

# Two new species of Pogonophora from the arctic mud volcano off northwestern Norway

Roman V. Smirnov

## SARSIA



Smirnov RV. 2000. Two new species of Pogonophora from the arctic mud volcano off northwestern Norway. *Sarsia* 85:141-150.

Collections of Pogonophora made by the research vessels *Håkon Mosby* and *Professor Logachev* in the Norwegian Sea in 1995-1996 contain two new species belonging to the genera *Sclerolinum* and *Oligobrachia*. Both species were obtained on the continental slope northwest of Norway in the area of an anomalous cold seep of a "mud volcano" type. *Sclerolinum contortum* sp. nov. differs from the congeneric species in having a rather long opisthosome with very few segments (4-5) and tubes open at both ends and strongly folded upon themselves to show regular S-bends. *Oligobrachia haakonmosbiensis* sp. nov. is well distinguished by a set of features, especially by the lack of glandular patches on the first two segments, that is very unusual for *Oligobrachia*. A detailed comparison of all species of the single genus in the subclass Monilifera, *Sclerolinum*, is given.

Roman V. Smirnov, Zoological Institute, Russian Academy of Sciences, St. Petersburg 199034, Russia.  
E-mail: [srw@zisp.spb.su](mailto:srw@zisp.spb.su)

Keywords: Arctic Ocean; Norwegian Sea; mud volcano; Pogonophora; taxonomy

## INTRODUCTION

Since its discovery in 1995 the so-called Haakon Mosby Mud Volcano (HMMV) has continued to attract the attention of geophysicists due to several uncommon features (some thermal anomalies, location at high latitude, lack of association with plate subduction, etc.) (Vøgt & al. 1997). Meanwhile zoological investigation of the HMMV is just beginning. Two pogonophoran species appeared to be abundant benthic animals associated with it. They were sampled during two expeditions on board Norwegian and Russian vessels, and most of the specimens were placed at my disposal. The material consists of one new species of the genus *Sclerolinum* and another of the genus *Oligobrachia*.

## MATERIAL AND METHODS

Nearly 200 tubes of *Sclerolinum contortum* sp. nov. and 32 tubes of *Oligobrachia haakonmosbiensis* sp. nov. were obtained employing both gravity and box cores to sample a muddy bottom on and near the HMMV off northwestern Norway in the Norwegian Sea during the 16th cruise of the RV *Håkon Mosby* (Stn 85, 72°00.46'N,

14°43.91'E, 1257-1303 m; Summer 1995) and 15th cruise of the RV *Professor Logachev* (Stn 36, 72°00.5'N, 14°43.35'E, 1250-1260 m; 7-8 Aug 1996). The material was fixed in 75 % alcohol. The drawings were made using a stereomicroscope with mirror attachment. For scanning electron microscopy different parts of several animals were prepared employing the cheap and gentle method of Markevich and Koreneva (Markevich 1993), the essence of which is that objects are firstly put through ethanol, diethyl ether and etheric solution of naphthalene consecutively and then dried by means of sublimation of naphthalene. The objects were finally coated with platinum and examined with a Hitachi-700 scanning electron microscope. All material is deposited at the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIRAS).

## CLASS POGONOPHORA

Since the higher taxonomy of pogonophores is still ambiguous I prefer to use here the system of three subclasses accepted by Ivanov (1991, 1994) and Southward (1988 and later) as the most adequate at present. The names of taxa follow Ivanov (1994) and partially Webb (1969).

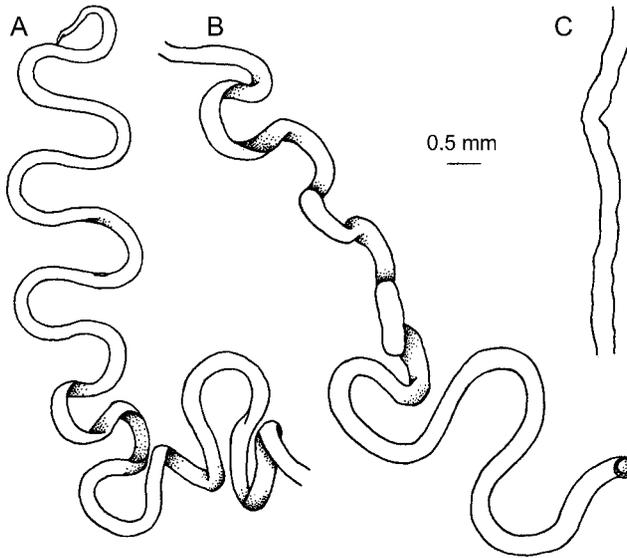


Fig. 1. *Sclerolinum contortum* sp. nov. Tube: form with S-bends in one plane. A. Anterior part. B. Middle part. C. Posterior part.

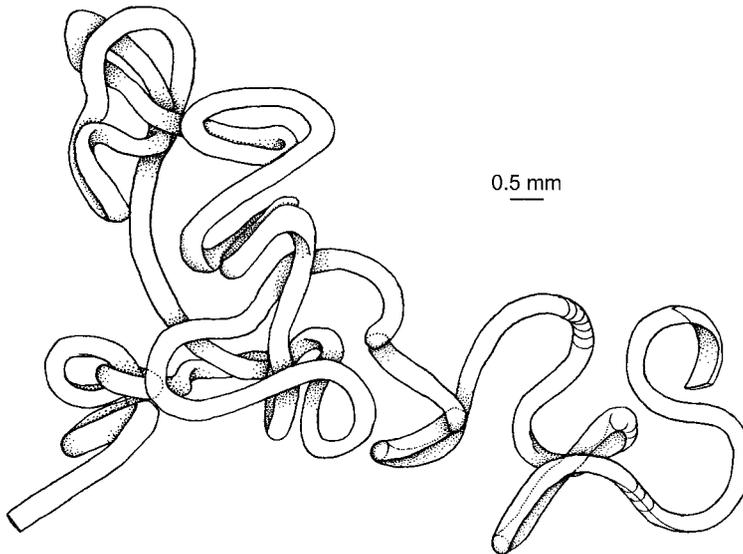


Fig. 2. *Sclerolinum contortum* sp. nov. Tube: very entangled form with S-bends situated in different planes.

#### TAXONOMIC PART

Subclass Monilifera  
 Order Sclerolinida  
 Family Sclerolinidae  
 Genus *Sclerolinum* Southward

*Sclerolinum contortum* sp. nov.  
 (Figs 1-5)

Type material. Holotype: ZIRAS N64.

Type locality. Norwegian Sea, Haakon Mosby Mud Volcano (72°00.46'N, 14°43.91'E), 1257-1303 m, grab, mud, RV *Håkon Mosby* (cruise 16), Stn 85, Summer 1995.

Other material examined. 136 specimens and 59 fragments of empty tubes from the locality of the holotype;

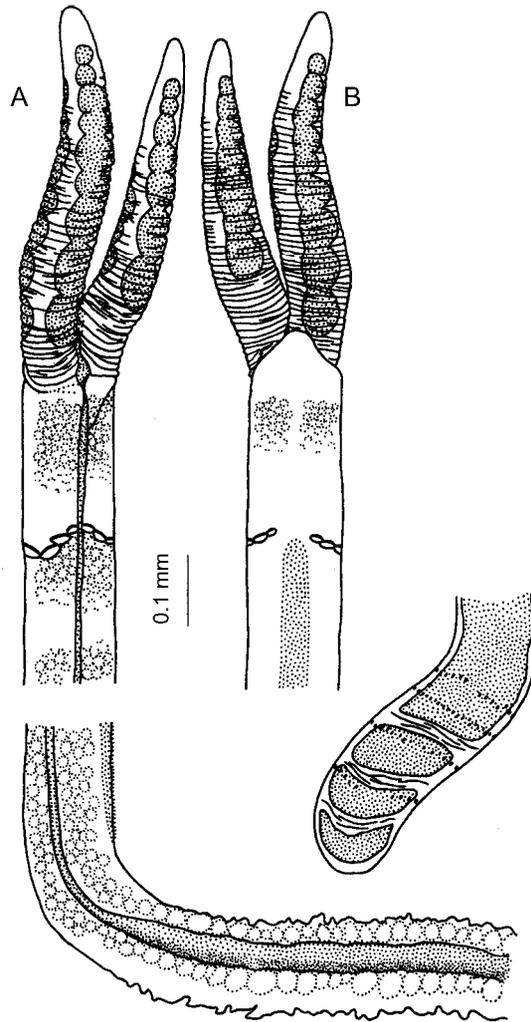


Fig. 3. *Sclerolinum contortum* sp. nov. A. Anterior zone, dorsal view. B. The same, ventral view. C. Posterior zone, dorsolateral view. D. Opisthosome.

Norwegian Sea, Haakon Mosby Mud Volcano (72°00.5'N, 14°43.35'E), 1250-1260 m, grab, mud, RV *Professor Logachev* (cruise 15), Stn 36, 7-8 Aug 1996. 11 animals and 6 empty tubes.

**Etymology.** The specific name *contortum* meaning twisted is given due to the peculiar appearance of the tubes.

**Description.** The tubes are very firm but elastic, slightly wrinkled, pale yellow in the middle and brownish posteriorly, except for the anteriormost and posterior regions which are colourless, thin-walled and collapsed. The front part is regularly twisted into a few S-bends

situated in one plane or several planes (Fig. 1A, B). If the latter, the tube can be so entangled that it resembles a knot (Fig. 2). This S-bend region ranges from 7 to 35 mm in length and is present in all the tubes. The wall-thickness may be up to 56 µm on the inside of curves, less on the outside.

The posterior part of the tube is more brittle in spite of its thinner walls and almost straight, but with traces of S-bends. It is apparently buried in mud whereas the twisted anterior part sticks out or lies on the surface of the substrate (Fig. 1C). The diameter of the tubes varies between 0.20-0.39 mm; the maximum length can be appraised as about 70 mm. The hind end is not closed.

Although the tube is very transparent, I have failed to

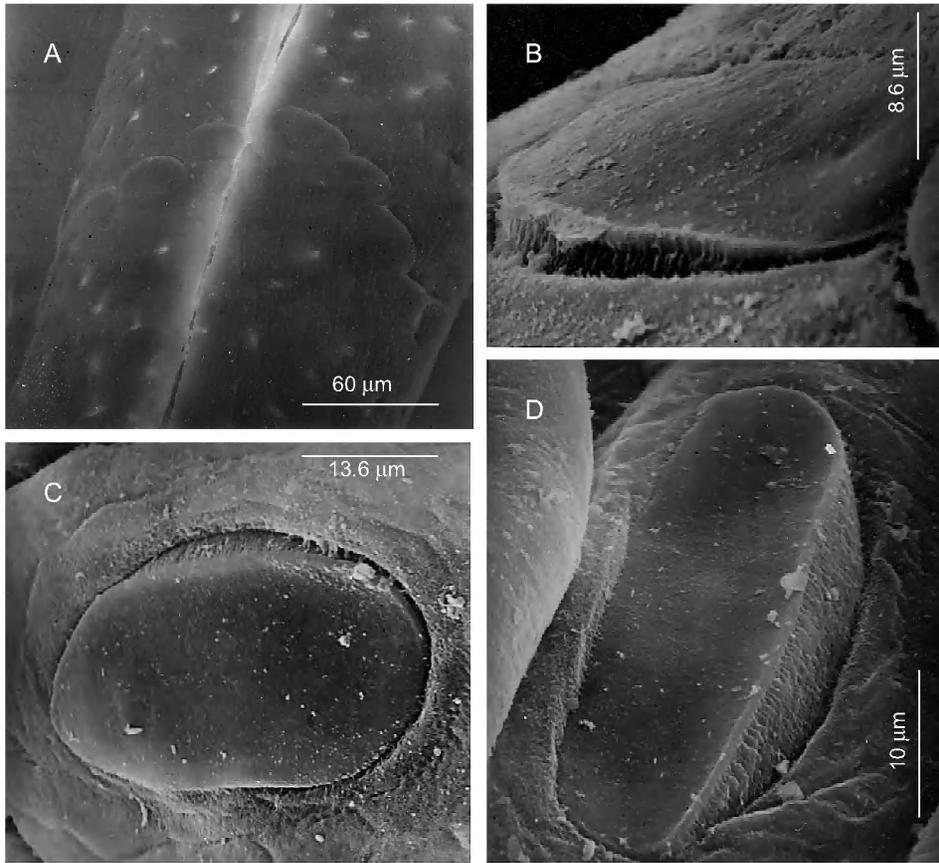


Fig. 4. *Sclerolinum contortum* sp. nov. A. Region of bridle, dorsal view (SEM). B. Cuticular plaque of the bridle (SEM). C, D. Different forms of cuticular plaques from the posterior zone (SEM).

discern sufficient details of the animal's external morphology through the wall. This has led me to dissect 18 specimens from their extremely tough, but, fortunately, elastic tubes.

The animal has two comparatively thick and more or less wrinkled tentacles 0.525-2.250 mm long. Two longitudinal blood vessels looking like series of yellowish oval formations (evidently because of fixation) are seen in direct light in the tentacles of some specimens (Fig. 3A, B).

Externally there is no useful criterion for the distinction of the forepart and the trunk. For descriptive convenience the body may be divided, following Webb (1964a, 1964b) and Southward (1972), into an anterior zone from the cephalic lobe to the end of the ciliated band and a posterior zone comprising all the rest backwards to the opisthosome.

A rather noticeable cephalic lobe measuring 50-70 μm is triangular with a rounded tip. It is not separated from the rest of the anterior zone, on the dorsal side of which

there is a deep, narrow longitudinal furrow stretching from the bases of the tentacles to cut across the bridle. The latter is situated approximately 0.29 mm behind the apex of the cephalic lobe. The bridle consists of two U-shaped dense rows of separate oval, colourless plaques, each with a thickened front edge (Fig. 4A, B). The number of plaques in the bridle varies between 10-14 and the size varies from 22 to 41 μm, the latter even in the same specimen. Both the bridle plaques and those on the posterior papillae can scarcely be discerned even on a tubeless animal, to say nothing of seeing them through the tube wall.

A wide ciliated band begins a short way behind the ventral plaques of the bridle and runs back to the end of the anterior zone, a distance of 2.0-4.5 mm. Numerous glands are visible from close to the bases of the tentacles, densely packed in the coelom. Posteriorly they become larger and at about the point of change from the anterior to the posterior zone give way to much larger glands of unequal size arranged in two rows (Fig. 3C).

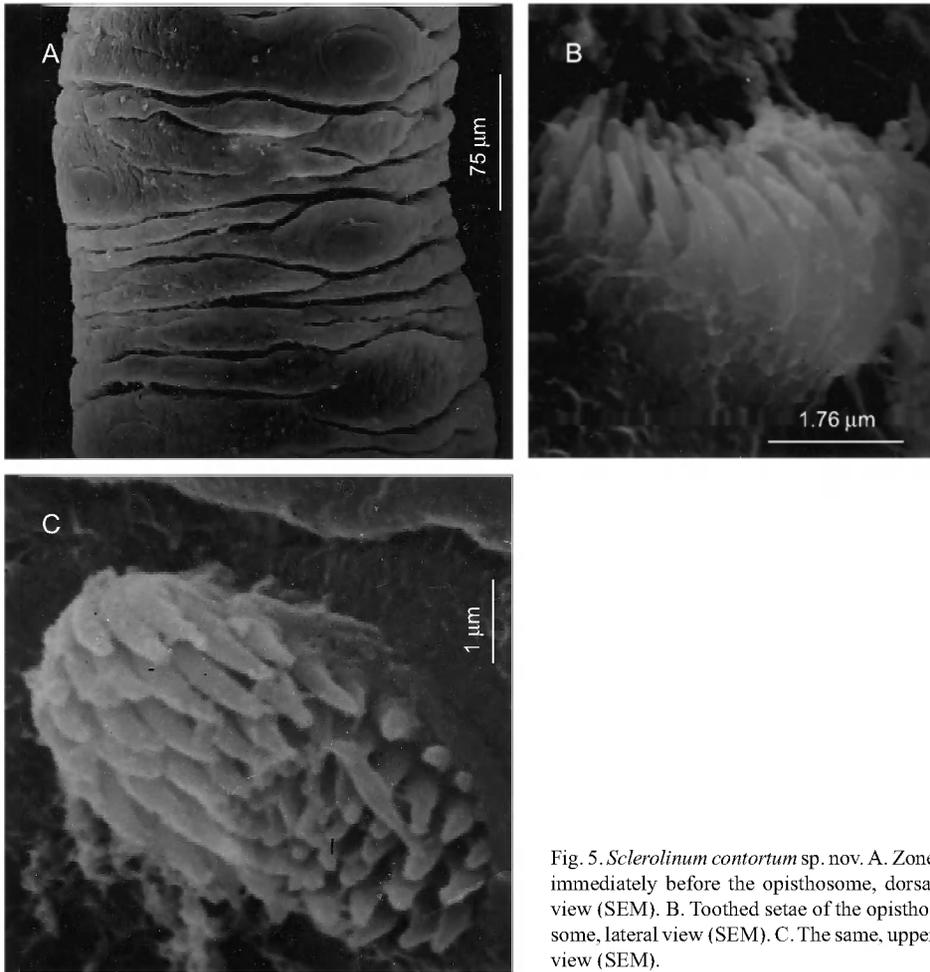


Fig. 5. *Sclerolinum contortum* sp. nov. A. Zone immediately before the opisthosome, dorsal view (SEM). B. Toothed setae of the opisthosome, lateral view (SEM). C. The same, upper view (SEM).

The transition between the anterior and posterior zones is well marked also by a broadening of the dorsal furrow, sometimes quite abrupt, and the change of the body outline from smooth to wavy. Further back, papillae topped by plaques similar to those in the bridle (Fig. 4C, D) appear gradually, scattered mainly on the dorsolateral sides of the trunk. Just before the opisthosome there is a zone with densely arranged papillae (Fig. 5A). The complete posterior zone is 30-50 mm long. The diameter of the body in the bridle area averages 0.2 mm.

The opisthosome, 0.45-0.60 mm long with no more than four or five segments, has been found in a few specimens. It is not separated from the trunk (Fig. 3D). There is a row of 10-20 tiny bristles on the first two-three segments, just behind the septa which are rather thick and easily visible. There are also two rings of similar bristles in front of the first septum, the anterior incomplete dorsally while the posterior is split ventrally. These are

close together and presumably homologous with the girdles of all frenulate pogonophores. The bristles are typical “toothed platelets” with oval serrated tips 5.5-6.3 µm long and two groups of teeth on each, the front slightly smaller than the hind group (Fig. 5B, C).

**Discussion.** This species undoubtedly belongs to the genus *Sclerolinum*. It is characterised by the absence of some typical frenulate features (external grooves dividing forepart and opisthosome from trunk, proper bridle and girdles, specialised regions on trunk, morphological differences between bristles in girdles and on opisthosome), and possesses a set of peculiar features, i.e. two comparatively short and thick tentacles without pinnules, very small cephalic lobe, separate plaques as a bridle, simple girdles (i.e. without muscular ridges) lying immediately next to the opisthosome, a ciliated band on both forepart and anterior papillaless part of the trunk,



transparent ringless and non-segmented tube with thick, tough walls in the middle part. Contrary to Ivanov's (1991, 1994) opinion the tubes are not posteriorly closed in all *Sclerolinum* species.

Six species have been described in this genus, all having the characteristics mentioned above. *S. contortum* sp. nov. belongs to a group of two mud-dwelling species while the other four inhabit decaying wood and other vegetable debris. Table 1 shows an entire list of features that are useful to distinguish *Sclerolinum* species. As appears from this, *S. contortum* sp. nov. stands apart from all, since it has a rather long opisthosome with very few

segments and the anterior part of the tube is strongly twisted to form several regular S-bends. Nevertheless, several characteristics indicate some similarity to *S. major* and *S. magdalenae* (Southward 1972) from the Caribbean Sea, especially to the latter, from which *S. contortum* sp. nov. differs additionally in the shorter opisthosome and in the fewer bristles per segment. As for *S. major*, it should not be closely related to the new species because of its wood-living habit and the nature of the bridle which is apparently the most primitive among all sclerolinids as it is composed of many plaques scattered higgledy-piggledy.

Table 1. Characteristics of the species of *Sclerolinum*. Symbols: + present; – absent; + – poor development; ++ strong development; ? unknown; s<sup>1</sup> boundary between cephalic lobe and rest of 1st segment; s<sup>2</sup> boundary between 1st and 2nd segments; s<sup>3</sup> boundary between 2nd and 3rd segments; s<sup>4</sup> boundary between 3rd segment and opisthosome; d dorsal; v ventral; l lateral; a anterior; p posterior

	<i>S. brattstromi</i>	<i>S. minor</i>	<i>S. major</i>	<i>S. javanicum</i>	<i>S. sibogae</i>	<i>S. magdalenae</i>	<i>S. contortum</i>
Tube, diameter (mm)	0.128	0.13-0.20	0.20-0.84	0.12	0.1-0.15	0.3	0.20-0.39
Tube, thickness of wall (µm)	32, uneven	?, even	?, uneven	?, even	15, even	?, even	56, uneven
Tube, general character	irregularly bent	irregularly bent	loose spiral	irregularly bent	straight	a-irregularly bent p-straight	a-regularly bent p-straight
Tube, character of surface	smooth	smooth	smooth	smooth	deeply wrinkled	a-smooth p-wrinkled	a-smooth p-slightly wrinkled
Tube, anterior part	filmy	firm	filmy	filmy	filmy	firm	filmy
Tube, posterior part	filmy	filmy	filmy	firm	?	filmy	filmy
Tentacles, character of surface	slightly wrinkled	slightly wrinkled	slightly wrinkled	smooth	wrinkled	wrinkled	wrinkled
Cephalic lobe	+	+	+	+	++	+	+
s <sup>1</sup>					+		
s <sup>2</sup>							
s <sup>3</sup>				+	+		
s <sup>4</sup>				?	?		
Distance from apex of cephalic lobe to bridle (mm)	0.133-0.159	0.09-0.18	0.22	0.132-0.200	0.22-0.32	0.35	0.27-0.3
Anterior zone, breadth (mm)	0.09-0.12	0.08-0.10	0.2-0.3	0.08-0.10	0.06-0.07	0.2	0.13-0.24
Dorsal groove on anterior zone		+	++			+	++
Ciliated band, character	broad, heterogeneous	narrow, homogeneous	broad, homogeneous	broad, homogeneous	narrow, homogeneous	?	narrow, homogeneous
Ciliated band, length (mm)	1.239-1.265	0.7	2-3	2	>0.37	?	2.0-4.5
Bridle, general character	unfused	unfused	unfused	unfused	unsteady fused	unfused	unfused
Bridle, arrangement of cuticular plaques	1 row, sparse	1 row, sparse	scattered	1 row, sparse		1 row, sparse	1 row, dense
Bridle, shape (dorsal view)	∩∩	∩∩	⊗⊗	∩	irregular	— —	∩∩
Bridle, position	(d)-l	d-l-(v)	(d)-l	d-l	d-l-v	d-l	d-l-(v)
Plaques of bridle, shape	elongated	oval	oval	oval		oval	oval
Plaques of bridle, size across (µm)	23	10-20	10-20	7-20		22-44	22-41
Plaques on papillae, size across (µm)	15	12-20	12-30	12-15	15-30	40	29-41
Transition between anterior and posterior zones	abrupt	gradual	gradual	gradual	gradual	gradual	abrupt
Anterior zone, length (mm)	1.398-2.929	0.79-0.88	3-4	2.132	1.80-3.35	?	2.3-4.8
Posterior zone, length (mm)	≥94.78	20	?	?	>30	?	30-50
Opisthosome, length (mm)	0.331-0.885	0.3-0.5	0.64	?	?	1	0.45-0.60
Opisthosome, number of segments	8-15	7-8	8-9	?	?	18-20	3-5
Bristles of opisthosome, number per segment	?	2-15	11-17	?	?	30-40	10-20
Bristles of opisthosome, size across (µm)	?	?	?	?	?	4-5	5.5-6.3
Spermatophores, length (mm)	?	?	?	?	0.1-0.15	?	?
Habitat	wood	wood	wood	wood	mud	mud	mud



*S. contortum* sp. nov. is well distinguished from the geographically closest (Hardangerfjorden, western Norway) species, *S. brattstromi* (Webb 1964a), by many characteristics. These, in addition to already mentioned, are thicker wall of the tube, the twice larger diameter of the tube; the narrower ciliated band; the plaques of the bridle are oval, not elongated; a distance from the apex of the cephalic lobe to the bridle in *S. contortum* is considerably larger as well as the length and breadth of the anterior zone, on which there is a strongly developed dorsal groove, absent from *S. brattstromi*; finally, the two species dwell different substrates: mud and wood (Webb 1964b).

Subclass Frenulata  
Order Athecanephria  
Family Oligobrachiidae  
Genus *Oligobrachia* Ivanov

*Oligobrachia haakonmosbiensis* sp. nov.  
(Figs 6, 7)

Type material. Syntypes: ZIRAS N65 (5 specimens).

Type locality. Norwegian Sea, Haakon Mosby Mud Volcano (72°00.5'N, 14°43.35'E), 1250–1260 m, grab, mud, RV *Professor Logachev* (cruise 15), Stn 36, 7–8 Aug 1996.

Other material examined. 7 animals and 19 empty tubes from the locality of the syntypes; Norwegian Sea, Haakon Mosby Mud Volcano (72°00.46'N, 14°43.91'E), 1257–1303 m, grab, mud, RV *Håkon Mosby* (cruise 16), Stn 85, Summer 1995. 1 empty tube.

Etymology. The specific name *haakonmosbiensis* refers to the locality (Haakon Mosby Mud Volcano) and the research vessel *Håkon Mosby* which discovered it.

Description. The tubes are brown to black in colour, being transparent only anteriorly and posteriorly, and rather stiff. The longest fragment measures 15 cm, the diameter near the front end reaches 0.83 mm diminishing backwards to 0.28–0.47 mm. The anterior end is colourless with slender wrinkles in limp, filmy walls, 2–5 mm long (Fig. 6I). In some specimens the rings appear just after this, without a gradual intensification, with coarse fibres in the interspaces, and the colour abruptly become brownish, soon darkening to black (Fig. 6J). Otherwise, at first the fibres are distributed evenly, then these form local condensations situated at unequal intervals which thus give the appearance of short rings. Further back the fibres disappear little by little, at first from the rings, then

altogether, and the rings become darker, they widen to about the tube diameter and become regular (Fig. 6K, L). The ringed part is, however, not very long, the rings soon become indistinct while the interspaces break up and finally vanish (Fig. 6M). The walls of the tube in the rings are noticeably concave. The semitransparent posterior part of the tube is characterised by the presence of weak longitudinal ribs on the surface, and, in some specimens, by a few segments about 1.1–1.2 mm long (Fig. 7).

All animals have slightly squashed anterior ends while other parts are worse preserved. The tentacles are broken, their number varies in different specimens from 5 to 12, pinnules are not seen, perhaps because of bad preservation. The forepart is 2.9–4.5 mm long with the diameter between 0.45 and 0.70 mm, according to the degree of the animals' contraction (Fig. 6A, B, C). A wide and short cephalic lobe is strongly flattened dorsoventrally and approaches an equilateral triangle in shape. On the ventral side at the level of attachment of the tentacles there is a slight transverse groove united with a longitudinal mid-dorsal furrow which continues to the bridle situated just in front of the middle of the forepart. The thin, dark brown bridle keels are always very close together ventrally and usually joined on the dorsal side, but not infrequently just separated by a tiny gap. The boundary between the trunk and the forepart is clearly marked by a slightly oblique groove. The narrow dorsal sulcus of the anterior part of the trunk is flanked by a pair of ridges inside which numerous crowded pyriform glands are easily visible by transparency since they stand out against a background of darkish epidermal patches. No other coloured or glandular areas are perceptible.

Very small (20–24  $\mu\text{m}$ ) black cuticular plaques are present on the anterior part of the trunk, starting 1–2 mm behind the diaphragm. Some papillae in the annular and postannular regions are furnished with plaques of another type. They are entirely colourless and without any ridge, measuring about 41  $\mu\text{m} \times 26 \mu\text{m}$  (Fig. 6G).

There are two girdles, close together, made up of two irregular rows of platelets which are 14–15  $\mu\text{m}$  long with the anterior group of teeth occupying no more than a quarter of the head area (Fig. 6F). Both girdles are incomplete dorsally (Fig. 6D, E).

The oocytes are oval with an average size 126  $\mu\text{m} \times 168 \mu\text{m}$ . The spindle-shaped spermatophores are about 700  $\mu\text{m}$  long and 40–50  $\mu\text{m}$  in diameter; the proximal end of the filament is drawn out sideways into two unarmed wings (Fig. 6H).

Dr. E.C. Southward has more specimens of *O. haakonmosbiensis* better preserved than mine, and she has kindly permitted her additions to the description to be quoted in this paper. According to her observations, there is a white patch on the ventral side of the cephalic lobe; pinnules are definitely absent from the tentacles;

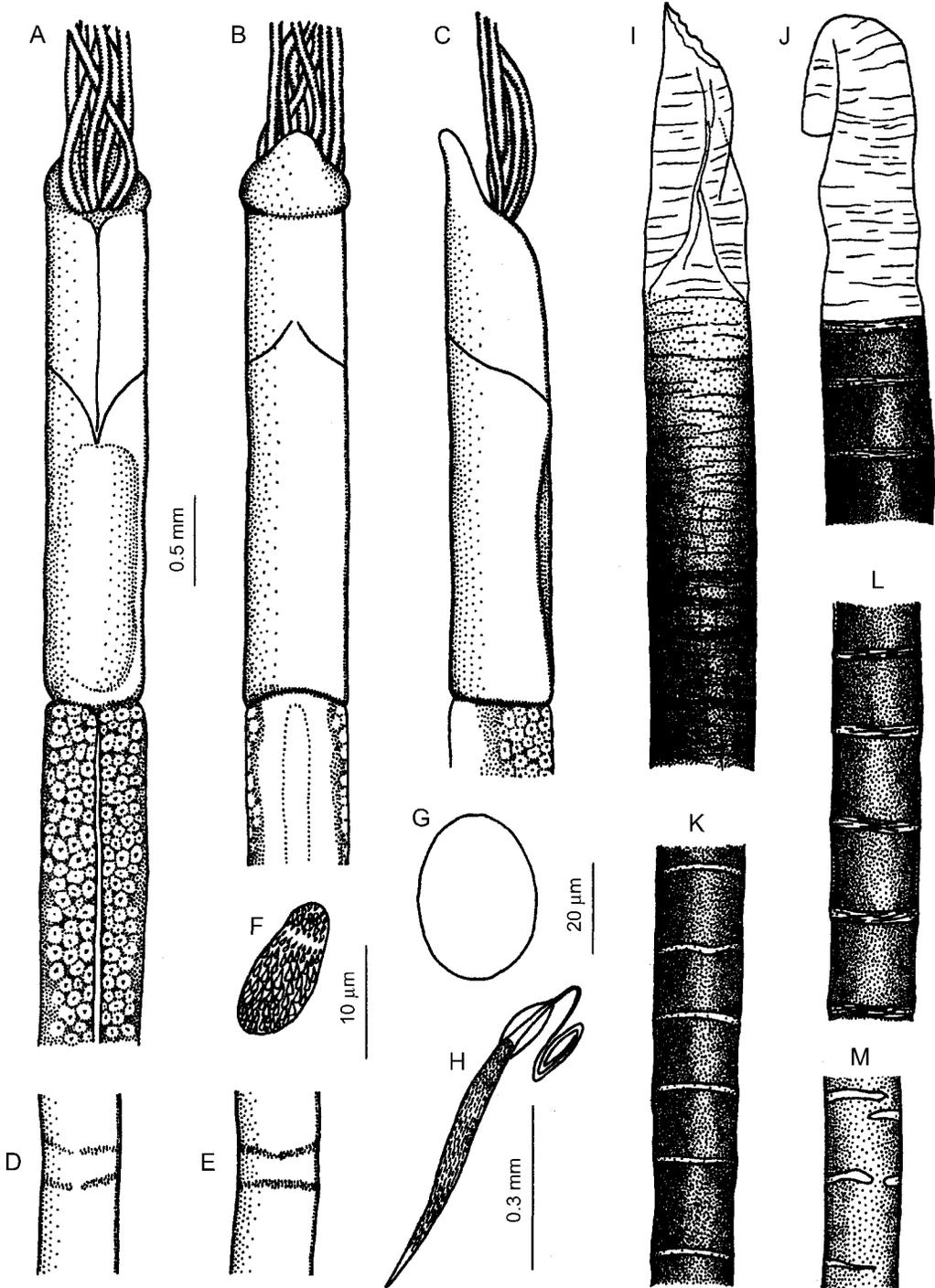


Fig. 6. *Oligobrachia haakonmosbiensis* sp. nov. A. Forepart, dorsal view. B. The same, ventral view. C. The same, lateral view. D. Girdles, dorsal view. E. The same, ventral view. F. Toothed setae of girdles. G. Cuticular plaque from the postannular region of the trunk. H. Spermatophore. I. Tube, one type of the anterior end. J. The same, another type. K, L. Tube, middle part. M. Tube, distal part.

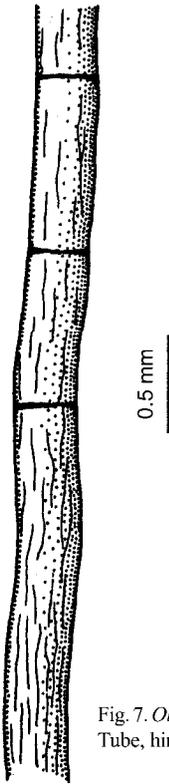


Fig. 7. *Oligobrachia haakonmosbiensis* sp. nov. Tube, hindmost part with segments.

there is a band of reddish-brown spots along each tentacle; the tubes are larger and some of them contain numerous embryos, the early spherical stage being about 180 to 200  $\mu\text{m}$  in diameter.

**Discussion.** *O. haakonmosbiensis* is a typical member of the genus *Oligobrachia* sharing all the characteristics among which the most striking are: a small number of

separate tentacles, continuous lateral ridges with non-metamerically arranged pyriform glands in the anterior part of the trunk, non-transparency of the forepart body wall, spermatophores with two wings at the base of the filament and dark tube, opaque in the middle, with rings.

In size, number of tentacles and number of rows of pyriform glands in the foremost (front 10–15 mm) part of the trunk *O. haakonmosbiensis* resembles four of ten previously known species to wit *O. dogieli* (Ivanov 1957), *O. mashikoi* (Imajima 1973), *O. ivanovi* (Southward 1959) and *O. webbi* (Brattegard 1966), the first two from the Pacific and the last from the northeast Atlantic, *O. webbi* being found near Tromsø in northern Norway. The new species comes closest to *O. ivanovi* because it has internal pyriform glands packed tightly cheek-by-jowl with a brown ring around the opening of each, a circular furrow lying in front of the bridle, and the tube is very similar (Southward 1978). The last two characters are in common also with *O. webbi*. *O. haakonmosbiensis* differs from both *O. ivanovi* and *O. webbi* in its lack of any patches of glandular epidermis on the forepart (not including the cephalic lobe) and lack of white-coloured bands covering the pyriform glands. From *O. ivanovi* it differs additionally in having much smaller anterior groups of teeth on the heads of the setae, split girdles, and in arrangement of the bridle keels which are always separate on the ventral side of the body and usually so on the dorsal side. In these respects it resembles *O. webbi*, but differs from this species in having a darker tube, a white patch on the cephalic lobe, and smaller and much more numerous embryos.

#### ACKNOWLEDGEMENTS

I am grateful to the crews on the RVs *Håkon Mosby* and *Professor Logachev* for obtaining the material.

#### REFERENCES

- Brattegard T. 1966. A new species of multitentaculate Pogonophora from northern Norway. *Sarsia* 22:55–63.
- Imajima M. 1973. A new species of the genus *Oligobrachia* (Pogonophora) collected from Tsukumo Bay, Noto Peninsula. *Annual Report of the Noto Marine Laboratory* 13:7–12.
- Ivanov AV (Ivanov AW). 1957. Neue Pogonophora aus dem nord-westlichen Teil des Stillen Ozeans. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 85:431–500.
- Ivanov AV. 1991. Monilifera - a new subclass of Pogonophora. *Doklady Akademii Nauk S.S.S.R.* 319:505–507.
- Ivanov AV. 1994. On the systematic position of Vestimentifera. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 121:409–456.
- Markevich GI. 1993. SEM observations on *Seison* and phylogenetic relationships of the Seisonidea (Rotifera). *Hydrobiologia* 255/256:513–520.
- Southward EC. 1959. Two new species of Pogonophora from the northeast Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 38:439–444.
- Southward EC. 1972. On some Pogonophora from the Caribbean and the Gulf of Mexico. *Bulletin of Marine Science* 22:739–776.



- Southward EC. 1978. Description of a new species of *Oligobrachia* (Pogonophora) from the North Atlantic, with a survey of the Oligobrachiidae. *Journal of the Marine Biological Association of the United Kingdom* 58:357-365.
- Southward EC. 1988. Development of the gut and segmentation of newly settled stages of *Ridgeia* (Vestimentifera): implications for relationship between Vestimentifera and Pogonophora. *Journal of the Marine Biological Association of the United Kingdom* 68:465-487.
- Vogt PR, Cherkashev G, Ginsburg, G, Ivanov G, Milkov A, Crane K, Lein A, Sundvor E, Pimenov N, Egorov A. 1997. Haakon Mosby Mud Volcano provides unusual example of venting. *Transactions of the American Geophysical Union* 78:549,556-557.
- Webb M. 1964a. A new bitentaculate pogonophoran from Hardangerfjorden, Norway. *Sarsia* 15:49-55.
- Webb M. 1964b. Additional notes on *Sclerolinum brattstromi* (Pogonophora) and the establishment of a new family, Scleroliniidae. *Sarsia* 16:47-58.
- Webb M. 1969. *Lamellibrachia barhami*, gen. nov., sp. nov. (Pogonophora), from the northeast Pacific. *Bulletin of Marine Science* 19:18-47.

*Accepted 22 June 1999 – Printed 9 June 2000*  
*Editorial responsibility: Jarl Giske*