	?	–
Girdle chaetae, rows	1	1	1	1	1	1–2	1–3	1–2	1
Girdle chaetae, size (mm)	17–23	15–22	12–14	10–12	13–14	9–12	10–18	12–15	13.2–19.2
Girdle chaetae, anterior teeth	++	++	++	++	++	+	++	++	++
Spermatophore, length (mm)	~200	300–380	120–150	120–190	?	?	?	?	?
Spermatophore, add filament	–	–	–	–	?	?	?	?	?

Table 2. Continued.

Species	<i>S. ceylonicum</i>	<i>S. pholidotum</i>	<i>S. longimanus</i>	<i>S. scotiense</i>	<i>S. weberi</i>	<i>S. lacteum</i>	<i>S. arabicum</i>	<i>S. sergeevi</i>	<i>S. debile</i>
Tube, $D_{th}$ (mm)	0.19	0.13–0.16	0.18–0.195	0.15–0.26	0.1–0.135	0.27	0.13	0.3	0.1–0.135
Tube, colour	brown	brown	brown	brown	brown	milk-white	–	–	whitish
Tube, character	thin-w, sm	thick-w, sm	thick-w, sm	thick-w, wr	thin-w, wr	thick-w, wr	thin-w, sm	thin-w, sm	thin-w, sm
Tube, segments	+	+	+	+	–	–	–	–	–
Tube, rings (character)	+	+	+	+	+	–	–	–	–
Tube anterior ringless part longer than ringed part	–	–	–	–	–	–	–	–	–
Tube, rings regularity	ana	ana	ana	perf, ana	ana	–	–	–	–
Tube, rings colour	brown	brown	brown	brown	brown	–	–	–	–
Tube, rings per segment	7–10	2–4	6–10	2–11	–	–	–	–	–
Tube, ring interspaces concave	–	–	–	–	–	–	–	–	–
Tentacle, $D_i/D_j$	0.92	0.63–0.74	0.85	0.74	0.54	0.2	0.3	0.39	0.39
Pinnules (length, mm)	+(200)	+(130–140)	+(200)	+(200)	+(60)	+(50–80)	–	–	+(60–80)
Cephalic lobe, $L_{ce}/D_i$	1.78	1.16	2.1	1.65	1.25	1.11	1.52	1.08	2.33
Forepart, $D_i$ (mm)	0.15–0.18	0.09–0.15	0.1–0.15	0.13–0.2	0.08–0.1	0.25	0.2	0.22–0.25	0.08–0.14
Forepart, $L_i/D_i$	4–8	4–7	6–10	5–6	7–12	9–10	8–9	3	5–11
Forepart, glandular patches	t belt	–	–	–	+, – (br belt)	spots, bands	spots, bands	–	–
Forepart multicellular glands visible by transparency (rows)	+(many)	+, – (1–2)	+(2)	+(3)	–	–	–	–	–
Forepart, segmental groove	–	+, – (circular)	circular	–	circular	+, – (circular)	–	–	–
Bridle, location on forepart	middle	middle	middle	middle	anterior	anterior	anterior	middle	middle
Bridle keels, structure	homogeneous	heterogeneous	homogeneous	homogeneous	homogeneous	homogeneous	homogeneous	homogeneous	heterogeneous
Bridle keels fused d	+	+	+	+	+	–	–	+	+
Bridle keels fused v	–	+, –	–	+, –	–	–	–	+	–
Trunk met reg, gl pat	–	–	–	bands	–	spots, bands	bands	–	–
Trunk met reg, cut pl ( $\emptyset$ , mm)	+(15)	+(17–35)	+(11–12)	+(16.2–29.7)	–	–	–	–	–
Trunk anteriormost part, cut pl	–	+	–	+	–	–	–	–	–
Enlarged papillae	1	–	–?	–	–	2	–	1	–
Postannular papillae	+	2–5	?	4–6	1	3–4	1	1	?
Postannular cut pl ( $\emptyset$ , mm)	+(?)	+(12–26)	?	+(19–24.3)	+(15)	+(15)	–	–	?
Girdle region, papillae (number)	$p^3(1)$	–?	?	$p^3(1)$	$p^2(\text{few})$	$p^3(1)$	$p^3(1)$	$p^2(1)$	–?
Girdle region, cut pl ( $\emptyset$ , mm)	?	?	?	+(24–25)	–	+(40)	–	–	–
Girdles, arrangement (mm apart)	2+1 (1.88)	2+1 (1–2.2)	?	2+1 (5.75–7)	1+1 (0.85–1.2)	2	2	2	2
First girdle fused d	+	–?	?	+	–?	–	–	–	–?
First girdle fused v	+, –	+	?	–	?	–	–	+	?
Second girdle fused d	–	+	?	–	–?	–	–	–	–?
Second girdle fused v	+	–?	?	+, –	?	–	–	–	–?
Third girdle fused d	–	–?	?	–	–	+	+	+	?
Third girdle fused v	+	+	?	–	–	–	–	–	–
Fourth girdle fused d	–	+	?	–	–	–	–	–	–
Fourth girdle fused v	–	–	?	–	–	–	–	–	–
Girdle chaetae, rows	1	1	?	1	1	2–3	1	1–2	1–3
Girdle chaetae, size (mm)	10–17	15–21	?	14.4–16.8	12–15	15–18	13–14	9–12	10–18
Girdle chaetae, anterior teeth	++	++	?	++	++	++	++	++	++
Spermatophore, length (mm)	~220	120–200	~150	168–184.8	40	?	?	?	?
Spermatophore, add filament	–	–	–	–	–	?	?	?	?



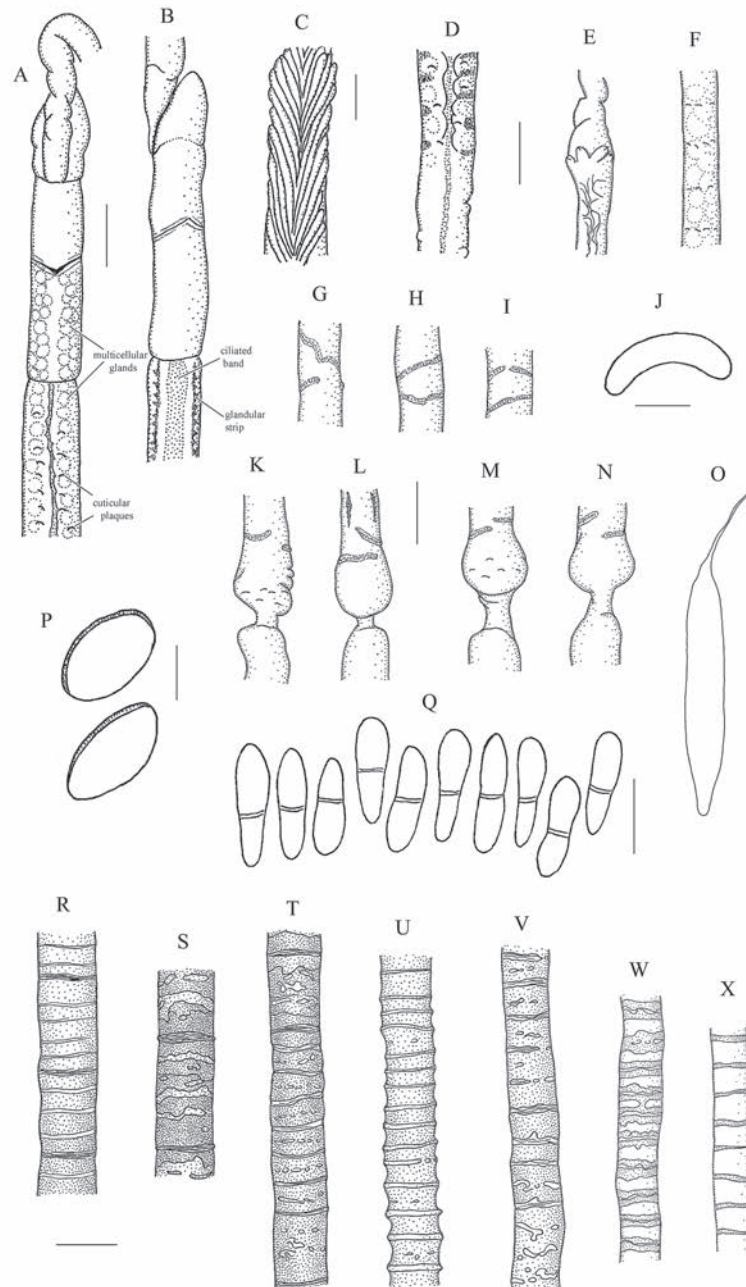
Table 2. Continued.

Species	<i>S. callosum</i>	<i>S. vinculatum</i>	<i>S. pellucidum</i>	<i>S. quadrumulatum</i>	<i>S. minutum</i>	<i>S. inerme</i>	<i>S. oregoni</i>	<i>S. gosnoldae</i>
Tube, D <sub>b</sub> (mm)	0.07–0.12	0.2–0.21	0.13–0.15	0.15–0.3	0.1–0.12	0.13–0.18	0.13–0.16	0.36–0.5
Tube, colour	brown	white	– (yellowish)	– (yellowish)	red-brown	brown	brown	brown
Tube, character	thick-w, sm	thick-w, sm	thin-w, sm	thick-w, wr	thick-w, sm	thin-w, sm	thin-w, sm	thin-w, sm
Tube, segments	+	–	–	–	–	–	–	–
Tube, rings (character)	+ (single)	+ (single)	+ (single)	+, – (single)	+ (single)	+ (single)	+ (single)	+ (single)
Tube, anterior ringless part longer than ringed part	–	–	+	+	–	–	–	–
Tube, rings regularity	perf, ana	regular	regular	ana	ana	ana	perf	regular
Tube, rings colour	brown	white	– (yellowish)	yellowish	red-brown	brown	brown	brown
Tube, rings per segment	3–4	–	–	–	–	–	–	–
Tube, ring interspaces concave	–	–	+	–	–	–	–	+
Tentacle, D <sub>v</sub> /D <sub>t</sub>	0.73	0.33–0.52	0.26	0.46	0.25	0.35	0.25	0.25–0.33
Pinnules (length, mm)	+(23)	+(75–80)	–	–	–	–	+(?)	+(60)
Cephalic lobe, L <sub>v</sub> /D <sub>t</sub>	1.86	1.82	1.47	1.5	1.13	1.06	1.17	1.13
Forepart, D <sub>t</sub> (mm)	0.054–0.069	0.15–0.17	0.1–0.14	0.11–0.25	0.08–0.1	0.14–0.15	0.1–0.115	0.22–0.28
Forepart, L <sub>v</sub> /D <sub>t</sub>	8–13	5–7	6–7	4–10	4.5–5	5–6	13–20	10–12
Forepart, glandular patches	–	–	–	br ring, dia ring	–	+, – (br belt)	br belt	br belt
Forepart multicellular glands visible by transparency (rows)	+(1)	–	+(2–3)	+(3–4)	–	–	–	–
Forepart, segmental groove	circular	circular	circular	+, – (circular)	–	circular	+, – (circular)	oblique
Bridle, location on forepart	middle	middle	middle	middle, anterior	middle	anterior	middle	middle
Bridle keels, structure	homogeneous	homogeneous	heterogeneous	homogeneous	heterogeneous	homogeneous	homogeneous	homogeneous
Bridle keels fused d	+	+	+	+	+	+, –	–	+
Bridle keels fused v	+	+	–	bands	–	–	–	–
Trunk met reg, gl pat	–	–	–	–	–	–	–	bands
Trunk met reg, cut pl (Ø, mm)	–	–	–	–	–	–	–	–
Enlarged papillae	–?	–20	–?	–	5	–?	–?	–
Postannular papillae	? ?	? ?	? ?	1–5	–	1	? ?	4–5
Postannular cut pl (Ø, mm)	? ?	? ?	? ?	+ (20–22)	–	? ?	? ?	+ (?)
Girdle region, papillae (number)	p <sup>3</sup> (3)	p <sup>1</sup> (1), p <sup>2</sup> (1)	? ?	p <sup>3</sup> (few)	p <sup>3</sup> (1)	p <sup>1</sup> (few), p <sup>3</sup> (1)	? ?	p <sup>1</sup> (-16), p <sup>3</sup> (1)
Girdle region, cut pl (Ø, mm)	+(9–10)	+(35–40)	–?	+(20)	+(?)	–?	–?	+(?)
Girdles, arrangement (mm apart)	2+2 (1–2)	2	1+1 (3)	4	2	2–3	1–2+1–2 (0.7–5.4)	2
First girdle fused d	spiral	–	?	–	–	–	–	–
First girdle fused v	spiral	–	?	+	?	– (+)	–	–
Second girdle fused d	spiral	–	?	+	–	–	–	–
Second girdle fused v	spiral	–	?	–	?	– (+)	–	+
Third girdle fused d	–	–	–	–	–	(–)	? ?	–
Third girdle fused v	+	+	+	+	–	(–)	? ?	–
Fourth girdle fused d	+	–	–	–	–	–	–	–
Fourth girdle fused v	–	–	–	–	–	–	–	–
Girdle chaetae, rows	1	2–3	1	1	1	1	1	2–3
Girdle chaetae, size (mm)	10–12	11–13	9–12	14–18	10–11	10–12	12–15	16–19
Girdle chaetae, anterior teeth	++	–	+	+	–	+	++	+
Spermatophore, length (mm)	130	300–314	140	64–80	110–118	50–60	100–130	270
Spermatophore, aed filament	–	–	–	+	–	–	–	+

Table 2. Continued.

Species	<i>S. longicollum</i>	<i>S. subligatum</i>	<i>S. mergophorum</i>	<i>S. caulleryi</i>	<i>S. ekmani</i>	<i>S. fiordicum</i>
Tube, $D_t$ (mm)	0.16–0.19	0.25–0.33	0.195–0.41	0.2–0.3	0.11–0.17	0.21–0.29
Tube, colour	brown	white-greyish	whitish	brown	brown	brown
Tube, character	thin-w, sm	thick-w, sm	thin-w, sm	thin-w, sm	thick-w, sm	thin-w, sm
Tube, segments	–	–	–	–	+	–
Tube, rings (character)	+ (single)	+ (single)	+ (single)	+ (single)	+ (single)	+ (single)
Tube anterior ringless part longer than ringed part	–	–	–	–	–	–
Tube, rings regularity	perf	ana	regular	regular	ana	regular
Tube, rings colour	brown	white-greyish	whitish	brown	brown	brown
Tube, rings per segment	–	–	–	–	5–10	–
Tube, ring interspaces concave	–	–	–	–	–	–
Tentacle, $D_t/D_f$	0.5	0.5	0.62	0.27	0.61–0.87	0.35
Pinnules (length, mm)	+ (25–33)	–	+ (200)	+ (48)	+ (70–83)	+ (39)
Cephalic lobe, $L_{ce}/D_f$	1.4	1.7	1.36	1.58	1.81	1.52
Forepart, $D_f$ (mm)	0.11–0.13	0.16–0.27	0.18–0.21	0.16–0.25	0.1–0.15	0.15–0.3
Forepart, $L_f/D_f$	12–16	8–10	7.5–11.5	6–7	6–9	4.5–9
Forepart, glandular patches	br belt	spots, bands	br belt, band	+, – (br belt)	+, – (br belt)	+, – (br belt)
Forepart multicellular glands visible by transparency (rows)	–	–	–	–	+ (3)	–
Forepart, segmental groove	+, – (circular)	circular	oblique	oblique	+, – (circular)	oblique
Bridle, location on forepart	middle	anterior	middle	middle	middle	anterior
Bridle keels, structure	heterogeneous	homogeneous	homogeneous	homogeneous	heterogeneous	homogeneous
Bridle keels fused d	–	–	+	+	+	–
Bridle keels fused v	–	–	–	–	+, –	–
Trunk met reg, gl pat	–	rings, bands	rings, bands	–	–	–
Trunk met reg, cut pl ( $\emptyset$ , mm)	–	–	–	–	–	–
Enlarged papillae	–	–	7–10	5	–	2–8
Postannular papillae	2–3	1	1–5	1	1–4	2–6
Postannular cut pl ( $\emptyset$ , mm)	+ (5–6?)	–	+ (?)	–?	+ (11.4)	+ (?)
Girdle region, papillae (number)	$p^3(1)$	$p(3-5), p^2(1)$	–	$p(2), p^2(1)$	–	$p(2-3), p^2(1)$
Girdle region, cut pl ( $\emptyset$ , mm)	+ (?)	–	–	–?	–	+ (38)
Girdles, arrangement (mm apart)	2+1 (1.5–2.2)	2	2	2	2+1 (0.8–1.8)	2
First girdle fused d	+	–	–	–	+	–
First girdle fused v	–	+	–	–	–	+
Second girdle fused d	–	–	–	–	–	–
Second girdle fused v	–	+	–	–	–	–
Third girdle fused d	–	+	+	+	+	+
Third girdle fused v	–	–	–	–	–	–
Girdle chaetae, rows	1	2–4	2	2	1	1
Girdle chaetae, size (mm)	12–17	14–16	15–17	15–20	12–19	11–20.7
Girdle chaetae, anterior teeth	++	+	+	+	++	+
Spermatophore, length (mm)	150	300–350	800–830	180	150–178	152–205
Spermatophore, add filament	–	+	–	–	–	–

Notes. + present; – absent; + + strong development; ? unknown or doubtful;  $\emptyset$  diameter;  $s^2$  segmental groove on forepart; t tentacle; br bridle; dia diaphragm between forepart and trunk; thin-w thin-walled tube; thick-w thick-walled tube; sm smooth tube; wr wrinkled tube; perf "perforations" on tube rings; ana anastomoses on tube rings; met reg metameric region of trunk; cut pl cuticular plaques; gl glandular patches; add additional;  $p^1$  papillae just before girdles;  $p^2$  papillae between girdles;  $p^3$  papillae just behind girdles; d dorsal/dorsally; v ventral/ventrally.

*Siboglinum Ekmanifilum scotiense*

**Fig. 3.** *Siboglinum Ekmanifilum scotiense* sp. nov.: A – forepart and anterior part of metameric region of trunk from dorsal side; B – forepart and anterior trunk, ventro-lateral view; C – tentacle with pinnules; D – border area between metameric and nonmetameric regions of trunk, dorsal view; E – dorsal view of groups of papillae from anterior part of postannular region; F – the same from posterior part of postannular region; G – two anterior girdles, dorso-lateral view; H, I – the same in different specimens, ventral view; J – cuticular plaque from postannular region; K, M – third girdle in two specimens, dorsal view; L, N – the same two specimens ventrally; O – spermatophore; P – two cuticular plaques from metameric region; Q – part of girdle (teeth on chaetae not shown); R–X – parts of tube in anterior-posterior series. Scales: A, B, D–I, K–N, R–X – 0.2 mm; C – 0.1 mm; J, P, Q – 10  $\mu$ m; O – 50  $\mu$ m.

between the adjacent glands. In the posterior part of the metameric region the glands are within prominent papillae (Fig. 3D). The length of the metameric region is 3–4 mm and it has a clear boundary with the nonmetameric region, which itself is 25–30 mm long. The latter bears small, scattered dorso-lateral papillae without plaques. There is no zone of enlarged papillae. The third girdle of chaetae is situated far behind the two anterior girdles, at a distance of 5.7–7 mm. The girdle configuration is variable (Fig. 3G–I, K–N). The first is usually oblique and has a gap on the ventral or lateral side, the second girdle is always widely interrupted dorsally, while ventrally its ends touch each other or join together. The third girdle is interrupted both dorsally and ventrally, and both its dorsal and ventral ends may be situated differently in different individuals: either the left end is higher than the right, or vice versa. Two narrow bands of glandular epidermis can be seen on the lateral sides of the body, between the girdles, in some specimens. Behind the third girdle is a huge papilla furnished with a few cuticular plaques (Fig. 3K, M). The plaques have the same structure as those in the metameric region and are 24–25  $\mu\text{m}$  in diameter. The chaetae are in single rows, 14.4–16.8  $\mu\text{m}$  in length, with the anterior teeth very well developed, occupying 45% to 60% of the chaetal head (Fig. 3Q). The front end of the head is usually wider than the hind end. The intermediate zone between the groups of teeth is narrow, but clearly noticeable. The postannular body region begins with a very strong waist behind the single papilla. Metameric groups of papillae appear at a considerable distance behind the girdles and consist of a dorso-lateral, transverse row of four to six papillae furnished with cuticular plaques 19–24.3  $\mu\text{m}$  across, accompanied by a ventral glandular shield (Fig. 3E). The plaques are shaped like curved rods, without a thickened rim (Fig. 3J). In the posterior part of the postannular region the papillae are indistinct and rows of plaques appear to lie directly on the body surface (Fig. 3F). The opisthosoma is missing in all specimens.

In the tubes of a few specimens some rather thick spermatophores with a peculiar, evenly rounded, a filamentar end were found (Fig. 3O). The length of the spermatophores is 168–184.8  $\mu\text{m}$ .

**Comparison.** Among all features of *S. E. scotiense* sp. nov. the most peculiar is the presence of cuticular plaques in the metameric region of the trunk, which is rare in the genus *Siboglinum*. Only four other spe-

cies possess this character: *S. Siboglinum gureevae* sp. nov. (see description below), *S. E. ceylonicum* Ivanov, 1963, *S. E. pholidotum* Southward and Brattegard, 1968 and *S. E. longimanus* Ivanov, 1971 (Ivanov 1963, 1971; Southward and Brattegard 1968) (see Table 2). *Siboglinum E. scotiense* sp. nov. differs from the first of these species by having a relatively thicker wrinkled tentacle with much longer pinnules, a segmented tube and different structure of the rings, and also by a great distance between the girdles and the presence of a particularly large papilla furnished with a few cuticular plaques in the region behind the girdles. *Siboglinum E. pholidotum* lacks papillae within the girdle region, while *S. E. ceylonicum* has a small, plaqueless papilla behind the girdles. *Siboglinum E. scotiense* sp. nov. appears to have the most widely separated girdles among pogonophorans. In the large size of the cuticular plaques on the metameric region and their presence almost throughout the latter, the new species differs from *S. E. longimanus* and approaches closest to *S. E. pholidotum*. The new species also shares with *S. E. pholidotum* the absence of glandular epidermal patches on the forepart and the presence of anastomosing rings on the tube, but it differs from *S. E. pholidotum* in having homogeneous bridle keels and in the presence of glandular epidermal bands on the metameric region, very obvious multicellular glands in the forepart coelom, a longer cephalic lobe and longer pinnules. The tube peculiarities also distinguish the new species.

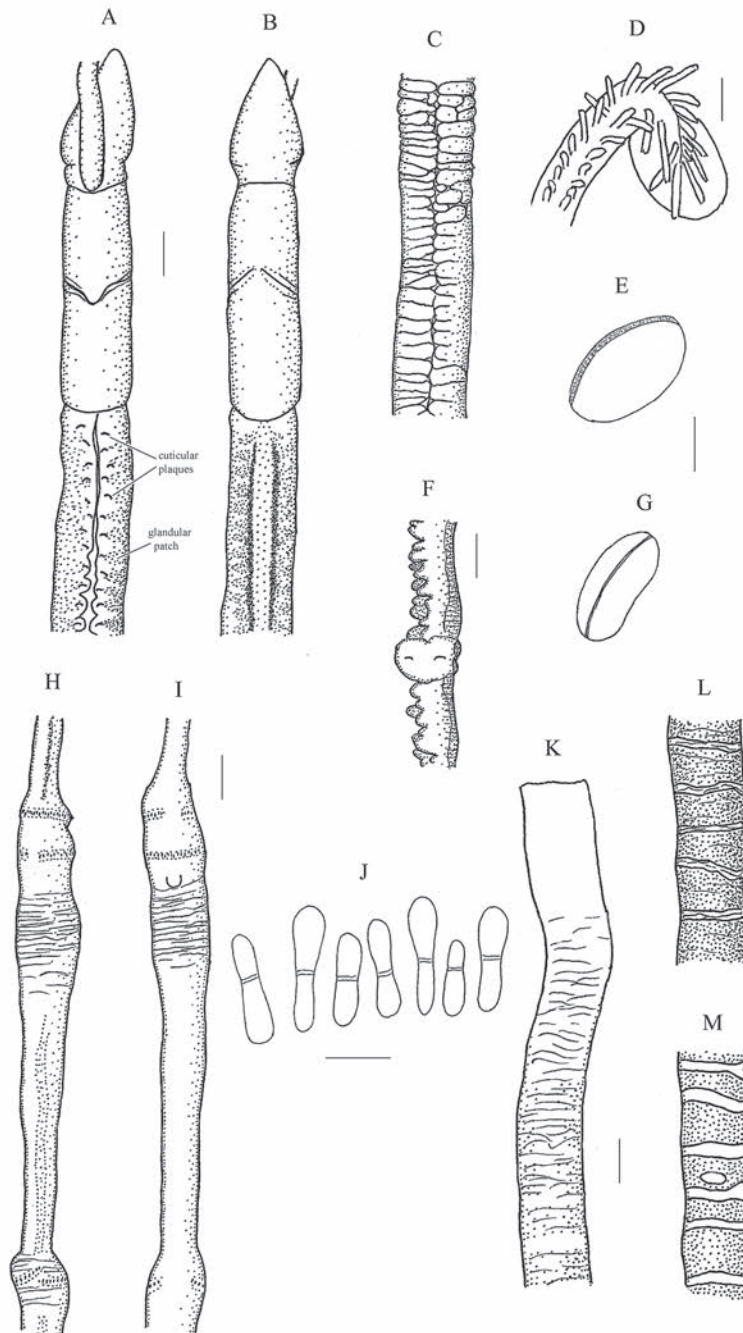
**Distribution.** Scotia Sea (central trench and off northern Elephant Island); Laurie Trench; Orkney Trench (3060–6070 m depth).

#### Subgenus *Siboglinum* Caullery, 1914

*Siboglinum Siboglinum gureevae* sp. nov.  
(Fig. 4)

**Material examined.** R.V. Akademik Kurchatov; station 909: 3 specimens, 5 empty tubes; st. 4882: 21 tubes, including 11 occupied. R.V. Dmitry Mendeleev; st. 4100: 1 specimen, 2 empty tubes. Type material. R.V. Akademik Kurchatov; st. 4882, holotype (ZIN HN73).

**Etymology.** The species is named in honour of Dr Margarita A. Gureeva, a known Russian zoologist and embryologist, in recognition of her considerable contribution to the investigation of Pogonophora.

*Siboglinum Siboglinum gureevae*

**Fig. 4.** *Siboglinum Siboglinum gureevae* sp. nov.: A – forepart and anterior part of trunk, dorsal view; B – forepart and anterior trunk, ventral view; C – posterior part of trunk metameric region, dorsal view; D – tentacle with pinnules; E – cuticular plaque from metameric region; F – postannular group of papillae, dorso-lateral view; G – cuticular plaque from postannular region; H – girdle region, ventral view; I – the same, dorsal view; J – part of girdle (teeth on chaetae not shown); K – tube, anterior part; L – tube, middle part; M – tube, posterior part. Scales: A–C, F, H, I, K–M – 0.1 mm; D – 50  $\mu$ m; E, G, J – 10  $\mu$ m.

## Description

**Tube.** The tube is slender, unsegmented, and entirely transparent. The ringless, anterior filmy end is very short (up to 4 mm), the longest tube fragment reaches 150 mm. A few fibres are present, mainly on the anterior filmy part (Fig. 4K) and in spaces between rings more posteriorly (Fig. 4L). Simple yellow rings with slightly uneven edges appear gradually (Fig. 4K), then become less regular and increase slightly in width, while the interspaces narrow (Fig. 4L, M). The hind part of the tube is uniformly grey in colour, without rings. The largest tube is 0.18 mm in diameter.

**Forepart.** This species has a very short forepart ( $L_f$  0.63–0.77 mm,  $L_f/D_f$  4–5) and a comparatively well-developed cephalic lobe whose maximum width sometimes exceeds the forepart diameter, 0.15–0.16 mm (Fig. 4A, B). The length of the cephalic lobe ranges from 0.21 to 0.24 mm, averaging 1.45  $D_f$ . The thin tentacle (up to 50  $\mu$ m,  $D_t/D_f$  ~0.31) is based medially. On the distal part of the tentacle, whose length reaches 5 mm, there are short (up to 56  $\mu$ m) pinnules forming two close rows (Fig. 4D). Only one groove is consistently present on the forepart, immediately behind the tentacle base. The quite thin yellowish bridle is situated in the middle of the forepart (Fig. 4A, B). The bridle keels are united dorsally and approach each other on the ventral side of the body.

**Trunk.** On the anterior part of the trunk the papillae are unclear, and the narrow dorsal furrow separates two continuous ridges. On each of the ridges cuticular plaques appear just behind the diaphragm in a more or less regular line (Fig. 4A). The plaques are 24.3–27  $\mu$ m across, with a thickened front edge (Fig. 4E). Multicellular glands are arranged in a row within the ridges; below the level of their pores there is a ventro-lateral band of brown glandular epidermis on each side, branching into the spaces between adjacent glands (Fig. 4A, B). The part of the ventral ciliated band nearest to the diaphragm is noticeably narrowed. The rows of plaques and the dorsal furrow end rather suddenly and, thus, the beginning of the nonmetameric region can be detected easily. From there to the girdles the body surface is transversely folded, giving the appearance of papillae (Fig. 4C). Cuticular plaques are absent from the nonmetameric region. The latter is about 5.25 mm in length, slightly more than twice the length of the metameric region (~2.25 mm). There is no zone of enlarged papillae.

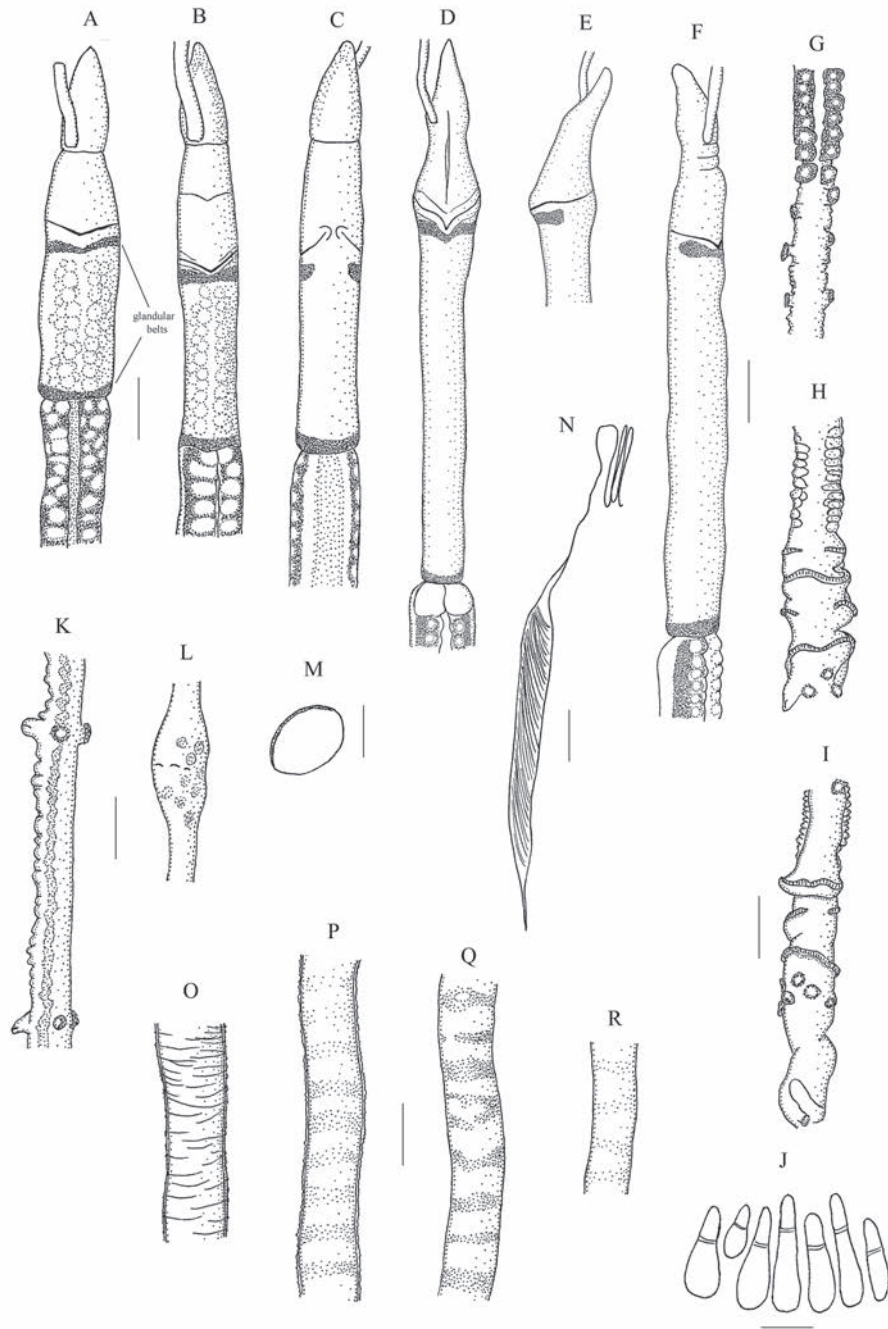
Three girdles of chaetae are arranged in a 2+1 pattern, with a distance of 0.9–2.75 mm between the second and the third ones (Fig. 4H, I). A longitudinal strip of glandular epidermis is visible for some distance before and behind the girdles and sometimes also between them. The first girdle is interrupted on the dorsal side, the second one on the ventral side and the third one on both sides. The heads of the chaetae are distinctly narrowed in the middle and are arranged in a single row in each girdle (Fig. 4J). A clear narrow intermediate zone separates two groups of teeth, of which the anterior one occupies from 40% to 50% of the head length. The front end of the head is wider than the hind end in the majority of chaetae. The chaetal head length varies between 13.2 and 19.2  $\mu$ m. Postannular groups of papillae begin a considerable distance behind the girdles. Each consists of three dorso-lateral, feebly separated papillae, accompanied by an aggregation of multicellular glands on the ventral side (Fig. 4F). Each papilla carries a cuticular plaque 19–27  $\mu$ m in diameter furnished with a medial ridge (Fig. 4G). On the ventral side between the papilla groups, the body surface is strongly wrinkled, and it forms numerous papilla-like folds dorsally. The opisthosoma and spermatophores remain unknown.

**Comparison.** *Siboglinum S. gureevae* sp. nov. belongs to a wide range of species, which are similar to *S. S. weberi* (see Smirnov 2014, Table 2). These species show wide morphological diversity, but all of them share this combination of four characters: well-developed anterior teeth on the chaetal heads, an unsegmented tube, an annular, if present, groove between segments on the forepart and short spermatophores (Caullery 1914a, b, 1944; Ivanov 1957, 1960, 1963, 1971; Southward and Southward 1958; Hartman 1961; Southward 1961, 1972; Cutler 1965; Southward and Brattegard 1968; Flügel and Langhof 1983). Among these species *S. S. gureevae* sp. nov. stands somewhat apart, since it possesses cuticular plaques in the metameric region of the trunk (Table 2).

**Distribution.** Laurie Trench; Scotia Sea (off northern Elephant Island); Bransfield Strait (1265–5480 m depth).

***Siboglinum Siboglinum quadrannulatum* sp. nov.**  
(Fig. 5)

**Material examined.** R.V. Akademik Kurchatov; station 909: 7 empty tubes; st. 4882: 10 tubes, of which 1 contained an animal. R.V. Dmitry Mendeleev; st.

*Siboglinum Siboglinum quadrannulatum*

**Fig. 5.** *Siboglinum Siboglinum quadrannulatum* sp. nov.: A, B, D, F – forepart and anterior part of trunk in different specimens, dorsal view; C – specimen shown in B, ventral view; E – specimen D forepart, lateral view; G – dorsal view of border area between metameric and non-metameric regions of trunk; H – girdle region, dorsal view; I – girdle region, ventral view; J – part of girdle (teeth on chaetae not shown); K – anterior part of postannular region, lateral view; L – posterior part of postannular region, lateral view; M – cuticular plaque from postannular region; N – spermatophore; O–R – parts of tube in anterior-posterior series. Scales: A–I, K, L, O–R – 0.2 mm; J, M, N – 10  $\mu$ m.

4097: numerous tubes, many with animals; st. 4100: 5 specimens and 1 empty tube; st. 4103: 1 empty tube; st. 4104: 1 empty tube. Type material. R.V. Dmitry Mendeleev; st. 4097, holotype (ZIN HN74) and 4 paratypes (ZIN PN74).

**Etymology.** The specific name refers to one of the most striking characters of the species, the number of girdles (from Latin *quattuor* meaning four, and Latin *annulus* meaning girdle).

## Description

**Tube.** The tube is very peculiar (Fig. 5O–R). It lacks segments throughout its length, and rings, if present, are only in the posterior-most part, not less than 45 mm from the anterior end. Only about 20 of several hundred tubes possess the rings. The latter are narrow, irregular yellowish areas (the rest of the tube is colourless) anastomosing infrequently with each other, often discernible only near the tube sides (Fig. 5P, Q). The wall of most of the tube is very thick, with numerous coarse fibres and wrinkles; nevertheless, the tube is entirely transparent. The tubes of juveniles are thin-walled and lack any structure. The anterior part of the tube of mature specimens is 0.15 to 0.3 mm in diameter and the longest fragment, 160 mm, has no rings.

**Forepart.** The forepart is capable of very strong contractions; its length (0.9–1.78 mm) may vary from four to ten times the diameter (0.11–0.25 mm). The shape of the forepart can also vary in different specimens from almost cylindrical to being considerably wider in the area of the bridle than before or behind it (Fig. 5A–F). The cephalic lobe is less variable,  $L_{cl}$  0.21–0.24 mm,  $L_{cl}/D_f \sim 1.5$ . The tentacle lacks pinules and can reach 9 mm in length and 90  $\mu$ m in diameter ( $D_t/D_f \sim 0.46$ ). It is attached distinctly to the left of the mid-line of the body, which is marked by a longitudinal groove. The tentacle surface is smooth or slightly wrinkled. Transverse grooves are variable. The most consistent one is behind the tentacle base. The bridle is situated near the middle of the forepart or anterior to this, depending on the contraction of the animal. The cutaneous-muscular ridges of the bridle are very well developed. The dorsal ends of the bridle keels are joined together, while the ventral ends are separate. There is a narrow glandular belt, white in colour, which is widely interrupted on the ventral side of the body and sometimes slightly divided on the dorsal side (Fig. 5A). Another glandular

belt, complete, is present around the diaphragm level. Behind the bridle large internal multicellular glands, arranged in three to four rows on each side, can easily be seen (Fig. 5A, B).

**Trunk.** The metameric region is represented by a pair of dorsal ridges in which the multicellular glands are seen as very large transparent spots (Fig. 5A, B, F). These are usually arranged in a single row in each ridge, but in some of the largest specimens duplication of the row is observed at the beginning of each ridge. The papillae are unclear. Brown glandular epidermis covers the whole dorsal surface of the ridges, except directly above the multicellular glands; therefore, the latter stand out especially sharply (Fig. 5A, B). In the posterior part of the metameric region the continuous ridges begin to separate, over 0.5–1 mm, into papillae incorporating one gland each (Fig. 5G). In some individuals the papillae are more or less distinct in the anterior part of the trunk too. The papillae possess a peculiar flattened top. The first pair of metameric papillae (genital papillae) in the males is distinguished by its larger size (Fig. 5D). The wide ventral ciliated band begins from either the front border of the trunk or slightly behind it, extending throughout the metameric region, for 3–15 mm. The beginning of the nonmetameric region is marked by the loss of the dorsal furrow and displacement of the papillae first to a lateral position and then to the ventral side (Fig. 5G). The papillae diminish markedly in size but retain their connection with multicellular glands and epidermal unicellular glands, which continue to aggregate on the surface of the papillae, around the internal gland duct pore. There are zones of folded epidermis, glandular shields, between the papillae on the sides of the body. There is no zone of enlarged papillae. The nonmetameric region is 9 to 31.5 mm in length. The girdle region is very characteristic (Fig. 5H, I). Four closely placed girdles of chaetae are situated on well-developed muscular ridges, each on its own ridge. Two girdles (first and third) are interrupted on the dorsal side, while two others (second and fourth) are interrupted ventrally. The ends of each girdle may be separated widely or may nearly touch each other. On both sides of the body, behind the last girdle, there is a group of rounded papillae. Some of these, including the largest mid-dorsal papilla, are furnished with oval cuticular plaques with a thickened front rim, about 20  $\mu$ m across. Juvenile specimens have only two girdles, both interrupted on both sides of the body. The chaetae are in single rows.



The chaetal heads are 14–18  $\mu\text{m}$  in length, narrowed in the middle or closer to the front end (Fig. 5J). There is a clearly visible intermediate zone between the groups of teeth. The anterior group of teeth occupies one-quarter to one-third of the head length, but the anterior teeth are not smaller than the posterior ones. The postannular region begins with a sharp waist behind the girdles. For some distance the body lacks any noteworthy features, then folded glandular epidermis and large conical papillae, with cuticular plaques on their rounded tops, appear on the dorsal side (Fig. 5K). The plaques are similar to those on the girdle region, but are slightly larger, 20–22  $\mu\text{m}$  across (Fig. 5M). Each papilla is opposite a few multicellular glands on the ventral side, each of which usually protrudes into a glandular shield with a flattened top. Unicellular glands form a dark rosette around the pore of the internal gland on the shield tops. The more posterior papilla groups have an entirely different structure. These consist of four to five papillae, which join together to form a continuous ridge with indistinct borders (Fig. 5L). The ridge simply looks like a huge thickening of the body, on whose ventral side several pores of multicellular glands are situated without the shields and glandular epidermis, and on the dorso-lateral sides there is a transverse row of cuticular plaques. The opisthosoma is missing in all specimens.

Tubes and genital ducts of many animals contained genital products. The spermatophores are narrow, with filaments on both ends, one much longer than the other (Fig. 5N). The length of the spermatophores (including the additional filament) varies between 64 and 80  $\mu\text{m}$ .

**Comparison.** The systematic affinities of *S. S. quadrannulatum* sp. nov. within the genus *Siboglinum* are somewhat doubtful. Certain features of the tube, tentacle, girdles, postannular region and spermatophore are considered characteristic of this species. Among the tube peculiarities, the very long ringless part, many times longer than the ringed part, deserves attention. In this *S. S. quadrannulatum* sp. nov. resembles *S. Taeniafilum lacteum* Southward, 1963, *S. T. arabicum* Ivanov, 1963, *S. Subtilifilum sergeevi* Ivanov, 1963 and *S. S. debile* Southward, 1961, all of which, however, have completely ringless tubes, and partly *S. Siboglinum pellucidum* Ivanov, 1957, which has a very long ringless part and almost colourless rings (Southward 1961, 1963; Ivanov 1963) (see Table 2). The tube in all these species, except for the

first, is thin-walled, and *S. S. pellucidum* differs additionally by having concave spaces between the rings and very regular rings. *Siboglinum T. lacteum* has a thick-walled and wrinkled tube, which, nevertheless, differs in being milk-white in colour. It seems to me that the tube of *S. S. quadrannulatum* sp. nov. corresponds best to a few unidentified empty tube fragments from the equatorial part of the Pacific Ocean (Milne-Edward Basin) (Ivanov 1971).

One of the most striking morphological features of the animal is the placement of the tentacle base to the left of the body mid-line. There is a slight shift in a few other *Siboglinum* species, but the shift is much greater in *S. S. quadrannulatum* sp. nov.

The number and arrangement of the girdles of *S. S. quadrannulatum* sp. nov. is very unusual. Only one other species has four distinct girdles: in *S. Spirannulifilum callosum* Ivanov, 1971, two anterior girdles are twisted spirally around the trunk, while two posterior ones are placed far behind them but close to one another (Ivanov 1971) (see Table 2). Four girdles could have originated in some ancestral form by separation of each of the two primary girdles into halves, which is in fact recapitulated in ontogeny of *S. S. quadrannulatum* sp. nov. The same tendency is observed in a few biannular species: *S. Subtilifilum vinculatum* Ivanov, 1960, *S. Minifilum minutum* Ivanov, 1957, *S. Siboglinum inerme* Southward and Southward, 1958, for example, with respect to one of the girdles, and in *S. S. oregoni* Southward, 1972, with respect to both girdles (Southward and Southward 1958; Ivanov 1963; Southward 1972). The girdles of *S. S. oregoni* were not figured by Southward (1972) and their arrangement and configuration are somewhat obscure. It is not unlikely that *S. S. oregoni* has indeed two pairs of separate girdles. However, only *S. S. quadrannulatum* sp. nov. has four girdles close together, with each girdle situated on its own muscular ridge and not touching adjacent girdles.

*Siboglinum S. quadrannulatum* sp. nov. shows rare variability in the arrangement of the papillae in the postannular region of the trunk. Single papillae coexist with transverse rows of four–five papillae in one individual. Only two other species share this feature, *S. Mergofilum mergophorum* Nielsen, 1965 and *S. Ekmanifilum ekmani* Jägersten, 1956 (Nielsen 1965; Webb 1964). Single or double papillae are more characteristic for *Siboglinum* species; however, papillae in rows are also known, e.g., in *S. E. pholidotum*, *S. E. scotiense* sp. nov., *S. E. davisiense* sp. nov., *S. Nereili-*

*noides gosnoldae* Southward and Brattegard, 1968, *S. Siboglinum longicollum* Southward and Brattegard, 1968 and *S. S. gureevae* sp. nov. (Southward and Brattegard 1968) (see Table 2).

The spermatophore of *S. S. quadrannulatum* sp. nov. is rather short, but has an additional filament found also in a few species similar to *S. Taeniafilum subligatum* Ivanov, 1963 (Table 2; see also Smirnov 2014, Table 2).

I consider the characters of the spermatophore, girdles and tube to have a high significance. Thus, I conclude that the new species, standing somewhat apart from the previous species, has a combination of characters that is shared by *S. S. gureevae* sp. nov. and other species similar to *S. S. weberi* (see the remarks on *S. S. gureevae* sp. nov.).

**Distribution.** Laurie Trench; Scotia Sea (off northern Elephant Island); Bransfield Strait; Weddell Sea (1265–5480 m depth).

## DISCUSSION

In spite of increased research on the benthos in the Antarctic seas, our knowledge of the pogonophoran fauna of the Southern Ocean is still very fragmentary. Until recently, only two species were recorded from this enormous basin: *Siboglinum S. meridiale* from the Davis Sea and *Spirobrachia leospira* Gureeva, 1975 from the South Sandwich Trench (Ivanov 1960; Gureeva 1975).

The finding of *Spirobrachia orkneyensis* Smirnov, 2000 in the Orkney Trench and the redescription of *S. leospira* and other congeneric species provided the basis for a revision of the genus *Spirobrachia* Ivanov, 1952 and the erection of a new genus, *Volvobrachia* Smirnov, 2000 (Smirnov 2000a, b).

Further study of the material obtained on the Russian Antarctic expeditions in 1971–1986 to the Atlantic Ocean Sector of the Antarctic contributed to our knowledge of pogonophorans of the Southern Ocean. The description of four new species in the genus *Polarsternium* Smirnov, 1999 and two new species in the genus *Polybrachia* Ivanov, 1952 (see the key to the Antarctic species of Pogonophora below) somewhat increased our knowledge of the morphology and biodiversity of Antarctic pogonophorans (Smirnov 2005a, b). However, all these materials, apart from a few samples from the Davis Sea, are limited to the Atlantic part of the Antarctic Ocean. The present study shows that these two widely separated areas of the

Antarctic, the Davis Sea and the Scotia Sea with the neighbouring basin, appear to be inhabited by different species (Fig. 1). In the Davis Sea only one species, *Siboglinum E. davisense* sp. nov., was obtained, and *Siboglinum S. meridiale*, which was described from this region by Ivanov (1960), was not found.

Each new species described in this paper has some morphological characters which are rare or even unique among the congeners. Two species, *S. S. gureevae* and *S. E. scotiense* spp. nov., possess cuticular plaques on the metameric region of the trunk, and the latter species is also characterised by an extremely long distance (up to 7 mm) between the girdles. A transverse row of interannular papillae occurs in *S. E. davisense* sp. nov., while *S. S. quadrannulatum* sp. nov. has four separate girdles of chaetae, a remarkable leftward shift of the tentacle base, and both main types of arrangement of postannular papillae (in rows and singly).

Little attention has been paid to the placement of the tentacle base in unitentaculate pogonophorans. Following Webb (1964, 1969), Ivanov (1994) and Southward (1999), the tentacular crown of Pogonophora develops from two primary tentacles, which are placed symmetrically to the left and the right of the forepart mid-line. One of these tentacles probably fails to develop in representatives of the genera *Siboglinum*, *Polarsternium* and *Unibrachium* Southward, 1972, while e.g. the genus *Siboglinoides* Ivanov, 1961, which is close to *Siboglinum*, retains two tentacles (Ivanov 1961, 1963). It is worth noting that atypical bitentaculate specimens, probably atavistic, were recorded in two species of *Siboglinum*, *S. Taeniafilum leucopleurum* Flügel and Callsen-Cencic, 1993 and *S. Nereilinoidea fiordicum* Webb, 1963 (Flügel and Callsen-Cencic 1993; Southward pers. comm.). However, Hilário et al. (2010) imply that some of the unidentified unitentaculate specimens in their collection may have been misclassified as *Siboglinum*, though these are likely related to multitentaculate clades. For example, multitentaculate *Polybrachia canadensis* Ivanov, 1962 passes indeed through unitentaculate stage in its ontogeny (Southward 1969b). In most species of unitentaculate genera the base of the single tentacle is situated in the mid-line of the body, but in a few species of *Siboglinum* and *Polarsternium* the tentacle has a more or less distinct leftward shift. In addition, the tentacle in *Siboglinum* is innervated asymmetrically from the left side of the brain (Ivanov 1963). Thus, the tentacle of *Siboglinum* probably

originates from the ancestral left tentacle and the leftward shift of the tentacle base is plesiomorphic for, at least, the genus *Siboglinum*. The type of arrangement of the postannular papillae was one of the main diagnostic characters of the orders in frenulates (Ivanov 1963). *S. S. quadrannulatum* sp. nov. provides evidence of a low taxonomic value of this character, as was previously stated by several authors (Nielsen 1965; Bubko 1970; Southward 1971b). Certainly, the origin of these characters would be interesting to test in the future through phylogenetic analysis.

The genus *Siboglinum* now includes 72 species (with the four new ones described here), comprising about half the species of all pogonophorans; it has the most complicated systematic structure among all pogonophoran genera. A recent review of the genus *Siboglinum* by Smirnov (2014) has resulted in the division of the genus into nine subgroups of a subgeneric value. The most valuable characters useful for distinguishing the subgenera have been defined (Smirnov 2014); these concern the disposition of opaque glandular areas on the forepart, the relative development of anterior teeth on chaetal heads, the number, shape and disposition of the girdles of chaetae, the shape of the segmental groove on the forepart (when present), the length and details of structure of the spermatophore, the colour of the tube, the presence or absence of segments (together with rings or separately) on the tube, the relative thickness of the tentacle and the presence of pinnules on the tentacle (Table 3). The subgenus *Mergofilum* Smirnov, 2014 (a single species, *S. M. mergophorum*) and the subgenus *Taeniafilum* Smirnov, 2014 (nine species), typified by *S. T. subligatum*, are characterised by the presence of one or two peculiar ribbons of opaque glandular epidermis on the forepart (Ivanov 1963; Nielsen 1965). The diagnostic character of the subgenus *Nereilinoidea* Smirnov, 2014 (six species), typified by *S. N. cauleryi* Ivanov, 1957, is the oblique position of the segmental groove on the forepart (Ivanov 1963). Spiral anterior girdles of chaetae characterise the subgenus *Spirannulifilum* Smirnov, 2014 (two species), typified by *S. S. callosum* (Ivanov 1971).

The other subgroups are distinguished by combinations of features. The species of the subgenus *Subtilifilum* Smirnov, 2014 (eight species), typified by *S. S. vinculatum*, possess a peculiar white or colourless tube, spermatophores with a very thick filament base and lack the anterior group of teeth on their chaetal heads (or it is rudimentary) (Ivanov 1963).

The diagnostic set of features for the subgenus *Variifilum* Smirnov, 2014, a single species *S. V. variabile*, is the following: a thin tentacle without pinnules, two annular girdles of chaetae, feebly developed anterior teeth on the chaetal heads and a ringed and segmented tube (Ivanov 1963). The subgenus *Minifilum* Smirnov, 2014, a single species *S. M. minutum*, is distinguished by the absence of anterior teeth on the chaetal heads and by the peculiar red-brown colour of the tube (Ivanov 1963).

The largest and most variable subgenus *Siboglinum* is typified by *S. S. weberi*, the type species of the genus *Siboglinum*. Twenty eight species are characterised by an unsegmented tube, well-developed anterior teeth on the chaetal heads, thin and short spermatophores and by a transverse (if present) groove between the segments on the forepart (Caulery 1914a, b, 1944; Ivanov 1957, 1960, 1963, 1971; Southward and Southward 1958; Southward 1961, 1972; Hartman 1961; Cutler 1965; Southward and Brattegard 1968; Flügel and Langhof 1983). *Siboglinum S. gureevae* and *S. S. quadrannulatum* spp. nov. share these characteristics. This subgenus may be polyphyletic, but for the present I am unable to find characters on the basis of which it can be further subdivided.

The subgenus *Ekmanifilum* is typified by *S. E. ekmani*. Sixteen species of *Siboglinum*, including *S. E. davisense* and *S. E. scotiense* spp. nov., are similar in having three annular or initially spiral girdles of chaetae, which are arranged in a 2+1 pattern, i.e. the third girdle is situated at a distance behind the two anterior girdles; there are very well developed anterior teeth on the chaetal heads, occupying about half of the head length; a thick (in relation to forepart diameter) tentacle furnished with pinnules and a ringed and segmented tube (Jägersten 1956; Ivanov 1957, 1960, 1963, 1970, 1971; Southward 1961, 1971a, 1980; Southward and Brattegard 1968; Gureeva 1981; Flügel 1990).

Southward and Brattegard (1968) proposed that *S. pholidotum* and *S. ceylonicum* (in this subgenus *Ekmanifilum*), together with other plaque-bearing species might be excluded from the genus *Siboglinum*. However, these two species have more in common with *S. longimanus* and *S. scotiense* sp. nov. (both from the same subgenus *Ekmanifilum*), than with the plaque-bearing *S. gureevae* sp. nov. (subgenus *Siboglinum*) (see remarks on *S. E. scotiense* sp. nov.). There are no specific characters, except for the presence of

**Table 3.** Diagnostic characters of *Siboglinum* subgenera.

Subgenus	<i>Mergofilum</i>	<i>Taeniafilum</i>	<i>Nereilinoides</i>	<i>Spirannulifilum</i>	<i>Subtilifilum</i>	<i>Variifilum</i>	<i>Minifilum</i>
Type species	<i>S. mergophorum</i>	<i>S. subligatum</i>	<i>S. caulleryi</i>	<i>S. callosum</i>	<i>S. vinculatum</i>	<i>S. variabile</i>	<i>S. minutum</i>
Tube, colour	white	white, yellowish, -	brown	brown, yellow	white, -	brown	red-brown
Tube, rings	+	+, -	+	+	+, -	+	+
Tube, segments	-	+, -	-	+	-	+	-
Tube, segments combined with rings		-		+		+	
Tentacle, $D_v/D_t$ (average)	0.62	0.2–0.5 (0.32)	0.25–0.63 (0.41)	0.7–1.2 (0.96)	0.28–0.65 (0.41)	0.35	0.25
Pinnules	+	+, -	+	+	+, -	-	-
Forepart, glandular bands (number)	+ (1)	+ (2)	-	-	-	-	-
Forepart, glandular sports anterior to bridle	-	+	-	-	-	-	-
Forepart, glandular belt	+	-	+, -	-	+, -	+	-
Forepart, segmental groove	oblique	+, - (circular, oblique)	oblique	+, - (circular)	+, - (circular)	circular	-
Forepart, $L_v/D_t$ (average)	7.5–11.5 (9.5)	7–14 (9.8)	4.5–12 (7.6)	8–13 (10.5)	3–11 (5.9)	5–6 (5.5)	4.5–5 (4.7)
Trunk, enlarged papillae	+	+, -	+	-	+, -	-	+
Girdles, arrangement	2	2, 3	2	2+1, 2+2	2	2	2
Girdles, shape	annular	annular	annular	spiral	annular	annular	annular
Girdle chaetae, anterior teeth (% of head length)	+ (-30)	+ (-30)	+ (-35)	+ (35–50)	+, - ( $\leq 20$ )	+ (-25)	-
Spermatophore, length (mm)	800–830	240–500	140–270	130–160	145–314	?	110–118
Spermatophore, thick filament base	+	-	-	-	+	?	+
Spermatophore, additional filament	-	+	-	-	-	?	-
Spermatophore, lanceolate appendix	-	-	-	-	-	?	+
Spermatophore, transparent terminal zones	-	-	+	-	-	?	-

**Table 3.** *Continued.*

Subgenus	<i>Siboglinum</i>	<i>Ekmanifilum</i>
Type species	<i>S. weberi</i>	<i>S. ekmani</i>
Tube, colour	brown, yellow, -	brown, yellow, red
Tube, rings	+, -	+
Tube, segments	-	+
Tube, segments combined with rings		+, -
Tentacle, $D_v/D_t$ (average)	0.16–0.58 (0.37)	0.43–1.0 (0.73)
Pinnules	+, -	+
Forepart, glandular bands (number)	-	-
Forepart, glandular sports anterior to bridle	-	-
Forepart, glandular belt	+, -	+, -
Forepart, segmental groove	+, - (circular)	+, - (circular)
Forepart, $L_v/D_t$ (average)	3.5–20 (8)	2.5–11 (7.1)
Trunk, enlarged papillae	+, -	+, -
Girdles, arrangement	2, 3, 4, 1+1, 2+1, 1+2, 2+2	2+1
Girdles, shape	annular	annular, initially spiral
Girdle chaetae, anterior teeth (% of head length)	+ (25–50)	+ (30–60)
Spermatophore, length (mm)	40–160	110–380
Spermatophore, thick filament base	-	-
Spermatophore, additional filament	+, -	-
Spermatophore, lanceolate appendix	-	-
Spermatophore, transparent terminal zones	-	-

*Note.* Same abbreviations as in Table 2.

the plaques, which might distinguish all these species from the affiliate species in the subgenera *Siboglinum* and *Ekmanifilum* (see Table 2). In my view, this feature has lower taxonomic significance, than some other features, e.g. the presence of a segmented tube (Table 3).

Halanych et al. (2001) have published molecular data showing that *S. ekmani* (subgenus *Ekmanifilum*) may be distinct from *S. fiordicum* (subgenus *Nereilinoides*) at the generic level. In my opinion, the known morphological differences between these two species of the genus *Siboglinum* do not support such a conclusion at present (see Table 2). Hilário et al. (2010) have analysed mitochondrial cytochrome-c-oxidase subunit 1 (CO1) sequences of numerous unidentified frenulate specimens in a new collection from mud volcanoes in the Gulf of Cadiz. Fifteen lineages were distinguished and grouped in five clades. Six of the eight unitentaculate lineages were grouped together in clade I, but two unitentaculate lineages appeared to be related to multitentaculate genera in other clades. Certainly, the morphological definitions of the subgenera must be confirmed by molecular information, which is insufficient at present but will be important if and when data can be obtained.

**Key to the subgenera of the genus *Siboglinum***

For explanations of all morphological features not illustrated in this paper, see Ivanov (1963), Smirnov (2000b, 2005a, b) and Southward et al. (2005).

- 1a. One or two longitudinal dorso-lateral opaque glandular ribbons behind bridle (frenulum) on forepart . . . . . 2
- 1b. No longitudinal glandular ribbons on forepart . . . . . 3
- 2a. One post-frenular elevated Y-shaped glandular ribbon on forepart. No glandular patches anterior to bridle on forepart . . . . . *Mergofilum*
- 2b. Two post-frenular glandular ribbons and two pre-frenular glandular spots on dorsal side of forepart . . . . . *Taeniafilum*
- 3a. Tube unsegmented. Rings, if present, white, sometimes with slightly brownish tinge. Unringed tube colourless or whitish. Anterior group of teeth on chaetal heads of girdles occupies less than one-quarter of head length (up to 20%), or absent . . . . . *Subtilifilum*
- 3b. Tube ringed, not infrequently also segmented. Rings yellow, red, brown or, rarely, colourless. Anterior group of teeth on chaetal heads of girdles, if present, occupies not less than one-quarter of head length . . . . . 4
- 4a. Tube segmented, at least anteriorly . . . . . 5
- 4b. Tube unsegmented . . . . . 7

- 5a. Tentacle thin ( $D_v/D_f \sim 0.35$ ), without pinnules. Each papilla in two rows on anterior part of trunk contains two multicellular glands. Two girdles of chaetae arranged close together. Anterior group of teeth on chaetal heads of girdles occupies about one-quarter of head length . . . . . *Varifilum*
- 5b. Tentacle thick ( $D_v/D_f 0.43-1.2$ ), with pinnules. Multicellular glands form one row on each side of dorsal furrow in anterior part of trunk, where papillae, if present, contain one gland each. Three or four girdles of chaetae arranged in 2+1 or 2+2 patterns. Anterior group of teeth on chaetal heads of girdles occupies 30 to 60% of head length . . . . . 6
- 6a. Two anterior girdles of chaetae distinctly spiral (not less than two full turns of spire). Main part of tube very rigid, thick-walled, brittle. Rings with very regular "perforation" . . . . . *Spirannulifilum*
- 6b. Girdles of chaetae usually annular, otherwise initially spiral with no more than 1.5 turns of spire. Tube medium-rigid or soft. Ring "perforation", if present, irregular . . . . . *Ekmanifilum*
- 7a. Segmental groove on forepart oblique . . . . . *Nereilinoides*
- 7b. Segmental groove on forepart transverse or absent . . . . . 8
- 8a. Cephalic region distinctly trilobed. No anterior group of teeth on chaetal heads of girdles. Postannular region of trunk has no serial papillae . . . . . *Minifilum*
- 8b. Cephalic lobe simple. Anterior group of teeth on chaetal heads of girdles occupies not less than one-third of head length. Papillae usually present in postannular region of trunk . . . . . *Siboglinum*

**Key to the species of Antarctic pogonophorans**

Thirteen species of Pogonophora are currently found in the Southern Ocean: *Siboglinum Siboglinum meridiale* Ivanov; *S. S. gureevae* sp. nov.; *S. S. quadrannulatum* sp. nov.; *S. Ekmanifilum davisense* sp. nov.; *S. E. scotiense* sp. nov.; *Polarsternium mirabile* Smirnov, 2005; *P. evrikae* Smirnov, 2005; *P. magnum* Smirnov, 2005; *P. australe* Smirnov, 2005; *Spirobrachia leospira* Gureeva; *S. orkneyensis* Smirnov; *Polybrachia macrolamellosa* Smirnov, 2005; *P. romanovi* Smirnov, 2005.

- 1a. One tentacle . . . . . 2
- 1b. More than one tentacle . . . . . 10
- 2a. Multicellular glands form three to five rows on each side of dorsal furrow in anterior part of trunk . . . . . (*Polarsternium*) . . . . . 3
- 2b. One or two rows of multicellular glands on each side of dorsal furrow in anterior part of trunk . . . . . (*Siboglinum*) . . . . . 6
- 3a. Bridle in posterior third of forepart, with strongly developed, thick keels on heavy muscular ridges. Bridle keels fused both dorsally and ventrally. No glandular patches on forepart. Segmental groove between fore-

- part and trunk absent. Tube lacks segments and rings . . . . . *Polarsternium mirabile*
- 3b. Bridle in anterior half or nearly in middle of forepart. Bridle keels thin, but straight and well-marked, split on ventral side of body. Glandular patches on forepart. Segmental groove between forepart and trunk well-marked. Tube ringed, sometimes also segmented . . . . . 4
- 4a. Tentacle attaches in body mid-line. Cephalic lobe large ( $L_{cl}/D_f \sim 1.8$ ). Glandular belt complete behind bridle ventrally on forepart. Multicellular glands of forepart not visible in transmitted light. Cuticular plaques 21–33  $\mu\text{m}$  across on preannular and annular regions of trunk. About thirty enlarged papillae. Tube rings single, regular . . . . . *Polarsternium evrikae*
- 4b. Tentacle base has leftward shift. Cephalic lobe comparatively small ( $L_{cl}/D_f < 1.3$ ). Glandular belt split behind bridle ventrally on forepart. Multicellular glands of forepart can be seen clearly by transparency. Cuticular plaques, if present on preannular or annular regions of trunk, 15  $\mu\text{m}$  or less across. No zone of enlarged papillae. Rings in middle part of tube double and/or irregular . . . . . 5
- 5a. Pinnules absent from tentacle. Two glandular belts on forepart behind bridle and near trunk border.  $D_f < 0.25$  mm,  $L_f < 1.5$  mm. Multicellular glands on each side of dorsal furrow in several rows at  $\sim 1$  mm of anterior part of trunk. Distance between third and two anterior girdles of chaetae less than 2 mm. First girdle split dorsally, second girdle split ventrally and complete dorsally. Three to five papillae furnished with cuticular plaques immediately behind third girdle. Postannular papillae with cuticular plaques 13–14  $\mu\text{m}$  across. Spermatophores  $< 150$   $\mu\text{m}$  in length. Single rings in anterior part of tube and double rings in other parts of tube. Both single and double rings  $\sim 1/2 D_{tb}$  in width. Tube unsegmented . . . . . *Polarsternium australe*
- 5b. Tentacle with pinnules. One glandular belt on forepart behind bridle.  $D_f > 0.4$  mm,  $L_f \sim 3$  mm. Multicellular glands on each side of dorsal furrow in several rows throughout metameric part of trunk (at  $\sim 10$  mm). Distance between third and two anterior girdles of chaetae  $\sim 3.1$  mm. First girdle complete dorsally, second girdle split dorsally and complete ventrally. One unarmed papilla immediately behind third girdle. Postannular papillae with cuticular plaques 40–45  $\mu\text{m}$  across. Spermatophores  $> 300$   $\mu\text{m}$  in length. Tube rings single, narrow ( $1/5$ – $1/6 D_{tb}$ ). Anterior filmy, unringed part of tube with segments . . . . . *Polarsternium magnum*
- 6a. Segments in anterior and middle parts of tube. Double and/or strongly “perforated” rings in middle and/or posterior parts of tube . . . . . (*Ekmanifilum*) . . . . . 7
- 6b. Segments absent from tube. Tube rings single, regular . . . . . (*Siboglinum*) . . . . . 8
- 7a. Cephalic lobe large ( $L_{cl}/D_f \sim 1.65$ ). Multicellular glands of forepart visible by transparency. Cuticular plaques and glandular ventro-lateral strips on metameric part of trunk. First girdle of chaetae interrupted ventrally. Distance between third and two anterior girdles of chaetae 5.7–7 mm. One large papilla furnished with several cuticular plaques immediately behind third girdle. Postannular papillae with cuticular plaques 19–24.3  $\mu\text{m}$  across . . . . . *Siboglinum E. scotiense*
- 7b. Cephalic lobe small ( $L_{cl}/D_f \sim 1$ ). Multicellular glands of forepart not visible in transmitted light. Cuticular plaques and glandular patches absent from metameric part of trunk. First girdle of chaetae interrupted on both ventral and dorsal sides of body. Distance between third and two anterior girdles of chaetae 3.5–4 mm. Several small papillae, each furnished with one cuticular plaque, immediately behind third girdle. Postannular papillae with cuticular plaques 14–15  $\mu\text{m}$  across . . . . . *Siboglinum E. davisiense*
- 8a. Tentacle attaches in body mid-line. Pinnules in two rows on tentacle. Cuticular plaques on metameric part of trunk . . . . . *Siboglinum S. gureevae*
- 8b. Tentacle base has leftward shift. Pinnules absent from tentacle. No cuticular plaques on metameric part of trunk . . . . . 9
- 9a. Cephalic lobe very small ( $L_{cl}/D_f \sim 0.84$ ). Multicellular glands of forepart not visible in transmitted light. Glandular patches absent from body. Anterior unringed part of tube not more than 25 mm long . . . . . *Siboglinum S. meridiale*
- 9b. Cephalic lobe comparatively large ( $L_{cl}/D_f \sim 1.5$ ). Multicellular glands of forepart visible by transparency. Glandular belts behind bridle and near trunk border on forepart, and dorso-lateral glandular strips on metameric part of trunk. Anterior unringed part of tube not less than 45 mm long . . . . . *Siboglinum S. quadrannulatum*
- 10a. Ten to fifteen free tentacles arranged in a circle.  $D_f < 0.5$  mm. No papillae on ventro-lateral sides of trunk. Dorsal papillae on trunk lack pulvilli. Cuticular plaques on anterior part of trunk have regular anterior thickened edge with pointed ends. Spermatophores wide, without wings . . . . . (*Polybrachia*) . . . . . 11
- 10b. About thirty or more tentacles fused together into a spiral plate.  $D_f > 0.6$  mm. Papillae on ventro-lateral sides of trunk. Dorsal papillae on trunk with pulvilli. Cuticular plaques on anterior part of trunk have bow-shaped anterior thickened edge with rounded ends. Spermatophores narrow, with narrow lateral wings below base of filament . . . . . (*Spirobrachia*) . . . . . 12
- 11a. Bridle keels homogenous, split on both sides of body. Cephalic lobe very large ( $L_{cl}/D_f \sim 2$ ).  $D_f \sim 0.25$  mm,  $L_f/D_f \sim 8$ . Cuticular plaques 21–33  $\mu\text{m}$  across on all papillae in metameric part of trunk . . . . . *Polybrachia romanovi*
- 11b. Bridle keels heterogenous, split on ventral side of body. Cephalic lobe comparatively small ( $L_{cl}/D_f \sim 1.2$ ).  $D_f$  0.37–0.45 mm,  $L_f/D_f$  3.5–4.5. Metameric papillae, except for anterior unarmed 8–11 pairs, have cuticular plaques 50–88  $\mu\text{m}$  across . . . . . *Polybrachia macrolamellosa*

- 12a. Less than fifty tentacles. No lophophore. No pinnules on tentacles. Spiral of tentacular plate makes no more than 2 turns. Papillae on posterior part of trunk preannular region grouped into dorsal clusters alternating with zones without papillae. Cuticular plaques 54–66 µm across on anterior part of trunk and ~68 µm across on postannular region of trunk. Three to ten enlarged papillae. Chaetae of girdles in 2–3 rows. Tube yellow-greenish, transparent, soft. Anterior filmy part of tube not less than 30 mm long . . . . . *Spirobrachia leospira*
- 12b. More than fifty tentacles, attached partly on lophophore. Tentacles with pinnules. Spiral of tentacular plate makes 3–4 turns. No clusters of dorsal papillae on trunk. Cuticular plaques ~82 µm across on anterior part of trunk and 78–88 µm across on postannular region of trunk. Several dozen enlarged papillae. Chaetae of girdles in 4–5 rows. Tube very stiff, opaque, white-grey anteriorly and brown posteriorly. Anterior soft, transparent part of tube 10–15 mm long, usually torn off . . . . . *Spirobrachia orkneyensis*

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#### REFERENCES

- Bubko O.V. 1970.** Data on the anatomy of *Choanophorus indicus* Bubko (Pogonophora, Polybrachiidae). In: *Contributions to Evolutionary Morphology of Invertebrates. I.P. Dubrovskaya (Ed.), Leningrad State University, Leningrad*: 114–129. [In Russian].
- Caullery M. 1914a.** Sur les Siboglinidae, type nouveau d'invertébrés recueilli par l'expédition du Siboga. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences, Paris*, **153**: 2014–2016.
- Caullery M. 1914b.** Sur les Siboglinidae, type nouveau d'invertébrés recueilli par l'expédition du Siboga. *Bulletin de la Société Zoologique de France*, **39**: 350–353.
- Caullery M. 1944.** *Siboglinum* Caullery 1914. Type nouveau d'invertébrés, d'affinités à préciser. *Siboga-Expeditie*, **25**(2): 1–26.
- Cutler E.B. 1965.** Pogonophora from the eastern tropical Pacific, including two new species of *Siboglinum*. *Pacific Science*, **19**(4): 422–426.
- Flügel H.J. 1990.** A new species of *Siboglinum* (Pogonophora) from the North Atlantic and notes on *Nereilinum murmanicum* Ivanov. *Sarsia*, **75**: 233–241.
- Flügel H.J. and Callsen-Cencic P. 1993.** A new species of the genus *Siboglinum* (Pogonophora) from the North Atlantic off Portugal. *Sarsia*, **78**: 255–264.
- Flügel H.J. and Langhof I. 1983.** A new hermaphroditic pogonophore from the Skagerrak. *Sarsia*, **68**: 131–138.
- Gureeva M.A. 1975.** A new *Spirobrachia* (Pogonophora) from the South-Sandwich Trench. *Trudy Instituta Okeanologii P.P. Shirshov*, **103**: 307–312. [In Russian].
- Gureeva M.A. 1981.** Pogonophora of the Caribbean Sea. *Trudy Instituta Okeanologii P.P. Shirshov*, **115**: 183–194. [In Russian].
- Halanych K.M., Feldman R.A. and Vrijenhoek R.C. 2001.** Molecular evidence that *Sclerolimum brattstromi* is closely related to vestimentiferans, not to frenulate pogonophorans (Siboglinidae, Annelida). *Biological Bulletin*, **201**: 65–75.
- Hartman O. 1961.** New Pogonophora from the Eastern Pacific Ocean. *Pacific Science*, **15**(4): 542–546.
- Hilário A, Johnson S.B., Cunha M.R. and Vrijenhoek R.C. 2010.** High diversity of frenulates (Polychaeta: Siboglinidae) in the Gulf of Cadiz mud volcanoes: a DNA taxonomy analysis. *Deep-Sea Research I*, **57**: 143–150.
- Ivanov A.V. 1951.** On including the genus *Siboglinum* Caullery in the class Pogonophora. *Doklady Akademii Nauk SSSR*, **76**: 739–742. [In Russian].
- Ivanov A.V. 1957.** Neue Pogonophora aus dem nordwestlichen Teil des Stillen Ozeans. *Zoologische Jahrbücher: Abteilung für Systematik, Ökologi und Geographie der Tiere*, **85**: 431–500.
- Ivanov A.V. 1960.** Pogonophory [Pogonophores]. Fauna of USSR, new series, volume 75, Moscow, 271 p. [In Russian].
- Ivanov A.V. 1961.** Deux genres nouveaux de Pogonophores diplobranchiaux *Nereilinum* et *Siboglinoides*. *Cahiers de Biologie Marine*, **2**: 381–397.
- Ivanov A.V. 1963.** Pogonophora. Academic Press, London, 479 p.
- Ivanov A.V. 1970.** *Siboglinum carpinei* sp. nov., the first representative of Pogonophora in the Mediterranean Sea. *Bulletin de l'Institut Océanographique, Monaco*, **69**(1409): 1–10.
- Ivanov A.V. 1971.** New Pogonophora from the Atlantic and Pacific Oceans. *Journal of Zoology*, **164**: 271–304.
- Ivanov A.V. 1994.** On the systematic position of Vestimentifera. *Zoologische Jahrbücher: Abteilung für Systematik, Geographie und Biologie der Tiere*, **121**: 409–456.
- Ivanov A.V. and Gureeva M.A. 1973.** Notes on the fauna of pogonophores of the Northern Pacific Ocean. *Trudy Instituta Okeanologii P.P. Shirshov*, **91**: 248–255. [In Russian].
- Jägersten G. 1956.** Investigations on *Siboglinum ekmani*, n. sp., encountered in the Skagerrak, with some general remarks on the group Pogonophora. *Zoologiska Bidrag från Uppsala*, **31**: 211–252.

- Nielsen C. 1965.** Four new species of Pogonophora from the Atlantic Ocean off southern Florida. *Bulletin of Marine Science*, **15**: 964–986.
- Smirnov R.V. 2000a.** A new species of *Spirobrachia* (Pogonophora) from the Orkney Trench (Antarctica). *Polar Biology*, **23**: 567–570.
- Smirnov R.V. 2000b.** A redescription of *Spirobrachia leospira* Gureeva (Pogonophora), with the erection of a new genus and a revision of the Spirobrachiidae. *Ophelia*, **53**(2): 151–158.
- Smirnov R.V. 2005a.** New species of the genus *Polarsterium* (Pogonophora) from the Scotia Sea and adjacent waters of the Antarctic. *Russian Journal of Marine Biology*, **31**(3): 146–154.
- Smirnov R.V. 2005b.** Two new species of abyssal pogonophores from the Antarctic Ocean. *Russian Journal of Marine Biology*, **31**(4): 251–255.
- Smirnov R.V. 2014.** On a new classification of the genus *Siboglinum* Caullery, 1914 (Annelida: Pogonophora). *Proceedings of the Zoological Institute RAS*, **318**(1): 48–69.
- Southward E.C. 1961.** Pogonophora. *Siboga-Expedition*, **25**(3): 1–22.
- Southward E.C. 1963.** *Siboglinum lacteum* sp. nov. In: *Ivanov A.V. 1963. Pogonophora. Academic Press, London, 479 p.*: 322–325.
- Southward E.C. 1969a.** New Pogonophora from the northeast Pacific Ocean. *Canadian Journal of Zoology*, **47**(3): 395–403.
- Southward E.C. 1969b.** Growth of a Pogonophora: a study of *Polybrachia canadensis* with a discussion of the development of taxonomic characters. *Journal of Zoology, London*, **157**(4): 449–467.
- Southward E.C. 1971a.** Pogonophora of the Northwest Atlantic: Nova Scotia to Florida. *Smithsonian Contributions to Zoology*, **88**: 1–29.
- Southward E.C. 1971b.** Recent researches on the Pogonophora. *Oceanography and Marine Biology, an Annual Review*, **9**: 193–220.
- Southward E.C. 1972.** On some Pogonophora from the Caribbean and the Gulf of Mexico. *Bulletin of Marine Science*, **22**(4): 739–776.
- Southward E.C. 1980.** Two new species of Pogonophora from Hawaii. *Pacific Science*, **34**(4): 371–378.
- Southward E.C. 1999.** Development of Perviata and Vestimentifera (Pogonophora). *Hydrobiologia*, **402**: 185–202.
- Southward E.C. and Brattegard T. 1968.** Pogonophora of the Northwest Atlantic: North Carolina Region. *Bulletin of Marine Science*, **18**(4): 836–875.
- Southward E.C., Schulze A. and Gardiner S.L. 2005.** Pogonophora (Annelida): form and function. *Hydrobiologia*, **535/536**: 227–251.
- Southward E.C. and Southward A.J. 1958.** On some Pogonophora from the northeast Atlantic, including two new species. *Journal of the Marine Biological Association of the United Kingdom*, **37**: 627–632.
- Ushakov P.V. 1933.** Eine neue Form aus der Familie Sabellidae (Polychaeta). *Zoologischer Anzeiger*, **104**: 205–208.
- Webb M. 1964.** A redescription of *Siboglinum ekmani* Jägersten (Pogonophora). *Sarsia*, **15**: 37–47.
- Webb M. 1969.** Regionation and terminology of the pogonophoran body. *Sarsia*, **38**: 9–24.

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