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ON A NEW CLASSIFICATION OF THE GENUS *SIBOGLINUM* CAULLERY, 1914 (ANNELIDA: POGONOPHORA)

R.V. Smirnov

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

ABSTRACT

The largest pogonophoran genus *Siboglinum* Caullery, 1914 is for the first time reviewed and divided into nine subgenera, diagnoses provided and species listed. The following characters in various combinations are considered to have subgeneric significance: disposition of glandular areas on the forepart, presence and relative development of anterior teeth on chaetal heads, number, shape and disposition of the girdles of chaetae, shape of a segmental groove on the forepart, length and details of structure of the spermatophore, colour of the tube, presence of segments (together with rings or separately) on the tube, relative thickness of the tentacle, presence of pinnules on the tentacle. Several species of *Siboglinum* from the ZIN collection have been re-examined to define their position in the proposed subgeneric classification.

Key words: Pogonophora, *Siboglinum*, revision

К НОВОЙ КЛАССИФИКАЦИИ РОДА *SIBOGLINUM* CAULLERY, 1914 (ANNELIDA: POGONOPHORA)

Р.В. Смирнов

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

РЕЗЮМЕ

Впервые проведена ревизия рода *Siboglinum* Caullery, 1914, крупнейшего среди погонофор. Выделено 9 подродов, для каждого из которых составлен диагноз и определен видовой состав. Следующие признаки в различных комбинациях предложено использовать для диагностики подродов: расположение железистых участков на переднем отделе, наличие и относительное развитие передних зубцов на головках щетинок, количество, форма и расположение поясков щетинок, форма сегментарной борозды на переднем отделе, длина и детали строения сперматофора, цвет трубки, наличие сегментов (в сочетании с кольцами или отдельно от них) на трубке, относительная толщина щупальца, наличие пиннул на щупальце. Материал по нескольким видам *Siboglinum* из коллекции ЗИН переисследован для уточнения их положения в новой подродовой классификации.

Ключевые слова: Pogonophora, *Siboglinum*, ревизия

INTRODUCTION

Pogonophorans are free-living tubicolous worms discovered nearly 90 years ago, whose most striking features are the absence of a gut, the endosymbiotic nutrition, living mostly in deep-sea habitats and the entangled taxonomic history. The taxonomic rank and phylogenetic affinities of this group have been changed many times throughout its investigation: a family or class status incertus (Caullery 1914a, b, 1944; Johansson 1937, 1939), a subfamily of sabellid polychaetes (Ushakov 1933), a separate phylum

classified among the Deuterostomia (Ivanov 1960, 1963, 1975, 1991; Malakhov and Galkin 1998), or the Protostomia (van der Land and Nørrevang 1975; Southward 1971a, 1988), an independent branch of coelomates (Ivanov 1994), two separate phyla (Jones 1985), or one family of polychaetous annelids (Rouse and Fauchald 1997; McHugh 1997; Rouse 2001; Halanych et al. 2001).

The employment of polychaete terminology for descriptions of pogonophoran morphology, e.g. prostomium, peristomium, palps, neurotroch, prototroch, telotroch, pygidium etc., may reflect the obviously close affinity of Pogonophora and Polychaeta, but in my opinion, their usage in taxonomic descriptions is unadvisable at present. Special studies would be required to confirm the homology between these polychaete structures and the proposed corresponding parts of the pogonophoran body (Fig. 1). Concerning the inclusion of all pogonophoran taxa in a single family (Siboglinidae, assigned to the class Polychaeta), the molecular data apart from the morphological evidence are not in my view sufficient for deciding the problem of taxonomic status of the group, though I accept the view of close affinity between these two groups of trochophoran animals. The high degree of pogonophoran ingroup morphological divergency and the peculiar structural plan including several synapomorphies, i.e. pinnules on the tentacles with two blood capillaries, tentacles (peristomial palps?) with two blood vessels, heart, protein-chitin tube, trophosome and absence of the gut, original multilevel trunk regionalization based on allometrical growth and uneven elongation of different trunk parts, allow me to retain the higher taxonomic rank for Pogonophora. Therefore, following Southward (1988), Southward et al. (2005), Ivanov (1994), and Malakhov and Galkin (1998), I would prefer to use in this paper the system of the class Pogonophora with three subclasses Frenulata, Monilifera, Vestimentifera, while the fourth one would probably comprise the enigmatic genus *Osedax* Rouse et al., 2004.

The genus *Siboglinum* so far includes 72 species of small unitentaculate Pogonophora. This genus is the largest one, accommodating about half of the total number of pogonophoran species. The taxonomic structure of the genus *Siboglinum* is still very complex and obscure. This paper represents the first attempt at a detailed revision of the genus, which is based on both the investigation of the recently described species of *Siboglinum* from Antarctica (Smirnov in press) and a review of all other species, whose descriptions have been published.

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

MATERIAL AND METHODS

The present study is a review, which is based mainly on the published data on the *Siboglinum* species. Some type and other materials from the world largest pogonophoran collection of the ZIN RAS were also investigated, totally a few dozen animals and some empty tubes. The re-examined type material came from the Indian Ocean and Okhotsk Sea (R.V. Vityaz, 31 cr., 1960: station 4543, 4498; 45 cr., 1952: station 1892). The new material was obtained by R.V. Akademik M.A. Lavrentiev, 28 cr., 1998 in the Okhotsk Sea (station Lv 28–16–2). Samples were taken by a Sigsbee trawl and an Ocean 0.25 grab. Sediments were various silts. The material was fixed in 70% ethanol. The observations, measurements, and drawings were performed using binocular and standard light microscopes with a camera lucida. All material is deposited at the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN).

SYSTEMATICS

Re-examination of type material

Siboglinum sumatrense Ivanov, 1963
(Fig. 2)

Type material. R.V. Vityaz, 31 cr.; station 4543; grab; 1960; Indian Ocean off southern Sumatra to the west of the entrance to Sunda Strait; 626 m; silty sand; one tube with an animal and one empty tube. Syntypes ZIN KN13.

Remarks. The new study of the type material was aimed to examine Ivanov's (1963) conclusion about the annular region structure, namely the presence of two girdles situated close together. It was this single character which made it difficult for me to assign *S. sumatrense* to any subgroup of *Siboglinum*. The specific combination of characters of *S. sumatrense* is: segmented and ringed dark-brown tube, thick tentacle with two rows of pinnules, annular girdles and well-developed group of anterior teeth on chaetal

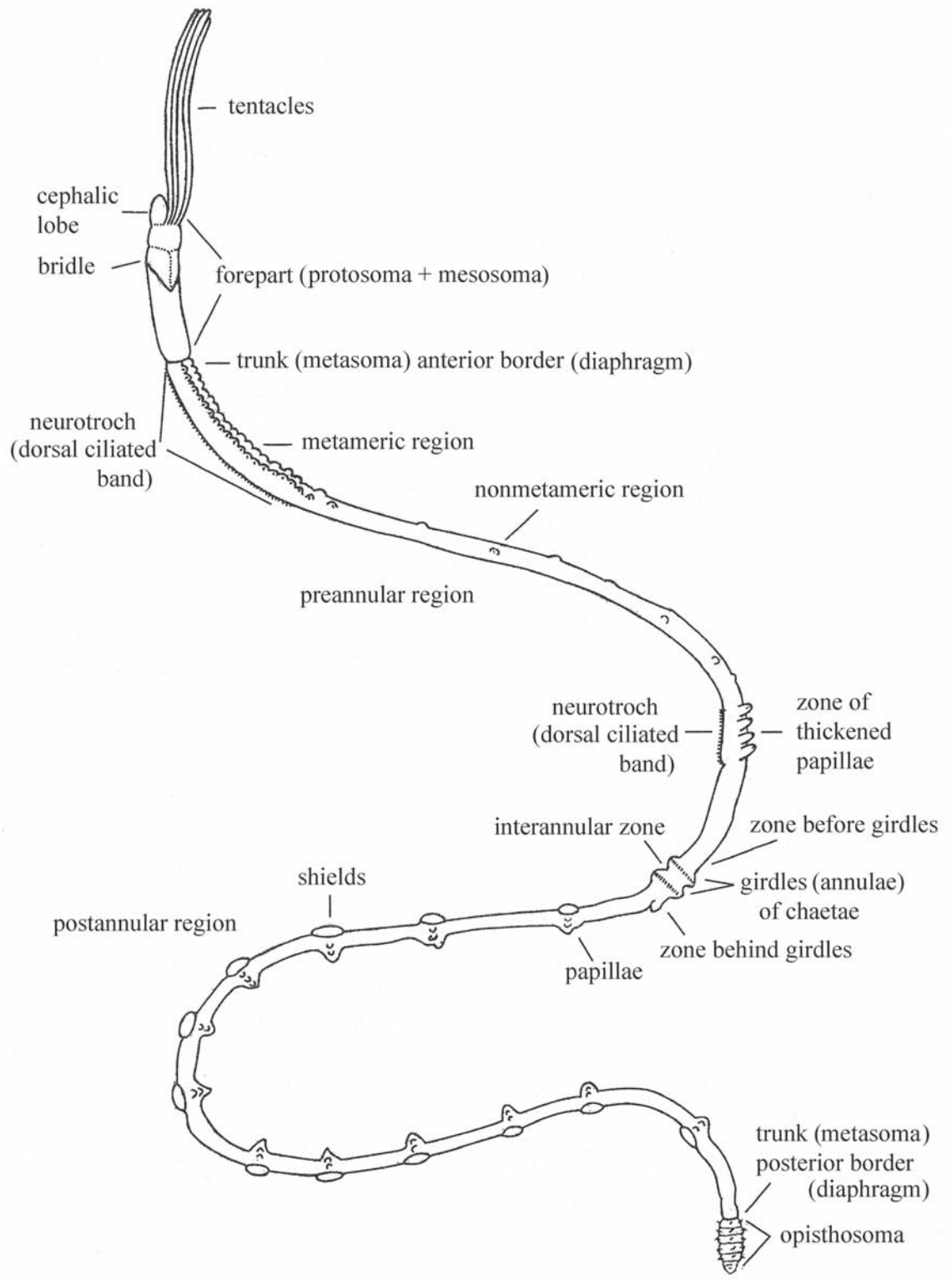

Fig. 1. General scheme of pogonophore (after Southward 1971a, with modifications).

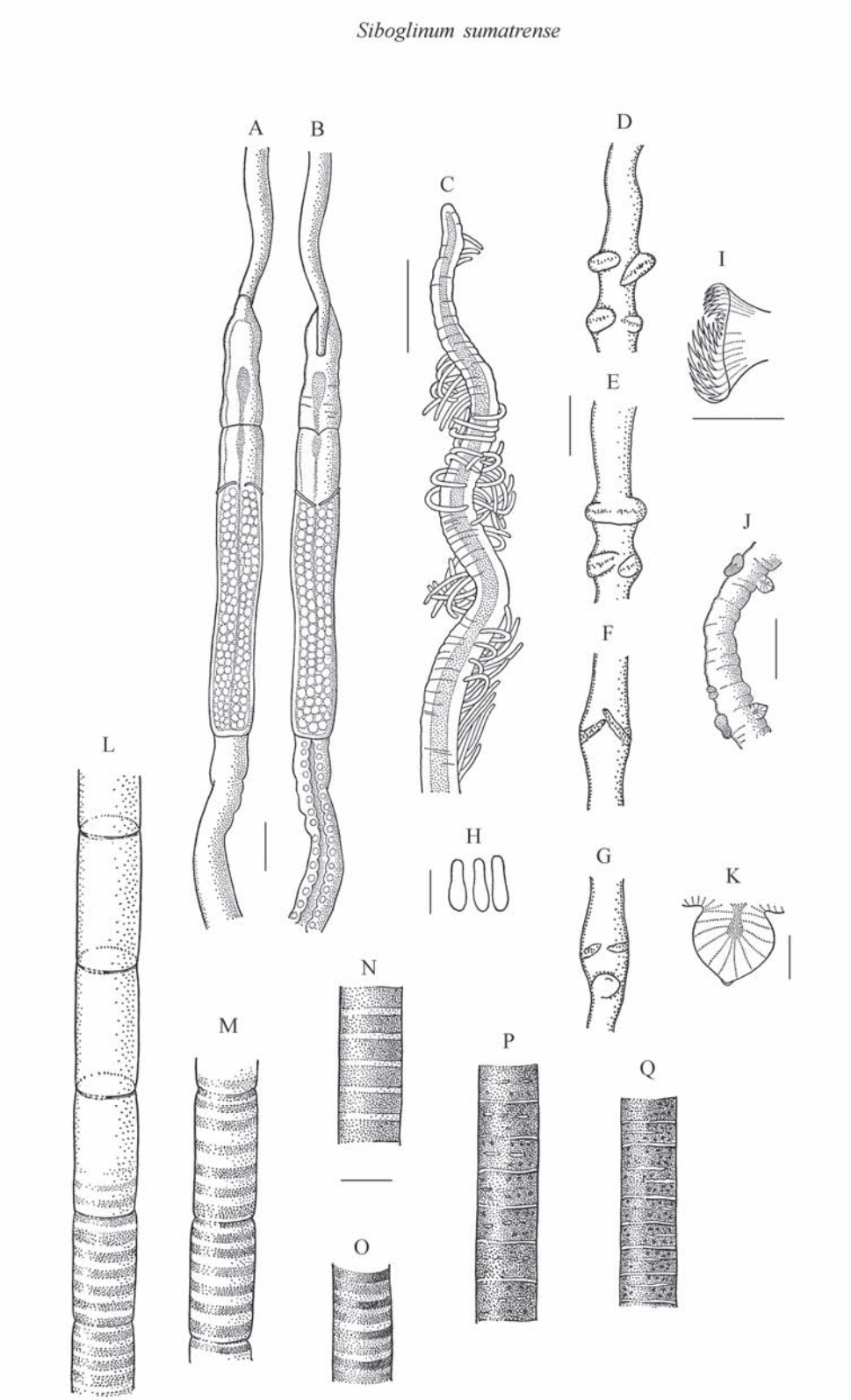

Fig. 2. *Siboglinum sumatrense*: A – forepart and anterior part of trunk, ventral view; B – forepart and anterior trunk, dorsal view; C – tentacle with pinnules; D – two anterior girdles, dorsal view; E – two anterior girdles, ventral view; F – third girdle, ventral view; G – third girdle, dorsal view; H – part of girdle; I – head of chaeta, lateral view; J – postannular region of trunk, lateral view; K – papilla from postannular region; L–Q – parts of tube, anterior-posterior series (after Ivanov 1963, modified). Scales: A–G, J, L–Q – 0.1 mm; H, K – 10 μm; I – 20 μm. A–C, H–K, from Ivanov (1963) fig. TT133; L–Q, from Ivanov (1963) fig. UU133. D–G, original figures.

heads. These features are distinctive for the subgroup typified by *S. ekmani* (see below), though all its species have three girdles of chaetae. The new study showed that *S. sumatrense* possesses three girdles of which the two anterior ones are so distant from the third girdle (3.25 mm) that it is not surprising that the first description missed the third one (Fig. 2D–G). All three girdles lie on very well-developed muscular ridges and show gaps on both sides of the body. A large papilla furnished by one cuticular plaque is situated behind the last girdle.

Siboglinum plumosum Ivanov, 1957

Type material. R.V. Vityaz, 45 cr.; station 1892; Sigsbee trawl; 1952; Okhotsk Sea off eastern Sakhalin Island 52°N, 144°30´E; 119–342 m; mud; one specimen and one empty tube. Holotype ZIN N1.

New material. R.V. Akademik M.A. Lavrentiev, 28 cr.; station Lv 28–16–2; Sigsbee trawl; 16.08.1998; Okhotsk Sea off northern Sakhalin Island 54°22.66´–21.36´N, 143°59.05´–04´E; 382–387 m; mud, cold methane seep; two empty tubes.

Remarks. The species was known only from short fragments of a single animal and one empty tube. The original diagnosis has large gaps leaving the position of *S. plumosum* in the genus system obscure. The new material allowed me to clarify the systematic position of the species. On the anterior end of the tube of *S. plumosum* there is a long (17–18 mm) filmy region with thin collapsed walls in which plenty of fibres are incorporated. When the rings begin to appear the fibres remain only in the interspaces. The tube diameter in this part is 0.5–0.6 mm. The tube lacks segments, and this feature makes it impossible to include *S. plumosum* in the subgroup typified by *S. ekmani*. Though the structure of the girdle region and spermatophore of *S. plumosum* remains unknown, the unsegmented, ringed dark-brown tube without regular "perforation", thick tentacle with two rows of pinnules, annular groove separating first two segments, and the absence of glandular bands on the forepart allow me to assign this species to the subgroup typified by *S. weberi* (see below) (Ivanov 1957, 1963).

Siboglinum modestum Bubko, 1967

Type material. R.V. Vityaz, 31 cr.; station 4498; Sigsbee trawl; 1960; Arabian Sea at the entrance to Gulf of Aden to the northwest of Socotra Island 12°48´N, 52°38´E; 2080–3300 m; mud; 78 tubes with animals and many empty. Holotype ZIN N34, two paratypes KN34.

Remarks. There is a detail in Bubko's (1967) original description, which, if confirmed, places the species quite apart from the genus *Siboglinum*. The matter concerns the number of multicellular glands incorporated in each papilla of the trunk metameric region. Bubko asserts that there are three to six glands in each papilla throughout the metameric region, and, thus, the maximum number of rows of glands could not be less than three (Bubko 1967). All other siboglinids have a maximum two or three glands, in anterior pairs of papillae, and the number of rows never exceeds two. These features are very significant for diagnosis of families of the order Athecanephria. By other features, *S. modestum* approaches the *Siboglinum* subgroup typified by *S. vinculatum* (see below). These are: feebly developed anterior teeth on the chaetal heads, spermatophores with a very thick base of filament, tube white in colour. The study of a few specimens of *S. modestum* from the ZIN collection allowed me to conclude that large laminar secretion bodies incorporated in each gland were mistaken in the original description for separate multicellular glands. Each papilla has in fact only one or two glands.

Notes on other species

Siboglinum cinctutum Ivanov, 1957 var. *subtile* Southward, 1961

Remarks. A comparison of the descriptions of the variety and *S. cinctutum* Ivanov indicates that characters significant enough for two species to be separated were found, but to which no special attention was paid in the first description. The relative length of spaces between the tube rings in *S. cinctutum* var. *subtile* is considerably greater (~0.53 of the ring length, while in *S. cinctutum* this is ~0.13), papillae are absent from the zone between the girdles and the postannular region (present in *S. cinctutum*), postannular papillae are single (absent in *S. cinctutum*), and, finally, an anterior group of teeth on the chaetal head is always present and occupies about 18% of the head length (up to 9% or absent in *S. cinctutum*) (Ivanov 1957, 1963; Southward 1961).

Siboglinum ekmani Jägersten, 1956 var. 1 and 2 of Southward, 1972

Remarks. Variety 1 fits the range of morphological features of the main species, while variety 2 is probably a separate species. Considerable differences in the length and shape of the spermatophores, in the diameter of the tube and forepart, in the relative width of the tube rings testify to this conclusion (see descriptions of *S. ekmani* by Jägersten 1956; Ivanov 1963; Webb 1963b, 1964; Southward and Brattegard 1968; Southward 1971b, 1972).

Siboglinum pholidotum Southward and Brattegard, 1968

Siboglinum fedotovi Ivanov, 1957

Remarks. These two species are considered here, following Southward (1972), Ivanov and Gureeva (1973), as senior synonyms of *S. armatum* Ivanov, 1971 and *S. vancouverense* Southward, 1969, respectively (Ivanov 1957, 1963, 1971; Southward and Brattegard 1968; Southward 1969).

RESULTS

Revision of the genus *Siboglinum*

The genus *Siboglinum* Caullery now includes 72 species comprising more than half the species in the subclass Frenulata and about 44% of the class Pogonophora (Table 1). The genus *Siboglinum* has the most complicated systematic structure among all pogonophoran genera. The genus belongs to the family Siboglinidae, whose chief diagnostic features are the presence of more or less developed papillae instead of continuous ridges on the anterior part of the trunk, and the arrangement of pyriform (multicellular) glands on the same region in one or initially two irregular rows on each side of the dorsal furrow. In spite of the great morphological diversity of the genus *Siboglinum*, there is one specific character, which is shared by all species of the genus, namely the presence of a single tentacle. The number of tentacles in *Siboglinum* cannot vary, probable teratoid bitentaculate specimens were recorded only twice in two species, *S. fiordicum* and *S. leucopleurum* (Flügel and Callsen-Cencic 1993; Southward pers. comm.). The two other known unitentaculate genera, *Unibrachium* and *Polarsternium*, belong to the family Oligobrachiidae and are characterised by the continuous ridges and multirowed arrangement of the multicellular glands in the anterior part of the trunk (Southward 1972, 1975; Smirnov 1999, 2005). The urgent problem of dividing of the genus *Siboglinum* into several subgenera has not hitherto been discussed, though existence of some subgroups inside the genus is accepted by many specialists (Ivanov 1971; Southward 1972; Flügel 1990; etc). Apparently, the revision of *Siboglinum* would make the systematic structure of the genus more regular and, therefore, considerably facilitate the identification of the species. In my view, the most valuable characters for distinguishing the subgroups concern the disposition of glandular areas on the forepart, presence and relative development of anterior teeth on chaetal heads, number, shape and disposition of the girdles of chaetae, shape of a segmental groove on the forepart, length and details of structure of the spermatophore, colour of the tube, presence of segments (together with rings or separately) on the tube, relative thickness of the tentacle, presence of pinnules on the tentacle. These features allow me to identify nine discrete subgroups in the genus *Siboglinum* (Table 2). The subgroups typified by *S. subligatum* and *S. mergophorum* are characterized by the presence of two or one peculiar ribbons of glandular epidermis on the forepart (Figs 3A, 4A). The diagnostic character of the subgroup typified by *S. caulleryi* is an oblique shape of the segmental groove on the forepart (Fig. 5B). The spiral anterior girdles of chaetae determine the subgroup typified by *S. callosum* (Fig. 6F, G). The other subgroups are distinguished by various combinations of features. The species of the subgroup typified by *S. vinculatum* possess the peculiar white or colourless tube, spermatophores with a very thick filament base, and lack the anterior teeth on the chaetal heads (or these are rudimentary) (Fig. 7J, K). The largest and most variable subgroup typified by *S. weberi* is characterised by the unsegmented tube, well developed anterior teeth on the chaetal heads, thin and short spermatophores and by annular (if present) groove between the segments on the forepart (Fig. 8A, B, G, I, J, K, L). The diagnostic set of features of the subgroup typified by *S. variabile* is the following: the thin tentacle lacking pinnules, two annular girdles of chaetae, feebly developed anterior teeth on the chaetal heads, tube ringed and segmented (Fig. 9A, D, F, G). The subgroup typified by *S. minutum* is distinguished by

Table 1. List of species of the genus *Siboglinum* with author references.

Species	Author	Species	Author	Species	Author
S. weberi	Caullery 1944	*S. japonicum*	Ivanov 1960	*S. longicollum*	Southward and Brattegard 1968
S. ekmani	Jägersten 1956	*S. velerone*	Hartman 1961	*S. fulgens*	Southward and Brattegard 1968
S. plumosum	Ivanov 1957	*S. subtile*	Southward 1961	*S. pholidotum*	Southward and Brattegard 1968
S. pellucidum	Ivanov 1957	*S. debile*	Southward 1961	*S. gosnoldae*	Southward and Brattegard 1968
S. cinctutum	Ivanov 1957	*S. macrobrachium*	Southward 1961	*S. carpinei*	Ivanov 1970
S. fedotovi	Ivanov 1957	*S. timorense*	Southward 1961	*S. fasciatum*	Ivanov 1971
S. caulleryi	Ivanov 1957	*S. zanzibaricum*	Ivanov 1963	*S. elongatum*	Ivanov 1971
S. minutum	Ivanov 1957	*S. exile*	Ivanov 1963	*S. risillum*	Ivanov 1971
S. inerme	Southward and Southward 1958	*S. subligatum*	Ivanov 1963	*S. longimanus*	Ivanov 1971
S. atlanticum	Southward and Southward 1958	*S. concinnum*	Ivanov 1963	*S. callosum*	Ivanov 1971
S. pusillum	Ivanov 1960	*S. arabicum*	Ivanov 1963	*S. bayeri*	Southward 1971b
S. microcephalum	Ivanov 1960	*S. sergeevi*	Ivanov 1963	*S. oregoni*	Southward 1972
S. bogorovi	Ivanov 1960	*S. ceylonicum*	Ivanov 1963	*S. nanum*	Southward 1972
S. tenue	Ivanov 1960	*S. sumatrense*	Ivanov 1963	*S. parvulum*	Southward 1972
S. meridiale	Ivanov 1960	*S. silone*	Ivanov 1963	*S. polystichum*	Southward 1975
S. robustum	Ivanov 1960	*S. fiordicum*	Webb 1963a	*S. ordinatum*	Southward 1981
S. buccelliferum	Ivanov 1960	*S. lacteum*	Southward 1963b in Ivanov 1963	*S. southwardae*	Gureeva 1981
S. norvegicum	Ivanov 1960	*S. holmei*	Southward 1963a	*S. poseidoni*	Flügel and Langhof 1983
S. hyperboreum	Ivanov 1960	*S. ecuadoricum*	Cutler 1965	*S. brevicephalum*	Flügel 1990
S. taeniaphorum	Ivanov 1960	*S. albatrossianum*	Cutler 1965	*S. leucopleurum*	Flügel and Callsen-Cencic 1993
S. frenigerum	Ivanov 1960	*S. mergophorum*	Nielsen 1965	*S. gureevae*	Smirnov in press
S. vinculatum	Ivanov 1960	*S. modestum*	Bubko 1967	*S. quadrannulatum*	Smirnov in press
S. pinnulatum	Ivanov 1960	*S. angustum*	Southward and Brattegard 1968	*S. scotiensis*	Smirnov in press
S. variabile	Ivanov 1960	*S. candidum*	Southward and Brattegard 1968	*S. davisiensis*	Smirnov in press

Table 2. Allocation of *Siboglinum* species to the new subgenera.

Siboglinum	*Ekmanifilum*	*Taeniafilum*	*Subtilifilum*	*Nereilinoides*	*Spirannulifilum*	*Mergofilum*	*Varifilum*	*Minifilum*
S. weberi	*S. ekmani*	*S. subligatum*	*S. vinculatum*	*S. caulleryi*	*S. callosum*	*S. mergophorum*	*S. variabile*	*S. minutum*
S. plumosum	*S. fedotovi*	*S. taeniaphorum*	*S. frenigerum*	*S. japonicum*	*S. polystichum*			
S. pellucidum	*S. pinnulatum*	*S. atlanticum*	*S. cinctutum*	*S. timorense*				
S. inerme	*S. macrobrachium*	*S. lacteum*	*S. subtile*	*S. fiordicum*				
S. pusillum	*S. ceylonicum*	*S. concinnum*	*S. debile*	*S. holmei*				
S. microcephalum	*S. sumatrense*	*S. arabicum*	*S. sergeevi*	*S. gosnoldae*				
S. bogorovi	*S. silone*	*S. candidum*	*S. modestum*					
S. tenue	*S. pholidotum*	*S. elongatum*	*S. fulgens*					
S. meridiale	*S. carpinei*	*S. leucopleurum*						
S. robustum	*S. bayeri*							
S. buccelliferum	*S. longimanus*							
S. norvegicum	*S. ordinatum*							
S. hyperboreum	*S. southwardae*							
S. velerone	*S. brevicephalum*							
S. zanzibaricum	*S. scotiensis*							
S. exile	*S. davisiensis*							
S. ecuadoricum								
S. albatrossianum								
S. angustum								
S. longicollum								
S. fasciatum								
S. risillum								
S. oregoni								
S. nanum								
S. parvulum								
S. poseidoni								
S. gureevae								
S. quadrannulatum								

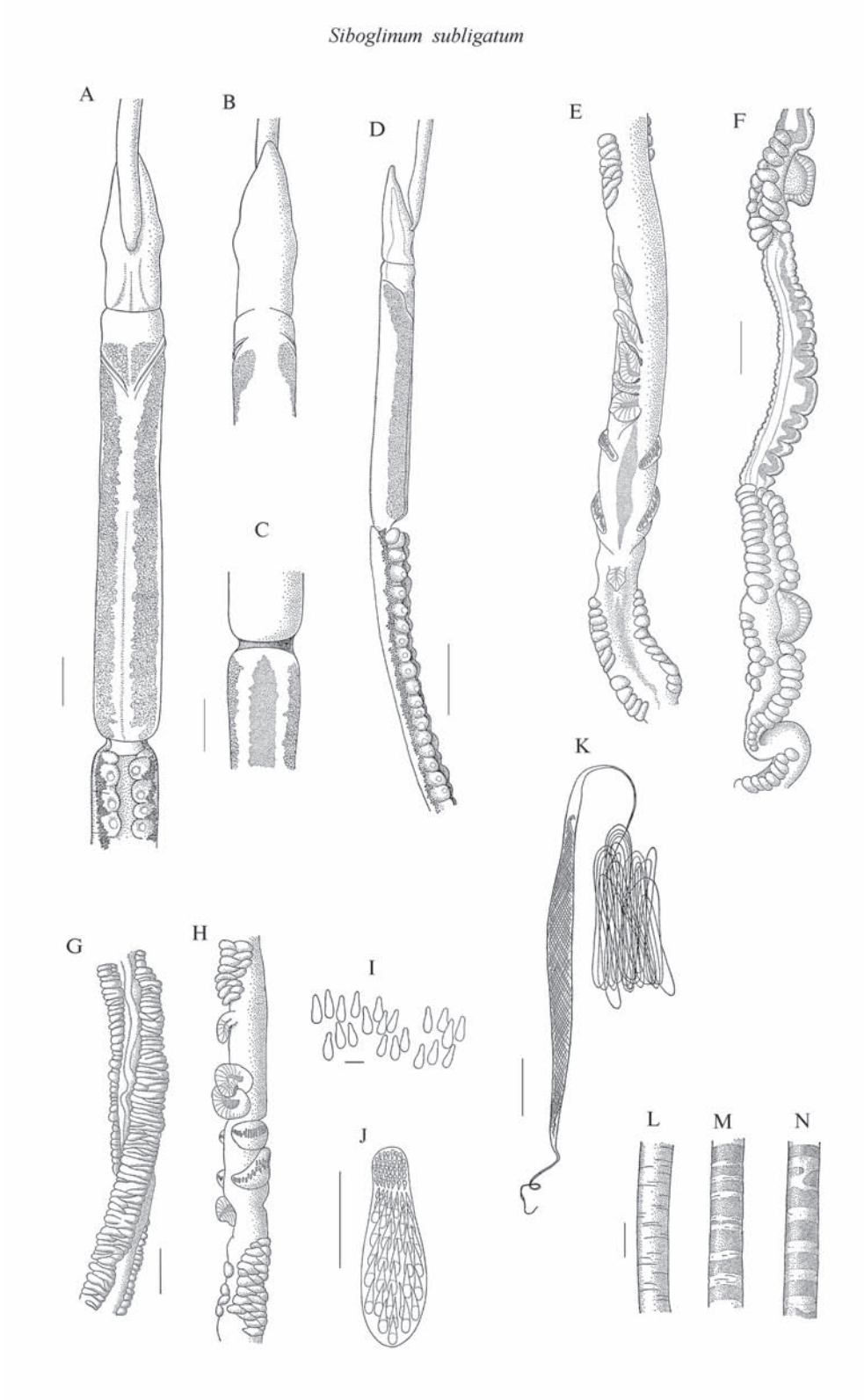

Fig. 3. *Siboglinum subligatum*: A – forepart, dorsal view; B – cephalic part, ventral view; C – anterior diaphragm area, ventral view; D – forepart and anterior part of trunk, side view; E – annular area, dorsal view; F – postannular region of trunk, lateral view; G – nonmetameric part of trunk, dorso-lateral view; H – annular area, dorso-lateral view; I – part of girdle; J – head of chaeta; K – spermatophore; L–N – parts of tube, anterior-posterior series (after Ivanov 1963). Scales: A–C, E–H – 0.2 mm; D – 0.5 mm; I – 10 μm; J – 50 μm; K – 0.05 mm; L–N – 0.3 mm.

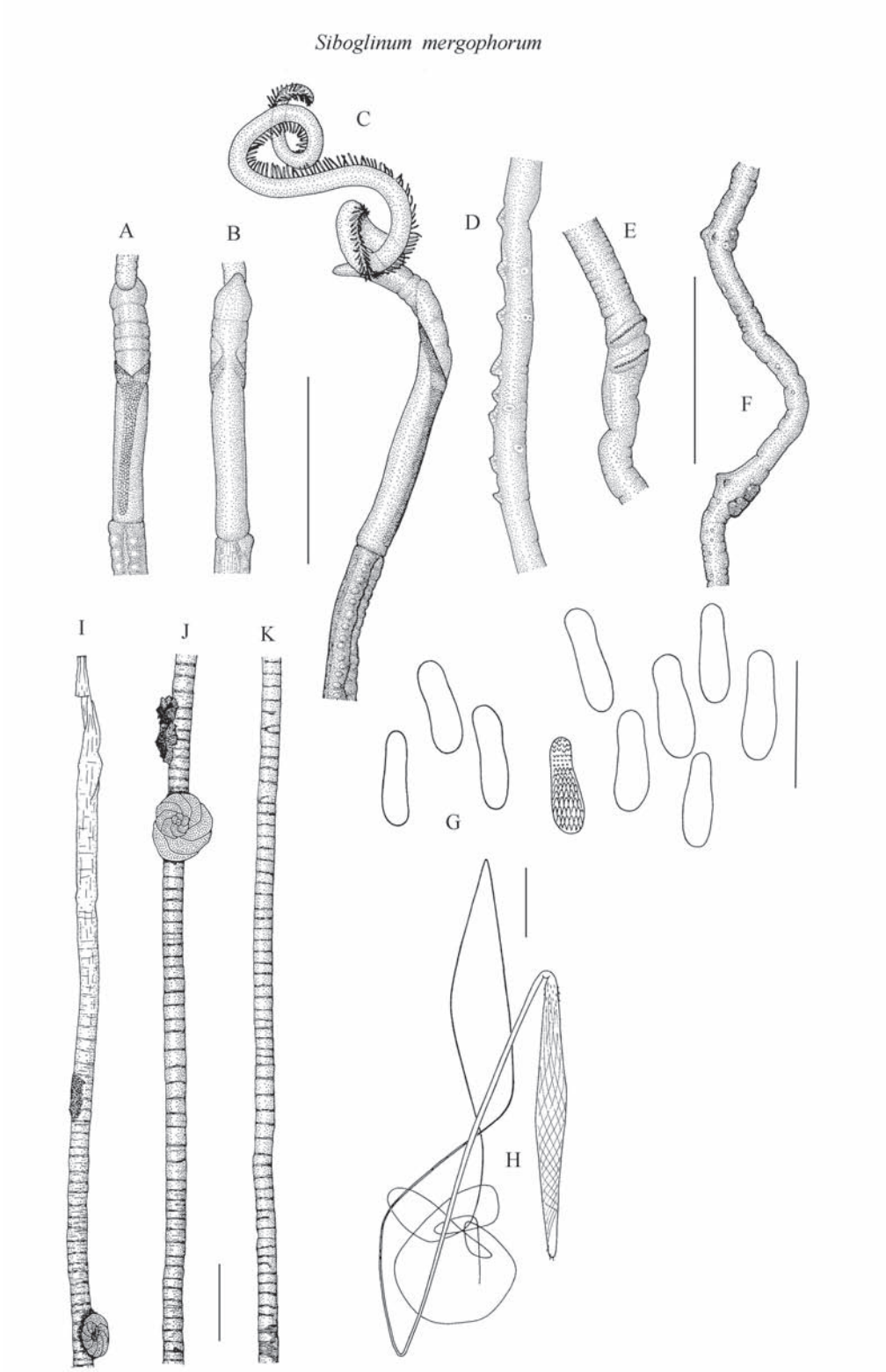

Fig. 4. *Siboglinum mergophorum*: A – forepart, dorsal view; B – forepart, ventral view; C – forepart, tentacle and anterior part of trunk, lateral view; D – zone of thickened papillae, lateral view; E – annular area, lateral view; F – postannular region of trunk, lateral view; G – part of girdle; H – spermatophore; I–K – parts of tube, anterior-posterior series (after Nielsen 1965). Scales: A–F, I–K – 1 mm; G – 20 μm; H – 0.2 mm.

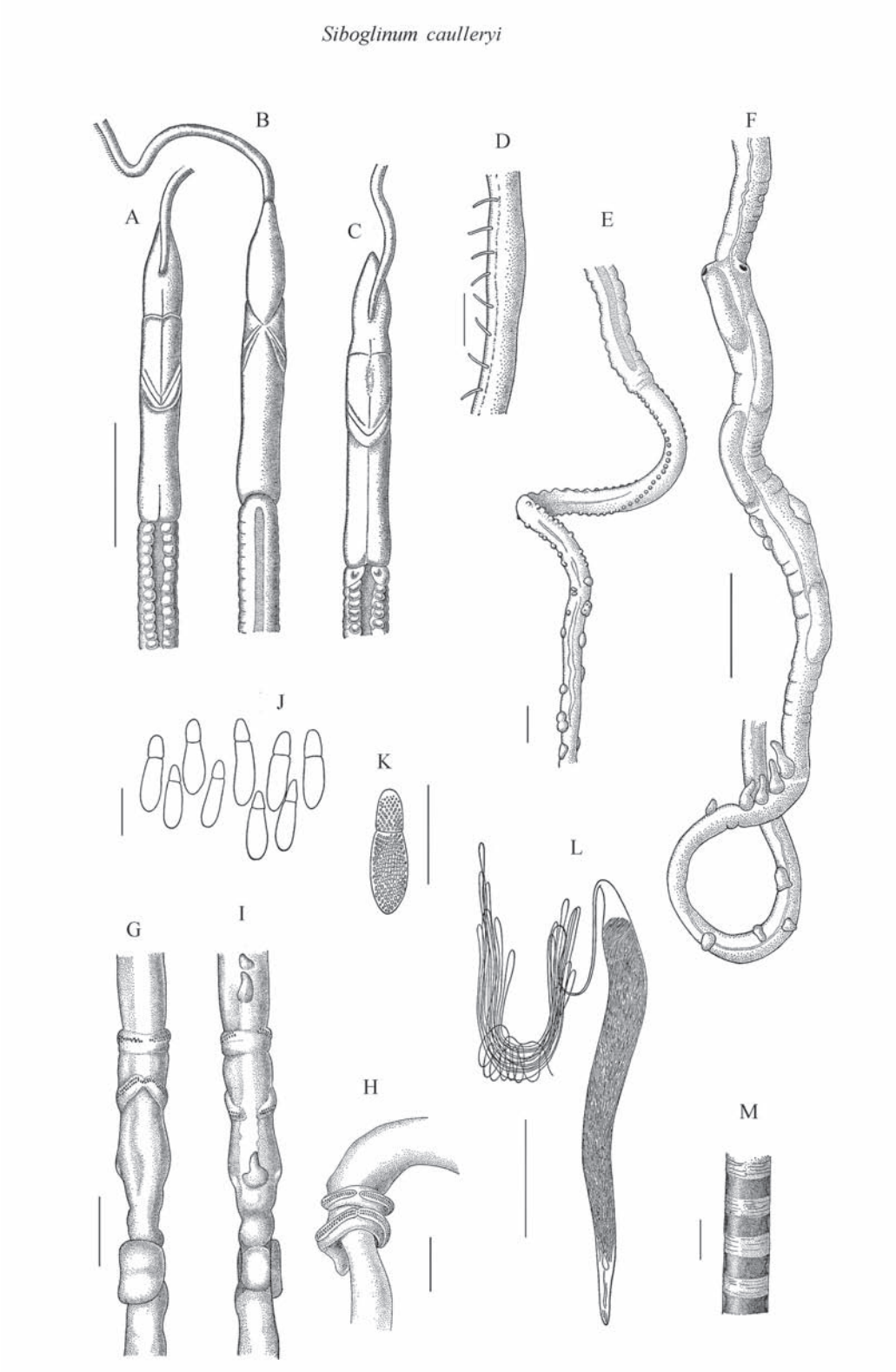

Fig. 5. *Siboglinum caulleryi*: A – forepart, tentacle and anterior part of trunk, dorsal view; B – forepart, tentacle and anterior trunk, ventral view; C – forepart, tentacle and anterior trunk of male, dorsal view; D – tentacle with pinnules; E – parts of metameric and nonmetameric regions of trunk, dorso-lateral view; F – nonmetameric part of trunk near female gonopores and zone of thickened papillae, dorso-lateral view; G, H – annular area in different specimens, ventral view; I – annular area, dorsal view; J – part of girdle; K – head of chaeta; L – spermatophore; M – middle part of tube (after Ivanov 1957). Scales: A–C, F – 0.5 mm; D – 0.1 mm; E, G, H, I, M – 0.2 mm; J – 10 μm; K – 20 μm; L – 50 μm.

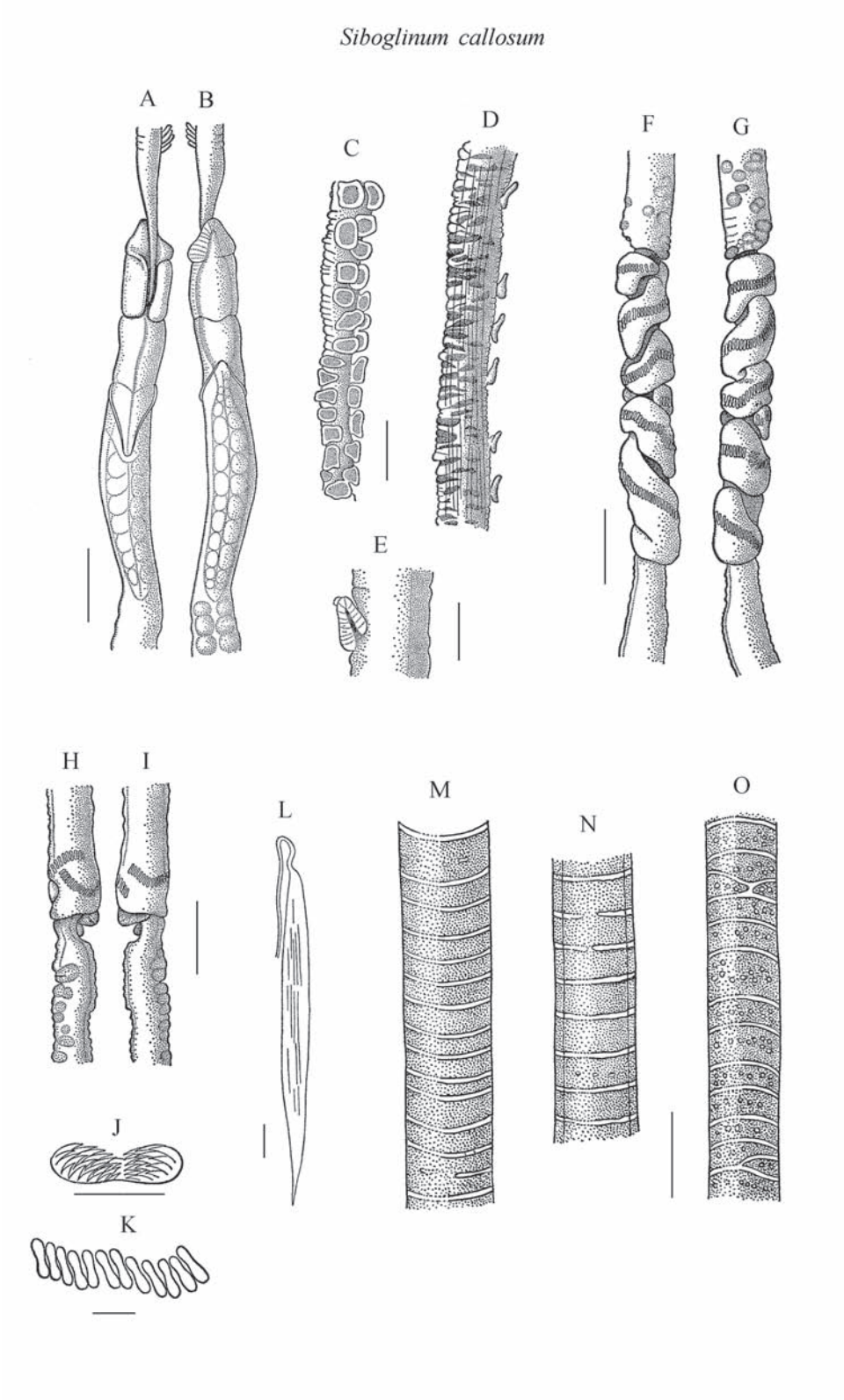

Fig. 6. *Siboglinum callosum*: A – forepart, dorsal view; B – forepart, ventral view; C – metameric part of trunk, dorso-lateral view; D – non-metameric part of trunk, lateral view; E – papilla from nonmetameric part of trunk; F – two anterior girdles, dorsal view; G – two anterior girdles, ventral view; H – third girdle, ventro-lateral view; I – third girdle, dorso-lateral view; J – head of chaeta; K – part of girdle; L – spermatophore; M–O – parts of tube, anterior-posterior series (after Ivanov 1971). Scales: A–D, F–I, M–O – 0.1 mm; E – 0.05 mm; J – 20 μm; K, L – 10 μm.

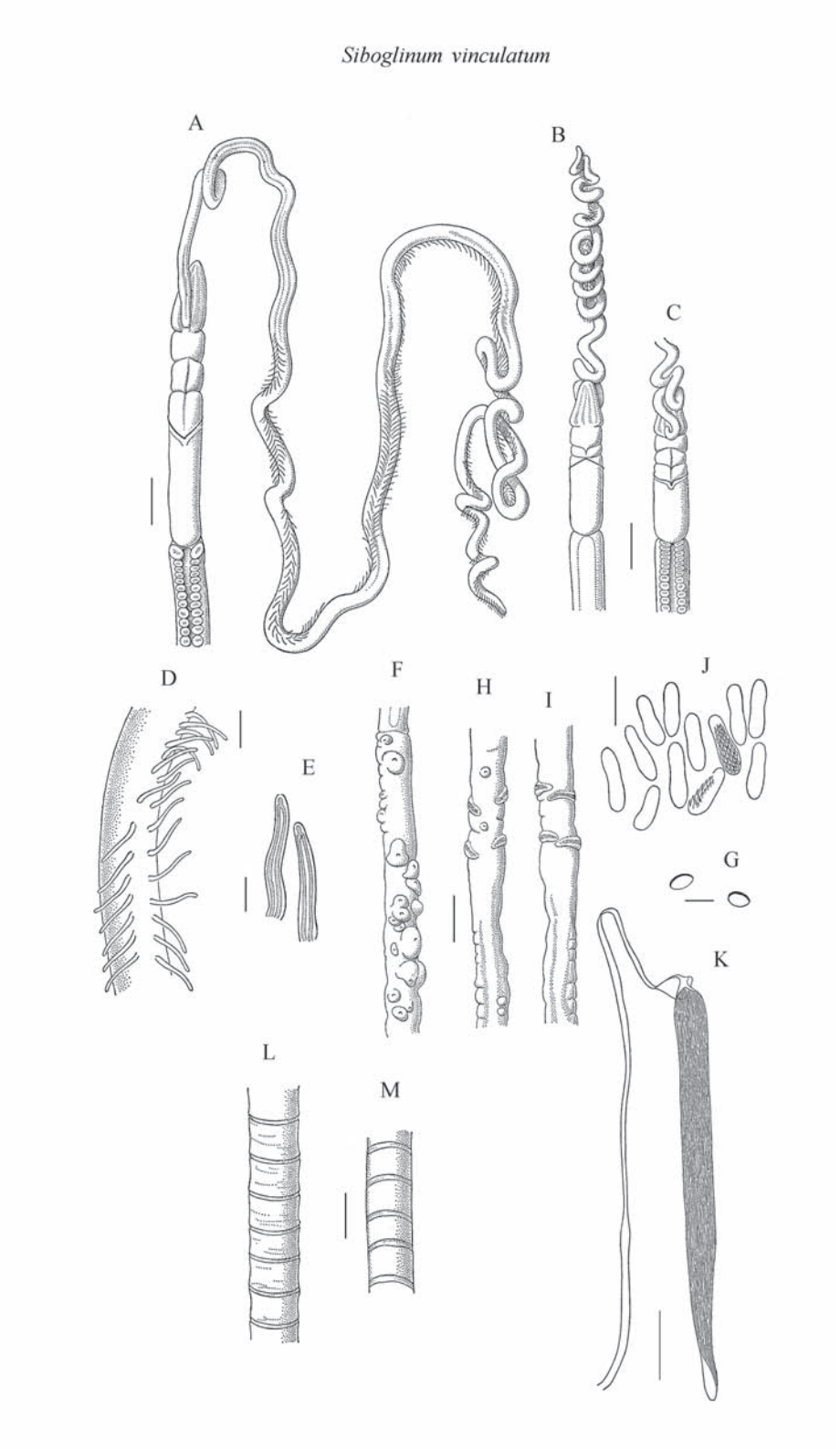

Fig. 7. *Siboglinum vinculatum*: A, C – forepart, tentacle and anterior part of trunk in different specimens, dorsal view; B – forepart, tentacle and anterior trunk, ventral view; D – tentacle with pinnules; E – pinnules; F – zone of thickened papillae, dorsal view; G – cuticular plaques from thickened papillae; H – annular area and anterior part of postannular region of trunk, dorsal view; I – annular area and anterior postannular trunk, ventral view; J – part of girdle; K – spermatophore; L – anterior part of tube; M – middle part of tube (after Ivanov 1960). Scales: A–C, F, H, I, L, M – 0.2 mm; D, G, K – 50 μm; E – 20 μm; J – 10 μm.

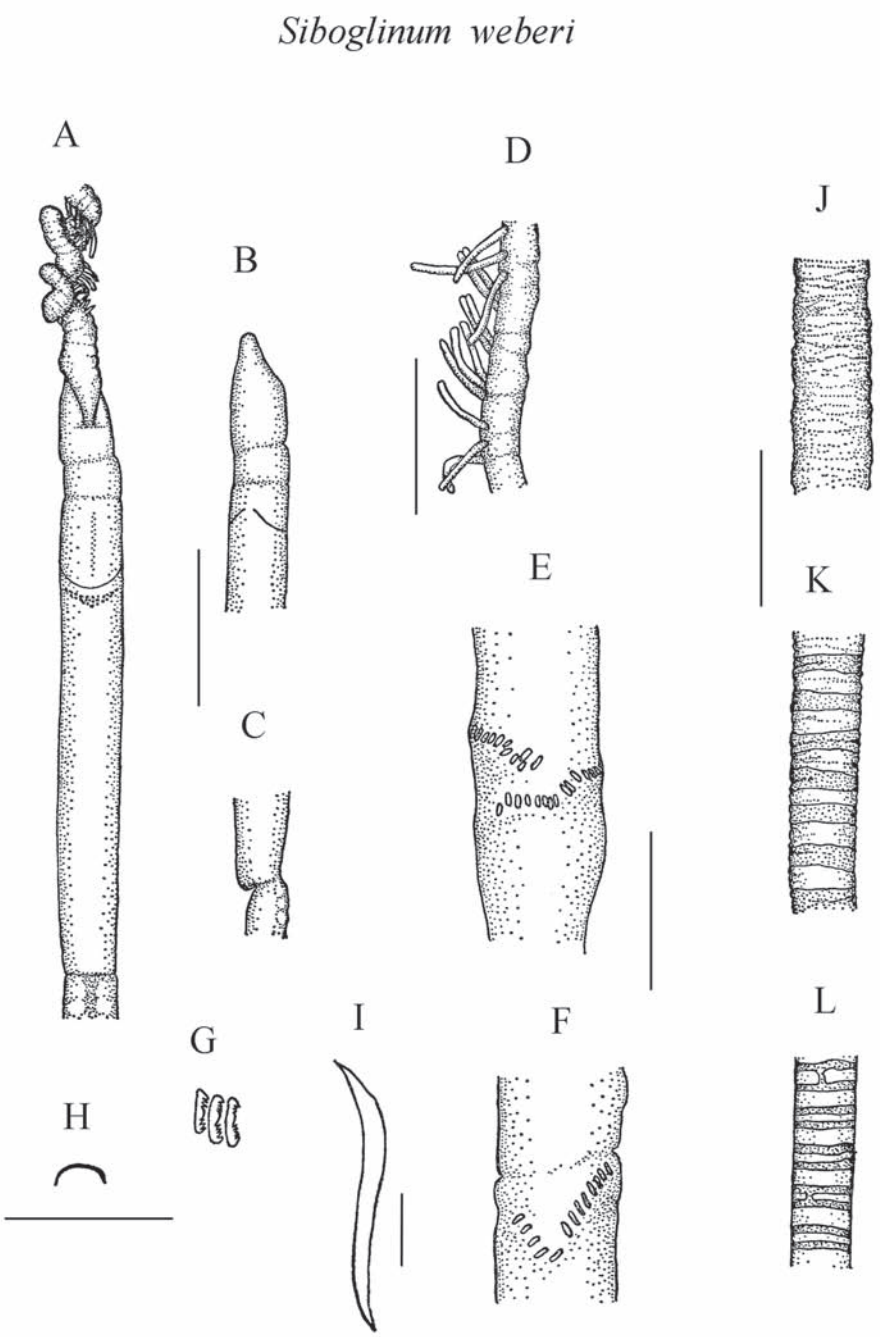

Fig. 8. *Siboglinum weberi*: A – forepart, ventral view; B – cephalic part, ventral view; C – anterior diaphragm area, lateral view; D – tentacle with pinnules; E – first girdle; F – second girdle; G – part of girdle; H – cuticular plaque from postannular region of trunk; I – spermatophore; J–L – parts of tube, anterior-posterior series (after Southward 1961). Scales: A–D, J–L – 0.2 mm; E, F – 0.1 mm; G, H – 50 μm; I – 10 μm.

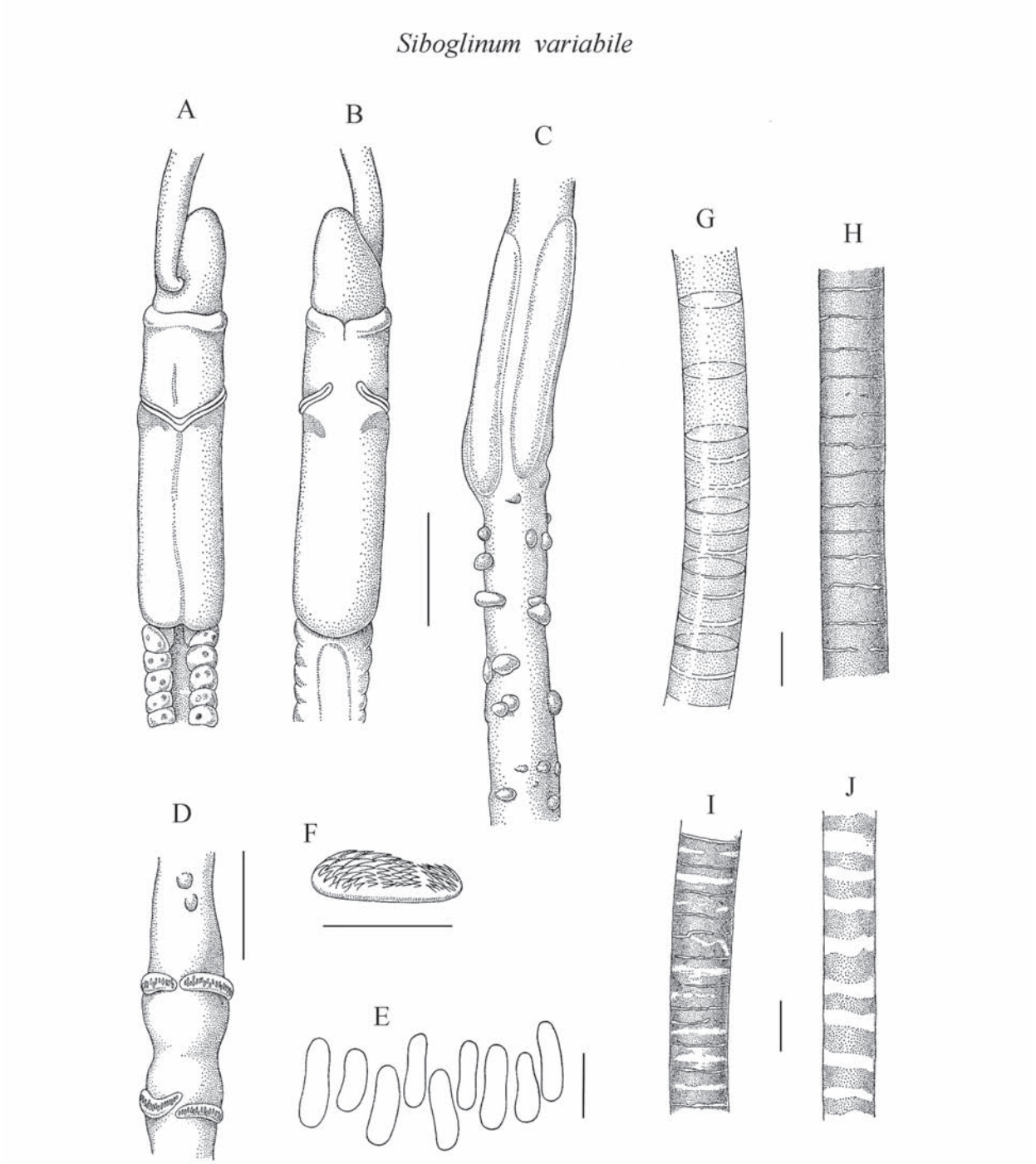

Fig. 9. *Siboglinum variabile*: A – forepart, dorsal view; B – forepart, ventral view; C – zone of thickened papillae, dorsal view; D – girdles, dorsal view; E – part of girdle; F – head of chaeta; G–J – parts of tube, anterior-posterior series (after Ivanov 1960). Scales: A–D – 0.2 mm; E – 10 μm; F – 20 μm; G–J – 0.1 mm.

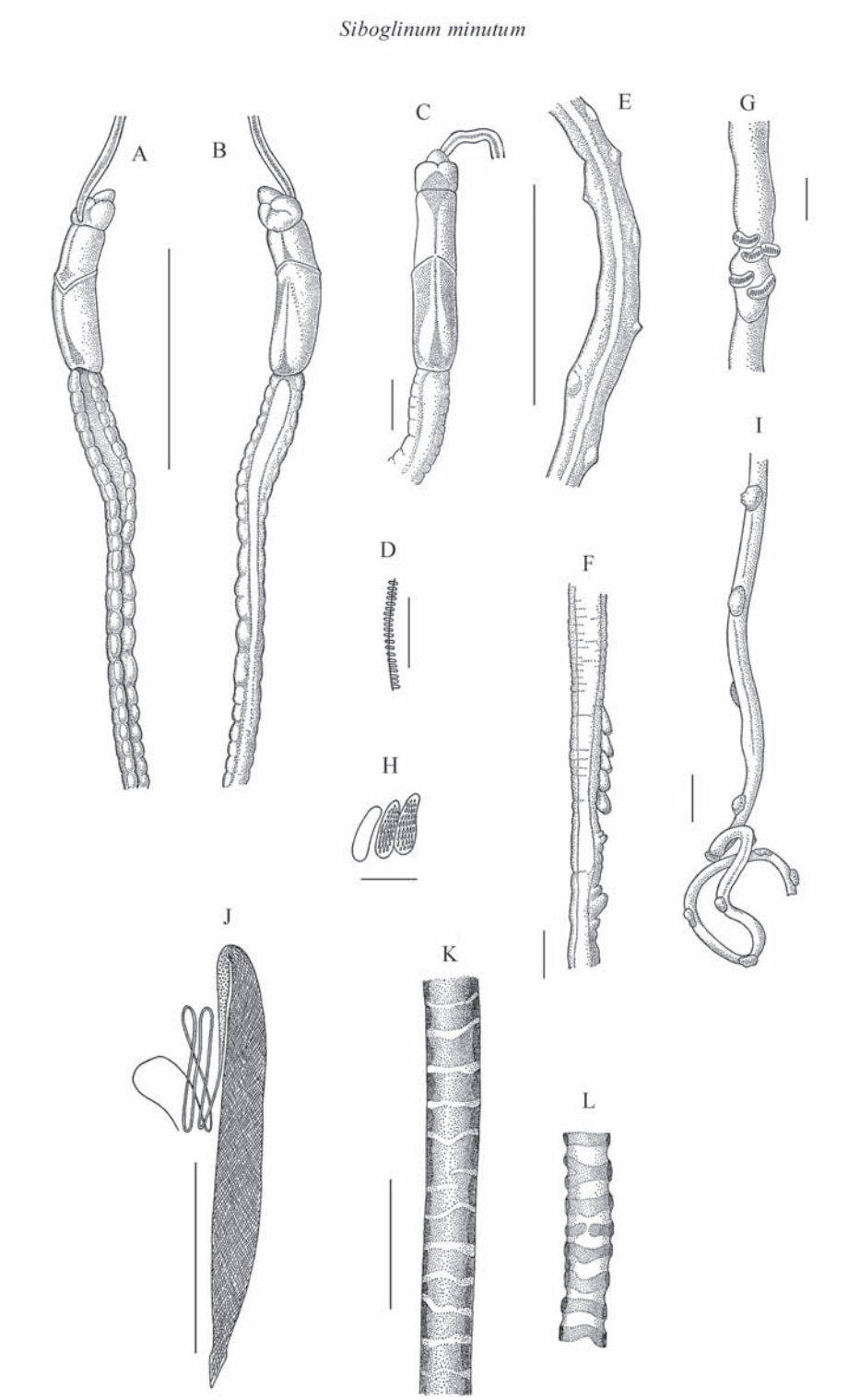

Fig. 10. *Siboglinum minutum*: A – forepart, tentacle and anterior part of trunk, dorso-lateral view; B,C – forepart, tentacle and anterior trunk of different specimens, ventral view; D – part of bridle; E – nonmetameric part of trunk, dorsal view; F – zone of thickened papillae, lateral view; G – girdles, dorsal view; H – part of girdle; I – postannular region of trunk; J – spermatophore; K – middle part of tube; L – posterior part of tube (after Ivanov 1957). Scales: A, B, E – 0.5 mm; C, F, G, I – 0.1 mm; D, J – 50 μm; H – 10 μm; K, L – 0.25 mm.

the absence of the anterior teeth on the chaetal heads and by peculiar red-brown colour of the tube (Fig. 10H). The subgroup typified by *S. ekmani* is characterised by the presence of three annular or initially spiral girdles of chaetae, which are arranged 2+1, i.e. the third girdle is situated at a distance behind the two anterior girdles; very well developed anterior teeth on the chaetal heads, occupied about a half of the head length; the thick (in relation to forepart diameter) tentacle furnished with the pinnules; the ringed and segmented tube (Fig. 11A, D, G, K, O). In my view, these subgroups deserve the subgeneric rank. Certainly, the morphological definitions must be confirmed by molecular taxonomy, but molecular information is insufficient at present. Halanych et. al. (2001) have demonstrated that *S. ekmani* and *S. fiordicum* are not monophyletic, as shown by analysis of their 16S mitochondrial rDNA and 18S nuclear rDNA genes. The morphological differences between these two species allow me to assign them only to different subgenera. Hilario 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. Much more work is certainly needed before a molecular phylogeny can be developed for *Siboglinum* species, but it will be important if and when data can be obtained.

A revised diagnosis of the genus and diagnoses of the newly proposed nine subgenera are provided below. The most important representative features, which could be recognised as necessary and sufficient for taxa diagnostics are listed first. The forepart is accepted to comprise two segments (formerly proto- and mesosome). For explanations of all morphological features, not illustrated in this paper, see Ivanov (1963) and Southward et al. (2005).

Genus *Siboglinum* Caullery, 1914

Type species. *S. weberi* Caullery, 1944 (redescribed Southward 1961).

Diagnosis. One tentacle. Papillae in metameric part of trunk, if present, contain one, sometimes two or three multicellular glands, which thus arranged in one, sometimes in two rows on each side of dorsal furrow. Girdles of chaetae two or three, very seldom four, arranged either close together or by schemes: 1+1, 2+1, 1+2 or 2+2.

Comparison. The genus differs from the other genus of the family Siboglinidae, *Siboglinoides* Ivanov, 1961, by the presence of single tentacle.

Composition. The genus comprises 72 species (see Table 1).

Subgenus *Siboglinum* Caullery, 1914 comb. nov.

Type species. *S. S. weberi* Caullery, 1944 (redescribed Southward 1961).

Diagnosis. Groove between body segments 1 and 2, if present, annular. Anterior teeth on chaetal heads well developed and occupy one-quarter to half of head length. Spermatophores thin and short (40–160 μm). Tube unsegmented. Glandular epidermis on forepart forms belt behind bridle and sometimes in diaphragm area, or not visible. On trunk glandular epidermis forms longitudinal lateral or latero-dorsal bands, rosettes around openings of ducts of multicellular glands of papillae, spots, or, more frequently, not visible. Forepart usually rather long (L_f/D_f : 3.5–20, average 8). Pinnules, if present, form one or two rows. Tentacle usually thin (D_t/D_f : 0.16–0.58, average 0.37). Zone of thickened papillae usually absent. Two, three or four annular girdles of chaetae arranged 1+1, 2+1, 1+2 or close together. Tube ringed brown, yellow, or very rarely almost colourless. Rings single or double, frequently irregular.

Comparison. The subgenus differs from the congeners by the specific combination of following characters: groove between body segments 1 and 2, if present, annular; anterior teeth on chaetal heads well developed and occupy one-quarter to half of head length; spermatophores thin and short (40–160 μm); tube unsegmented.

Composition. The subgenus comprises 28 species (see Table 2).

Subgenus *Taeniafilum* subgen. nov.

Type species. *S. subligatum* Ivanov, 1963.

Etymology. The name refers to the white glandular epidermal ribbons (from Latin *taenium* meaning ribbon), and Latin *filum*, a thread, referring to the appearance of the tube.

Diagnosis. On forepart glandular epidermis forms two spots anterior to bridle dorsally and two

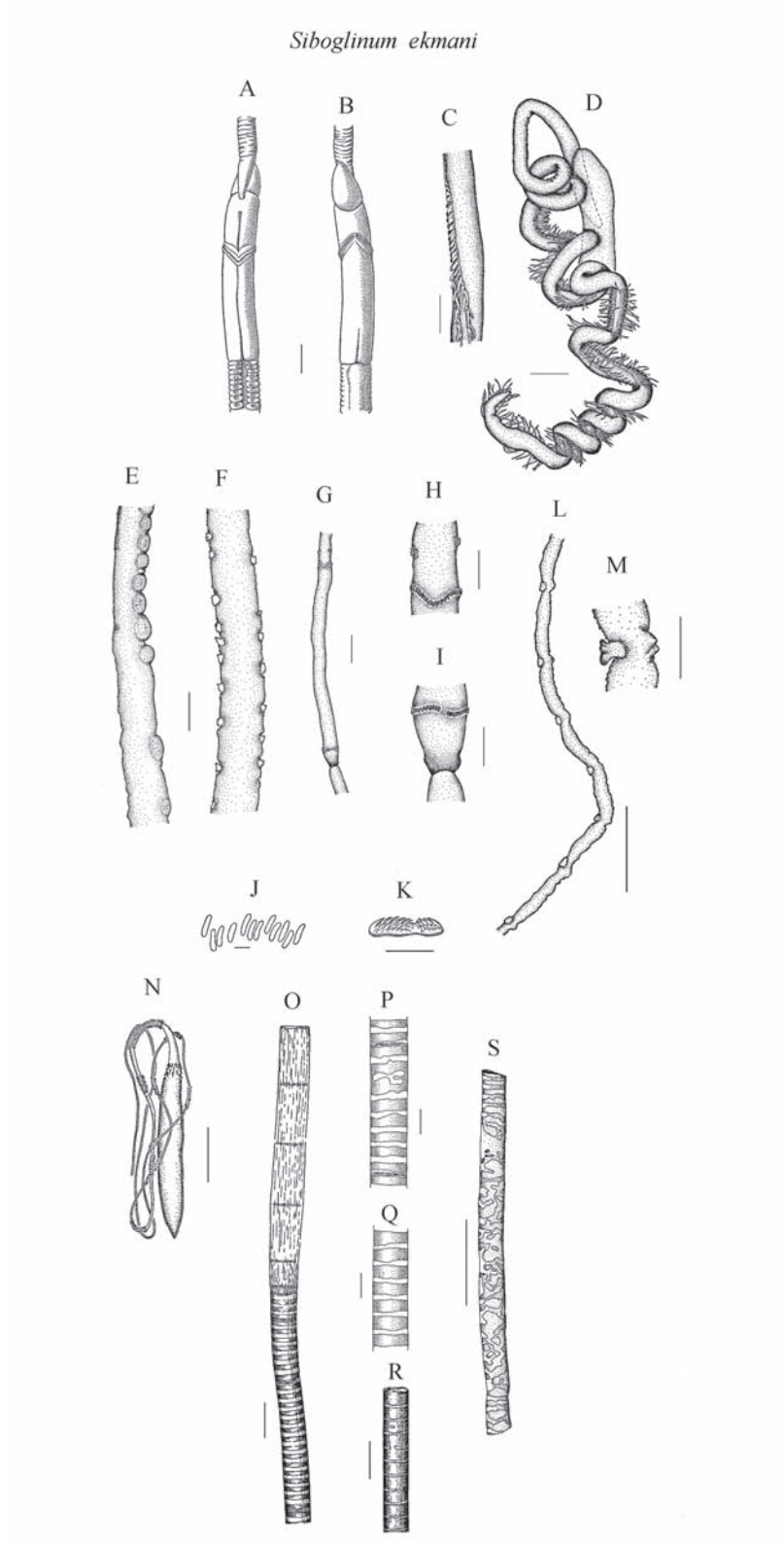

Fig. 11. *Siboglinum ekmani*: A – forepart, dorsal view; B – forepart, ventral view; C – cephalic part and tentacle; D – tentacle with pinnules; E – boundary between metameric and nonmetameric part of trunk, lateral view; F – nonmetameric region, dorsal view; G – girdles, ventral view; H – two anterior girdles, ventral view; I – third girdle, ventral view; J – part of girdle; K – head of chaeta; L – postannular region of trunk, lateral view; M – postannular papillae and glandular shield, lateral view; N – spermatophore; O–S – parts of tube, anterior-posterior series (after Jägersten 1956; Ivanov 1960; Webb 1963b, 1964; Southward 1972). Scales: A, B, D–F, H, I, M, P, Q – 0.1 mm; C, N – 50 μm; G – 0.25 mm; J, K – 10 μm; L, S – 0.5 mm; O, R – 0.2 mm. A, B, J, K from Ivanov (1960); C–I, L, M, S from Webb (1964); N from Webb (1963b); O, R from Jägersten (1956); P, Q from Southward (1972).

latero-dorsal longitudinal ribbons behind bridle. On metameric part of trunk glandular epidermis forms pair of longitudinal bands. Forepart long (L_f/D_f : 7–14, average 9.8). Boundary between body segments 1 and 2, if present, usually annular groove, rarely oblique groove. Pinnules, if present, form single or semidouble row. Tentacle rather thin (D_t/D_f: 0.2–0.5, average 0.32). Zone of thickened papillae usually present. Two annular girdles of chaetae (sometimes another rudimentary one present), situated close together. Anterior teeth on chaetal heads very small, occupying not more than one-third of head length, usually much less. Spermatophores thin, 240–500 μm long. Tube unsegmented or has feeble segmentation anteriorly, not reaching ringed part, colour white, yellowish, greenish or absent. Rings, if present, single, with rare anastomoses.

Comparison. The subgenus differs from the congeners by the specific form and arrangement of glandular epidermis on the forepart: two latero-dorsal longitudinal ribbons behind the bridle and two spots anterior to the bridle dorsally.

Composition. The subgenus contains nine species (see Table 2).

Subgenus *Mergofilum* subgen. nov.

Type species. *S. mergophorum* Nielsen, 1965.

Etymology. The name refers to the forked shape of glandular ribbon (Latin *mergum*) and is derived from the name of the single species, assigned to this subgenus.

Diagnosis. On forepart, glandular epidermis forms elevated Y-shaped longitudinal latero-middorsal ribbon and two dorsal spots behind bridle. On metameric part of trunk glandular, epidermis forms one pair of lateral bands. Anterior boundary of second segment oblique. Forepart long (L_f/D_f: 7.5–11.5, average 9.5). Tentacle thick (D_t/D_f ~0.62), with two rows of pinnules. Zone of thickened papillae present. Two annular girdles of chaetae lying close together. Group of very small anterior teeth of chaetal heads occupies less than one-third of head length (26–30%). Spermatophores thick and very long (~800 μm), with spines on both ends. Tube unsegmented, ringed whitish, sometimes with brownish areas. Rings single, with rare anastomoses.

Comparison. The subgenus differs from the congeners by the specific form and arrangement of glandular epidermis on the forepart: one elevated Y-shaped longitudinal latero-middorsal ribbon and two dorsal spots behind bridle.

Composition. The subgenus contains one species: *S. M. mergophorum* Nielsen, 1965 (see also Southward and Brattegard 1968).

Subgenus *Subtilifilum* subgen. nov.

Type species. *S. vinculatum* Ivanov, 1960.

Etymology. The name is derived from the Latin *subtilis*, i.e. slender, and describes the appearance of the tube.

Diagnosis. Group of very small anterior teeth on chaetal heads occupies much less than one-third of head length (up to 20%), or absent. Spermatophores with very thick filament base. Tube white, sometimes with slightly brownish tinge, or colourless. Glandular epidermis either not visible on forepart and trunk or forms belt behind bridle. Groove between two first body segments, if present, annular. Forepart short (L_f/D_f : 3–11, average 5.9). Pinnules, if present, usually arranged as single row, occasionally forming semidouble or double row. Tentacle usually rather thin (D_t/D_f: 0.28–0.65, average 0.41). Zone of thickened papillae usually present. Two annular girdles of chaetae lying close together. Spermatophores thin, 145–314 μm long. Tube unsegmented. Rings, if present, simple.

Comparison. The subgenus differs from the congeners by the specific combination of following characters: group of very small anterior teeth on chaetal heads occupies much less than one-third of head length (up to 20%), or absent; spermatophores with very thick filament base; tube white, sometimes with slightly brownish tinge, or colourless.

Composition. The subgenus comprises eight species (see Table 2).

Subgenus *Ekmanifilum* subgen. nov.

Type species. *S. ekmani* Jägersten, 1956 (revised Webb 1964).

Etymology. The name is derived from the most widespread species of the present subgenus, *S. ekmani*.

Diagnosis. Tentacle thick (D_t/D_f: 0.43–1.0, average 0.73). Three girdles of chaetae, annular or initially spiral (not more than 1.5 turns), arranged 2+1. Anterior teeth on chaetal heads very well developed and occupy 30–60% (usually about half) of chaetal head.

Tube segmented at least in anterior part. Glandular epidermis may form patches on different parts of forepart, rosettes around duct openings of multicellular glands of papillae and longitudinal lateral bands on trunk, or may be absent. Forepart usually rather long (L_f/D_f : 2.5–11, average 7.1). Anterior boundary of segment 2, if recognizable, annular groove. Pinnules usually arranged in two, sometimes in four rows. Zone of thickened papillae rarely present. Spermatophores quite long (110–380 μm), usually thick. Tube ringed, segments almost always combined with rings. Tube main part yellow, red, brown in colour. Rings single or double, often irregular.

Comparison. The subgenus differs from the congeners by the specific combination of following characters: tentacle thick (D_t/D_f : 0.43–1.0, average 0.73); three girdles of chaetae, annular or initially spiral (not more than 1.5 turns), arranged 2+1; anterior teeth on chaetal heads very well developed and occupy 30–60% (usually about half) of chaetal head; tube segmented at least in anterior part.

Composition. The subgenus comprises 16 species (see Table 2).

Subgenus *Varifilum* subgen. nov.

Type species. *S. variabile* Ivanov, 1960.

Etymology. The name is derived from the single hitherto known species and is descriptive of the considerable range of variability of the tube in this species (Latin *variabilis*, i.e. variable).

Diagnosis. Tentacle thin (D_t/D_f ~0.35). Pinnules absent. Two annular girdles of chaetae lie close together. Anterior teeth of chaetal heads feebly developed and occupy about one-quarter of head length. Tube with segments combined with rings. Glandular epidermis forms postfrenular patches. Forepart short (L_f/D_f : 5–6). Groove delimiting body segments 1 and 2 annular. No sharply defined zone of thickened papillae. Tube main part brown, rings irregular, double in posterior part of tube.

Comparison. The subgenus differs from the congeners by the specific combination of following characters: tentacle thin (D_t/D_f ~0.35); pinnules absent; two annular girdles of chaetae lie close together; anterior teeth of chaetal heads feebly developed and occupy about one-quarter of head length; tube with segments combined with rings.

Composition. The subgenus contains one species: *S. V. variabile* Ivanov, 1960.

Subgenus *Spirannulifilum* subgen. nov.

Type species. *S. callosum* Ivanov, 1971.

Etymology. The name is formed from Greek σϖείρα meaning twisted or spiral, and Latin *annulus*, a girdle, and refers to the spiral shape of the girdles of chaetae.

Diagnosis. Two anterior chaetal girdles spiral (not less than two turns). Glandular epidermis on body not visible or forms ventral spots in nonmetameric region of trunk. Forepart long (L_f/D_f : 8–13, average 10.5). Groove between first two body segments, if present, annular. Tentacle very thick (D_t/D_f : 0.7–1.2, average 0.96). Pinnules form two rows. Zone of thickened papillae absent. Three or four chaetal girdles arranged 2+1 or 2+2. Anterior teeth on chaetal heads well developed and occupy one-third to half of head length. Spermatophores thin, short (130–160 μm). Tube with rings and with segmented anterior part, yellow-brown in colour. Rings with very regular "perforation".

Comparison. The subgenus differs from the congeners by the specific form and arrangement of two anterior girdles of chaetae: these are spiral (not less than two turns).

Composition. The subgenus comprises two species (see Table 2).

Subgenus *Nereilinoides* subgen. nov.

Type species. *S. caulleryi* Ivanov, 1957.

Etymology. Representatives of the present subgenus resemble very much species of the genus *Nereilinum* Ivanov, 1961 (Oligobrachiidae) by the shape of the segmental groove on the forepart, that was referred to in the subgeneric name.

Diagnosis. Groove between body segments 1 and 2 oblique. Spermatophores with one or two peculiar transparent terminal zones. On forepart glandular epidermis represented by belt behind bridle and often by longitudinal latero-dorsal bands on trunk. Forepart rather long (L_f/D_f : 4.5–12, average 7.6). Tentacle usually quite thin (D_t/D_f : 0.25–0.63, average 0.41). Pinnules form usually one or two rows, rarely up to five rows. Zone of thickened papillae present. Two annular girdles of chaetae lying close together. Anterior group of teeth well developed on chaetal heads, occupies about one-third of head length. Spermatophores rather thin and long (140–270 μm). Tube

unsegmented, ringed. Rings simple. Colour of tube middle part brown with tinges of green, yellow, gray.

Comparison. The subgenus differs from the congeners by the specific form and arrangement of the groove between body segments 1 and 2: it is oblique.

Composition. The subgenus contains six species (see Table 2).

Subgenus *Minifilum* subgen. nov.

Type species. *S. minutum* Ivanov, 1957.

Etymology. The name refers to the small dimensions of the single hitherto known species and is derived from *minimus* (Latin) meaning "very small".

Diagnosis. Anterior teeth on chaetal heads absent. Tube red-brown in colour. Visible areas of glandular epidermis on body absent. Forepart short (L_f/D_f : 4.5–5). First two body segments not separated externally from each other. Tentacle thin (D_t/D_f ~0.25). Pinnules absent. Zone of thickened papillae present. Two annular girdles of chaetae situated close together. Spermatophores short (~110 μm) with very thick base of filament furnished by spines and lanceolate appendix on afilamentar end. Tube unsegmented, ringed, very rigid in main part. Rings single, irregular.

Comparison. The subgenus differs from the congeners by the specific combination of following characters: anterior teeth on chaetal heads absent; tube red-brown in colour.

Composition. The subgenus contains one species: *S. M. minutum* Ivanov, 1957.

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