

On some frenulate species (Annelida: Polychaeta: Siboglinidae) from mud volcanoes in the Gulf of Cadiz (NE Atlantic)

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SUMMARY: Collections of Frenulata made by the RV Professor Logachev in the Gulf of Cadiz in 2006 contain two new species, one belonging to the genus *Spirobrachia*, and another that was assigned to a new genus. *Spirobrachia tripeira* n. sp. is the first record of the genus in the North Atlantic Ocean; it has a very stiff, straight, orange tube; its tentacles have pinnules and are arranged in a spiral crown without a lophophore. *Bobmarleya gadensis* n. gen. et n. sp. is characterised by an unusually long tentacular crown composed of about 40 free tentacles. It shares many characteristics with the genus *Oligobrachia* but the large number and extreme length of the tentacles and a combination of other characters justify the designation of a new genus. The specimens of *Lamellisabella denticulata* Southward, 1978 collected during the M.S. Merian 03/01 cruise provide the first record of this species in the Gulf of Cadiz.

Keywords: Siboglinidae, Frenulata, Pogonophora, mud volcano, Gulf of Cadiz.

RESUMEN: SOBRE ALGUNAS ESPECIES DE FRENULADOS (ANNELIDA: POLYCHAETA: SIBOGLINIDAE) DE LOS VOLCANES DE FANGO EN EL GOLFO DE CÁDIZ (NE ATLÁNTICO). – Las colecciones de Frenulata realizadas por el RV Professor Logachev en el Golfo de Cádiz en 2006 contienen dos especies nuevas, una perteneciente al género *Spirobrachia*, y la otra asignada a un género nuevo. *Spirobrachia tripeira* sp. nov. constituye la primera cita del género para el Atlántico norte; tiene un tubo muy rígido, recto y naranja; los tentáculos tienen pinnulas y se disponen en forma de corona espiralada y sin lofóforo. *Bobmarleya gadensis* n. gen. et n. sp. se caracteriza por su corona tentacular inusualmente larga compuesta por aproximadamente 40 tentáculos libres. Comparte muchas características con el género *Oligobrachia*, pero el elevado número y la longitud extrema de sus tentáculos, junto con una especial combinación de caracteres, justifica la designación de un género nuevo. Los especímenes de *Lamellisabella denticulata* Southward, 1978 recolectados durante la campaña M.S. Merian 03/01 constituyen la primera mención de esta especie para el Golfo de Cádiz.

Palabras clave: Siboglinidae, Frenulata, Pogonophora, volcán de fango, Golfo de Cádiz.

INTRODUCTION

Siboglinids (also called Pogonophora) include three groups of marine protostomes, frenulates, moniliferans and vestimentiferans. The group has a varied and complex taxonomic history in that they have been placed in both Deutorostomia (Ivanov and Petrunkevitch, 1955; Southward, 1963) and Protostomia (van der Land and Nørrevang, 1975; South-

ward, 1988) and have been assigned to all taxonomic ranks from family to phylum. The first member of this group, *Siboglinum weberi* was not found until early in the 20th century. Caullery (1914) named the genus *Siboglinum* and the family Siboglinidae, without assigning the animal to a particular phylum. The species was only described in 1944 (Caullery, 1944). Annelid affinities are now supported by both morphological and genetic studies. Rouse and Fauchald (1997) con-

ducted a series of cladistic analysis of the morphology of polychaetes and stated that: "The Pogonophora should now be reclassified as members of the clade Sabellida". They argued that "since the name Pogonophora was misleading at this level, the name of the group should revert to that of the first family name originally formulated for members of the group, that of Siboglinidae Caullery, 1914". This name change was also proposed by McHugh (1997), it has been used by other authors (Schulze, 2003; Halanych, 2005) and it will be used in this paper. For the taxonomy within the Siboglinidae, Rouse (2001) used the names Frenulata, Monilifera and Vestimentifera for three clades. For objections to the replacement of the group name Pogonophora by Siboglinidae see Southward *et al.* (2005) and Bartolomaeus *et al.* (2005).

All siboglinids inhabit reducing environments, mostly in the deep-sea, although the levels of sulphide and methane and the type of substrate vary. Frenulates are generally found in anoxic sediments with the anterior end of the tube extending into the oxygenated bottom water. They have been found in hydrocarbon seeps, on continental slopes, and at the bottom of fjords. An increasing effort put into deep-sea sampling in the Atlantic is gradually disclosing more species as well as more genera of frenulates, and reducing the apparent deficiency of genera in the Atlantic compared with the Pacific Ocean.

Chemosynthetic-based communities, often dominated by frenulates, have been found in several mud volcanoes in the Gulf of Cadiz (Cunha *et al.*, 2001; Rodrigues and Cunha, 2005). Here we describe two new frenulate species collected from the Porto and Carlos Ribeiro mud volcanoes during the TTR16 cruise (Training Through Research Programme, IOC-UNESCO) on board the RV Professor Logachev, and report the first record of *Lamellisabella denticulata* in the Gulf of Cadiz, collected during the MSM01/03 cruise. Specimens of *Siboglinum* and *Polybrachia* were also collected from several mud volcanoes, but because further morphological and molecular studies are necessary to elucidate their taxonomy, these genera will be reported elsewhere.

METHODS

Study area

For more than a decade, the international marine scientific community has deployed considerable ef-

forts in studying the occurrence of mud volcanism, cold seepage and gas hydrates in the Gulf of Cadiz (Baraza and Ercilla, 1996; Pinheiro *et al.*, 2003; Somoza *et al.*, 2003). Since the discovery of the Gulf's first mud volcano in 1999, research cruises have steadily unveiled one mud volcano after another (Gardner, 2001; Pinheiro *et al.*, 2003; Somoza *et al.*, 2003; Van Rensbergen *et al.*, 2005). Located in a compressional tectonic province, the mud volcanoes in the Gulf of Cadiz are more numerous than anywhere else on the European Atlantic margins. The compression between the Eurasian and African tectonic plates creates an interesting geophysical template (Sartori *et al.*, 1994; Maldonado *et al.*, 1999; Gutcher *et al.*, 2002) shaped by volcanic activity and by the interaction between the topography and the circulation of the Atlantic and Mediterranean Waters (Peliz *et al.*, 2007). Found in water depths between 200 and 4000 m, these mud volcanoes are clustered in several fields on the Portuguese, Spanish, and Moroccan margins and show considerable variations in dimension, morphology and composition of erupted material and fluids (Pinheiro *et al.*, 2003; Van Rensbergen *et al.*, 2005; Hensen *et al.*, 2007; Niemann *et al.*, 2006).

Sample collection and processing

Specimens of the two new species were obtained from TV-guided grab samples collected on the Porto mud volcano (35°33.77'N, 8°30.42'W, 3902 m depth) and the Carlos Ribeiro mud volcano (35°47.23'N, 8°25.27'W, 2200 m depth), respectively. Specimens of *Lamellisabella denticulata* were collected on the Porto mud volcano with a USNEL box core. The specimens were carefully picked from the sediment, and preserved in 70 or 96% ethanol (the latter will be used for future molecular studies).

All drawings were made using a camera lucida attached to a stereomicroscope. Air-dried pieces of the girdle of specimens of both species were mounted onto stubs using adhesive carbon disks, sputter-coated with gold-palladium (Polaron E500; 3x30s) and observed with a JEOL JSM-5400 scanning electron microscope.

For the histological study of the internal anatomy the specimens were slowly dehydrated by transfer to 90% ethanol overnight followed by a period of 9 hours in 100% ethanol with change of solution every 3 hours. The segments were cleared with 100% Histoclear™ for 12 hours depending on the size of

the segment and impregnated in paraffin wax at 70°C for 12 to 24 hours. The tissue was then embedded in wax, sectioned at 5 µm, and stained with Mayer's hematoxylin and eosin.

Abbreviations

BNHM: British Natural History Museum; DBUA: Departamento de Biologia da Universidade de Aveiro; MSM: Maria S. Merian; TTR: Training Through Research.

SYSTEMATICS

Family SIBOGLINIDAE Caullery, 1914
Genus *Bobmarleya* n. gen.

Diagnosis. More than 30 free tentacles packed in a regular arrangement at their base, with pinnules. Pale and thin bridle keels. Small cephalic lobe with an irregular tip. Two rows of plaqueless metameric papillae separated by a furrow. Two girdles lying on well-developed ridges, with the two halves of both girdles being separated dorsally by a relatively large group of papillae. The tube is soft and ringed; semi-transparent at the anterior end, brown with darker rings in the middle and white/greyish in the posterior end.

Type species. *Bobmarleya gadensis* n. sp.

Etymology. The generic name is given as an allusion to the shape of the tentacular crown in which the tentacles largely resemble dreadlocks, a hairstyle popularised by the reggae singer and songwriter Bob Marley.

Bobmarleya gadensis n. sp.
(Figs. 1, 2, 4 and 5)

Type material. Atlantic Ocean, Gulf of Cadiz, Carlos Ribeiro mud volcano. Holotype: One incomplete male specimen (BNHM 2007.978), TTR16 cruise, station AT615GR, 35°47.23'N, 8°25.27'W, 2200 m depth, 31/05/2006. Paratypes: one incomplete male (DBUA 00929.01), one incomplete male used for histological sections (DBUA 00929.01S), same data as holotype.

Etymology. The specific name comes from the Roman name of the city of Cadiz, Gades, in reference to the Gulf of Cadiz.

Diagnosis. As this genus is currently monotypic, the diagnosis is as the generic diagnosis.

Description. This is a large, rather dark frenulate, living in a soft ringed tube about 2 mm in diameter. The tube is white, semi-transparent on the first 5 to 10 mm, but it becomes dark brown in the middle and then lighter again to reach a white/greyish colour at the posterior end (Fig. 1). The rings are black, with a length equal to the diameter of the tube on its anterior portion, but on the middle section they become incomplete and closer together. On the posterior portion the rings are almost absent and the tube is smooth. The longest occupied tube was 975 mm.

The most obvious feature of this species is the long, up to 65 mm long, orange-brown tentacular crown (Fig. 4C); it consists of about 40 free tentacles arranged regularly at their base (Fig. 5A), with two rows of pinnules along the inner side (Fig. 4A).

The forepart of the body is short (2.33 to 3.66 mm) and thick (1.40 to 1.73 mm), with a pronounced dorsal convexity (Fig. 2A-C). The anterior end is irregular, has a mid-dorsal swelling and partially encloses the base of the tentacles (Fig. 2A). The cephalic lobe is small and has an irregular end. Between the cephalic lobe and the bridle there is a mid-ventral patch of granular cells (Fig. 2B).

The colourless, narrow keels of the bridle lie on well-developed ridges and are not fused dorsally or ventrally. Anterior to the bridle are 2 dorso-lateral ridges (Figs. 2A-C). A mid-dorsal furrow begins behind the bridle and runs as far as the junction with the trunk (Fig. 2A).

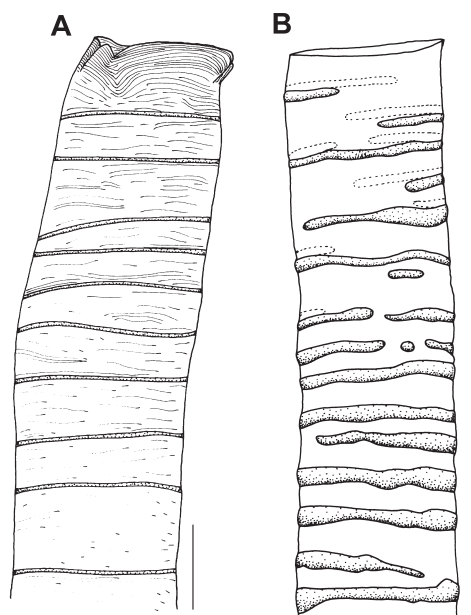


FIG. 1. – *Bobmarleya gadensis* n. sp. tube: (A) near anterior end; (B) middle. Scale bar: 1 mm.

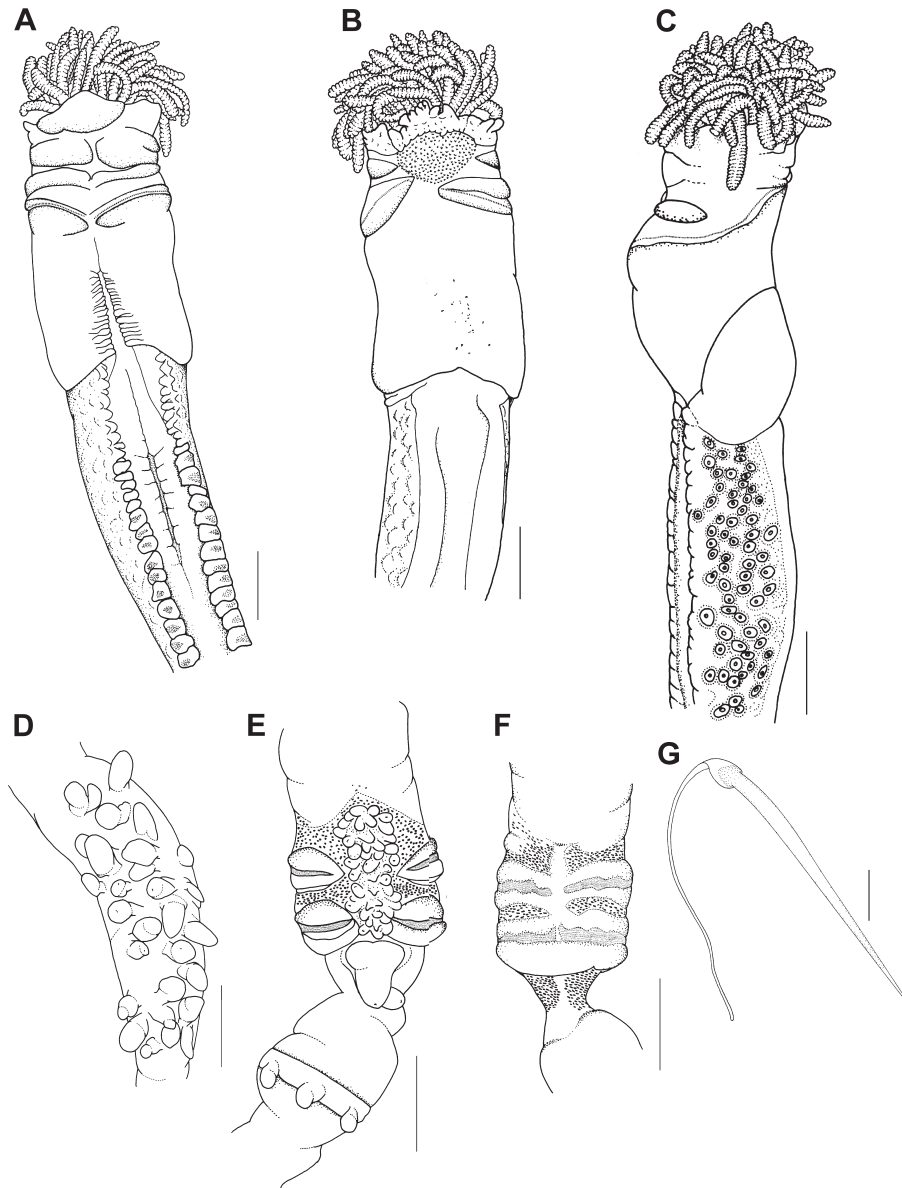


FIG. 2. – *Bobmarleya gadensis* n. sp. (A) forepart and anterior part of the trunk, dorsal view; (B) forepart and anterior part of the trunk, ventral view; (C) forepart and anterior part of the trunk, lateral view; (D) enlarged papillae; (E) girdle region, dorsal side; (F) girdle region, ventral side; (G) spermatophore. Scale bar: 0.5 mm (A-F); 250 μ m (G)

The metameric region at the anterior end of the trunk is 8 to 11 mm long and has two wide glandular ridges, separated by a median dorsal furrow that runs along most of the length of the pre-annular region. Anteriorly the glands are not grouped, but after 1 mm they are grouped inside two rows of plaqueless papillae (Fig. 2A). Laterally there are smaller pyriform glands with rings of brown epidermal cells around their openings forming two longitudinal brown stripes (Fig. 2C); the ventral side is smooth and flat (Fig. 2B).

Posterior to the metameric region the trunk is brownish with scattered darker spots, and after the

posterior end of the mid-dorsal furrow there is a region with more than 25 enlarged papillae on the dorsal side (Fig. 2E). Some of these enlarged papillae are tipped by singular cuticular plaques. The two girdles lie on well-developed ridges surrounded by rather dark pigment spots, and are separated from the enlarged papillae by a section of 5 to 11 mm. Anteriorly to the girdles starts a strip of 40 small papillae that separates dorsally the two halves of both girdles. Ventrally they are also both interrupted, but the posterior gap is very narrow (Fig. 2E and F). The chaetae of the girdles are arranged in 8 rows; they are 12 to 15 μ m long and elongate in shape with two

groups of teeth facing opposite directions. The anterior group is small, with smaller and very curved teeth (Fig. 5C). After the posterior girdle there is a conical enlarged papilla. The post-annular papillae are arranged in transverse rows of 5 to 7. The opisthosoma was missing in all the specimens collected.

The spermatophores are 1.6 mm long, spindle-shaped with a pair of small wings at the base of the filament (Fig. 2G and 4D).

Distribution. Known only from the type locality, Carlos Ribeiro mud volcano, at a depth of 2200 m.

Remarks. The arrangement of the tentacles of this genus is unique among Frenulata. There are several other genera with more than two free tentacles (Table 1), but in all of them the base of the tentacular crown is horseshoe-shaped, although in *Cyclobrachia* and *Zenkevitchiana* the ends bend round to complete the ring (Ivanov, 1963). Because histological sections to study the base of the tentacular crown were made in only one of the specimens, it is open to discussion whether this character is sufficient to create a new genus. However, a number of other characters justify the creation of a new genus. The number of tentacles corresponds to that of *Polybrachia* but the species of this genus are characterised by a segmented tube with funnel-like collars on each segment, whereas the species described here has a soft ringed tube similar to that of species of *Oligobrachia*. The structure of the spermatophore is also similar to that of *Oligobrachia* (Southward, 1978a). On the other hand, species of *Oligobrachia* are characterised by the strong bridle keels (Southward, 1978a), which are pale and narrow in the genus here described.

Bobmarleya gadensis shows a general resemblance to *Birsteinia* but the latter has a stiff tube and plaques on the metameric papillae (Ivanov, 1952, 1963). Cuticular plaques on the metameric papillae are also present in *Polybrachia*, *Diplobrachia*, *Cyclobrachia*, *Heptabrachia* and *Galathealimum*.

Although size characteristics are not diagnostic of the superspecific taxa of Frenulata, it is pertinent to note the length of the tentacular crown of the genus, which is the longest ever recorded (up to 65 mm). However, in all the specimens collected the tentacles deteriorated very quickly and at the time of fixation they were no longer than 1 mm and had no pinnules in this region (Figs. 2A-C and 4B).

TABLE 1. – Frenulate genera with more than two free tentacles

Genus	Number of tentacles
<i>Oligobrachia</i> Ivanov, 1957	2-18
<i>Birsteinia</i> Ivanov, 1952	12
<i>Polybrachia</i> Ivanov, 1952	18-70
<i>Diplobrachia</i> Ivanov, 1960	2-6
<i>Heptabrachia</i> Ivanov, 1952	5-19
<i>Cyclobrachia</i> Ivanov, 1960	9
<i>Zenkevitchiana</i> Ivanov, 1957	14
<i>Galathealimum</i> Kirkegaard, 1956	78-268
<i>Choanophorus</i> Bubko, 1965	18
<i>Bobmarleya</i> n. gen.	ca. 40

Genus *Lamellisabella* Ushakov, 1933

Lamellisabella denticulata Southward, 1978

Lamellisabella denticulata Southward, 1978: 713-716, Fig. 1 and 2.

Material examined. One incomplete specimen of undetermined gender (DBUA 00928.01), Porto mud volcano, MSM01/03 cruise, station 151, 35°33.77'N, 9°30.20'W, 3863 m, 22/04/2006.

Distribution. *L. denticulata* is the only species of *Lamellisabella* described from the Atlantic Ocean (Southward, 1978b). It was first found in the Bay of Biscay at 4000 m depth, but Southward (1978b) proposed that its range extends along the continental rise as far south as the Gulf of Guinea. In the Gulf of Cadiz it was found on the Porto mud volcano at a depth of 3902 m.

Genus *Spirobrachia* Ivanov, 1952

Spirobrachia tripeira n. sp. (Figs. 3, 4 and 5)

Type material. Atlantic Ocean, Gulf of Cadiz, Porto mud volcano. Holotype: One incomplete specimen of undetermined gender (BNHM 2007.977), TTR16 cruise, station AT622GR, 35°33.77'N, 9°30.42'W, 3902 m, 03/06/2006. Paratypes: one incomplete male and 12 specimens of undetermined gender (DBUA 00929.01), one incomplete female used for histological sections (DBUA 00929.01S), all same data as holotype.

Diagnosis. Tentacular spiral consisting of 80 to 110 tentacles with a quadruple row of pinnules each. Lophophore absent. Brown/orange tube, hard for most of its length.

Etymology. The specific name *tripeira* is given in reference to the nickname of the inhabitants of the city of Porto, which originates from the typical dish of the city, *tripas*.

Description. The light brown/orange tube is straight and very stiff, with thick, strong walls tapering towards the posterior end, which becomes slightly sinuous but remains thick-walled. There is

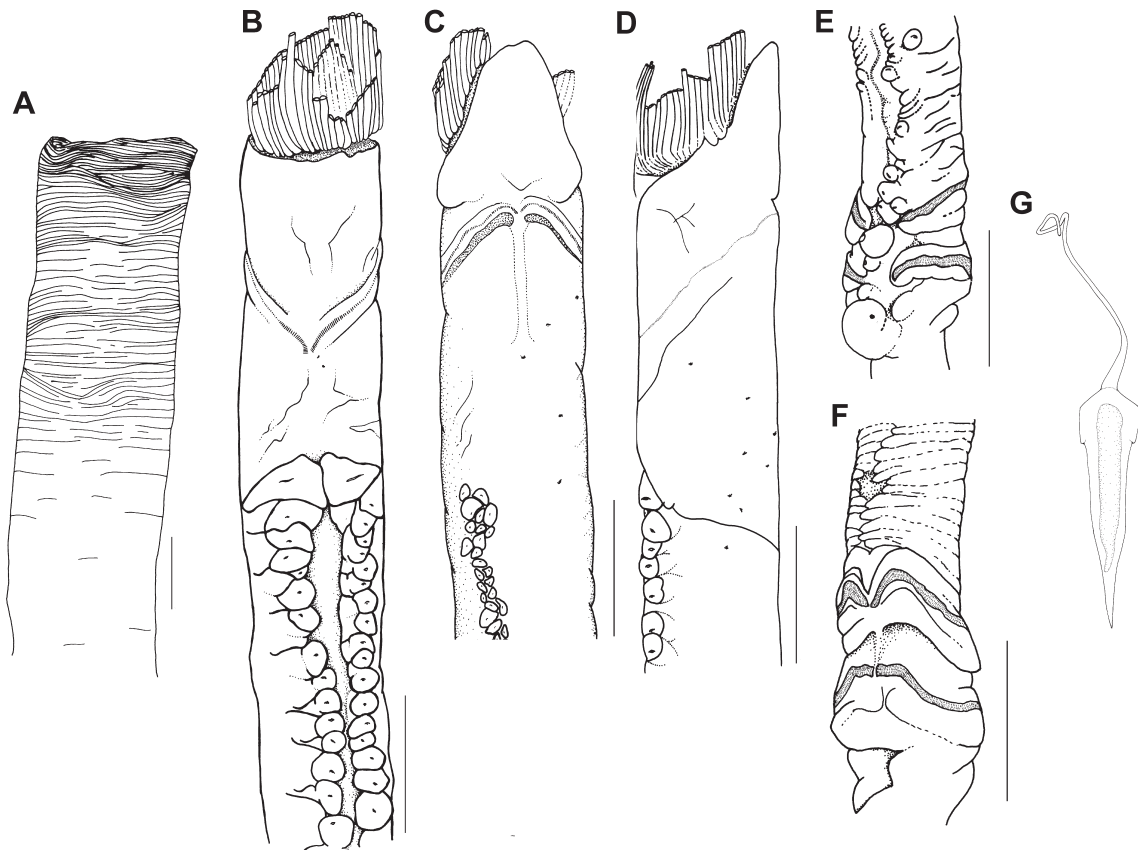


FIG. 3. – *Spirobrachia tripeira* n. sp. (A) tube; (B) forepart and anterior part of the trunk, dorsal view; (C) forepart and anterior part of the trunk, ventral view; (D) forepart and anterior part of the trunk, lateral view; (E) girdle region, dorsal side; (F) girdle region, ventral side; (G) spermatophore. Scale bar: 1 mm (A – F); 500 µm (G)

a short, transparent anterior part, which is soft and thin walled (Fig. 3A). The diameter of the tube varies from 0.57 to 2.05 mm.

The tentacles (80 to 100) are arranged in a spiral crown with 5 turns (Fig. 3B-D, 4E, 5B). The spire is leotropic, its direction of turn (when viewed from the anterior end) being anti-clockwise in all the specimens examined. The tentacles adhere side by side and have pinnules in a quadruple row on the zone facing the inside of the crown. The bases of the tentacles are situated on one plane on a table-like broadening of the forepart, without a lophophore. The whole tentacular crown is up to 22.8 mm in length.

The forepart of the body is 2 to 4 times as long as wide, the maximum length and diameter recorded being respectively 4.7 mm and 1.2 mm. The cephalic lobe is very wide and dorso-ventrally flattened (Fig. 3C and D). A mid-dorsal longitudinal groove extends along the whole length of the dorsal side of the forepart; on the ventral side there is a shallow groove that extends posteriorly from the ends of the bridle keels. The brown bridle keels are always separate,

turning posteriorly and running parallel on both the dorsal and ventral side (Fig. 3B and C).

A slight external groove separates the forepart from the trunk. On the anterior part of the trunk there are two rows of about 40 metamerically arranged papillae separated by a deep and narrow median furrow (Fig. 3B). Each papilla is topped by an oval cuticular plaque, about 70 x 40 µm, with a thickened, bow-shaped front edge. Posteriorly, the mid-dorsal furrow widens and another up to 100 papillae, not so tightly arranged, with plaques, continue along its edges. The ventral side of the trunk is slightly concave and latero-ventrally there are numerous small, plaqueless papillae tightly arranged (Fig. 3C). On the ventral side, anterior to the girdles, there is a series of digitiform ridges forming a deep sulcus (Fig. 3F). On the dorsal side there is a group of about 10 enlarged papillae anterior to and between the girdles, and a larger papilla behind the posterior girdle (Fig. 3E).

The two girdles, lying on very thick muscular ridges, are close together, approximately 0.5 mm apart, and are both interrupted dorsally and ventrally (Fig. 3E and F). The chaetae are arranged in 5 rows,

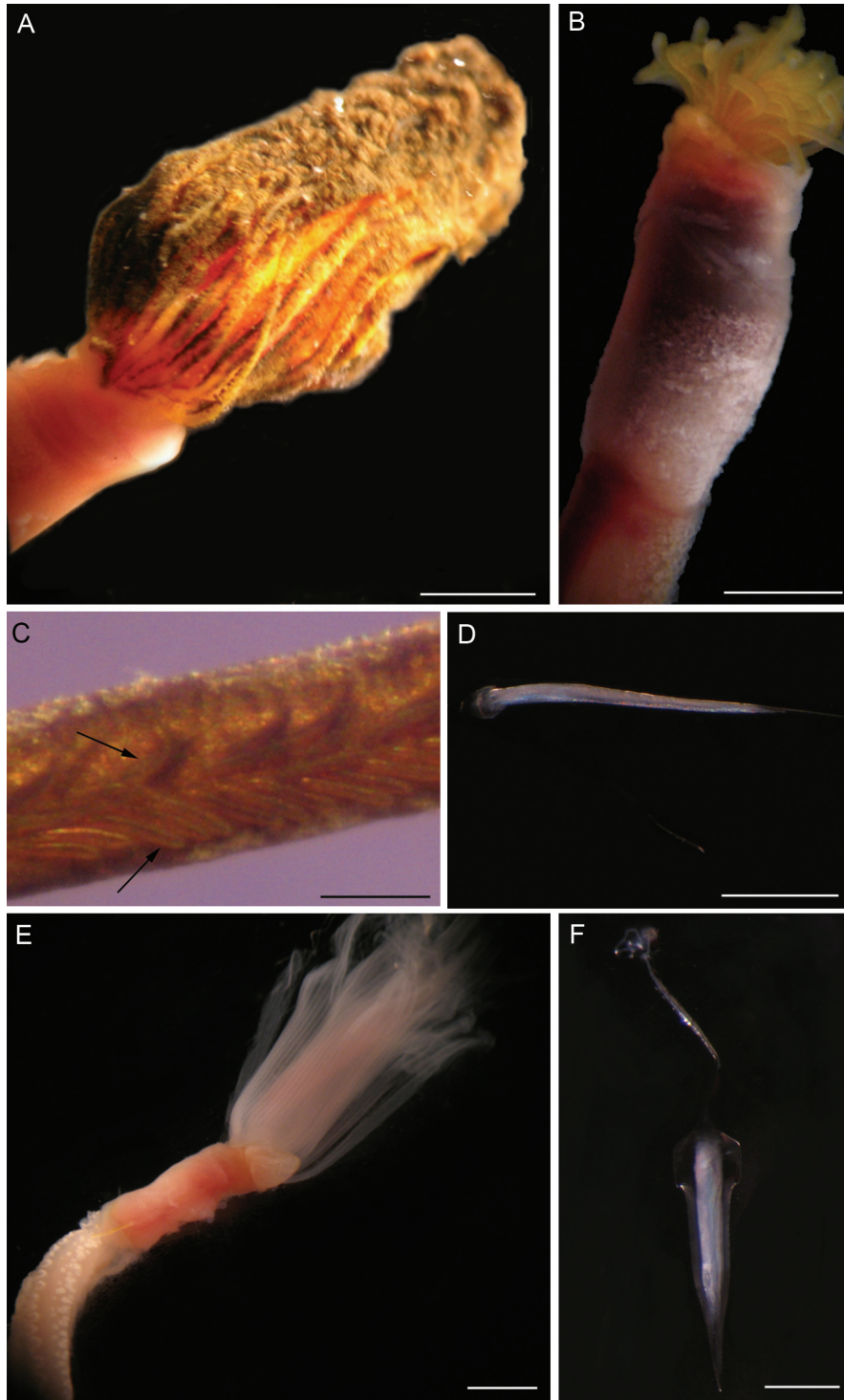


FIG. 4. – *Bobmarleya gadensis* (A) forepart and anterior part of the trunk, after some tentacular deterioration; (B) forepart and anterior part of the trunk, just before fixation; (C) tentacles with pinnules (arrows); (D) spermatophore. *Spirobrachia tripeira* n. sp. (E) forepart and anterior part of the trunk; (F) spermatophore. Scale bar: 1 mm (A, B and E); 0.5 mm (D and F); 0.1 mm (C)

their heads are slipper-shaped, 22 to 24 μm long, with a small anterior group of smaller teeth and a larger posterior group of larger teeth facing opposite directions (Fig. 5D).

On the dorsal side of the postannular region of the

trunk, at regular intervals of about 2 mm, there are transverse rows of 4 or 5 papillae with oval plaques with a median ridge. On the ventral side there is little or no development of glands. The opisthosoma was missing in all the specimens analyzed.

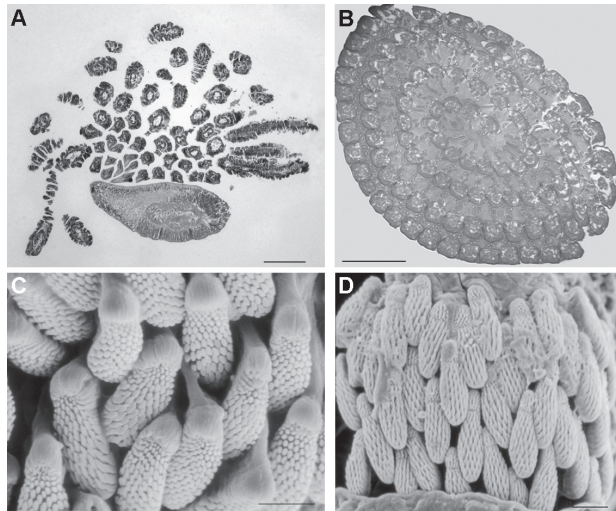


FIG. 5. – *Bobmarleya gadensis* n. sp. (A) cross-section of the tentacular crown; (C) heads of chaetae. *Spirobrachia tripeira* n. sp. (B) cross-section of the tentacular crown; (D) heads of chaetae. Scale bar: 0.2 mm (A and B); 5 µm (C); 10 µm (D).

Additional male characters. The male genital papillae are large and overlap the posterior end of the forepart. The spermatophores are narrow and about 1.75 mm long, with trapezoidal wings and a very long filament (Fig. 3G and 4F).

Distribution. Known only from the type locality, Porto mud volcano, at a depth of 3902 m. *Spirobrachia tripeira* is the first species of this genus to be described from the Atlantic ocean, so far this genus has only been known from high latitudes, both South and North (Table 2).

Remarks. The genus *Spirobrachia* was proposed by Ivanov (1952) and was recently revised by Smirnov (2000b). In this revision, the species formerly

ascribed to *Spirobrachia* were separated based on the structure of the spermatophore and tube, and *Volvobrachia* was erected. The spermatophores of *Volvobrachia* are wide, without clearly differentiated wings, and its tube has a rigid funnel-like mouth, whereas *Spirobrachia* possesses narrow spermatophores, with a pair of wings at the base of the filament, and the tube has a soft anterior end. The characteristics of the new species described herein are consistent with those of the genus *Spirobrachia*.

In *S. tripeira* the arrangement of the bridle is similar to that of *S. orkneyensis*. The number of tentacles and the presence of tentacular pinnules are also comparable to those of both *S. orkneyensis* and *S. grandis*, but *S. tripeira* differs from these species by the absence of the lophophore. *S. leospira*, which does not have a lophophore either, can be easily distinguished by having less than half the number of tentacles (Table 2).

DISCUSSION

It was not until 1962 that the first record of frenulates from the western Atlantic was made (Bayer, 1962) and for a long time the number of records from the Atlantic Ocean was surprisingly low when compared with that of the Pacific. But with the increased effort put into deep-sea sampling during the 1960s and 1970s, 46 species belonging to 10 genera were described from both sides of the Atlantic (Nielsen, 1965; Southward, 1968, 1971, 1972, 1978a,b; Southward and Southward, 1958, 1967). In the following two decades 3 species of *Siboglinum* from the Eu-

TABLE 2. – Characteristics of the species of *Spirobrachia*.

	<i>S. grandis</i>	<i>S. leospira</i>	<i>S. orkneyensis</i>	<i>S. tripeira</i> n. sp.
Tube colour	brown/ black	yellow/ greenish	grey/white and brown	grey/white and orange
Maximum anterior diam. of tube (mm)	3	1.8	2.4	1.8
Tube segmentation	?	yes	yes	yes
Number of tentacles	30-223	to 43	59-110	80-110
Maximum length of tentacles (mm)	27.0	19.0	27.5	22.8
Tentacular pinnules	yes	no	yes	yes
Presence of lophophore	yes	no	yes	no
Length of forepart (mm)	4.2-5.1	1.5-4	3.75-6.75	2.2-4.6
Diam. of forepart (mm)	1.2-2.5	0.9	1.1-1.7	0.7-1.7
Ventral bridle fusion	yes	no	no	no
Dorsal bridle fusion	yes	yes	no	no
Number of metameris papillae	220	to 25	?	80-110
Presence of cuticular plaques	yes	yes	yes	yes
Distance between girdles (mm)	?	0.1	2	0.4-0.6
Length of chaetae head (µm)	?	16-22	21-25	23-25
Length of spermatophore (µm)	2500	1200	1350-1750	1750
Occurrence	Bering Sea	S. Sandwich Trench	Orkney Trench	Gulf of Cadiz
Depth (m)	3260	7694-8004	6130-6420	3800

ropean margin were discovered (Flügel and Langhof, 1983; Flügel, 1990; Flügel and Callsen-Cencic, 1993), and more recently Smirnov (2000c) described one new species found in the Haakon Mosby mud volcano (off northwestern Norway). From the South Atlantic Sector of the Antarctic 7 new species were recently described (Smirnov, 2000a, 2005a,b) and one redescribed (Smirnov, 2000b).

In spite of this increase in the number of species, the knowledge on the distribution of frenulates is still fragmentary, with the latest update for the Atlantic Ocean dating from 1979 (Southward, 1979). The current distribution of frenulates in the North Atlantic can be divided into 3 main areas: the northwest Atlantic (from Nova Scotia to Florida), the Caribbean and Gulf of Mexico, and the northeast Atlantic along the European coast. In both the southeast and the southwest Atlantic only one species has been recorded (Table 3).

Three genera of Frenulata, *Siboglinum*, *Polybrachia* and *Oligobrachia* were reported by Pinheiro *et al.* (2003) for the Gulf of Cadiz, but the latter might have been misidentified because their identification was based solely on the tube. It is possible that these specimens belong to the new genus *Bobmarleya* but their poor state of preservation did not allow their identity to be confirmed.

The three genera reported herein were collected from Carlos Ribeiro (*Bobmarleya*) and Porto (*Spirobrachia* and *Lamellisabella*) mud volcanoes. While the megafauna assemblage is diverse on the flanks of the Carlos Ribeiro mud volcano, the top,

at a depth of 2200 m, is almost devoid of megafauna with the exception of scattered ophiuroids and *Bobmarleya gadensis*, which inhabits small depressions of the seafloor. Gas hydrates have been recovered from the sediment and methane concentrations measured on the Carlos Ribeiro mud volcano are some of the highest from the Gulf of Cadiz. On the other hand, the top of the Porto mud volcano, at a depth of 3900 m, is covered by a continuous field of clumps of 20 to 50 individuals of *Spirobrachia tripeira* and an undetermined number of adult and juvenile specimens of *Polybrachia* sp. These clumps are accompanied mainly by the frenulate *Lamellisabella denticulata*, stalked hexactinellid sponges and crinoids. Many old tubes and sponge stalks are colonised by epifaunal organisms (hydrozoans, actinarians, cirripeds and other). Mobile fauna (galatheid lobsters, ophiuroids and holothurians), life traces (burrows with star-shaped feeding marks) and scattered *Acharax* shells were also observed among the tubes.

However, frenulates were also found in all the other mud volcanoes from which biological samples are available. Although not all the species have been identified yet, molecular studies show that there are at least 9 different species belonging to 5 genera (Hilário *et al.*, in prep.), including the new genus *Bobmarleya* and two genera, *Spirobrachia* and *Polybrachia*, not yet known from the NE Atlantic. These observations increase the number of genera present in the NE Atlantic to 8, the same as in the NW Atlantic.

TABLE 3. – Frenulata species from the Atlantic Ocean. Species from the South Atlantic Sector of the Antarctic are not included.

NW Atlantic	Caribbean and Gulf of Mexico	SW Atlantic	NE Atlantic	SE Atlantic
<i>Oligobrachia floridana</i>	<i>Oligobrachia erythrocephala</i>	<i>Crassibrachia brasiliensis</i>	<i>Oligobrachia gracilis</i>	<i>Polybrachia talboti</i>
<i>Siboglinum angustum</i>	<i>Siboglinum ekmani</i>		<i>O. haakonmosbiensis</i>	
<i>S. bayeri</i>	<i>S. angustum</i>		<i>O. ivanovi</i>	
<i>S. candidum</i>	<i>S. callosum</i>		<i>O. webbi</i>	
<i>S. ekmani</i>	<i>S. nanum</i>		<i>Siboglinum angustum</i>	
<i>S. fulgens</i>	<i>S. oregoni</i>		<i>S. atlanticum</i>	
<i>S. gosnoldae</i>	<i>S. parvulum</i>		<i>S. brevicephalum</i>	
<i>S. holmei</i>	<i>S. pholidotum</i>		<i>S. carpinei</i>	
<i>S. longicollum</i>	<i>S. risillum</i>		<i>S. ekmani</i>	
<i>S. mergophorum</i>	<i>S. southwardae</i>		<i>S. fiordicum</i>	
<i>S. pholidotum</i>	<i>Siboglinoides caribbeanus</i>		<i>S. holmei</i>	
<i>Siboglinoides caribbeanus</i>	<i>Unibrachium colombianum</i>		<i>S. hyperboreum</i>	
<i>Crassibrachia sandersi</i>	<i>Polybrachia</i> sp. 1		<i>S. inerme</i>	
<i>Nereilinum punctatum</i>	<i>Diplobrachia grenadiensis</i>		<i>S. lacteum</i>	
<i>Polybrachia eastwardae</i>	<i>Lamellisabellid</i> sp. 1		<i>S. leucopleurum</i>	
<i>P. lepida</i>	<i>Lamellisabellid</i> sp. 2		<i>S. norvegicum</i>	
<i>Siphonobrachia ilyophora</i>			<i>S. pholidotum</i>	
<i>Diplobrachia floridiensis</i>			<i>S. poseidoni</i>	
<i>D. similis</i>			<i>Diplobrachia capillaris</i>	
			<i>D. similis</i>	
			<i>Lamellisabella denticulata</i>	
			<i>Nereilinum murmanicum</i>	

This diversity is probably due to the variety of geological and physical settings. Apart from differences in activity and fluid composition (Pinheiro *et al.*, 2003; Van Rensbergen *et al.*, 2005; Hensen *et al.*, 2007; Niemann *et al.*, 2006), mud volcanoes situated in the deeper areas of the Gulf of Cadiz are under the influence of deep Atlantic water masses, whereas the shallower mud volcanoes are strongly influenced by the Mediterranean Outflow Water (Peliz *et al.*, 2007). This environmental heterogeneity, acting on larvae dispersal and settlement, is likely to lead to high diversity of frenulates. The Gulf of Cadiz is presently the most extensive cold seepage area known on the European margins, ranging between depths of 200 and 4000 m and including over 30 mud volcanoes. It should therefore be considered of utmost importance for the study of distributional patterns of Frenulata.

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