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Calcareous tubeworms (Polychaeta, Serpulidae) of the Arctic Ocean

KMK Scientific Press
Moscow 2014

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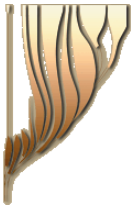

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Alexander V. Rzhavsky, Elena K. Kupriyanova, Andrei V. Sikorski, Salve Dahle. Calcareous tubeworms (Polychaeta, Serpulidae) of the Arctic Ocean. Moscow. KMK Scientific Press, 2014. 191 pp., 1 table, 37 figures, 2 colour plates.

The book is a taxonomic guide to serpulid polychaetes (including the subfamily Spirorbinae) of the Arctic Ocean. Identification keys include 37 serpulid taxa, all of which are described and illustrated in detail. Taxonomic treatment of species includes discussion of taxonomic problems, nomenclatural types, synonyms, and differential diagnoses. Information is also available on species reproduction, ecology, distribution, and habitat and locality. Species illustrations are presented as scanning electron micrographs and light micrographs, as well as line drawings. A comprehensive glossary and literature reference section is included. The study is based on extensive material (more than 600 samples) collected all over the Arctic and deposited in Russia, Iceland, Germany, Norway, and Australia. This fully illustrated laboratory guide is intended for invertebrate zoologists, marine ecologists, environmental consultants, as well as students and naturalists.

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CONTENTS

INTRODUCTION

Serpulidae are obligatory sedentary polychaetes inhabiting calcareous tubes. They share the presence of a radiolar crown and division of the body into thoracic and abdominal regions. Their thorax is flanked by lateral thoracic membranes and the border between thorax and abdomen is marked by chaetal inversion, the chaetal arrangement where thoracic uncini switch from neuropodial to notopodial in the abdomen, while the chaetae switch from dorsal (notopodial) in the thorax to ventral (neuropodial) in the abdomen.

Traditionally the family Serpulidae was divided into three subfamilies: Spirorbinae, Serpulinae, and Filograninae (e.g., Rioja, 1923; Fauvel, 1927). Pillai (1970) elevated the Spirorbinae to the family status. Later, a number of authors (e.g., ten Hove, 1984; Smith, 1991; Kupriyanova, 2003; Kupriyanova et al., 2006), based on the results of phylogenetic analyses of morphological and molecular data, concluded that spirorbins are monophyletic and are nested within the Serpulidae. Kupriyanova's (2003) results of morphology-only analyses placed Spirorbinae as a sister group to Serpulinae. However, the results of analyses of both molecular (Lehrke et al., 2008; Kupriyanova et al., 2009) and combined morphological and molecular data (Kupriyanova et al., 2006) indicate that neither Serpulinae nor Filograninae are monophyletic and that Spirorbinae is a sister group to a clade containing mostly "filogranins" and some "serpulins". Therefore, the rank of the spirorbids has been lowered to the subfamily and all six former sub-families of the spirorbins are now placed at tribal ranks (Rzhavsky et al., 2013). Moreover, the traditional subfamilies Serpulinae and Filograninae have been abandoned pending revision and re-formulation as a result of a nearly comprehensive combined phylogenetic analysis (Kupriyanova et al., in prep.).

Identification keys are given separately for non-spirorbins and Spirorbinae because of differences in their morphology. Two separate keys (one based on tube morphology and another on the body and chaetal morphology) are given for non-spirorbins, which is impossible to accomplish for Spirorbinae.

In non-spirorbins (p. 21) tubes are straight, irregularly twisted or coiled, ranging from only several mm to over 20 cm in length; the body is symmetrical even in worms living in spirally coiled tubes and their chaetal inversion is complete, so the abdomen appears to be turned 180 degrees relative to the thorax; there are 4–12 (normally 6 or 7) thoracic chaetigers; larvae are planktotrophic or lecithotrophic coupled with various types of incubation.

In Spirorbinae (p. 69) tubes are usually planospiral, coiled dextrally or sinistrally, although the last whorls may be straightened or facing upward from the substrate. The coil diameter of adult tubes is usually 1.5–3 mm (up to 8 mm); the body is asymmetrical, so that the abdomen appears to be turned for 90 degrees relative to the thorax in the achaetigerous zone between thorax and abdomen; typically there are 3–4 (rarely 5 (7?)) thoracic chaetigers; the lecithotrophic larvae are always incubated either in the tube or in an opercular brood chamber.

GENERAL MORPHOLOGY

The description of serpulid morphology (including that of spirorbins) below is more detailed than one would need to identify only Arctic serpulids. However, this additional information may be useful for understanding of terminology used in other papers on

GLOSSARY

abdomen: body region posterior to the thorax.

achaetous: without chaetae.

alveolus (*pl.* alveoli): small depression or hole, usually numerous, on the tube wall surface (Fig. 19A)

ampulla: proximal part of operculum, mostly bulbous, often distally covered by calcareous or chitinous endplate.

***Apomatus* chaeta:** sigmoid to overall sickle shaped thoracic chaeta, with a proximal denticulate zone and distal flat zone with rectangular teeth (Fig. 2D; 6G, see also **sickle-chaeta**).

apron: membranous flap formed by thoracic membranes joining ventrally past the last thoracic chaetigers (Fig. 14B; 8C; 1C; 1D).

basal groove: in spirorbins a depression in the basal part of blade on limbate collar chaetae.

bayonet chaeta: collar chaeta with one or two (sometimes more) large proximal bosses (or "teeth") at the base of a distal limbate zone (e.g., Fig. 14D).

blade: distal, seemingly flat portion of a chaeta (see, however, **capillary** or **limbate** chaeta).

boss: small projection or knob-like process in collar chaetae of *Hydroides* and *Serpula* (Fig. 8F, 14F).

brood chamber: a structure for incubation of embryos; generally associated with tube surface or operculum (e.g., Fig. 2B, 24B, C, 30E-H).

brush-type chaetae: abdominal flat-geniculate chaetae in spirorbins with very short sharply narrowing blades and small number of denticles (around 10). Romanchellini only (see Knight-Jones P. & Fordy, 1979, fig. 68E-G).

capillary chaeta: slender, often long, chaeta tapering to a fine point; a collective term for elongate, needle-like chaetae of otherwise variable shape and ontogeny.

chaeta (*pl.* chaetae): chitinous bristle protruding from an epidermal pocket in the body wall.

chaetal inversion: in serpulids and sabellids the thorax bears notochaetae dorsally and neurochaetae (uncini) ventrally; in the abdomen the position of chaetae and uncini is reversed. Unlike the abdomen of other serpulids that is turned 180° relative to the thorax, the abdomen of spirorbins is turned relative to the thorax by approximately 90°. In sabellariids uncini are notopodial and chaetae are neuropodial, whereas uncini are missing in the parathorax. The neuropodial chaetal composition changes gradually from parathorax to abdomen (Kieselbach & Hausen, 2008). Thus, the chaetal arrangement in Sabellariidae cannot be described as a true chaetal inversion.

chaetiger: segment bearing chaetae.

collar: an encircling membranous fold or flap covering the base of the radiolar crown (also see **thoracic membranes**).

collar chaetae: notochaetae located on the collar chaetiger, mayby **modified** or non-modified (**limbate** or **capillary**).

collar chaetiger: first chaetiger bearing an anterior collar and notochaetae (**collar chaetae**), but lacking uncini.

THE FORMER "SERPULINAE" AND "FILOGRANINAE"

Practical recommendations for identification of non-spirorbin genera

1. Removing serpulids from their tubes without any tube damage is rarely possible. Therefore one needs to examine the tube carefully before breaking it to extract the animals.

2. To determine the number of thoracic chaetigers, one needs to count the number of rows of thoracic uncini on any side of the body and then add 1 for the collar segment (generally, but not always, marked by a bundle of chaetae only).

3. To study the details of the soft body structures (e.g., collar, thoracic membranes) worms should be stained with methylene blue, malachite green or a similar dye immediately before examination.

4. Because non-spirorbins are generally larger (with some exceptions) than spirorbins, mounting of the entire specimen (= destruction of the specimen) on a slide can be avoided. Thoracic chaetae, including collar chaetae, can be pulled with the finest dissecting forceps (watchmaker's forceps), and mounted on a slide. For examination of uncini and abdominal chaetae, a piece of the torus should be carefully extracted from the animal using a dissecting needle, placed on a slide, and covered with a cover slip. Slight pressure should be applied to the cover slip to position the uncini flat on their sides. Alternatively, dissected chaetae and tori with uncini can be placed on a stub and examined with SEM (preferable option).

Key to non-spirorbins based on tube morphology

1a) Tube unattached, tusk-shaped (Fig. 5A) ..... ***Ditrupa arietina*** (p. 37)
1b) Tube attached to substrate at least in the proximal part **2**

2a) Tubes forming pseudo-colonies consisting of numerous greyish/whitish branching wire-like tiny tubes with diameter up to 1 mm, usually "free", not encrusting substrate (Fig. 6A, B) ..... ***Filograna implexa*** (p. 40)
2b) Tubes solitary, incidentally forming gregarious masses encrusting substrate **3**

3a) Tube with 3 keels made of long curved spines (Fig. 2A .... ***Bathyvermilia eliasoni*** (p. 29)
3b) Tube with single main non-denticulate keel, more or less triangular in cross-section or cylindrical, without a main keel **4**

4a) Tube with a single main keel, more or less triangular in cross-section **5**
4b) Tube cylindrical, without a main keel, sometimes with several low or indistinct keels **8**

5a) Tube vitreous, thick-walled, may be attached to substrate only by proximal part, distal part usually free and triangular in cross section; tube mouth with three elongated spines (Fig. 10A, B) ..... ***Placostegus tridentatus*** (p. 50)
5b) Tube opaque, with low or high main keel, attached to the substrate throughout its whole length; tube mouth without elongated spines **6**

6a) Tube with very high distinct keel (Fig. 11A) ..... ***Protis akvaplani*** (p. 54)
6b) Tube with low median keel, straight or wavy **7**

7a) Tube surface smooth, without distinct striations, median keel smooth, wavy (Fig. 15A, B), distal paired tube ovicells always absent ..... ***Spirobranchus triqueter*** (p. 66)
7b) Tube surface rough, with distinct striations, median keel sharp, straight and slightly denticulate (Fig. 4A), distal paired tube ovicells may present (Fig. 4B) .... ***Chitinopoma serrula*** (p. 34)

8a) Tube surface more or less smooth, sometimes with distinct growth rings **9**
8b) Tube surface very characteristic pitted by shallow oblong alveoli bounded by small ridges (Fig. 9A) ..... ***Metavermilia arctica*** (p. 49)

9a) Tube surface very smooth, porcellaneous **10**
9b) Tube surface rough, non-porcellaneous **11**

10a) Tube attached to substrate only by proximal end, distal end mostly free (Fig. 7B); tube surface with indistinct straight growth lines; ring-shaped thickenings (not peristomes directed towards tube mouth) sometimes present (Fig. 7A) .... ***Hyalopomatus claparedii*** (p. 44)
10b) Tube attached to substrate throughout entire length, only most distal part slightly raised from substrate; tube surface with very slight wavy growth lines; undulating peristomes sometimes present (Fig. 3A, B) ..... ***Bathyvermilia islandica*** (p. 31)

Genus *Apomatus* Philippi, 1844

Type-species: *Apomatus ampulliferus* Philippi, 1844

Tube white, opaque, circular in cross-section, keels and collar-like rings absent. Granular overlay may be present. Operculum a soft membranous vesicle without endplate borne on unmodified pinnulated radiole. Opercular constriction may be present. Pseudoperculum may be present on unmodified radiole. Radioles may be exceptionally flat ribbon-like; arranged in semi-circles (may be up to 3/4 of a circle), maximum number up to 40 per lobe in larger species. Inter-radiolar membrane present. Radiolar eyes in form of ocellar clusters. Stylodes absent. Mouth palps present. Seven thoracic chaetigerous segments. Collar trilobed with smooth margin. Thoracic membrane long, forming ventral apron across anterior abdominal segments. Tonguelets between ventral and lateral collar lobes absent. Collar chaetae limbate and capillary, may exceptionally be supplemented by *Apomatus* chaetae. *Apomatus* chaetae present in fascicles of other thoracic chaetae. Thoracic uncini saw-to-rasp-shaped with approximately 30 teeth in profile, up to 3–6 teeth in a row above and continuing onto peg; anterior peg long, blunt, almost rectangular. Ventral thoracic triangular depression absent. Abdominal chaetae sickle-shaped with finely denticulate blades; uncini rasp-shaped with approximately 30 teeth in profile. Short achaetous anterior abdominal zone present. Posterior capillary chaetae present. Posterior glandular pad present. (Diagnosis mainly after Kupriyanova & Nishi, 2010).

Remarks. The genera *Protula* Risso, 1826 and *Apomatus* Philippi, 1844 are distinguished by mainly by the presence (*Apomatus*) or absence (*Protula*) of a soft vesicular operculum on an unmodified radiole. The controversy whether *Apomatus* and *Protula* should be regarded as separate genera (e.g., ten Hove & Pantus, 1985) or synonymized under *Protula* (e.g., Kupriyanova & Jirkov, 1997) has not been resolved yet (ten Hove & Kupriyanova, 2009). Ten Hove & Pantus (1985) examined operculate and non-operculate forms in the Mediterranean and listed further differences in thoracic blood-vessel patterns, distribution of *Apomatus* chaetae and rows of compound eyes in radioles as differentiating *Protula* and *Apomatus*. However, with the exception of the *Apomatus* chaetae distribution, the characters suggested by ten Hove & Pantus (1985) can be observed only in fresh material and the results are still confusing as significant variability exists. Ben-Eliahu & Fiege (1996: 27) further elucidated the differences between *Apomatus* and *Protula* in a key, but none of the studies includes all species of the genera, so a proper revision is much-needed.

Nine species (ten Hove & Kupriyanova, 2009; Kupriyanova & Nishi, 2010), one known from the Arctic, however, Bastida-Zavala (2008) stated that *Apomatus timsii* Pixell, 1912 is a junior synonym of *Apomatus geniculatus* (Moore & Bush, 1904).

Apomatus globifer Théel**,** 1879

(Fig. 1A-E, Pl. 1G)

Apomatus globifer Théel, 1879, p. 66, pl. IV, fig. 63-65; Levinsen, 1887, p. 300, tab. XXV, fig. 11; Marenzeller, 1892, p. 430-432, tab. 19, fig. 8; Wollebæk, 1912, p. 112-113, pl. XLI, fig. 1-3, pl. fig. 4-6; Friedrich, 1940, 127-128, 131; Wesenberg-Lund, 1950b, p. 137; Zatsepin, 1948, p. 167, tab. XXXIX, 27 đ, i, h; Uschakov, 1957, p. 1669.

Protula globifera: Kupriyanova & Jirkov, 1997, p. 222-225, fig. 9A-J, map 9; Jirkov & Kupriyanova, 2001, p. 569-570, text figures 1-7, map.

Material examined. Table 1. # 48 (6); # 72 (1); # 73 (4); # 90 (1); # 91 (1 and tubes); # 92 (8); # 93 (2); # 94 (9); # 95 (1); # 96 (1); # 97 (1); # 98 (5); # 99 (3); # 100 (1); # 101 (1); # 102 (1); # 103 (7); # 104 (1); # 105 (10); # 106 (55); # 107 (? 1000); # 109 (8); # 110 (2); # 111 (5); # 112 (3); # 113 (4); # 114 (tubes); # 115 (3); # 116 (1); # 117 (3);

118 (8); # 119 (1); # 120 (tubes); # 121 (2); # 122 (4); # 188 (1); # 190 (tubes); # 191 (1); # 194 (1); # 235 (1); # 237 (1 and tubes); # 244 (2); # 248 (1 and tubes); # 250 (tubes); # 251 (3); # 253 (tubes); # 254 (123); # 258 (4); # 259 (2); # 260 (91); # 261 (1); # 262 (15); # 263 (2); # 265 (3); # 266 (1); # 267 (3); # 268 (1 and tubes); # 272 (6); # 273 (2); # 274 (9); # 279 (13); # 280 (21); # 281 (2 and tubes); # 283 (1); # 285 (2); # 286 (12); # 287 (tubes); # 288 (10); # 289 (8); # 290 (4); # 291 (3 and tubes); # 292 (8 and tubes); # 293 (1); # 294 (4 and tubes); # 430 (tubes); # 432 (8 and tubes); # 433 (1); # 434 (1); # 435 (2); # 437 (1); # 441 (2); # 442 (46); # 446 (2); # 447 (52); # 452 (8); # 453 (6); # 454 (9); # 455 (4); # 458 (2); # 459 (1); # 485 (1); # 505 (6); # 512 (1 and tubes); # 521 (2); # 522 (1 and tubes); # 528 (3); 576 (5); # 577 (7); # 578 (3); # 579 (1); # 580 (2 and tubes); # 581 (1 and tubes).

Description. Tubes (Fig. 1A) up to 5 mm in diameter, circular in cross section, white, opaque. Tubes usually attached to substrate at base only, distal part free. Tube surface with poorly expressed "honeycombed" structure (Fig. 1B).

Body length without radioles up to 26 mm. Live specimens with white or red radiolar crown, body red.

Number of radioles varying from 10-40 pairs depending on animal size. Radioles connected by inter-radiolar membrane at base. Radiolar lobes long, radioles arranged pectinately. Radiolar eyes present, but not seen in preserved material**.**

Operculum a globular membranous transparent vesicle on a normal pinnulated radiole. (Fig. 1C). Sometimes an additional similar operculum (pseudoperculum?) present.

Collar entire, short, not covering bases of radiolar lobes. Thoracic membranes wide, continuing to last thoracic segment and forming wide apron ventrally (Fig. 1D, E). Prostomium fused with peristomium.

Seven thoracic chaetigers, including 6 uncinigerous (Fig. 1D). Thoracic neuropodia at least three times longer than abdominal notopodia (Fig. 1E). Neuropodia situated at mid-lateral line of thorax, not shifting ventrally. Collar chaetae limbate (Fig. 1F) and capillary. Other thoracic chaetae limbate and *Apomatus* chaetae. Uncini rasp-shaped, with numerous teeth per row above elongated rounded anterior peg.

Achaetous anterior abdominal zone long. Up to 120 abdominal chaetigers. Abdominal chaetae short, sickle-shaped with finely denticulate blades on anterior and middle chaetigers, long capillaries posteriorly. Abdominal uncini similar to thoracic uncini, but smaller. Posterior glandular pad present.

Remarks. The tentative record of *Apomatus similis* Marion & Bobretzky, 1875 from the Central Arctic (Knox, 1959) is based on empty tubes and tube fragments from three stations. The information provided (cylindrical tubes with "circular ridges at intervals") is insufficient to attribute these tubes to *A. globifer*, *P. tubularia*, or *P. arctica*. Fauvel (1927) and Hartmann-Schröder (1971) placed *A. globifer* into synonymy of *A. similis*. As in the case with *Protis simplex* Ehlers and *P. arctica* (see below), without a comparative study, and based on literature only, we cannot tell with confidence whether the material from the Arctic and that from more southern locations belong to the same species. Therefore, we maintain *A. globifer* as a separate species.

A. globifer is most similar to another Arctic species, *P. tubularia*, but they can be easily distinguished, apart from the presence of opercula, by the length of thoracic notopodia and collar structure. Thoracic neuropodia (rows of uncini) are of the same length as abdominal notopodia (rows of uncini) and the collar is trilobed in *P. tubularia*, whereas the thoracic notopodia are several times longer than the abdominal neuropodia and the collar is entire in *A. globifer*.

The species within the genus are very similar morphologically, all having a membranous semi-transparent operculum borne on a non-modified radiole. The only easily recognizable species is *Apomatus voightae* Kupriyanova & Nishi, 2010 that has unusual

flattened radioles. The remaining species were all described in the 19th – early 20th century and are impossible to distinguish based on the old descriptions only. As a result, the specimens have been given specific names mostly based on geographic location of the records.

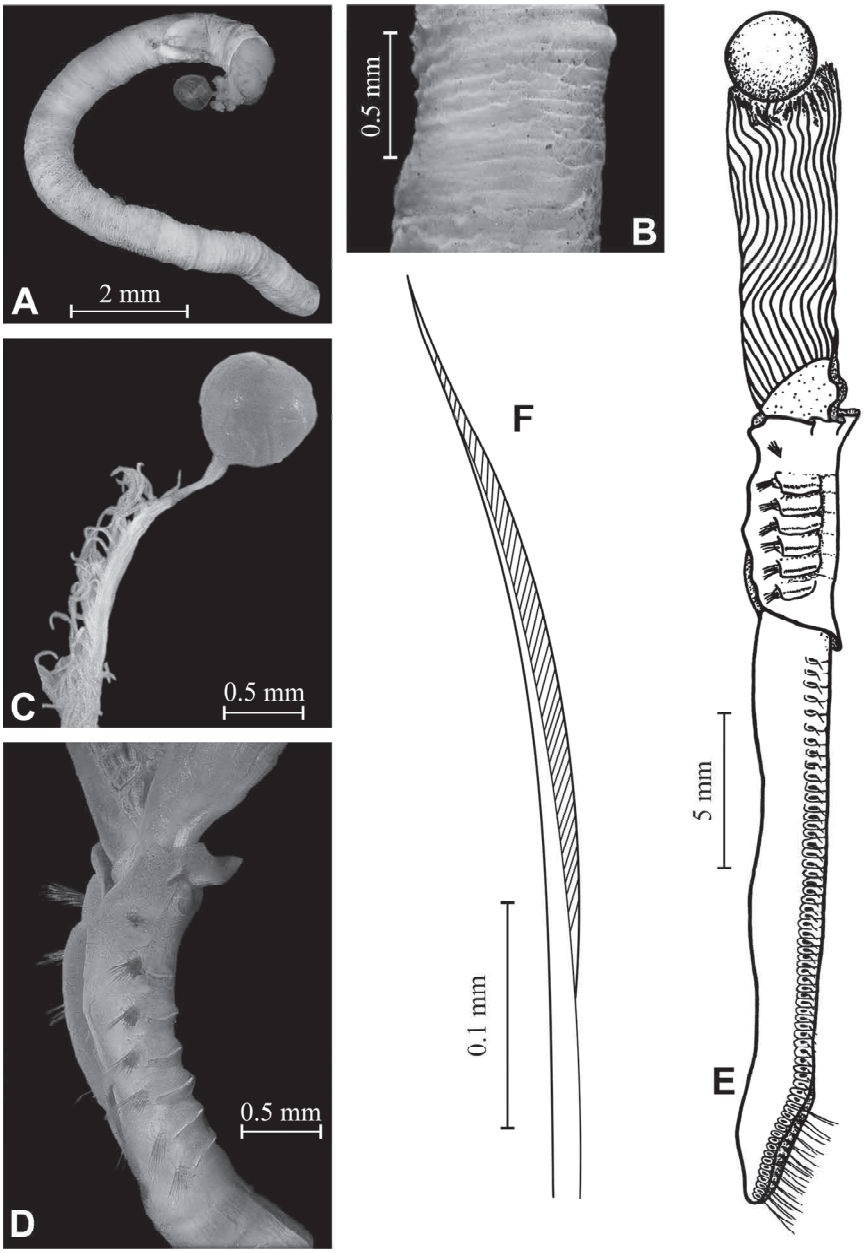

Figure 1. *Apomatus globifer*. A – animal in tube; B – tube fragment; C – operculum on pinnulated radiole; D – thorax; E – entire body, lateral view; F – limbate collar chaeta. E-F – from Kupriyanova & Jirkov (1997). A-D – photo E. Wong.

Ecology. In the Arctic found at depths of 18-3384 m corresponding to an average temperature of 2.01ºC, attached to rocks, gravel in various soft substrates excluding fine sands and rarely on coarse sand (Kupriyanova & Badyaev, 1998). Reproduction unknown.

Distribution. Widely distributed in the Arctic in the Chukchi, East-Siberian, Laptev, Kara, Barents, Norwegian, Greenland Seas, central part of the Arctic, and around Iceland (Kupriyanova & Jirkov, 1997). Outside the Arctic recorded from European waters (Bellan, 2001), but see questionable synonymy with *A. similis*, above.

Genus *Bathyvermilia* Zibrowius, 1973a

Type-species: *Bathyvermilia challengeri* Zibrowius, 1973a.

Tube white, opaque, circular in cross-section, keel(s) may be present. Collar-like rings present. Granular overlay absent. Operculum sub-globular, with simple flat to slightly conical chitinous endplate, which may be encrusted by calcareous deposit. Peduncle cylindrical, smooth or wrinkled, without distal wings; inserted as second dorsal radiole on one side, constriction present. Pseudoperculum absent. Arrangement of radioles in semicircles, up to 35 per lobe. Inter-radiolar membrane absent. Radiolar eyes not observed. Stylodes absent. Mouth palps may be present. 7 thoracic chaetigerous segments. Collar trilobed or non-lobed with entire edge, tonguelets absent. Thoracic membranes variable, ending at 2nd–7th thoracic segments. Collar chaetae limbate and capillary. *Apomatus* chaetae present. Thoracic uncini saw-shaped, with 6 to 10 teeth. Anterior fang pointed. Abdominal chaetae flat narrow geniculate with blunt teeth; abdominal uncini saw-shaped, except in a few far posterior segments, with rasp-shaped uncini. Short achaetous anterior abdominal zone present. Posterior capillary chaetae present. Posterior glandular pad present.

Remarks. Zibrowius (1973a) established the genus *Bathyvermilia* for the deep-water *Vermiliopsis langerhansi* Fauvel, 1909 and the newly described *Bathyvermilia challengeri* (new name for *Placostegus ornatus* not Mörch, 1863 but *sensu* McIntosh, 1885). Later, three species (*Bathyvermilia zibrowiusi* Kupriyanova, 1993b, from Kurile-Kamchatka trench, *B. islandica* Sanfilippo, 2001 from off Iceland, and *B. kupriyanovae* Bastida-Zavala, 2008, off California) were added and *Vermiliopsis? eliasoni* Zibrowius, 1970 was transferred to *Bathyvermilia* by Kupriyanova & Nishi (2010).

Six species, two known from the Arctic.

Bathyvermilia eliasoni (Zibrowius, 1970)

(Fig. 2A-G)

Vermiliopsis langerhansi **non** Fauvel, 1909: Southward, 1963, p. 584.

Vermiliopsis (gen?) *eliasoni* Zibrowius, 1970, p. 121-122; ten Hove, 1975, p. 55, 58.

Vermiliopsis eliasoni: Campoy, 1979, p. 760; Tyler & Zibrowius, 1992, p. 220; Lommerzheim, 1979, p. 154; 1981, p. 31 (a discussion of the operculum only); Barrier et al., 1989, p. 790-791, fig. 2; Ben-Eliahu & Fiege, 1996, p. 36; Leahy et al., 2003, p. 48; ten Hove & Kupriyanova, 2009, p. 91, 102.

Bathyvermilia eliasoni: Kupriyanova & Nishi 2010: 57-60, fig. 3, 4.

Material examined. Table 1. # 207 (1); # 208 (1).

Description. Tubes white opaque, up to 2.0 mm in diameter, more or less circular in internal cross-section, with three denticulate keels, no peristomes, with smooth surface, attached to the substrate throughout their length (Fig. 2A).

Body length, without radioles, up to 21 mm. Colour of live specimens unknown.

SPIRORBINAE
Practical recommendations for identification of spirorbins

1. To determine the direction of the spirorbin tube coiling, it should be observed "as is": opposite the substrate, as being projected onto the substrate. Some earlier workers reported the coiling direction as seen from the substrate and this still leads to confusion sometimes. It is recommended to place the tubes in the same position as they are usually illustrated herein, i.e., with their mouths on the top. Examining the tubes in other positions, especially upside down, can easily result in a mistaken tube coiling direction.

2. To determine the number of thoracic chaetigers, one needs to count the number of rows of thoracic uncini on the concave body side and then add 1 for the collar segment. It should done so because 1) notochaetae usually are present only on three first chaetigers; 2) number of tori may be incomplete on the convex side of body, and 3) tori are absent from 1st chaetiger.

3. To study the details of the soft body structures (e.g., thoracic membranes) the worms should be stained by methylene blue, malachite green or a similar dye immediately before the examination.

4. Mature oocytes lying freely (released spontaneously or because of damage in the tube-during preparation) may be confused with embryos.

5. To study the chaetal structure, spirorbin specimens should be mounted on slides in glycerine, Fore liquid or any other clearing medium. The animal should be positioned in such a way that the body side that is turned to the substrate in the tube is facing up. Chaetal structure should be studied using an objective magnification of at least 40X, using phase contrast is helpful. This is a destructive study method (excluding glycerin) and should be done after the external morphology is examined under a dissecting microscope.

6. The collar chaetae should be observed when positioned strictly laterally. If the fin is small or the gap separating the fin from the blade is short, modified fin-and-blade collar chaetae may be mistaken as limbate chaetae.

7. The denticulate distal part of the sickle-shaped chaetae often is optically transparent and thus poorly visible. Besides, because there may be only 1-2 sickle chaetae in a fascicle or their distal denticulate part may be broken off, these chaetae may be overlooked. The best way to examine the chaetal structure is to prepare the entire specimen for SEM when possible.

Key to spirorbins

1a) Tube dextral (e.g., Fig. 16A, B, 18A), occasionally sinistral specimens recorded, however not from the Arctic **2**
1b) Tube sinistral (e.g., Fig. 22A, 23A) **6**

2a) Tube thick-walled, hard, vitreous; inner lining of tube or body of live specimens seen through the translucent tube walls may make tubes to appear coloured (Pl. 2 A, B). Embryos stuck to each other and directly to inside of tube wall. Four thoracic chaetigers (rarely juveniles with three thoracic chaetigers). Only sickle (*Apomatus*) chaetae (Fig. 18E, 20G) in 3rd thoracic chaetiger **3**
2b) Tube thin-walled, fragile, white opaque, porcellaneous or not (e. g. Fig. 16A, 17B, 21A); bodies usually coloured, but colouration not visible through tube walls. Embryos incubated in tube or in brood chamber associated with operculum. Three thoracic chaetigers. Chaetae of 3rd thoracic chaetiger limbate only or supplemented with sickle (*Apomatus*) (Fig. 21I) chaetae **4**

3a) Tube planospiral. Peripheral tube alveoli (Fig. 19A) present (sometimes alveoli absent in juveniles or adult tube may be broken along alveoli line if tube detached from substrate). Body of live animals colourless, inner tube lining absent, so tubes always looking greyish-white. Opercular endplate cup-shaped, but often covered by thin brown domed membrane, talon thick, shovel-shaped (Fig. 19B). Large collar chaetae modified fin-and-blade cross-striated (Fig. 19D); gap between fin and blade may be very small. Serrated distal part of sickle (*Apomatus*) chaetae about of 1/2–1/3 of blade length .....
..... ***Paradexiospira* (*Spirorbides*) *cancellata*** (p. 86)
3b) Tube planospiral, tube alveoli absent. Deep violet or brown (in live and preserved specimens respectively) inner tube lining visible through tube walls making tubes appear almost black (Fig. 18A, Pl. 2B). Opercular endplate (Fig. 18B, C) flat or slightly convex, covered by brown (likely chitinous) membrane. Talon massive with two oval lateral incisions. Large collar chaetae modified cross-striated (Fig. 18D); serrated distal part of sickle (*Apomatus*) chaetae (Fig. 18E) about of 1/4–1/5 of blade length .....
..... ***Paradexiospira* (*Paradexiospira*) *violacea*** (p. 84)
3c) Tube planospiral (Fig. 20B) or with overlapping whorls making tubes turret-shaped (Fig. 20A) when their height is equal to or exceeding diameter up to 1.5–2 times. Tube alveoli absent. Red body of live animals visible through transparent tube wall making the tube appear brightly pink (Pl. 2A). Body and tubes colourless (whitish) in long-preserved specimens. In juveniles narrow wavy transparent zones of tube wall alternate with milky-white ones. Opercular endplate (Fig. 20C-E) thin, likely slightly calcified, cup-shaped. Talon absent or vestigial cone-shaped. Large collar chaetae modified fin-and-blade cross-striated. (Fig. 20F); serrated distal part of sickle (*Apomatus*) chaetae about of 1/2–1/3 of blade length (Fig. 20G) ..... ***Paradexiospira* (*Spirorbides*) *vitrea*** (p. 88)

4a) Tube (Fig. 21A) non-porcellaneous, unsculptured or with 1-3 (up to 4) keels. Embryos incubated in inverted cuticular cup outside opercular endplate. Primary operculum with flat calcareous endplate and long pin-like peripheral talon (Fig. 21B); completely fused with first brood chamber, which thus has a talon on lateral wall facing out of radiolar crown (Fig. 21C). Subsequent brood chambers lacking talons (Fig. 21D-G). All brood

Circeini Knight-Jones P., 1978

Type genus *Circeis* Saint-Joseph, 1894.

Embryos stick to each other and directly to inside of tube wall. Operculum in form of a distal plate usually with a talon. Larvae without white attachment glands. Thoracic uncini wide, rasp-shaped, with 3–15 longitudinal rows of teeth and blunt anterior peg. Abdominal uncini distributed quite asymmetrically, on convex body side they may be present on last chaetigers only or absent altogether. Largest abdominal tori on concave body side in anterior half of the abdomen. Abdominal chaetae flat-geniculate, pennant-shaped, usually with a thick (optically dense) projecting heel; their blade lengths not exceeding that of largest collar chaetae, width decreasing gradually towards tips. Abdominal companion capillary hooked chaetae usually absent or present only on last chaetigers.

Two genera, *Circeis* and *Paradexiospira,* both known from the Arctic.

Genus *Circeis* Saint-Joseph, 1894

Type species: *Circeis armoricana* Sŕint-Jîsĺđh, 1894.

Tubes usually dextral, with one species regularly and several species occasionally coiled sinistrally. Margins of collar and thoracic membrane not fused over thoracic groove. Large collar chaetae modified, bent (usually strongly), with vestigial lateral cross-striation or cross-striated from "frontal side" of blade, not visible laterally under a dissecting microscope. Sickle (*Apomatus*) chaetae absent. Always three thoracic chaetigers.

Six species, two are known from the Arctic.

Circeis armoricana Saint-Joseph, 1894

(Fig. 16A-K)

Circeis armoricana Saint-Joseph, 1894 p. 350, tab. XIII, fig. 387; Knight-Jones P. & Knight-Jones E.W., 1977, p. 468-470, fig. 5A-C, E-M (non *Circeis armoricana paguri*, p. 470, fig. 5D); Knight-Jones P. et al., 1979, p. 427-429, fig. 3A(a-d); Knight-Jones P. et al., 1991, p. 192, fig. 2; Rzhavsky, 1989, p. 51-52, fig. 1A; 1992a, p. 7-8; 1992[1994], p. 100, fig. 1; 2001, p. 582-583, text figures 1-8, 1-2, map; Jakovis, 1997, p. 40-41, fig. 3a-g; Gagaev, 2008, p. 94-95.

Spirorbis spirillum **non (**Linnaeus, 1758): Zenkevich, 1925, p. 5; Annenkova, 1932, p. 189; Pergament, 1945, p. 131; Zatsepin, 1948, p. 166, tab. XXXIX, 21 (partim?); Bock, 1953, p. 200-201, Abb. 1; Streltzov in Kuznetsova & Zevina, 1967, p. 22; Denisenko & Savinov, 1984, p. 105; Sikorski, 1989, p. 60.

Spirorbis (*Dexiospira*) *spirillum* **non (**Linnaeus, 1758):: Bergan, 1953b: 41-42, fig. 6a-c (partim?); Pettibone, 1954, p. 344-345; Uschakov, 1955, p. 430, non fig. 162Z (partim); 1965, p. 403-404, non fig. 162H (partim).

Dexiospira spirillum **non (**Linnaeus, 1758): Imajima & Hartman, 1964, p. 379.

Dexiospira spirilla **non (**Linnaeus, 1758): Chlebovitsch in Kussakin, 1975, p. 62; Bagaveeva, 1980, p. 92.

Spirorbis armoricana: Aleksandrov, 1981, p. 89, tab. XIII, fig. 1.

Circeis spirillum **non (**Linnaeus, 1758): Tzetlin, 1985, p. 44, fig. 1A-Zh.

Material examined. Table 1. # 17 (? 15); # 21 (? 50); # 22 (many); # 26 (2 samples, many); # 31 (many); # 32 (~ 30); # 39 (many); # 40 (many); # 42 (4); # 45 (6); # 47 (~ 30); # 51 (10); # 79 (many); # 83 (1); # 84 (many); # 87 (many); # 199 (~ 30); # 201 (? 50); # 210 (? 20); # 213 (7); # 215 (2); # 223 (many); # 226 (9); # 228 (12); # 231 (6); # 270 (many); # 456 (many); # 479 (3); # 486 (3); # 496 (1); # 500 (~ 100); # 504 (10); # 509 (many); # 513 (many); # 514 (~ 25); # 517 (many); # 519 (many); # 523 (14); # 534 (10); # 541 (many); # 550 (many); # 556 (~ 15); # 563 (many); # 564 (2); # 568 (~ 20); # 570 (3); # 573 (~ 30); # 575 (~ 100); # 583 (? 10); N 585 (~ 150); # 589 (20); # 591 (1); # 593 (3); # 595 (~ 30); # 597 (many); # 606 (~ 20); # 607 (~ 15); # 612 (many); # 613 (many); # 614 (many); # 616 (~ 25); # 620 (~ 25); # 622 (1).

Description. Tube normally dextral, some sinistral specimens were recorded from Pacific coast of North America (Knight-Jones P. et al., 1979) and Kiel, Baltic Sea (Bock,

1953, as "*spirillum*"). Up to 2–2.5 mm in coil diameter. Tube walls typically unsculptured or bearing one (rarely up to three) keels. Whorls usually planospiral (Fig. 16A), on filamentous algae and uneven substrates whorls overlapping (Fig. 16B), sometimes ascending over substrate or last whorl may be erected. Tube walls white, opaque, sometimes with narrow semitransparent transverse rings, slightly porcellaneous. Live specimens with colourless radiolar crown and light orange body; preserved specimens colourless or flesh-coloured.

Opercular endplate slightly concave, rarely flat. Talon eccentric, usually small, conical in frontal view, though sometimes rather large and flattened, its terminal margin rarely split into 2–3 lobes (Fig. 16C-F).

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 3rd chaetiger forming apron. Three thoracic chaetigers.

Large collar chaetae modified, strongly bent, their blades almost perpendicular to chaetal shaft on convex side of body (Fig. 16G), but not that strongly curved on concave side (Fig. 16H). Vestigial cross-striation on the "frontal side" of the blade not visible

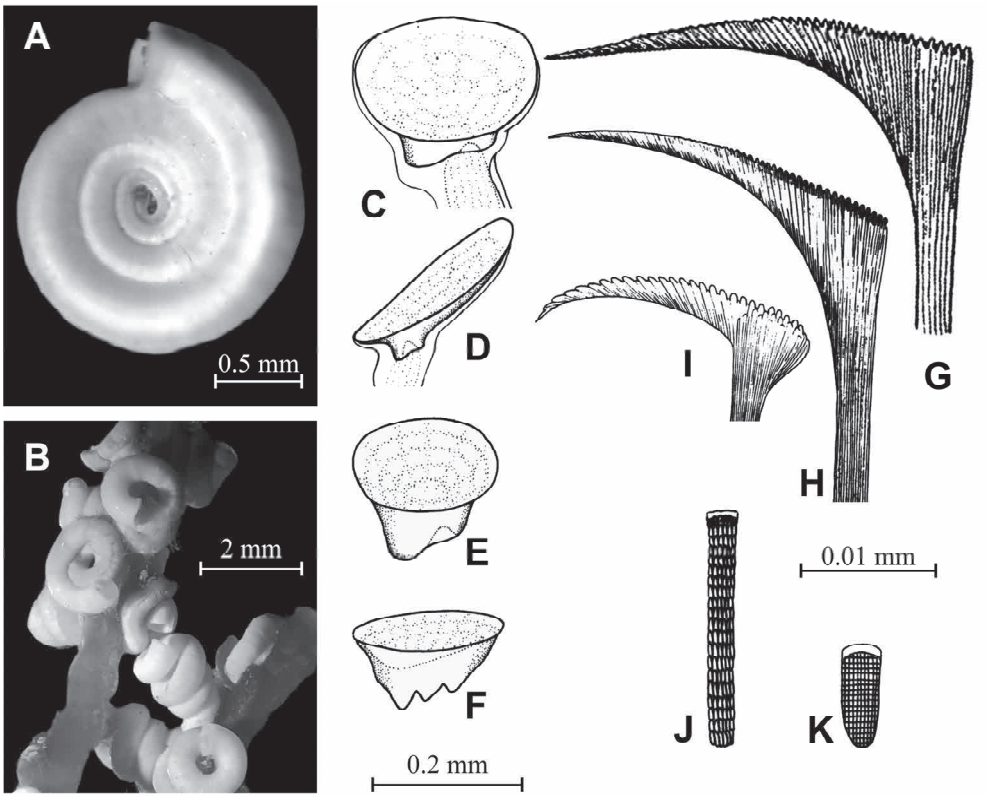

Figure 16. *Circeis armoricana*. A – planospiral tube, B – tubes with overlapping coils, C, D – typical operculum, front and lateral views; E, F – opercular variability, frontal view; G – modified collar chaeta from concave body side; H – modified collar chaeta from convex body side; I – abdominal flat geniculate notochaeta; J – thoracic uncinus, front view; K – abdominal uncinus, front view. C-F, H-K – from Knight-Jones P. & Knight-Jones E.W. (1977), G – from Knight-Jones P. et al. (1979). A, B – photo A.V. Rzhavsky.

laterally under a dissecting microscope (SEM examination is needed). Under dissecting microscope blades looking somewhat serrated, without any cross-striation. Capillary chaetae present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae absent.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini rasp-shaped (Fig. 16J), largest with about 5–6 and smallest with about 7–9 longitudinal rows of teeth throughout length of uncinus and blunt anterior pegs. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 20 chaetigers. Usually two chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and distinctly serrated tapering blade (Fig. 16I). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae. Companion capillary hooked chaetae not observed. Uncini (Fig. 16K) rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, distributed quite asymmetrically, on convex body side they may be present on last chaetigers only or absent altogether. Largest abdominal tori in anterior half of abdomen on concave body side.

Remarks. For a long time *C. armoricana* was confused or even synonymized with *C. spirillum*. These two species are similar in their morphology, but clearly distinct by a number of features. Tubes of *C. spirillum* (Fig. 17A, B; Pl. 2H) are typically ascending over substrate like stretched springs, more brightly porcellaneous than those of *C. armoricana* (Fig. 16A, B) and somewhat semi-transparent. Modified collar chaetae of *C. spirillum* (Fig. 17F, G) are not that obviously geniculate (blades are never perpendicular to the chaetal shaft) as those of *C. armoricana* (Fig. 16G-H), and have vestigial cross-striation in the basal part of the blade on convex body side; the opercular talon is always large and flattened (Fig. 16C, D; Fig. 17C, D). In addition, these two species usually significantly differ ecologically. *C. spirillum* almost exclusively uses bryozoans and hydrozoans as a substrate, its specimens are only occasionally found on byssus of the mussel *Crenomytilus grayanus* (Dunker, 1853) (Rzhavsky, 2001) and some red algae (Knight-Jones P. & Knight-Jones E.W., 1977; Jakovis, 1997). Larvae of *C. armoricana* settle on any substrates and in shallower water (see "Ecology"). Most Russian Arctic records of *C. spirillum* attached to substrates other than hydrozoans and bryozoans (Zachs, 1923; Gurjanova, 1924; Gurjanova et al., 1926, 1930; Uschakov, 1927, 1931, 1939, 1948; Derjugin, 1928; Gurjanova & Uschakov, 1928; Gorbunov, 1946; Kuznetsov & Matveeva, 1948; Rusanova, 1949; Polyanski, 1950; Filatova & Zenkevich, 1957; Slastnikov, 1957; Petrovskaja, 1960; Kuznetsov, 1963; Brotzkaja et al., 1963; Kussakin, 1963; Streltzov, 1966; Kuderskij, 1966; Kuznetsova, 1967; Propp, 1971; Averintzev, 1977; 1990; Golikov & Averintzev, 1977; Brjazgin et al., 1981) most probably completely or partially belong to *C. armoricana.* Because all these records were not described and illustrated, and we could not examine the material, they were excluded from the synonymy.

Re-examined Russian material identified by Tzetlin (1985) as *C. spirillum* belongs to *C. armoricana,* although his line drawings may illustrate either of these two species. Zatsepin (1948) compiled data on distribution of *C. spirillum* in the Arctic Ocean, but his description and drawings correspond to *C. armoricana*.

Three subspecies of *C. armoricana* (*C. a. armoricana, C . a. fragilis* and *C. a. paguri*) described from the North Atlantic are practically identical in adult morphology, but may be distinguished by their ecology and larval morphology (Knight-Jones E.W. et al., 1975; Knight-Jones P. & Knight-Jones E.W., 1977). Later *C. a. paguri* was elevated to full

species rank as *Circeis paguri* Knight-Jones P. & Knight-Jones E.W., 1977, associated only with hermit crabs (Al-Ogily & Knight-Jones P., 1981). Nevertheless, Knight-Jones P. et al. (1979) did not recognize any subspecies within *C. armoricana* in the North Pacific. A study of spirorbins off East Kamchatka (Rzhavsky & Britayev, 1988) did not mention a valid species of *Circeis* associated with hermit crabs only. It is likely that *C. armoricana* is a species complex and needs further study.

Chaetal pattern and tube morphology of *C. armoricana* are identical to that of *Circeis gurjanovae* Rzhavsky, 1992a known from the Commander Islands, but the operculum of *C. armoricana* is different. *Circeis vitreopsis* Rzhavsky, 1992c from the Sea of Japan also has the same collar chaetae as *C. armoricana* and *C. gurjanovae*, but differs from these two species not only in opercular morphology, but also in having a tube unusual for this genus: sinistral, thick-walled and completely vitreous.

Ecology. *C. armoricana* is one of the most common and abundant species in arctic and boreal waters. It attaches to various substrates such as rocks, stones, shells, live crustaceans, algae and sea grasses, polychaete tubes, ascidians, artificial substrates, rarely bryozoans and hydrozoans. Animals often live mixed with other spirorbins such as *P.* (*S.*) *vitrea, B.* (*J.*) *quadrangularis, B.* (*J.*) *similis, B.* (*B.*) *evoluta, J. heterostropha,* intertidally on fuci with *Spirorbis* spp. In the Arctic basin it was recorded from the intertidal zone up to 271 m deep, in other oceans it penetrates up to 170 m, though its preferred bathymetric range is 0–50 m.

As mentioned above (see Remarks), three subspecies were distinguished in the North Atlantic mainly on the basis of their ecology, one of them later was elevated to full species rank (Knight-Jones E.W. et al., 1975; Knight-Jones P. & Knight-Jones E.W., 1977; AI-Ogily & Knight-Jones E.W., 1981).

Distribution of *C. armoricana* on hermit crabs was studied in the intertidal zone of East Kamchatka Peninsula (Rzhavsky & Britayev, 1988). In this region the species broods from April to September, though sometimes embryos may be found throughout the winter. Life cycle and biology of *C. armoricana* in the northern part of the Japan Sea was studied by Ivin et al. (1990) and Ivin (1995; 1997). In this region the species breeds throughout the entire year. Most specimens bear embryos in summer and only 10–20 % do so in winter. The number of embryos may vary from 6 to 295 (Kupriyanova et al., 2001). Larval development was described in detail by Okuda (1946, as "*spirillum*" on material from Akkeshi Bay, Hokkaido, Japan). Oksov et al. (1987) described behaviour and setting of *C. armoricana* in the White Sea. Polyanski (1951) studied the effects of salinity and temperature changes probably on this species (as "*spirillum*", on material from the White Sea). Data on reproduction of "*spirillum*" (Bergan, 1953a, Oslofjord, Norway; Potswald, 1967, San Juan Isl., Washington, USA) also probably should be attributed to *C. armoricana*.

Distribution. Our extensive Arctic material was collected from the Chukchi, East-Siberian, Laptev, Kara, Barents, White, Norwegian (the mainland coast), Greenland Seas (Spitsbergen coast) and the central part of the Arctic Ocean. The species is also reported from Barrow Point, Arctic coast of Alaska (Knight-Jones P. et al., 1979; 1991) and the Iceland coast of the Greenland Sea (Knight-Jones P. et al., 1991). In the North Pacific its distribution range to the south reaches Possiet Bay (Japan Sea, Russia), Japan and Acapulco (Mexico); in the North Atlantic it extends to Brittany, France and Nova Scotia, Canada (for details see Knight-Jones P., Knight-Jones E.W., 1977; Knight-Jones P. et al., 1979; 1991; Rzhavsky, 1992a, 1992[1994]).

Table 1. List of station for the serpulid material examined. Abbreviations. **R/V, expedition or collector**: **“SP-3”, “SP-4”, “SP-22”, “SP-23”** – Drifting Polar Station “Severnyj Poljus” – 3, 4, 22,23; **Exp. BIOICE** – Expedition of the program “Benthic Invertebrates of Icelandic Waters); Expedition of **Exp. FMRI** – Expedition of the Floating Marine Research Institute; **Exp. IEE** – Expedition of the Severtsov Institute of Ecology and Evolution; **Exp. NIMRB** (**MAREANO**) – Expedition of the Norwegian Institute of Marine Research, Bergen, MAREANO Survey; Exp. **SHI**- Expedition of the State Hydrographic Institute; **Exp. ZI** – Expedition od the Zoological Institute; **Exp. ZI & MMBI** – Expedition of the Zoological Institute and Murmansk Marine Biological Institute; **B. – Birulja A.A.** – Bjalynitskij-Burulja A.A. **Seas: C. Arctic** – Central Arctic; **E. Siberian** – East Siberian. **Locations: F.J.L.** – Franz Joseph Land; **N.Z.** – Novaya Zemlya; **W.S.** – West Spitsbergen; **Deposition: AMRI** – Australian Museum Research Institute, Sydney, Australia; **AN** – Akvaplan-Niva, Tromsø , Norway; **DHMSU** – Department of Hydrobiology of Moscow State University, Moscow, Russia; **IEE** – A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow; **IINH** – Icelandic Institute and of Natural History; **IO** – Shirshov Institute of Oceanology RAS, Moscow, Russia; **MMBI** – Murman Marine Biological Institute of Kola Science Center, Russian Academy of Sciences, Murmansk, Russia; **SNHM** – Senckenberg Natural History Museum, Frankfurt, Germany; **ZISP** – Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia; **ZMBN** – University Museum of Bergen, University of Bergen, Norway; **ZMMU** – Zoological Museum of Moscow State University, Moscow, Russia.

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
1	“Akademik Berg”	st. 6	01.06.1954	Norwegian	no data	80	ZISP
2	“Akademik Berg”	st. 7	01.06.1954	Norwegian	61°58'N, 6°58'W	265	ZISP
3	“Alaid”	st. 6	01.07.1980	Barents	74º14'N, 19º20'E	62-65	DHMSU
4	“Alaid”	st. 7	04.07.1980	Barents	74°30'N, 32°30'E	385-390	DHMSU
5	“Alaid”	st. 10	06.07.1980	Barents	71°03'N, 30°00'E	330	IEE
6	“Alaid”	st. 13	11.07.1980	Barents	68°51'N, 37°20'E	75	
7	“Alaid”	st. 323	20.06.1980	Barents	71°10'N, 33°15'E	340	DHMSU
8	“Aleksey Otkupschikov ”			Barents	69°10'N, 36°00'E	84	DHMSU
9	“Aleksey Otkupschikov ”	st. 24	24.07.1978	Barents	69°17’N, 35°22'E	130	IEE
10	“Aleksey Otkupschikov ”			Barents	69°28'N, 34°11'E	111	DHMSU
11	“Alexander Kovalevsky”	no data	1908-1909	Barents	Kola Bay	no data	ZISP
12	“Alexander Kovalevsky”	st. 71	1909	Barents	Kola Bay	no data	ZISP
13	“Alexander Kovalevsky”	st. 157, 227	1909	Barents	Kola Bay	no data	ZISP
14	“Alexander Kovalevsky”	st. 187	1909	Barents	Kola Bay	no data	ZISP
15	“Alexander Kovalevsky”	st. 27	1916	Barents	Kola Bay	no data	ZISP
16	“Alexander Kovalevsky”	st. 170	1916	Barents	Kola Bay	no data	ZISP
17	“Alexander Kovalevsky”	st. 38	1926	Barents	Kola Bay	no data	ZISP
18	“Alexander Kovalevsky”	st. 146	1926	Barents	Kola Bay	no data	ZISP
19	“Andrei Pervozvannyj”	no data	1898	Barents	no data	littoral	ZISP
20	“Andrei Pervozvannyj”	12	05.06.1899	Barents	69°40'N, 35°15'E	190	ZISP
21	“Andrei Pervozvannyj”	no data	21.06.1899	Barents	between Ekaterininskij Isl. & Bolshoj Olenij Isl.	10	ZISP

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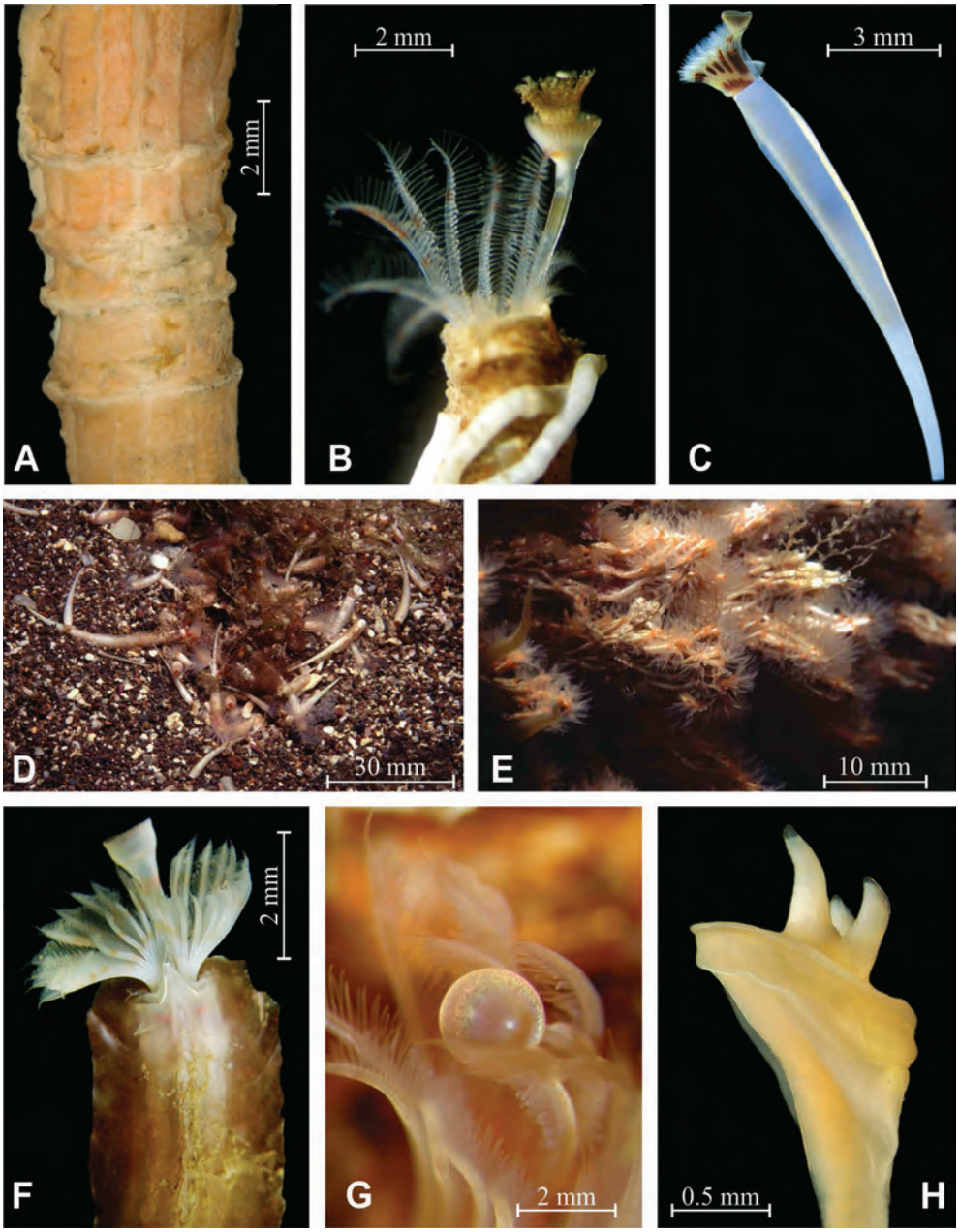

Plate 1. A – tube fragment of *Serpula vermicularis*,; B – branchial crown and operculum of *Hydroides norvegicus*; C – *Ditrupa arietina*, tube with the animal inside; D – *Ditrupa arietina*, animals *in situ*; E – *Filograna implexa*, colony of tubes *in situ*; F – *Placostegus tridentatus*, anterior part of the tube with branchial crown and operculum; G – operculum of *Apomatus globifer*; H – operculum of *Spirobranchus triqueter*. A, H – photo E. Wong, C – G. Rouse, B, D, E – P. Wirtz, F, G – S. Strömberg.

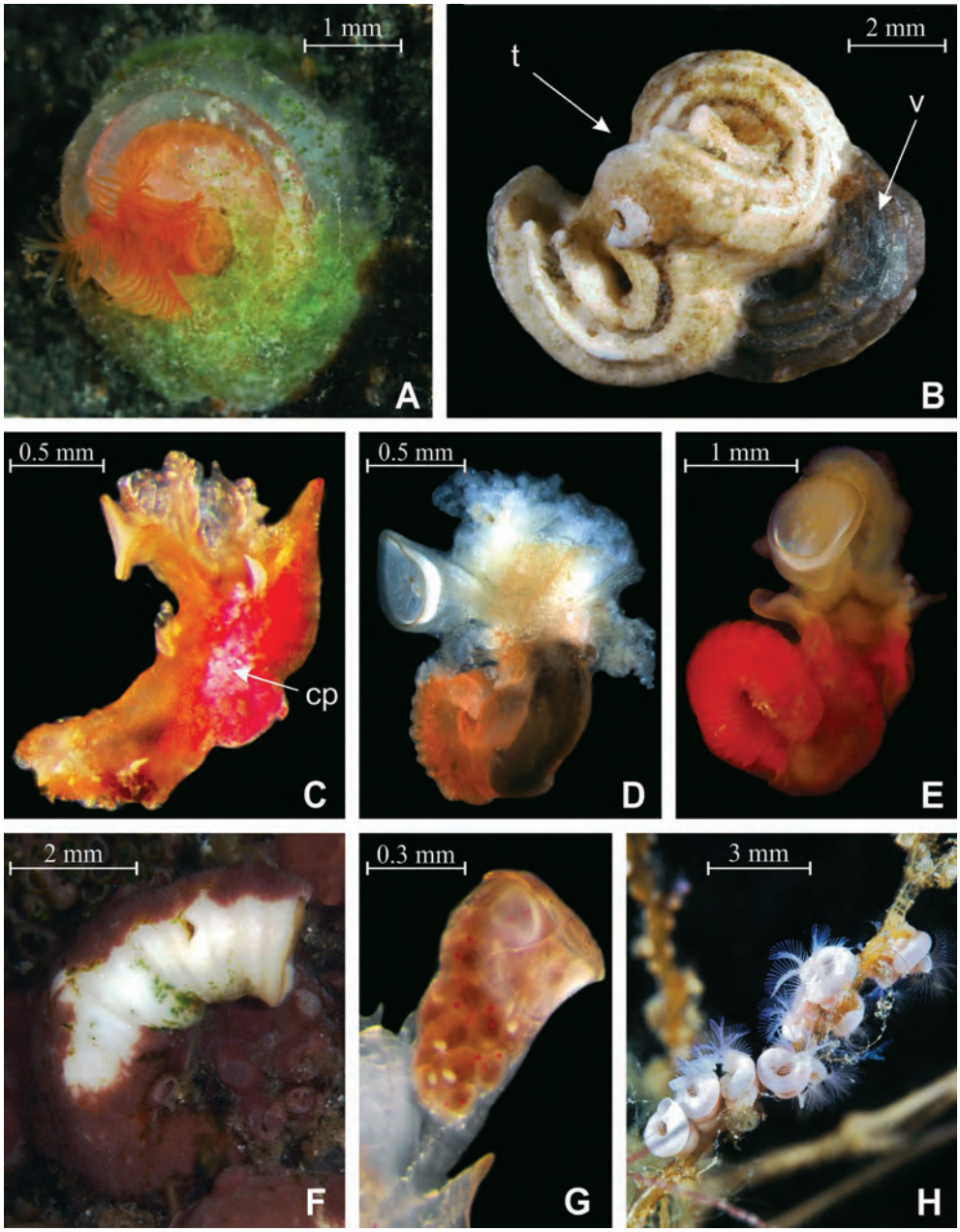

Plate 2. A – *Paradexiospira* (*Spirorbides*) *vitrea*, tube with body; B – tubes conglomerate of *Paradexiospira* (*Paradexiospira*) *violacea* (p) and *Spirorbis* (*Spirorbis*) *tridentatus* (t); C –*Pileolaria* ex gr. *berkeleyana*, entire body (cp – crystalline patches); D – *Spirorbis* (*Spirorbis*) *inornatus* entire body; E – *Spirorbis* (*Spirorbis*) *rupestris*, entire body; F - *Spirorbis* (*Spirorbis*) *rupestris*, tube overgrown by calcareous algae *Phymatholithon*; G – *Bushiella* (*Jugaria*) *similis*, brood chamber with embryous; H – settlement of *Circeis spirillum* on hydrozoan. A-G – photos A.V. Rzhavsky, H – photo A.A. Semenov.