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Calcareous tubeworms (Polychaeta, Serpulidae) of the Arctic Ocean

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Moscow 2014

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Akvaplan-niva

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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 serpulid taxonomy. The most comprehensive review of the serpulid morphology (excluding spirorbins) accompanied by numerous illustrations can be found in ten Hove & Kupriyanova (2009).

Tubes. Serpulid tubes are composed of crystalline calcium carbonate (calcite, aragonite, or both) interspersed with a mucopolysaccharide matrix. The adult tube is secreted by glands located on the collar and tube additions are molded by the collar folds when the worm is in a feeding position. Tubes are usually chalky (**opaque**) white (e.g., Fig. 2A, 22A, 31A, Pl. 1B, E), with rough or more or less smooth surface (e.g., *Hydroides* spp. (Fig. 8B, Pl. 1B), *Protis* spp. (Fig. 12A), *Protula* spp. (Fig. 13A), *Bushiella* spp., (Fig. 22 A), *Protoleodora* spp.(Fig. 31A)) or white with smooth shiny (porcellaneous) surface (e.g., *Spirorbis* spp. Fig. 36A, 37A), *Bathyvermilia islandica* Sanfilippo, 2001 (Fig. 3A), *Ditrupa* spp. (Fig. 5A, Pl. 1C, D)); rarely these tubes may be completely or partially semitransparent because of the thin wall, e.g., *Circeis spirillum* ((Linnaeus, 1758), *Spirorbis* (*Spirorbis*) *corallinae* L'Hardy, Quievreux, 1962. Completely transparent tubes are termed **vitreous,** e.g., *Placostegus* spp. (Pl. 1F), *Paradexiospira* spp (e.g., Pl. 2A).

Although tubes are mostly white, they may be completely or partly pink, bluish, orange (e.g., *Serpula vermicularis* Linnaeus, 1767, Pl. 1A), purple, mustard, or even white with dark-brown transverse stripes. In spirorbins with vitreous tubes the inner tube lining (Fig. 18A, Pl. 2B) or body of live specimens (Pl. 2A) may be visible through tube walls, thus making the tubes appear coloured (e.g., *Paradexiospira* spp.).

Spirorbins live in small spiral (hence the name) tubes 1.5 - 4 (up to 8) mm in diameter. Normally the spirals are flat (e.g., Fig. 16A), but the distal parts may be uncoiled and raised above the substrate (e.g., Fig. 17A, 27A), whorls being positioned on top of each other (e.g., Fig. 16B) or attached to the substrate, not forming a spiral (e.g., Fig. 26A). *Helicosiphon biscoeensis* Gravier, 1907 (from the Southern Hemisphere) has free tubes submerged into silt after the initial juvenile attached tubes have broken off. Spirorbin tubes may be coiled clockwise (**sinistral**) (e.g., Fig. 22A) or counter clockwise (**dextral**) (e.g., Fig. 16A). Most species show only one coiling direction, but tubes of some *Spirorbis* coil in either direction. Rarely, some Circeini and Januini (most of which are right-coiled) have specimens with opposite coiling directions. Dextral forms have never been recorded for typically sinistral species.

In non-spirorbin serpulids the tube shape is variable, and coiling, when present, is irregular. Most tubes are attached by at least the proximal older parts and some tubes are attached to the substrate throughout their entire length. Notable exceptions are the free-living *Ditrupa* (Pl. 1D, one species is known from the Arctic) and some deep-sea taxa, e.g., *Bathyditrupa hovei* Kupriyanova, 1993b and *Nogrobs grimaldii* (Fauvel, 1909).

Serpulid tubes are usually circular (e.g., Fig. 16A) or sub-circular in external cross-section. Longitudinal **keels** (ridges) usually do not change the tube cross-section (e.g., Fig. 11A, 32A), but some species may have triangular (Fig. 10A, B, 24A), quadrangular (Fig. 28A), pentangular (Fig. 27A, B) or even octangular cross-sections. Within a single tube cross-section may change from trapezoidal to multiangular or from triangular, trapezoidal or semi-circular to circular.

The external ornamentation (**sculpture**) of the tube surface typically consists of **longitudinal** and **transverse** elements. A single major prominent **keel** (e.g., Fig. 11A, 15A, B; 24A) (often termed **longitudinal ridge** in spirorbins) or several identical keels may be present (e.g., Fig. 22A, 28A, Pl. 1A). The major keel may be supplemented by secondary ones. The keels may either be sharp or smooth, high or low, straight or wavy, or in the form of longitudinal rows of denticles (Fig. 2A).

Transverse tube ornamentation in spirorbins may be presented by growth lines (**transverse striations)** (e.g., Fig. 30A) or rarely by transverse ridges (e.g., see Knight-Jones E.W. et al., 1974, fig. 2d; Knight-Jones P. et al., 1979, fig. 7B(a)). In non-spirorbins transverse sculpturing includes subtle growth striations, more distinct incomplete ridges or complete circular growth rings, and large flaring anteriorly directed **peristomes** that might be smooth or denticulate.

A combination of numerous longitudinal keels and transverse ridges may form characteristic honey-comb structures as e.g., in *Metavermilia arctica* Kupriyanova, 1993 (Fig. 9A). Sculpturing may differ between the free distal and the attached proximal parts of a tube. Tube surface may also be completely or partially pitted by numerous **alveoli**, e.g., *Neodexiospira alveolata* (Zachs, 1933)*, P.* (*S.*) *cancellata* (Fabricius, 1780**)** (Fig. 19A) that may completely perforate tube keels. **Tabulae** or transverse tube elements may partition the oldest parts of the tube as response to tube damage in some serpulids (e.g., *Spirobranchus*). Attached parts of the tubes often form flattened **peripheral flanges** (e.g., *B. islandica* (Fig. 3A), *Spirorbis* (*Spirorbis*) *inornatus* L'Hardy, Quievreux, 1962 (Fig. 34A) and may also contain alveolar structures (e.g., *Neodexiospira alveolata*).

Genera such as *Salmacina* and *Filograna* (formerly Filograninae) build characteristic aggregations (often incorrectly termed **colonies**) made of numerous branching tubes (Fig. 6A, Pl. 1E). These aggregations is a result of both asexual budding and gregarious larval settlement; they are different from the aggregations resulting from gregarious larval settlement only.

Morphological structures used for embryo incubation. All spirorbins have lecithotrophic larvae and incubate their embryos either inside their tubes or in opercular **brood chambers**. The methods of embryo brooding have been used to subdivide spirorbins into 6 subfamilies (now tribes).

Tube brooding:

1) Embryos positioned freely in the abdominal faecal groove – Paralaeospirini (see Knight-Jones P. & Walker, 1972, fig. o);

2) Embryo positioned in a sac fixed to the thorax or to the abdomen by an epithelial stalk – Romanchellini (see Knight-Jones E.W. et al., 1972, fig. 1e, f);

3) Embryos adhering to each other and directly to the internal tube wall – Circeini (see Knight-Jones E.W. et al., 1972, fig. 1c);

4) Embryo string attached posteriorly to the internal tube wall by a filament – Spirorbini (see Knight-Jones E.W. et al., 1972, fig. 1b);

Opercular brooding:

5) Embryos brooded in the re-usable **brood chamber** formed by invagination of the operculum – Pileolariini (e.g., Fig. 30F, H, Pl. 2G; see also Knight-Jones P. & Thorp, 1984, fig. 6);

6) Embryos brooded in a cuticular brood chamber formed outside the **distal part of the operculum**, a new chamber is formed for each brood – Januini (Fig. 21C-G; see also Knight-Jones P. & Thorp, 1984, fig. 1, 2).

Only the species of the tribes Spirorbini, Circeini, Pileolariini and Januini are found in the Arctic.

While most non-spirorbin serpulids are free-spawners with feeding larvae, some brood embryos inside the tube (e. g., *Filograna*), in various tube ovicells (e.g., *Chitinopoma,* Fig. 4B), inside the radiolar crown, in pockets of the thoracic membranes, or in a gelatinous mass near the tube mouth (e.g., *Protula*), also see Kupriyanova et al. (2001) for details.

Body. The body of non-spirorbin serpulids is bilaterally symmetrical even in animals that live in spirally coiled tubes. The thorax bears notopodial chaetae (dorsally) and neuropodial uncini (ventrally), whereas in the abdomen the position of chaetae and uncini is reversed, that is, the abdomen appears to be turned 180° relative to the thorax. Unlike torsion of molluscs, this chaetal inversion does not affect internal organs of the animal, it only affects the insertion of the chaetae. Both thorax and abdomen are facing the substrate by the dorsal side (bearing notochaetae in thorax and uncini in abdomen). Spirorbin bodies are always asymmetrical and curved in the direction of the tube's coil; their abdomen is turned by approximately 90° relative to the thorax (e.g., Fig. 31C; see also Knight-Jones P. & Fordy, 1979, fig. 1,3). It is unclear whether spirorbin morphology is an early stage in the evolution of chaetal inversion or a result of secondary untwisting. The thoracic region of spirorbins is turned to the substrate by the dorsal side (bearing notochaeta), while the abdomen faces the substrate laterally. Therefore, it is impossible to use such common terms as "dorsal" and "ventral", "right side" and "left side" for spirorbin morphology. Instead, the terms "facing the substrate" and "facing away from substrate", "convex side" and "concave side" are used.

Body colour. Serpulids are often very brightly coloured (red, pink, orange, brown, blue, greenish, yellow, or flesh-coloured). However, the colouration is of little taxonomic value because colour fades in preservatives, particular in alcohol, and may also be a subject to significant interspecific variability. The only exception is the genus *Spirorbis* where body colour is used as a taxonomic character.

In some Pileolariini, the posterior thorax on the side attached to the substrate has iridescent crystalline red, pink, purple patches (Pl. 2 C) that normally maintain their colour after fixation, although sometimes change to dark brown or almost black. These patches are likely not epithelial pigments but a secretion of some glands; they are located on top of the epithelium and can be easily removed by a preparation needle.

The radiolar crown. The crown, used for feeding and respiration, with each radiole bearing rows of paired ciliated pinnules, is a distinct feature of serpulids (and sabellids). The radioles are attached to paired lobes located laterally on both sides of the mouth. The bases of the radioles in some serpulids are joined by an **inter-radiolar membrane** (e.g., Fig. 15D). Such a membrane is always absent in spirorbins.

In all spirorbins and most small remaining serpulids, radioles are arranged in two semi-circles when in feeding position outside the tube. Spiralled radiolar arrangement occurs when the ventral margins of the radiolar lobe continue to grow, adding radioles and spiralling along the inner margin of the crown. In some large serpulids, especially in the large species of the genus *Spirobranchus,* the crown is a pair of beautiful spiralled cones.

The operculum. A modification of the distal part of a radiole, the **operculum**, serving as a tube plug, is present in most serpulids and always in spirorbins. Some serpulid taxa are non-operculate, e.g., *Protula* (Fig. 13C), although normally operculate genera may include non-operculate species (e.g., *Spirobranchus*) and normally non-operculate genera may include operculate species (*Protis*). The opercular structure has been considered one of the most important taxonomic characters.

In non-spirorbin serpulids and all tube-brooding spirorbins, opercular structure remains essentially the same throughout adult life. Opercular structure varies from soft vesicular (e.g., *Apomatus*, Fig. 1C, Pl. 1G, *Protis*, Fig. 12B, D) or spoon-shaped (e.g., *Filograna*, Fig. 6D, E) to very elaborate. The operculum mostly consists of a basal bulbous part (**ampulla**) and a distal part often reinforced with chitinous **endplates**. The chitinous endplates may be additionally reinforced by calcareous deposits, sometimes with non-movable spines (e.g., *Spirobranchus,* Fig. 15C, Pl. 1H). In the genus *Metavermilia* a range of opercular shapes is found, from a soft spherical to a complex multi-tiered chitinous structure. The funnel-shaped opercula of *Hydroides* (Fig. 8D, Pl. 1B) and *Serpula* (Fig. 14C) are composed of numerous **radii** and covered with a thickened **cuticle**. While the operculum in *Serpula* is a simple funnel, it is armed with a distal **verticil** of chitinous **spines** in *Hydroides*.

In tube-brooding spirorbins the operculum usually consists of a calcified **endplate** with smooth surface and its outgrowth (**talon**) is directed inside the opercular ampulla (often poorly expressed), sometimes continuing into the opercular peduncle. The talon shape is often species-specific. Only several species of the subfamily Spirorbinae have non-calcified endplates or lack talons.

In operculum-incubating spirorbins of the tribes Pileolariini and Januini the opercular structure changes throughout adult life. The structure of the **primary operculum** before the **brood chamber** formation is the same in that of tube-incubating groups. But as the brood chamber develops, the opercular structure may change significantly (e.g., Fig. 30B-H).

In most Pileolariini genera, the primary operculum is separated from the brood chamber soon after the formation is completed. Brood chambers vary from open nest-like structures (e.g., *Nidificaria* Knight-Jones P., 1984) to closed deep invaginations completely covering the embryos with a pore that may open for embryos penetration and larvae release (e.g., *Pileolaria* (Fig. 30D-H), *Protoleodora* (Fig. 32C-F), and *Bushiella* (e.g., Fig. 25B, C). In *Protoleodora* the primary operculum remains attached to the distal part of the brood chamber only with the distal talon end (e.g., Fig. 31E, F) and is easily separated (e.g., Fig. 31G). In *Bushiella* the brood chamber is closely associated with the primary operculum to which it remains connected. Normally the endplate of the primary operculum is completely fused with the distal part of the chamber (e.g., Fig. 24C) and the talon is fused with the lateral chamber wall on the side facing outside the radiolar crown. In some species of *Bushiella* the primary operculum attaches to the lateral wall of the chamber by the talon only, so that some small space remains between the distal endplate of the primary operculum and the distal plate of the opercular chamber (e.g., Fig. 25B, C).

Most Januini species have cylindrical cuticular brood chambers with slightly calcified semitransparent walls. The talon is completely fused with the first brood chamber, thus, the talon is attached to the lateral wall of the brood chamber facing away from the radiolar crown (Fig. 21C). By the time the embryos leave, the chamber separates from the operculum (e.g., see Okuda, 1934, Fig. 10; Knight-Jones P. et al., 1979, Fig. 4C(a)). The distal part of the next chamber becomes the basal part of the previous, which does not form its own talon (Fig. 21D-G) in most species.

The non-spirorbin genera *Hydroides* (Fig. 8C, Pl. 1B) and *Serpula* (Fig. 14B) are characterized by a **pseudoperculum**, a club-shaped underdeveloped operculum carried on a short rudimentary radiole on the side of the radiolar crown opposite the operculum.

The pseudoperculum can develop into a functional operculum if the latter is shed or lost. Sometimes, two functional opercula can be found simultaneously, or some taxa from that group may have two rudimentary opercula only.

The opercular peduncle. In some genera the radiole that bears the operculum is identical to other radioles, e.g., *Filograna* (Fig. 6E), *Apomatus* (Fig. 1C), and *Protis* (Fig. 12D). In most other serpulids (Fig. 9 C, 10 D) and in all spirorbins (e.g., Fig. 23B) the operculum is borne on a distinct **peduncle**, a modified thickened radiole **lacking pinnules**. One of the notable exceptions is the genus *Hyalopomatus*, with the peduncle as wide as the normal radioles (Fig. 7C, F). The peduncle may gradually merge into the basal opercular ampulla (Fig. 5D), or be separated from it by a **constriction** (e.g., Fig. 2B, 3D). In cross-section, the opercular peduncle is most often cylindrical, but it is nearly triangular in some non-spirorbin genera (e.g., *Spirobranchus*). The genus *Metavermilia* has a very characteristic flat ribbon-like peduncle (Fig. 9C).

The peduncle in non-spirorbins is usually inserted more or less below and between the first and second normal radioles, outside the line of radioles. It may be also located at the base of radiolar crown, covering several radioles, or be positioned as the second modified radiole (e.g., *Metavermilia*). In spirorbins the operculum-bearing radiole normally is located inside the radiolar crown, except for *Protoleodora,* where it is positioned outside the crown.

Below the operculum, the peduncle may be modified to form **distal wings,** e.g., *Spirobranchus* (Fig. 15D). It is unclear whether small latero-dorsal distal "winglets" found on the peduncle of some other non-spirorbin genera (e.g., *Dasynema*, *Neovermilia*) and spirorbin *Helicosiphon platyspira* Knight-Jones P., 1978 (=*Knightjonesia platyspira sensu* Pillai, 2009a) are homologous to the larger wings described above or are caused by flattening of the peduncle.

The collar and the thoracic membranes. The base of the radiolar crown is surrounded by a membranous peristomial **collar.** Spirorbin taxonomists (e.g., Knight-Jones P. & Knight-Jones E.W., 1977) did not distinguish between the thoracic membranes and the collar, but used the term "collar" probably collectively for both.

In spirorbins and some other serpulids the collar is non-lobed, but in most non-spirorbins it is trilobed, that is, sub-divided into one medio-ventral and two latero-dorsal lobes (e.g., Fig. 7C, 9B, 12C, 13C). The medio-ventral lobe may have an additional incision(s), thus making the collar quadrilobed or pentalobed. Small tongue-shaped outgrowths, the **tonguelets**, located between the dorso-lateral and ventral lobes of the collar are present in e.g., *Spirobranchus*. In some spirorbins the collar may form a large lateral flap on the convex body side (e.g., *Spirorbis (S.) spirorbis*, Fig. 34B, 36C). The collar chaetiger lacks neuropodial uncini and bears only notopodial **collar chaetae**. These collar chaetae are absent e.g., in *Ditrupa*, *Placostegus*, and some *Spirobranchus*.

The latero-dorsal collar lobes continue into the **thoracic membranes** that may end at the first or the second thoracic chaetiger (e.g., *Chitinopoma serrula*, Fig. 4C), reach the mid-thorax (e.g., *Vermiliopsis*), or continue throughout the length of the thorax and end posterior to the last thoracic chaetiger (e.g., *Protis arctica*, Fig. 12B, C). Thoracic membranes continuing past the end of the thorax often fuse ventrally over the first abdominal segment(s), forming the **apron,** e.g., *Serpula* (Fig. 14B), *Hydroides* (Fig. 8C), *Protula* (Fig. 13C), and *Spirobranchus* (Fig. 15D). In non-spirorbin genera, margins of thoracic membranes are fused dorsally only in *Ficopomatus uschakovi.*

In spirorbins collar and thoracic membranes are usually with free dorsal (the side facing the substrate) margins, e.g., Fig. 23B, 31C, but may be completely or partially fused, e.g., in *Neodexiospira*, see Knight-Jones P. et al., 1979, fig. 4C(a). Species with fused collar and thoracic membranes are unknown from the Arctic. Normally the thoracic membranes are slightly asymmetrical, continueing to the last thoracic segment and fusing ventrally to form the apron, but in *Protoleodora* the thoracic membranes on the convex body side may continue to the end of achaetigerous zone and even beyond the abdominal segments (Fig. 31C, 32B).

The thorax. The number of thoracic chaetigers is fairly constant in most taxa and traditionally constitutes an important taxonomic character. In most non-spirorbin genera, the thorax of adults consists of 7 thoracic chaetigerous segments (including the collar segment). Some taxa have 5–6, 9 or even more chaetigerous segments as adults. A variable number of thoracic chaetigers is e.g., known in *Filograna* (6–12). Some genera with an otherwise fixed number of thoracic segments (7) occasionally have species with a variable number of thoracic segments (e. g., *Serpula*, *Hydroides*).

Spirorbins usually have only 3 or 4 thoracic chaetigerous segments (including the collar segment). Rarely species with a 4-segment thorax as adults (e.g., *Paradexiospira*) may have only 3 thoracic segments as juveniles. *Amplicaria* and *Anomalorbis* have 5 chaetigers, whereas *Neomicrorbis*, a questionable spirorbin, has up to 7 thoracic segments (Kupriyanova unpubl.). All Arctic species have 3 or 4 thoracic chaetigers.

Thoracic chaetae. The inconsistency in terminology relating to the structure of serpulid chaetae (not including spirorbins) has been discussed by ten Hove & Kupriyanova (2009), who pointed out the importance of SEM observations in revealing true chaetal structure. Spirorbin chaetal morphology using the SEM was studied by Knight-Jones P. & Fordy (1979).

Thoracic chaetigers normally bear chaetae termed limbate and capillary. Limbate chaetae are comparatively larger and are subdivided into the basal shaft and the “blade” (limbus) that might be slightly bent relative to the shaft axis; the basal part of the limbus is wider than the shaft and it gradually narrows distally. Capillary chaetae are smaller than limbate, they gradually narrow distally and are not subdivided into the shaft and the blade. SEM examination shows that the “blade” of limbate chaetae is made of numerous microfibres (e.g., Fig. 2C). Moreover, capillary chaetae have a small limbus not visible under a light microscope. It is unclear whether capillary chaetae are underdeveloped limbate chaetae as suggested by Hove & Kupriyanova (2009) or a separate type of chaetae. In spirorbins capillary chaetae (also termed **companion capillary** chaetae) are present in the collar fascicle only, while in non-spirorbin serpulids, they are probably found in all thoracic chaetigers. Thus, here we keep limbate and capillary chaetae separate.

The fascicle of serpulid collar chaetae may contain only limbate and capillary chaetae (e.g., *Bathyvermilia* spp., *Protula* spp., *Protoleodora* spp., subgenus *Bushiella*). In non-spirorbin genera collar chaetae may include a range of modified chaetae in addition to limbate and capillary ones. Here we use the term **large collar chaetae** to distinguish limbate and modified chaetae from capillary chaetae in a collar fascicle. Ten Hove & Kupriyanova (2009) distinguish four types of modifications found in these chaetae. The first three are **basal modifications** characterized by the presence of a more-or-less distinct extension below the distal blade:

1) Bayonet-type chaetae have only one or two (rarely more) large proximal bosses at the base of the distal blade (e.g., *Serpula*, Fig. 14D, *Hydroides,* Fig. 8E, F);

2) Fin-and-blade chaetae have the basal "fin" (the term is a result of initial observations under a light microscope and incorrectly assumes a structure as flat as a fish fin) made of relatively few teeth of intermediate size; the "fin" can be separated by a distinct smooth gap from the distal blade (e.g., *Chitinopoma* Fig. 4E, *Protis,* Fig. 11C);

3) *Spirobranchus*-type chaetae have a proximal "fin" consisting of very numerous tiny hair-like spines (e.g., *Spirobranchus,* see ten Hove & Kupriyanova, 2009, Fig. 47A);

The fourth type is the **distal modification** found in ***Ficopomatus*-type** collar chaetae (*Ficopomatus* only) that are characterized by very coarse curved teeth alongside the distal part of chaetae (ten Hove & Kupriyanova, 2009, Fig. 16A).

Most spirorbin species have only modified chaetae replacing limbate ones in the collar segment. Both basal and distal types of modifications may be found on the same modified collar chaeta. Three types of spirorbin modified collar chaetae can be distinguished. Chaetae with basal only modification include:

1) Fin-and-blade (e.g., *Spirorbis,* Fig. 33F, G) are the same as fin-and-blade chaetae of other serpulids, with a distinct basal fin clearly separated from the limbate blade.

With distal only modification include:

2) Cross-striated chaetae found only in spirorbins (e.g., *Paradexiospira* (*P.*) *violacea* (Levinsen, 1884), Fig. 18D), *Neodexiospira pseudocorrugata* (Bush, 1905)). The blades of these chaetae are bent and have denticles organized into distinct long transverse rows; under a compound microscope this looks like a cross-striation. Collar chaetae on the convex body side are usually larger and with larger denticles on the blades. Cross-striation may be vestigial, when rows are short, with 3-4 denticles per row (e.g., *Neodexiospira lamellosa* (Lamarck, 1818) and asymmetrical, when the rows are present only on the one "lateral side" of chaetal blade (e.g., *Circeis spirillum* (Fig. 17F). Unusual modified strongly bent collar chaetae (Fig. 16G, H) of some *Circeis* spp. (e.g., *Circeis armoricana*) appear to bear vestigial cross-striation on the "frontal side" of the blade only (not visible laterally under a dissecting microscope) and probably represent just a variation of cross-striated chaetal type (see Knight-Jones P. & Fordy, 1979, fig. 11).

Chaetae with both distal and basal modifications include:

3) Fin-and-blade cross-striated chaetae have a combination of cross-striated blade separated from a basal denticulate fin by a smooth gap. Cross-striation may be distinct (e.g., *Pileolaria* ex gr. *berkeleyana* (Fig. 30I), *Paradexiospira* (*Spirorbides*) *vitrea* (Fig. 20F.)), or vestigial (e.g., *Pileolaria heteropoma* (Zibrowius, 1968a), *Bushiella* (*Jugaria*) *atlantica* Knight-Jones P., 1978).

Generally, spirorbins have the same types of collar chaetae in fascicles on both body sides, although the modified chaetae from the concave and convex sides of the body may differ in size, length of the gap between the fin and the blade, and the degree of cross-striation development. The collar chaetae of some species may be modified fin-and-blade (e.g., *Spirorbis* (*S.*) *tridentatus,* Fig. 37F) or cross-striated (e.g. *N. pseudocorrugata*), only on the convex side of the body while they are limbate on the concave side (Fig. 37G). In *Eulaeospira* spp. chaetae of different types (limbate and fin-and-blade) may be present in the same fascicle.

Modified chaetae of the posterior thorax supplementing limbate chaetae (if present) usually start from the third segment (e.g., Fig. 2D, 6G). These chaetae, termed ***"Apomatus"* chaetae** (or **sickle chaetae** in spirorbins, e.g., Fig. 20G), are sigmoid to sickle-shaped with a proximal denticulate zone (looking like fine striation under a compound microscope) and a long flat curved blade with a row of blunt regular teeth distally. Exceptionally, these chaetae are found in the collar fascicle (*Apomatus voightae* Kupriyanova & Nishi 2010) The sickle ("*Apomatus*") chaetae are absent in some spirorbins (e.g., *Circeis* spp., *Neodexiospira* spp.), while only sickle chaetae are present in the 3rd fascicle in *Paradexiospira* spp.

Thoracic uncini. Uncini are flattened comb-shaped chaetae with a number of curved teeth on their edge. Depending on the number of vertical rows of teeth in the uncini, they are termed **saw-shaped** (one row of teeth along the edge), **saw-to-rasp-shaped** (from one tooth on edge distally to a row of up to five teeth proximally near the peg), or **rasp-shaped** (several rows of teeth along the entire edge). Juvenile specimens of otherwise "saw-shaped" species may show rasp-shaped uncini and the shape of the uncini may change from saw-shaped in the anterior thorax to rasp-shaped posteriorly.

The shape of the anterior tooth of uncini is usually referred to in earlier publications as either simple or bifurcate. However, SEM examinations reveal that ultrastructure of the anterior tooth is very variable. A pointed anterior tooth is termed **fang** in serpulid genera such as e.g., *Filograna* (Fig. 6H), *Hydroides* (Fig. 8I), *Serpula* (Fig. 14F) and spirorbins of the tribe Pileolariini. However, what under a compound microscope appears to be a bifurcate tooth is in fact a gouged structure, bluntly truncate flattened with lateral edges curved underneath. For all blunt "wedge"-shaped, not acute, anterior teeth the collective term **peg** is used.

The uncini of serpulids are arranged side by side in a single row in a torus, transverse relative to the long axis of the body, with the dentate distal edge of the uncini directed anteriorly. Thoracic tori generally are positioned along the lateral side of the thorax, but in some taxa they are widely separated in front, gradually approaching one another posteriorly, so that the posterior thoracic tori may touch each other, forming a **triangular depression** ventrally.

The abdomen. The number of abdominal segments is very variable depending on size of the animal; it can be as low as 10-30 in spirorbins and other small serpulids, or up to over 200 segments in large species. Several anterior abdominal segments may lack chaetae and uncini, forming an **achaetous abdominal zone**. An abdominal segment bears a dorsal uncinigerous torus and a ventral fascicle of chaetae. A glandular zone on the dorsal side of the last abdominal segments in serpulids called the **glandular pad** might be involved in forming tabulae, closing off damaged posterior tube parts. The pygidium is usually bilobed and bears a terminal slit-like anus.

Abdominal chaetae. In serpulids the simplest forms of abdominal chaetae are capillary or nearly capillary. The term "trumpet-shaped chaetae", commonly used by various authors to describe the abdominal chaetae in e.g., *Hydroides,* Fig. 8G and *Serpula* Fig. 14E) is misleading (ten Hove & Kupriyanova, 2009). Although the distal parts of these chaetae, when examined under a compound microscope, are widened into what in profile looks like a chalice or trumpet with apparently two rows of thin teeth on edge; examination with SEM shows that these chaetae are not hollow, but flat, with a single row of teeth (see ten Hove & Kupriyanova, 2009, fig. 46D). Therefore, they are termed **flat trumpet-shaped** chaetae by ten Hove & Kupriyanova (2009). **True trumpet-shaped** chaetae, (e.g., in *Placostegus* and *Spirobranchus*) are distally hollow, with two parallel rows of sharp denticles, extending into a long lateral spine (see ten Hove & Kupriyanova, 2009, Fig. 47D).

In older literature serpulid abdominal chaetae are often referred to as "geniculate", the term generally defined in dictionaries as "having a knee-like joint" or "bent sharply". The term is misleading because there is no joint between the proximal and distal part of the chaetae and not all of them are bent. Because it is hard to see with a compound microscope whether such chaetae have a single or double row of teeth bordering the blade, true trumpet-shaped chaetae have been lumped together with the completely different **flat geniculate** abdominal chaetae (see ten Hove & Kupriyanova, 2009). The latter possess a capillary shaft and a flat blade with a single row of rounded to sharp denticles along its edge. The following types of flat geniculate chaetae are distinguished:

1) Sickle-shaped: fairly straight to weakly sickle-shaped abdominal chaeta with long concave edge bordered by very regular rounded teeth (typical for *Apomatus* and *Protula,* see ten Hove & Kupriyanova, 2009*,* fig. 8E and 39B respectively).

2) Flat triangular, with a knee-like bend and with dentition on the outside of a wide triangular distal blade (e.g., *Chitinopoma,* Fig. 4F);

3) Flat narrow geniculate, as 2), but with more elongated not so sharply bent blade (e.g., *Bathyvermilia*, Fig. 2E);

Spirorbin abdominal chaetae are **flat geniculate** only, usually sharply bent with denticulate blade, 1-2 (up to 10) per fascicle. The basal part of the blade may extend beyond the shaft of the chaeta forming a **heel**. Three main types of spirorbin abdominal chaetae (can be considered as sub-types of flat triangular) are:

1) Brush-type chaetae with very short sharply narrowing blades and around 10 denticles (typical for Romanchellini, see Knight-Jones P. & Fordy, fig. 68E-G).

2) Wide-bladed chaetae with large wide blades that are of the same width along its entire length and sharply narrowing only at the distal end; heel absent or vestigial (typical for Januini, Fig. 21J).

3) Pennant-shaped chaetae with the blade of the intermediate length gradually narrowing towards the distal end (Spirorbinae, Circeini, Paralaeospirini, and Pileolariini, as a rule with a heel, e.g., Fig. 16I).

In most serpulids abdominal chaetae usually become progressively longer posteriorly, and the most posterior chaetae are capillaries or elongated modified chaetae. If capillary, chaetae of the most posterior abdominal segments are at least an order of magnitude longer than those of anterior and middle abdominal segments, they are referred to as "long capillary chaetae". In spirorbins **companion capillary hooked** chaetae (e.g., Fig. 22 F) may be present in addition to flat geniculate chaetae on all abdominal chaetigers or only posteriorly. Long capillary chaetae are absent in spirorbins.

Abdominal uncini. In non-spirorbins saw- and/or rasp-shaped uncini vary according to their position. Rasp-shaped uncini are always found in the most posterior segments. Since polychaetes grow by addition of segments posteriorly, serpulids can shed their juvenile rasp-shaped uncini and replace them with saw-shaped adult uncini as they grow. Thus, juveniles always have rasp-shaped uncini.

In all spirorbins abdominal uncini are rasp-shaped with flat or slightly rounded anterior peg (Fig. 32J). Uncini may be either fairly symmetrically distributed along both body sides, as in Spirorbini, Januini and Pileolariini, or their distribution may be sharply asymmetrical as seen in Circeini, Paralaeospirini, and Romanchellini. In the latter group, abdominal uncini on the convex body side are absent or very few only on 2-3 posterior abdominal segments.

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.

companion capillary hooked chaeta: capillary chaetae with curved tip which may accompanying abdominal flat geniculate chaetae in all chaetigers or posteriorly only (e.g., Fig. 22F).

constriction: narrowing of the opercular peduncle or a transverse groove, at basis of funnel or ampulla (e.g., Fig. 2B; 3D).

crenulated: having a margin with small, low, rounded teeth.

cross-striation of collar chaetae: rows of denticles on blades of modified collar chaetae blades that look like transverse lines under a compound light microscope (e.g., Fig. 17F; 19D).

crown of brood chamber: thin-walled circular rim surrounding distal part of opercular brood chamber, entire or consisting of petals (Fig. 31C, G).

crystalline patches: in spirorbins iridescent crystalline spots (red, pink, purple) located dorsally on middle-posterior part of thorax and anterior part of achaetigerous zone (Pl. 2 C); likely not epithelial pigments, but a secretion of some glands because they are located on the epithelium and can be easily removed by a preparation needle. Normally maintaining their colour after fixation, though sometimes changing to dark brown or almost black.

cuticle: thin, non-cellular protective layer produced by, and overlying, the epidermis; probably not chitinous but consisting of scleroprotein.

dentate: toothed, see **denticulate**.

denticulate: with small teeth, see **dentate**.

distal wings: paired lateral outgrowths of the peduncle located just below the operculum (Fig. 15D).

eccentric: to one side of the centre; referring to the talon in spirorbins, located between the centre and the periphery.

entire edge (margin): smooth edged, without projections.

fang: sharply pointed anterior tooth of uncinus (e.g., Fig. 2F; 6H; 11E).

filamentous: shaped like a filament or fine thread.

filiform: thread-like, very slender.

fin: basal extension of modified collar chaetae made of relatively few teeth of intermediate size; originally assumed flat as a fish fin (hence the name) as seen under a compound microscope (e.g., Fig. 4E; 12E; 19D).

fin-and-blade chaeta: collar chaeta with basal "fin" more or less separated by a toothless zone (a gap) from the distal blade (e.g., Fig. 4E; 6F; 19D; 20F).

flat trumpet-shaped chaeta: chaeta with a thin, flat distal part with small teeth on its edge (Fig. 8G; 14E).

funnel: descriptive term used to indicate the inverted cone-like proximal part of the operculum in *Hydroides* (Fig. 8D) and the entire operculum in *Serpula* (Fig. 14C).

geniculate: "having a knee-like joint" or "bent sharply"; traditionally used in serpulids for a variety of abdominal chaetae, redefined on p. 15.

glandular pad: glandular zone on the dorsal side of the last abdominal segments in some serpulids.

heel: projection beyond the chaetal shaft of the blade of an abdominal chaeta (e.g., Fig. 16I; 18F).

inter-radiolar membrane: thin membrane connecting basal parts of radioles in some Serpulidae.

keel: longitudinal ridge running along the tube length (termed longitudinal ridge in older spirorbid literature, e.g., Fig. 11A; 15A, B; 22A; 24A).

lappet: lobe or flap-like projection.

large collar chaetae: name used for both **limbate** and **modified** collar chaetae.

limbate chaetae: stiff, elongate, pointed chaetae made of densely packed fibrils; under a compound microscope they seem to have a distal limbus or flat blade, which on inspection with SEM is an outer layer where the fibrils are packed less tightly than in the central shaft.

limbus: seemingly flattened distal border of chaetae, longitudinal flange, however, see **limbate chaetae**.

modified collar chaetae: collar chaetae with any modification such as basal **fin**, proximal **boss**, **cross-striation** as compared to **limbate chaetae.**

mouth: anterior opening of the alimentary canal; in serpulids also used for the anterior opening of the tube.

mouth palp: filiform projections of the dorsal lip of the Sabellida mouth.

neurochaeta: chaeta of a neuropodium.

neuropodium (*pl.* neuropodia): ventral branch of a parapodium.

notochaeta: chaeta of a notopodium.

notopodium (*pl.* notopodia): dorsal branch of a parapodium.

ocellar clusters: loose groupings of approximately 2–20 ocelli, generally with as many lenses.

operculum (*pl.* opercula): tip of modified radiole used to plug the tube when the worm is retracted (e. g., Fig. 2B; 12D; 14C; 15C).

opercular endplate (plate): terminal reinforcement of opercular ampulla, usually chitinous (e.g., Fig. 10D) or calcareous (e.g., Fig 2B).

opercular frontal view: in spirorbins, operculum as seen from the side of the talon location (from the convex side of the thorax; e.g., Fig. 16C, E, F; 21B; 27D; 30B, E, F; 33D).

opercular lateral view: in spirorbins, operculum as seen from the side perpendicular to the frontal view (from the side opposite to substrate or from the side of substrate; e.g., Fig. 16D; 21C-G; 27C; 30G, H; 33C).

parapodium (*pl.* parapodia): fleshy lateral projection from a body segment that usually bears chaetae.

pectinate: comb-like; with series of projections like the teeth of a comb. An arrangement of radioles in serpulids.

peduncle: modified radiole lacking pinnules and bearing the operculum (e.g., Fig. 9C; 10D).

peg: wedge shaped, not sharply pointed anterior tooth of uncinus (e.g., Fig. 4G; 5E, F; 7H).

pennant-shaped chaetae: flat geniculate abdominal chaetae in spirorbins with blade of intermediate length that gradually narrows towards the distal end (e.g., Fig. 16I; 16F).

peripheral flange: flattened area spreading over the substrate at the attachment of the tube; increases the surface for attachment (e.g., Fig. 3A; 34A).

peristome: collar-like widening of tube (former tube-mouth).

peristomium: pre-segmental region of the body surrounding the mouth.

petal: a lobe of a brood chamber crown in spirorbins of genus *Protoleodora* (Fig. 31C, G).

pinnules: small paired side branches of the radioles, giving each radiole a feathery appearance.

planospiral: having the tube coiled in one plane (e.g., Fig. 16A).

primary operculum: in spirorbins Pileolariini and Januini where embryo incubation is associated with the operculum, the latter before development of the brood chamber; in the genus *Hydroides* the first operculum in ontogeny, a one-tier funnel as typical for the genus *Serpula* (see ten Hove & Ben-Eliahu, 2005, p. 128).

prostomium: anterior-most, pre-segmental region of body, bearing the radioles and sometimes eyes.

pseudoperculum (*pl.* pseudopercula): underdeveloped operculum on modified radiole (usually the second dorsal one), generally shortened and without pinnules in *Hydroides* (Fig. 8C) and *Serpula* (Fig. 14B); can develop into a new functional operculum when the latter is lost.

pygidium: post-segmental terminal body-part surrounding the anus.

radiolar crown: a usually bilaterally symmetrical branched structure consisting of two separate lobes, each with a number of radioles bearing pinnules; often including an operculum with peduncle on one lobe and sometimes also a pseudoperculum on the opposite lobe.

radioles: pinnulate filaments of radiolar crown, used for respiration and feeding.

radius (pl. radii): radial projection of the funnel in *Serpula* and *Hydroides*.

rasp-shaped uncinus: with two or more rows of teeth (e.g., Fig. 2G; 11F)

saw-shaped uncinus: with only one row of teeth (e.g., Fig. 2F; 11E).

segment: one of the serially repeated units comprising the trunk; often separated internally by septa or dissepiments.

shaft: proximal hair-like part of a chaeta.

sickle chaeta: a recurved abdominal chaeta with tiny dentition on the inside of the curve (e.g., Fig. 20G). N.B. used in spirorbin literature for thoracic *Apomatus* chaetae.

spinule: each of the tubercular or tooth-like projections of a spine in the verticil of the genus *Hydroides*.

***Spirobranchus*-type chaeta:** bayonet-like collar chaeta with a proximal fin consisting of very numerous tiny hair-like spines (see ten Hove & Kupriyanova, 2009, fig. 47A).

tabulae: transverse internal tube elements partitioning off the oldest parts of the tube, generally as response to tube damage.

talon: outgrowth of the opercular plate, directed inside the opercular peduncle (e.g., Fig. 17C, D; 21 B, C; 22B, C; 30B, C; 36D, E). Distal part of talon is the part situated farthest from the endplate.

thoracic membranes: thin folds on both sides of thorax, extending from dorsal part of collar to lateral and/or ventral side of posterior thorax (e. g., Fig. 13C; 15D). **N.B**. Thoracic membranes have been included in the term collar by some spirorbin taxonomists.

thorax: anterior region of the body behind the head.

tonguelet: lappet located between dorso-lateral and ventral lobes of the collar in, e.g., *Spirobranchus*.

torus (*pl.* tori): transverse elevation of parapodium surrounding the uncini.

transversal ridge: annular elevation of tube, less pronounced than peristome.

triangular depression: area between thoracic uncinigerous tori when gradually approaching and almost touching one another posteriorly and ventrally.

trumpet chaetae: abdominal chaetae in e.g., *Serpula*, *Hydroides*, formerly thought to be hollow; however, more recently proven to be flat, not hollow. See preferred term **flat trumpet-shaped** chaetae.

true trumpet-shaped chaetae: distally hollow chaetae, with two parallel rows of sharp denticles, extending into a long lateral spine (Fig. 10F; 15F, see ten Hove & Kupriyanova, 2009, fig. 47D).

unciniger: segment carrying uncini.

uncinus (*pl.* uncini): deeply embedded comb-shaped chaeta with only its dentate edge protruding from the body wall; uncini usually arranged in tori, elevated rows transverse to the axis of the animal (e.g., Fig. 8H; 9F; 13E; 15G).

unsculptured tube: usually circular in cross-section not bearing any sculptural elements such as keels, ridges, alveoli, or spines (e.g., Fig. 16A). In spirorbin literature are often called "smooth".

verticil: distal part of operculum in *Hydroides* usually made of chitinous spines (Fig. 8D).

verticil spine: any of the radial elements, generally around a central disc, together forming the verticil in *Hydroides* (Fig. 8D).

wide-bladed chaetae: flat geniculate abdominal chaetae in spirorbins with large wide blades that are of the same width along its entire length and sharply narrowing only at the distal end (Fig. 21J).

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)

11a) Tubes pinkish (Pl. 1A); wide distal peristomes usually present; several low denticulate keels sometimes present in proximal tube part (Fig. 14A) .... ***Serpula vermicularis*** (p. 63)
11b) Tubes white or greyish, ring-shaped thickenings (not peristomes directed towards tube mouth) sometimes present **12**

12a) Growth rings wavy, tubes white, usually attached to the substrate throughout its length; distinct tube collars always absent, two indistinct keels present (Fig. 8B) .... ***Hydroides norvegicus*** (p. 46)
12b) Growth rings straight; attached to substrate only by proximal end, distal end free; tube collars sometimes present, no keels **13**

13a) Tube surface with poorly expressed "honeycombed" structure (Fig. 1A, B) .... ***Apomatus globifer*** (p. 26)
13b) Tube surface without "honeycombed" structure .... ***Protis arctica*** (Fig. 12A), ***Protula tubularia*** (Fig. 13A) (pp. 56, 60)

Key to non-spirorbins based on specimen morphology

1a) Operculum may be absent or present, inserted on normal unmodified radiole **2**
1b) Operculum present (when accidentally lost, place of its insertion usually obvious) on smooth, non-pinnulate peduncle **6**

2a) Two equally developed spoon-shaped membranous opercula (Fig. 6D, E); worms small (up to 6 mm). Forming pseudo-colonies of greyish/whitish tubes (Fig. 6A, B) .... ***Filograna implexa*** (p. 40)
2b) Operculum absent or one (rarely more) membranous, globular transparent operculum. Worms larger (up to 60 mm), not colonial (aggregates may occasionally occur) **3**

3a) Thoracic membranes ending at 4th – 7th thoracic segment, no ventral apron; large collar chaetae modified fin-and-blade in addition to limbate ones; thoracic uncini with up to 7 teeth in one row **4**
3b) Thoracic membranes forming ventral apron; large collar chaetae limbate only; thoracic uncini with more than 15 teeth in several rows **5**

4a) Six thoracic chaetigerous segments, 5 of which with uncini, thoracic membranes ending at 4th segment (Fig. 11B) .... ***Protis akvaplani*** (p. 54)
4b) Seven thoracic chaetigerous segments, 6 of which with uncini, thoracic membranes ending at 7th segment (Fig. 12B, C) .... ***Protis arctica*** (p. 56)

5a) Collar entire, not divided into lobes; thoracic neuropodial uncinigerous tori several times longer than abdominal notopodial uncinigerous tori (Fig. 1E) .... ***Apomatus globifer*** (p. 26)
5b) Collar trilobed; length of thoracic uncinigerous neuropodial tori similar to that of abdominal uncinigerous notopodial tori (Fig. 13C) .... ***Protula tubularia*** (p. 60)

6a) Collar chaetae absent (N.B. first chaetiger with both chaetae and uncini) **7**
6b) Collar chaetae (not accompanied by uncini) present **8**

7a) First and second pairs of thoracic neuropodia widely separated laterally (Fig. 5C) .... ***Ditrupa arietina*** (p. 37)
7b) First and second pairs of thoracic neuropodia not widely separated laterally (Fig. 10C) .... ***Placostegus tridentatus*** (p. 52)

8a) Six thoracic chaetigers (including collar chaetae); operculum pear-shaped, membranous, without end plate (Fig. 7F, C) .... ***Hyalopomatus claparedii*** (p. 44)
8b) Seven thoracic chaetigers (including collar chaetae); operculum at least partly calcified or chitinized **9**

9a) Pseudoperculum present; operculum composed of shallow funnel of fused radii with or without distal verticil of chitinized spines **10**
9b) Pseudoperculum absent; operculum inverted cone with chitinous or calcareous endplate **11**

10a) Operculum as funnel only, without distal verticil of chitinized spines (Fig. 14C) .. .. ***Serpula vermicularis*** (p. 63)
10b) Operculum made of basal funnel with distal verticil of chitinized spines (Fig. 8D) .. .. ***Hydroides norvegicus*** (p. 46)

11a) Peduncle with distal wings, very thick, triangular in cross section; operculum with calcified endplate often bearing three horns (Fig. 15C, D) .... ***Spirobranchus triqueter*** (p. 66)
11b) Peduncle without distal wings, cylindrical or flat **12**

12a) Peduncle flat, ribbon-like, with regular annulations (Fig. 9C); large collar chaetae limbate only (Fig. 9D) .... ***Metavermilia arctica*** (p. 49)
12b) Peduncle cylindrical, smooth, without regular annulations; large collar chaetae limbate only or limbate and modified fin-and-blade **13**

13a) Large collar chaetae modified fin-and-blade (Fig. 4 E) and limbate .... ***Chitinopoma serrula*** (p. 34)
13b) Large collar chaetae limbate only.. **14**

14a) Chitinous endplate not encrusted by calcareous deposits; thoracic membranes ending at 7th thoracic segments (Fig. 3C) ....***Bathyvermilia islandica*** (p. 31)
14b) Chitinous endplate encrusted by calcareous deposits (Fig. 2B); thoracic membranes ending at 3rd thoracic segments ....***Bathyvermilia eliasoni*** (p. 29)

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.

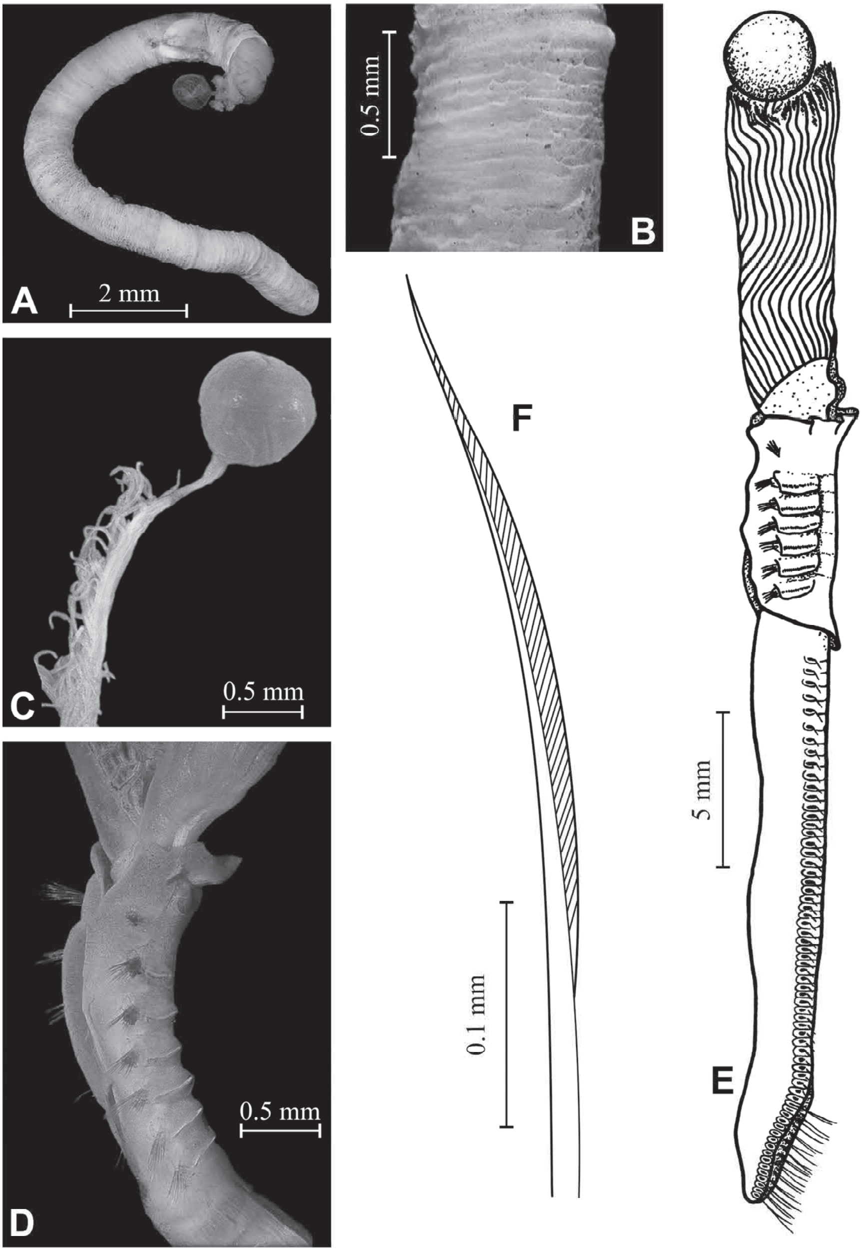

Figure 1. *Apomatus globifer*. A – animal in tube; B – tube fragment; C – operculum on pinnulated radiole; D – thorax; E – entire body, lateral view; F – limbate collar chaeta. E-F – from Kupriyanova & Jirkov (1997). A-D – photo E. Wong.

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.

Seven to ten pairs of radioles arranged into semicircles. No inter-radiolar membrane, no stylodes. Radiolar eyes unknown, not observed in preserved material**.**

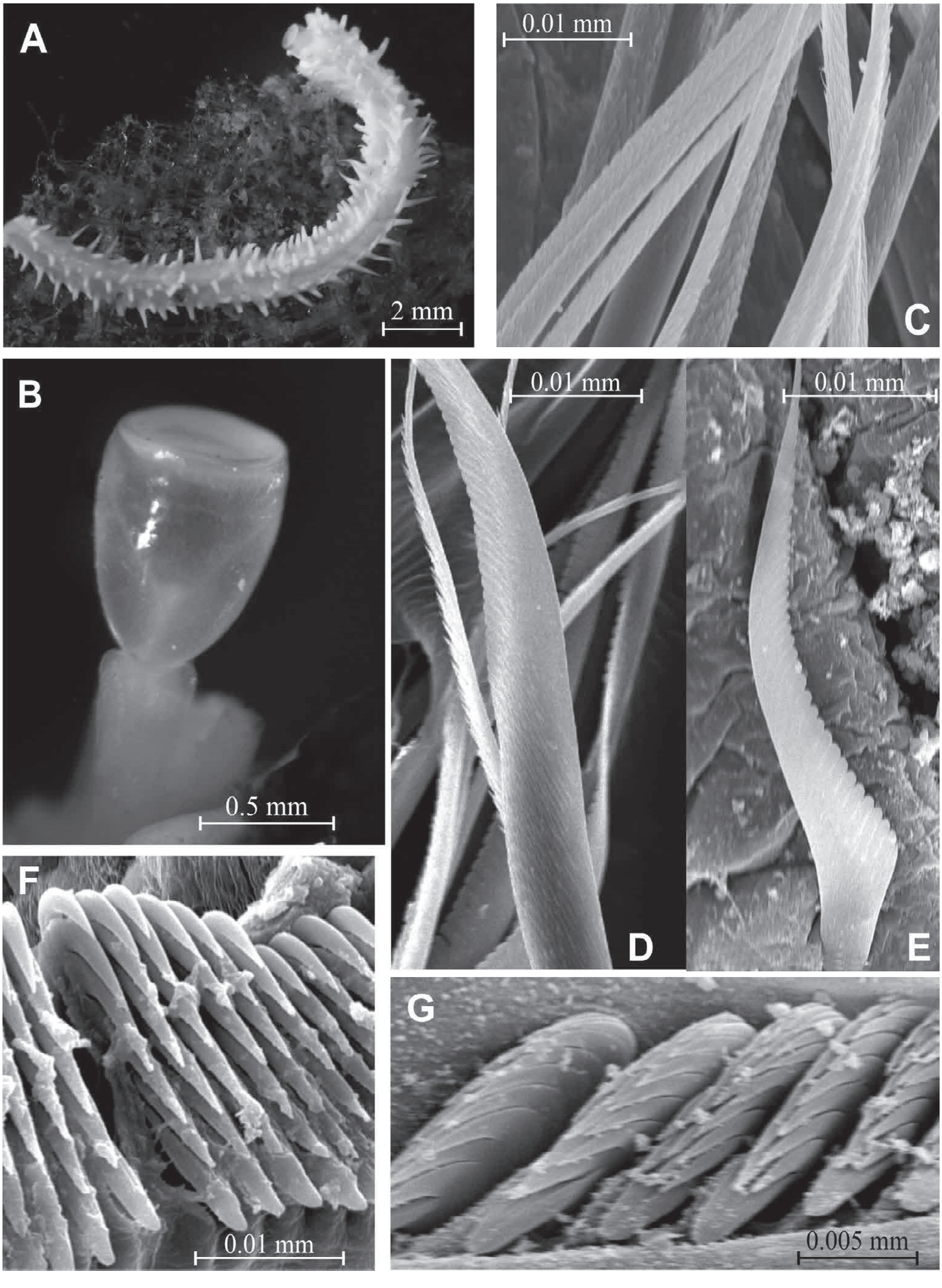

Figure 2. *Bathyvermilia eliasoni*. A – tubes; B – operculum with calcareous endplate; C – collar chaetae; D – *Apomatus* chaeta; E – abdominal chaeta; F – thoracic uncini; G – abdominal uncini. All photos from Kupriyanova & Nishi (2010).

Peduncle smooth, more or less circular in cross-section, slightly thicker than normal radioles and clearly inserted as second radiole. Deep constriction at junction of ampulla and peduncle (Fig. 2B). Operculum inverted cone with white, calcareous, slightly depressed endplate (Fig. 2B). Pseudoperculum absent.

Collar penta-lobed, with two latero-dorsal lobes and a ventral lobe divided into three lobes. Tonquelets absent. Thoracic membranes short, continuing to 3rd thoracic chaetiger. No distinct prostomium.

Thorax with seven thoracic segments, six of them with uncini. Thoracic tori slightly shifted ventrally from mid-lateral line of thorax, but distinct triangular depression absent. Collar chaetae limbate and capillary (Fig. 2C). Remaining thoracic chaetae limbate and *Apomatus* chaetae (Fig. 2D). Thoracic uncini saw-shaped with 5-6 teeth and pointed anterior fang (Fig. 2F).

Achaetous anterior abdominal zone short. Up to 60 abdominal chaetigers. Abdominal tori short. Anterior abdominal chaetae flat narrow geniculate with blunt teeth (Fig. 2E), replaced by capillary chaetae on the most posterior segments. Anterior abdominal uncini saw-shaped with 5–6 teeth and pointed anterior fangs. Uncini of middle and posterior abdominal segments rasp-shaped, with 6 teeth in profile and 2–3 teeth per row (Fig. 2G) above pointed fangs. Posterior glandular pad present.

Remarks. According to Zibrowius (1973a) who examined Southward's (1963) material identified as *V. langerhansi*, her specimens should be attributed to *V. eliasoni* (now *B. eliasoni*). This species differs from all other *Bathyvermilia* spp., including *B. islandica* from the Arctic (see below), by its very characteristic tube, lacking peristomes, but with three keels made of distinct long spines.

Ecology. In the Arctic known from 3570 m at Jesup Rise (see below). Barrier et al. (1989) provided a table summarizing depth distribution from 200-2000 m in the Mediterranean. In the Pacific (Patton-Murray Seamounts) reported from 484–1190 m on basalt (Kupriyanova & Nishi 2010). Reproduction unknown.

Distribution. In Arctic the species is known from a single record (Jesup Rise 84°5.9'N 14°24.88'E – 85°25.1' N 12°7.06' E, previously unpublished material from Senckenberg Museum, Frankfurt). Outside the Arctic reported from the North Atlantic (off England, Ireland), Mediterranean (Spain, Sicily, Portugal) and North Pacific Ocean (Patton-Murray Seamounts in Gulf of Alaska (Kupriyanova & Nishi, 2010). Another unpublished record (ten Hove, pers. comm.) comes from the Tydeman Selvagens-Canary Island Expedition, 30°03'N 15°52'W, depth 2100–2500 m, ZMA V.Pol. 4247.

Bathyvermilia islandica Sanfilippo, 2001

(Fig.3A-H)

Bathyvermilia islandica Sanfilippo, 2001, p. 178-181, fig. 2A-F, 3A-G.

Material examined. Table 1. # 503 (holotype).

Description. Tube white and solid, circular in cross section with porcellaneous surface, attached to substrate throughout entire length, forming a peripheral basal flange (Fig. 3A). Distal tube part may be slightly raised from substrate (Fig. 3 B). Undulating peristomes rarely present along tube (Fig. 3A). Tube mouth simple, with one dorsal and two lateral lobes resulting in an undulating edge, widened into a peristome (Fig. 3B). Incision on lower side of tube mouth continuing as a suture along tube wall. Tube surface with very slight wavy growth lines, with undulations similar to those observed in tube mouth. Tube diameter up to 3.8 mm. Tube wall with crystals more closely packed and sub-parallel outwards, giving transparency to outer tube layer (see Sanfilippo, 2001, fig. 3F, G).

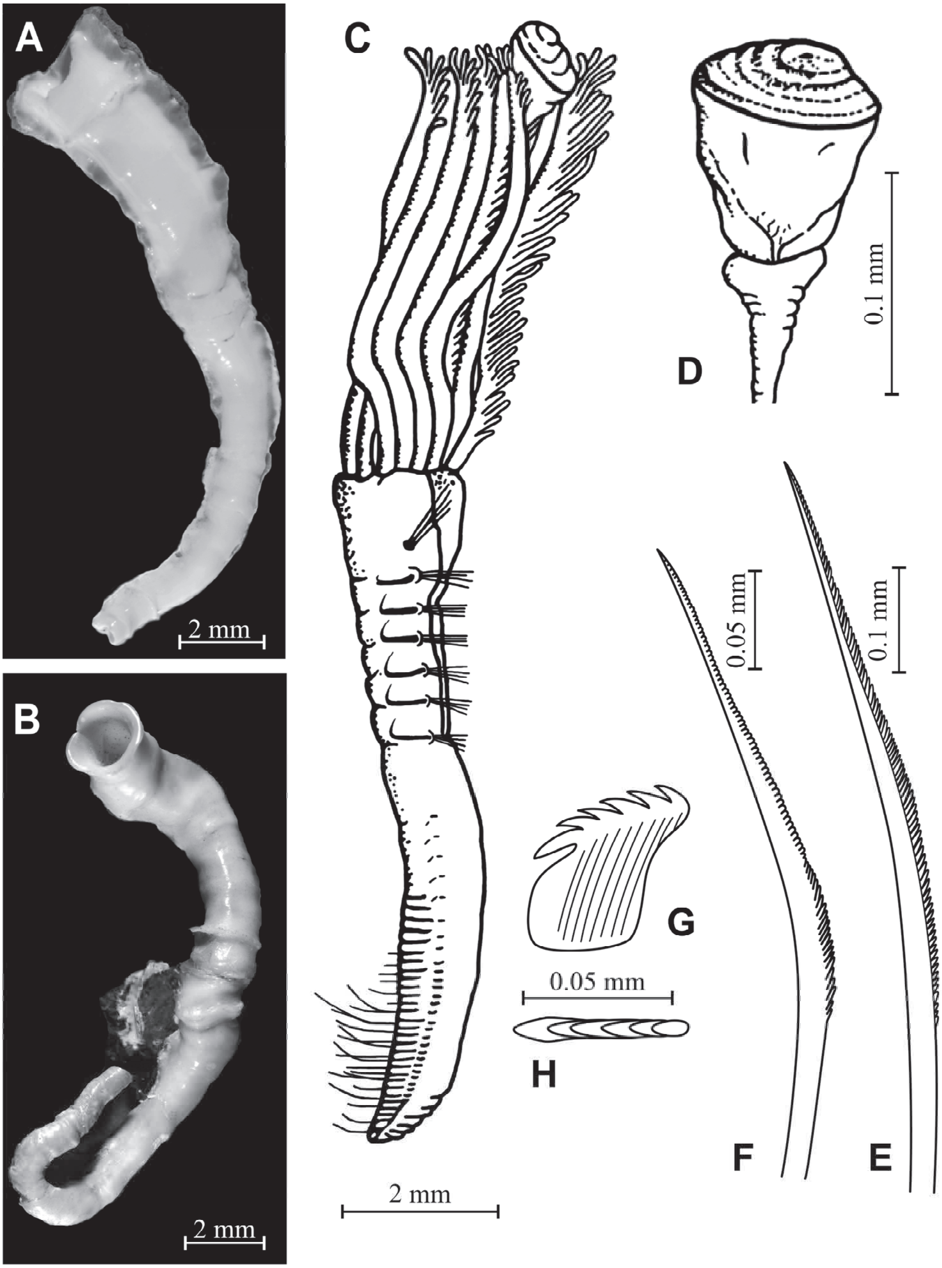

Figure 3. *Bathyvermilia islandica* Sanfilippo, 2001. A, B – tubes; C – entire body, lateral view of holotype; D – operculum; E – collar chaeta; F – *Apomatus* chaeta; G – thoracic uncinus, lateral view; H – thoracic uncinus, profile view. A, C-F – from Sanfilippo (2001). A, B – photo R. Sanfilippo.

Body length, without crown, up to 14 mm. Colour of live specimens unknown.

Twelve to thirteen pairs of long radioles not connected by inter-radiolar membrane. Radiolar eyes unknown, not observed in preserved material.

Peduncle smooth, more or less circular in cross-section, slightly thicker than normal radioles and clearly inserted as second radiole. Deep constriction at junction of ampulla and peduncle (Fig. 3D). Operculum an inverted cone (Fig. 3D), hollow (with a smaller soft operculum inside), covered with a slightly convex, light-yellow, chitinous endplate, with two or more concentric indistinct zones, without any calcareous deposit. Pseudoperculum absent.

Collar unlobed, short, of uniform width, barely covering base of radioles (Fig. 3C). Thoracic membranes wide up to 2nd segment and then narrowing sharply, ending at 7th thoracic chaetiger, but not forming apron (Fig. 3C). No distinct prostomium.

Thorax with seven thoracic chaetigers, six of them with uncini (Fig. 3C). Thoracic tori slightly shifted ventrally from mid-lateral line of thorax, but distinct triangular depression absent. Up to 20 collar chaetae: stouter limbate and less numerous capillary ones (Fig. 3 E). In the remaining thoracic segments limbate chaetae increase in number (25–30 per chaetiger), the 7th segment also with some (up to 5) *Apomatus* chaetae (Fig. 3 F). Thoracic uncini saw-shaped, with 6 teeth and pointed anterior fang (Fig. 3G, H).

Achaetous zone in anterior abdomen present. Up to 60 abdominal chaetigers. Abdominal tori short. Anterior abdominal chaetae flat geniculate, with broad triangular denticulate blades, replaced by numerous (up to 15 per chaetiger) very long capillary chaetae on posterior segments. Anterior abdominal uncini saw-shaped with 5–6 teeth and pointed anterior fangs. Uncini of most posterior abdominal segments with 7–8 teeth in profile and 2 teeth per row. Posterior glandular pad unknown.

Remarks. The smooth shiny porcellaneous nature of *B. islandica* tubes is due to relatively regular crystal arrangement, which show a common crystallographic axis perpendicular to outer surface (see ten Hove & Zibrowius, 1986; Zibrowius & ten Hove, 1987; Sanfilippo, 2001; 1998).

The species differs from the other Arctic representative, *Bathyvermilia eliasoni*, by its tube, circular in cross section with smooth shiny surface and rare undulating peristomes and by an operculum covered with a slightly convex, chitinous endplate, lacking any calcareous deposit as opposed to the calcareous endplate in *B. eliasoni*. *B. islandica* is also distinct in having long thoracic membranes ending at the 7th thoracic chaetiger, whereas the thoracic membranes end at the 3th – 4th thoracic chaetiger in all other species of the genus.

Ecology. Deep- and cold-water species found at depths from 770–2399 m corresponding to temperatures of 2–6 °C, on volcanic rock, “soap-stones”, corals, mollusc and brachiopod shells (Sanfilippo, 2001). Reproduction unknown.

Distribution. South of Iceland, from 61°N–64°N, known from type locality only (Sanfilippo, 2001).

Genus *Chitinopoma* Levinsen, 1884

Type-species: *Chitinopoma fabricii* Levinsen, 1884.

Tube white, opaque, with single keel, triangular or sub-triangular in cross-section, with brood chambers. Hyaline granular overlay absent. Operculum inverse conical, with chitinous endplate. Peduncle cylindrical, smooth, without distal wings, constriction present; inserted as second dorsal radiole on one side. Pseudoperculum absent. Radioles arranged in semi-circles, up to 7 radioles per lobe, inter-radiolar membrane absent. Radiolar eyes and stylodes absent. Mouth palps not observed. 7 thoracic chaetigerous segments. Collar trilobed with entire edge, tonguelets between ventral and lateral collar parts absent. Thoracic membranes short, ending at 2nd thoracic chaetiger. Large collar chaetae modified fin-and-blade, fin well separated from blade, and limbate. *Apomatus* chaetae present. Thoracic uncini saw-shaped, with about 12 teeth; anterior peg rounded. Thoracic triangular depression absent. Abdominal chaetae with large flat distal denticulate triangular blade; uncini rasp-shaped. Achaetous anterior abdominal zone absent. Posterior capillary chaetae absent. Posterior glandular pad absent.

Remarks. The partial revision of the genus conducted by Zibrowius (1969) showed that the tube-incubating *C. serrula* is the only species widely distributed in the Arctic and boreal North Atlantic. Later, brooding *Chitinopoma arndti* Zibrowius, 1983 was added and *Chitinopoma rzhavskii* (Kupriyanova, 1993c) was transferred from *Filogranula* (Kupriyanova et al., 2001) because of brooding chambers similar to those found in *C. arndti* and *C. serrula*. However, various forms of brooding of embryos, the main character distinguishing *Chitinopoma* from *Filogranula*, are very common for small serpulid species (Kupriyanova et al., 2001). These two genera are currently under revision (ten Hove & Kupriyanova, in prep).

Three species, one species in the Arctic. ?*Chitinopoma capensis* Day, 1961 listed by ten Hove & Kupriyanova (2009) was shown to belong to *Pseudochitinopoma* Zibrowius, 1969 by Kupriyanova et al. (2012).

***Chitinopoma serrula* (Stimpson, 1854)**

(Fig. 4A-G)

Vermilia serrula Stimpson, 1854, p. 29-30.

Chitinopoma fabricii Levinsen, 1884, p. 199, 203, tab. II, fig. 4, 8, tab. III, fig. 20; Ditlevsen, 1929, p. 54; Friedrich, 1940, p. 127-128, 131; Zatsepin, 1948, p. 166, tab. XXXIX, 24 t, a, gb; Gurjanova, 1957, p. 256; Slastnikov, 1957, p. 423.

Chitinopoma greenlandica: Bush, 1904, p. 224, 229, pl. 37, fig. 3, 9, pl.40; Nelson-Smith, 1967, p. 37, fig. 29.

Chaetinopoma greenlandica: Sumner et al., 1913, p. 631.

Chitinopoma serrula: Zibrowius, 1969, p. 2-6; Hartmann-Schröder, 1971, p. 533, Add. 185; Kupriyanova & Jirkov, 1997, p. 205-207, fig. 1 A-H, map 1; Jirkov & Kupriyanova, 2001, p. 559, text figures 1-8, map; Trott, 2004, p. 286.

Mikroserpula inflata: Thorson, 1936, p. 35.

Microserpula serrula: Hartman 1959, p. 582.

Miroserpula inflata: Dons, 1930, p. 3-5; 1934, p. 24-27, fig. 2-3; Brattström & Thorson, 1941, p. 21; Brattström, 1945, p. 1-22; Thorson, 1946, p. 135-136, 141, 145, fig. 77; Wesenberg-Lund, 1950a, p. 61; 1950b, p. 136; 1951, p. 129, 140, 155, 181; 1953a, p. 6-7; Nelson-Smith, 1967, p. 36, fig. 27-28.

Material examined. Table 1. # 3 (tubes); # 6 (6); # 502 (10).

Description. Tubes (Fig. 4A) white, opaque, almost triangular in cross section, with more or less sharp denticulate median keel; attached to substrate throughout entire length. Tube of adults with one or more pairs of brood chambers (Fig. 4B). Anterior aperture of tube sometimes widened into uneven lobes.

Body length, without radiolar crown, up to 15 mm. Radiolar crown of live animals white, body red.

Five to seven pairs of radioles, not connected by inter-radiolar membrane. Radiolar eyes absent.

Peduncle smooth, more or less circular in cross-section, slightly thicker than normal radioles and clearly inserted as second radiole. Operculum inverted cone covered with brown endplate of chitin-like material (Fig. 4C, D), separated from peduncle by constriction. Pseudoperculum absent.

Collar large and trilobed, lateral notches deep, ventral lobe longer than lateral lobes. Tonguelets absent. Thoracic membranes short, ending at 2nd thoracic chaetiger. No distinct prostomium.

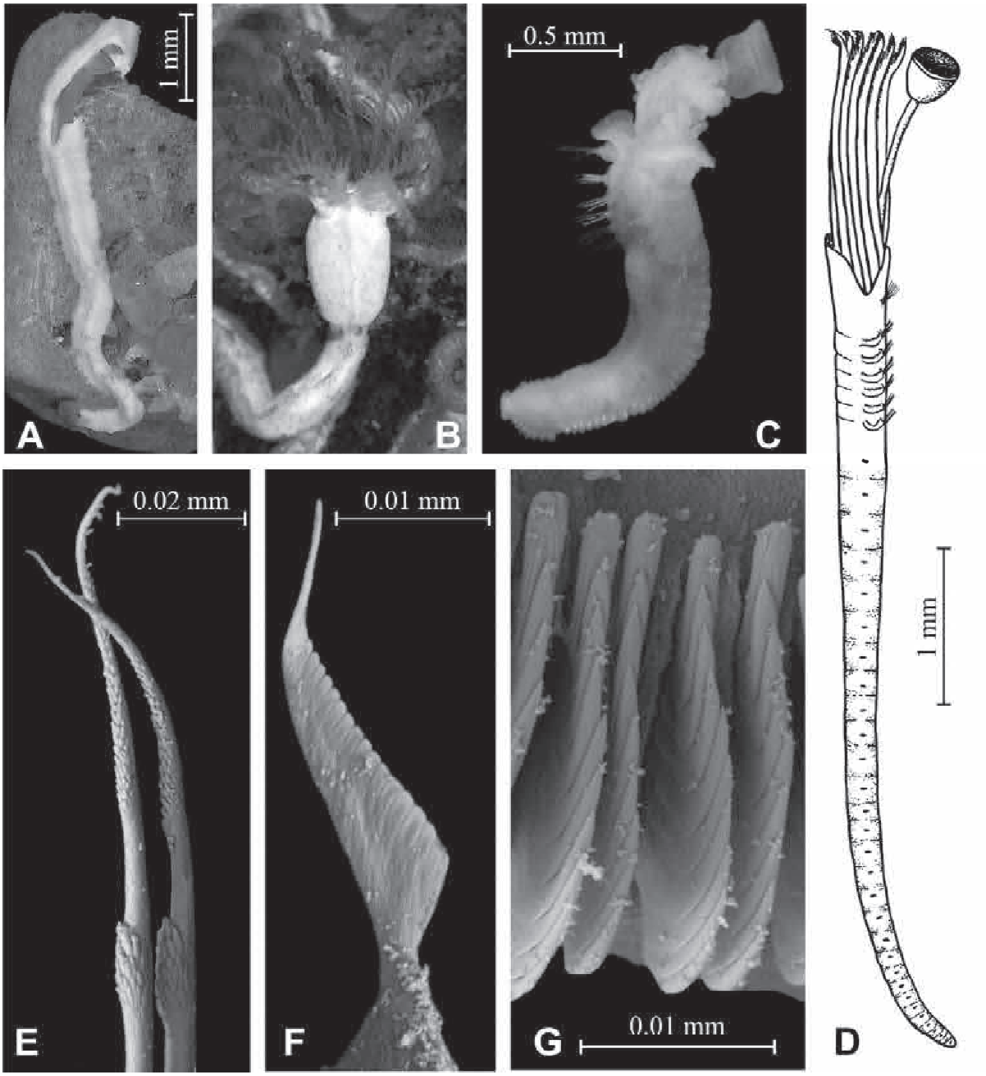

Figure 4. *Chitinopoma serrula*. A – specimen in tube; B – live specimen in a tube with brood ovicells; C – general view of a specimen removed from tube; D – entire body, lateral view; E – modified fin-and-blade collar chaetae; F – abdominal chaeta; G – thoracic uncini. D – from Kupriyanova & Jirkov, 1997. A, C – photo E. Wong, B – photo G. Rouse.

Seven thoracic chaetigers, 6 of them with uncini (Fig. 4D). Thoracic neuropodia at mid-lateral line of thorax, triangular depression absent. Large collar chaetae limbate and modified fin-and-blade, with distal limbus separated by a gap from proximal denticulate fin (Fig. 4E). Remaining thoracic chaetae limbate and *Apomatus* chaetae. Thoracic uncini (Fig. 4G) saw-shaped with 9–12 teeth and blunt anterior pegs. Rows of thoracic uncini 5–6 times longer than rows of abdominal uncini.

Achaetous anterior abdominal zone absent. Up to 60 abdominal chaetigers. Abdominal tori short. Abdominal chaetae with flat wide triangular denticulate blade (Fig. 4F). Abdominal uncini rasp-shaped with 9–12 teeth in profile and 4–5 teeth per row. Posterior glandular pad absent.

Remarks. *Miroserpula* has been misspelled as *Mikroserpula* and *Microserpula* and *Chitinopoma* was misspelled as *Chaetinopoma* (see synonymy). There are two other species currently included in this genus. *C. arndti* Zibrowius, 1983 from bathyal depths off Saint-Paul Island, Southern Indian Ocean is known based on a single dry specimen lost during rehydration. It clearly differs from *C. serrula* by tubes that are roughly pentagonal, with three denticulate keels, one median and two lateral one and the structure of the brood chambers that are always single, never paired as in *C. serrula*. *C. rzhavskii* has paired brood chambers, like *C. serrula*, but unlike *C. serrula*, it has a non-denticulate tube keel and a membranous funnel-shaped operculum without chitinous endplate. The nominal genus *Chitinopoma* will be synonymised with *Filogranula* Langerhans, 1884 by ten Hove & Kupriyanova (in prep.)

Ecology. Found from the tidal zone down to over 300 m (Zibrowius, 1969) on stones and shells (Kupriyanova & Jirkov, 1997).

Spermatozoa have elongated heads as characteristic of species with sperm storage, but spermathecae have not been described. Egg diameter is 180-200 µm, which is typical for lecithotrophic larvae, up to 20 of which are brooded in paired tube ovicells located at the tube mouth (Dons, 1933; Thorson, 1946; Kupriyanova et al., 2001).

Distribution. Widely distributed in the Arctic (Greenland, Norway, Barents, White and Kara Seas) and Boreal Atlantic Ocean from the Strait of Belle Isle (Canada) to the Gulf of Maine (USA) along the North American coast and from the entire coast of Norway, West Coast of Sweden, Oresund, North-West of Jutland, Scotland and UK coasts in Europe (summary from Zibrowius, 1969 and Kupriyanova & Jirkov, 1997).

Genus *Ditrupa* Berkeley, 1835

Type species: *Dentalium arietinum* Müller, 1776.

Tube free, tusk-like, not attached to substrate, circular in cross-section, open at both ends, broadening anteriorly though exterior tapers just prior to tube mouth. Outer layer hyaline or white, inner layer opaque. Granular overlay of tube absent. Operculum inverse conical with chitinous endplate. Peduncle cylindrical, smooth, without wings, gradually merging into operculum, no constriction; positioned as first dorsal left radiole. Pseudoperculum absent. Radioles arranged in two semi-circles on pectinate base; up to 15 radioles per lobe. Inter-radiolar membrane, radiolar eyes and stylodes absent. Pair of filiform dorsal mouth palps present. 6 thoracic chaetigerous segments. Large entire (unlobed) collar continuous with short thoracic membranes, ending at first chaetiger (second thoracic segment); tonguelets absent. Collar chaetae absent. First thoracic chaetiger uncinigerous with limbate chaetae and with uncini; sometimes with modified chaetae.

Apomatus chaetae absent. Thoracic uncini saw-to-rasp-shaped or rasp-shaped; about 25 teeth in profile, with 2 or 3 teeth in a row above peg; anterior peg blunt, curved upwards and gouged underneath. Triangular depression absent. Abdominal chaetae and certainly posterior ones thin, almost capillary, with very faint narrow geniculate tip (to completely capillary in *Ditrupa gracillima* Grube, 1878). Abdominal uncini rasp-shaped, with 20–25 teeth in profile, up to 8 teeth in a row above peg; anterior peg blunt, almost rectangular. Achaetous anterior abdominal zone absent; however, anterior half of abdomen with uncini only. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. The genus found living unattached in soft sediment marine environments around the world has been partially revised by ten Hove & Smith (1990). Like many serpulid genera, *Ditrupa* has a history of taxonomic confusion to the extent that its tubes were included in the Mollusca (genera *Cadulus* and *Dentalium*) by some authors. Unattached free tubes similar to those of *Ditrupa* are known only for *Bathyditrupa hovei*, "*Ditrupa*" *groenlandica* McIntosh, 1877, and *Spirobranchus latiscapus* (Marenzeller, 1885). However, tubes of the latter taxa are triangular to octagonal in cross-section, not circular. Moreover, "*Ditrupa*" *groenlandica* McIntosh, 1877 known from an empty unattached tube, octagonal in cross-section, does not belong to this genus, but is closely related to *Bathyditrupa* and *Nogrobs* (Kupriyanova & Ippolitov, in review).

Two species, one of them known from the Arctic.

Ditrupa arietina **(Müller, 1776)**

(Fig. 5A-D, Pl. 1C, D)

Dentalium subulatum Deshayes, 1825, p. 373, pl. 16, fig. 29.

Ditrypa arietina: McIntosh, 1923, p. 380-383, pl. CXXII, fig. 5-6, pl. CXXXII, fig. 1.

Ditrupa arietina: Wollebæk, 1912, p. 119-120, pl. XLVI, fig. 4-9, pl. LI, fig. 4; Augener, 1925, p.116; Ditlevsen, 1929, p. 54; Wesenberg-Lund, 1950a, p. 60-61; 1953, p. 6; Nelson-Smith & Gee, 1966, p. 350, fig. 13B; Nelson-Smith, 1967, p. 39; Zibrowius, 1968a, p. 169-171; 1968b, p. 383-385; Hartmann-Schröder, 1971, p. 527; Bianchi, 1981, p. 124-125, fig. 47; ten Hove & Smith, 1990, p. 104-107; Kupriyanova & Jirkov, 1997, p. 207-209, fig. 2A-H, map 2; Gambi & Jerace, 1997; Grémare et al., 1998, p. 447-457; Medernach et al., 2000, p. 171-184; Jirkov & Kupriyanova, 2001, p. 560, text figures 1-7, map; Riisgård et al., 2002; Morton & Salvador, 2009, p. 145-156; Guizien et al., 2010, p. 239-251.

Ditrupa groenlandica **non** McIntosh, 1877: Wesenberg-Lund, 1950b, p.136.

Material examined. Table 1. # 298 (1 and tubes); # 312 (~100); # 316 (tubes); # 321 (4); # 339 (tubes); # 340 (1 and tubes); # 346 (94 and tubes); #347 (2 and tubes); # 350 (tubes); # 351 (3 and tubes); # 354 (tubes); # 355 (tubes); # 362 (tubes); # 363 (tubes); # 364 (1 and tubes); # 365 (tubes); # 366 (tubes); # 382 (tube); # 383 (1); # 388 (tubes); # 395 (89); # 401 (3 and tubes); # 406 (3 and tubes); # 413 (3 and tubes); # 416 (tubes); # 417 (tube); # 420 (12 and tubes); # 421 (tube); # 424 (tubes); # 462 (3 and tubes); # 468 (2 and tubes); # 469 (1).

Description. Tubes (Fig. 5A) tusk-shaped, circular in cross section, up to 2.0 mm in diameter, white, without distinct growth marks, consisting of external transparent and internal white (or sometimes brownish/reddish) opaque layers.

Body length, without radioles, up to 20 mm (Fig. 5B). Colour of crown in live specimens white or red, body red.

Six thoracic chaetigers, all with uncini, collar chaetae absent (Fig. 5B, C). Thoracic neuropodia shifted ventrally, those of 6th chaetiger meeting ventrally forming triangular depression. Five to seven pairs of radioles, not connected by inter-radiolar membrane. Radiolar eyes absent.

Peduncle smooth, more or less circular in cross-section, slightly thicker than normal radioles and inserted as first second radiole. Operculum inverted cone covered with flat or slightly convex brown endplate of chitin-like material (Fig. 5B, D), not separated from peduncle by constriction. Pseudoperculum absent.

Collar entire, very long, covering to one-half of length of radioles. Tonguelets absent. Thoracic membranes short, ending at 2nd thoracic chaetiger. No distinct prostomium

Lateral distance between first and second pair of thoracic neuropodia several times longer than that between other pairs of neuropodia. Thoracic chaetae capillary and

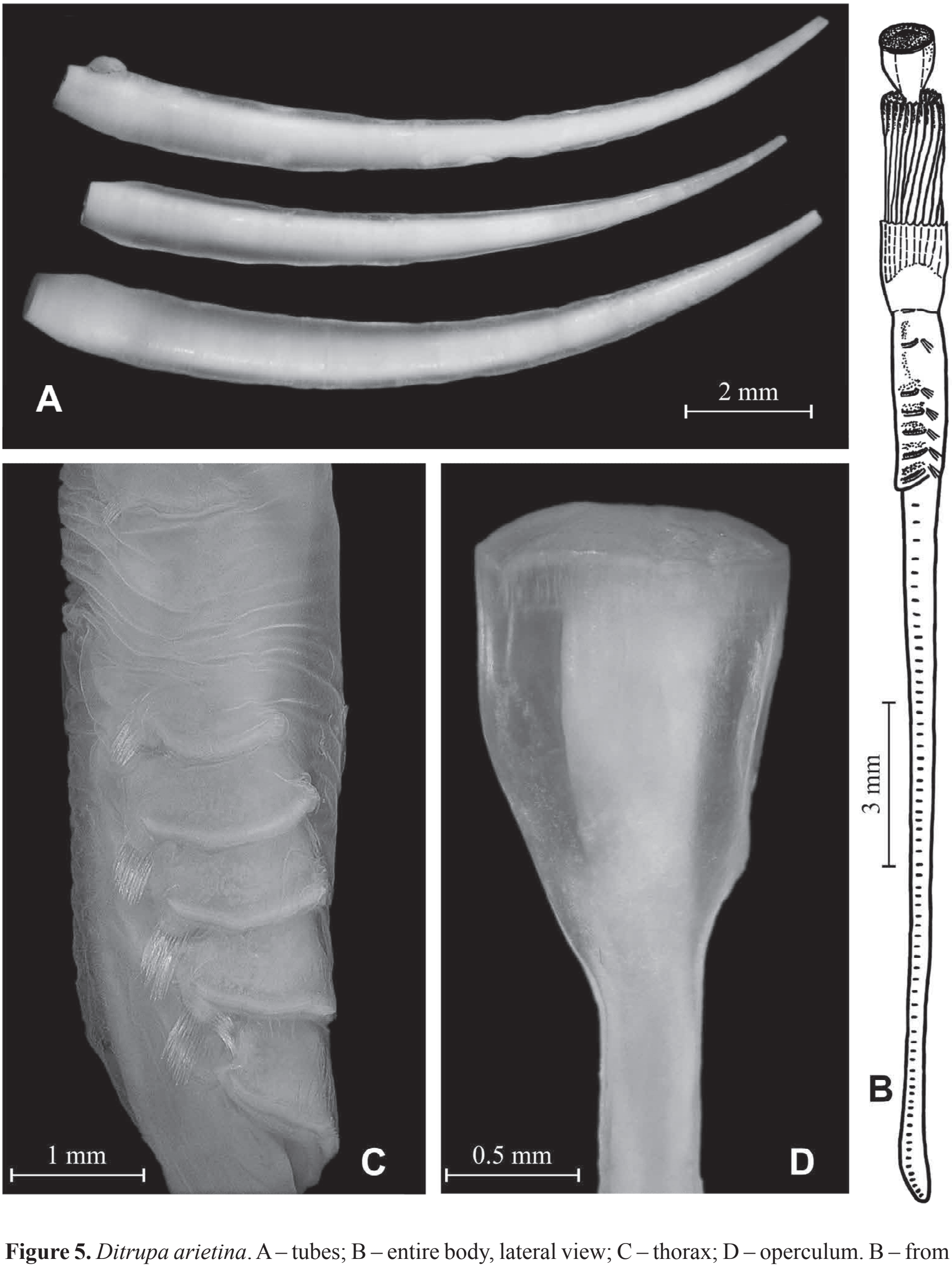

Figure 5. *Ditrupa arietina*. A – tubes; B – entire body, lateral view; C – thorax; D – operculum. B – from Kupriyanova & Jirkov (1997). A, C, D – photo E. Wong.

limbate. Thoracic uncini rasp-shaped with about 20 teeth in profile view, 3–4 teeth per row.

Achaetous abdominal zone absent; however, anterior half of abdomen with uncini only. Up to 60 abdominal chaetigers. Abdominal chaetae very small, capillary, tips slightly geniculate, hollow, bordered with two rows of denticles (true trumpet-shaped chaetae *sensu* ten Hove & Kupriyanova, 2009), 1–3 per fascicle. Tori very short rows of uncini. Abdominal uncini similar to thoracic ones, rasp-shaped with numerous teeth in each row. Posterior glandular pad absent.

Remarks. The partial generic revision by ten Hove & Smith (1990) showed that the distribution of *D. arietina* is restricted to East Atlantic and Mediterranean, whereas a separate species, *D. gracillima*, inhabits Indo-Pacific. The two species are very similar morphologically and differ mainly by the details of the tubes that are tusk-shaped and slender, with a smooth hyaline layer in *D. arietina*, whereas there are three tube morphotypes – "smooth"(characterized by highly polished porcellaneous finish), "rough"(with chalky and opaque outer layer) and "monifera"(with irregular spaced annular thickening along their length).

Tubes of *Ditrupa* are similar to scaphopod (Mollusca) shells, but the latter are made of one uniformly white layer only and the thickness of the shell's wall at approximately 10 times smaller than the mouth diameter. *Ditrupa* tubes are composed of transparent and opaque layers and in *D. arietina* thickness of the tube wall is approximately the same as the tube mouth diameter. The tube wall in *Ditrupa* is composed of two layers of Mg-calcite. The outer, hyaline layer has a unique type of ultrastructure, regularly ridged prismatic structure (RRP) unknown in other invertebrate skeletons. This structure is characterized by ridged lateral surfaces of the prisms, which interlock the prisms and exclusively characterizes the genus *Ditrupa.* RRP structure could have evolved as an adaptation to the unattached life style, with the ability to move around, which could have placed an increased demand on the tube's mechanical properties (Vinn et al., 2008).

The longitudinal thickenings and denticulate edge of the collar of *D. arietina* mentioned in the description of Kupriyanova & Jirkov (1997) is an artefact of fixation not found in fresh material**.**

Ecology. In the Arctic the species occurs in depths from subtidal down to 445 m, corresponding to an average temperature of 7.58ºC, usually on a variety of soft substrates except fine sand; it prefers silt and coarse sand without additional large rocks (Kupriyanova & Badyaev, 1998). Ten Hove & Smith (1990) state that tubes have been collected from depths down to 530 m, but specimens are known to a depth of 150 m only.

Sexes are strictly separated in *D. arietina*. Spermatozoa have spherical heads, characteristic of broadcast spawning species, and the average number of oocytes per female before spawning is close to 9000. Planktotrophic larvae feed in the plankton close to 3 weeks and completion of metamorphosis occurs very rapidly after larval settlement. Competent larvae do not show any selective behaviour relative to sediment particle size (Charles et al., 2003).

Distribution. In the Arctic known from the Barents, Norwegian, Greenland and North Seas, Iceland (Kupriyanova & Jirkov, 1997). Outside the Arctic recorded from the East Atlantic to the Azores, Canary Islands, and Senegal; Mediterranean and questionably Black Sea (summarized by ten Hove & Smith, 1990).

Genus *Filograna* Berkeley, 1835

Type species: *Filograna implexa* Berkeley, 1835.

Worms form aggregates (pseudo-colonies) consisting of large numbers of small greyish/whitish tubes, circular in cross-section. Granular overlay and keels absent. A pair of membranous spoon-shaped opercula on first normal pinnulate radiole. Radioles arranged into semi-circles, up to four radioles per lobe. Radiolar eyes absent. Inter-radiolar membrane and stylodes absent. Prominent prostomium with ocellar clusters. Mouth palps present. 6–12 thoracic chaetigerous segments. Collar trilobed, tonguelets between ventral and lateral collar parts absent. Thoracic membranes long, forming apron. Large collar chaetae fin-and-blade and limbate. *Apomatus* chaetae present. All uncini are rasp-shaped with up to 10 teeth in profile, 2–4 teeth in a transverse row; anterior fang pointed. Triangular depression absent. Achaetous anterior abdominal zone present, short. Abdominal chaetae flat narrow geniculate with rounded teeth along edge. Long posterior capillary chaetae and glandular pad absent.

Remarks. The nominal genera *Filograna* and *Salmacina* are distinguished mainly by the presence of two (rarely one) membranous opercula in the former, absent in the latter. Some authors consider them distinct genera (Iroso, 1921; Fauvel, 1927; Pillai, 1960; Straughan, 1967), whereas others treat sympatric representatives as a single species (McIntosh, 1923; Faulkner, 1929; Day, 1955; 1967). More recent authors (Nelson-Smith, 1967; Gee, 1973; Zibrowius, 1968a; 1973b; Uchida, 1978; Kupriyanova & Jirkov, 1997) regard operculate and non-operculate forms to be separate species within the genus *Filograna*. Nogueira & ten Hove (2000) gave an extensive discussion and adapted the heuristic view that the operculate cold-temperate Atlantic *Filograna* better be kept separate from the non-operculate ubiquitous *Salmacina.*

Evidence has accumulated in the last several decades strongly suggesting that opercular absence alone cannot be used for reliably identifying serpulids to species, leave alone to genus. Some serpulids are known to shed and regenerate opercula (Okada, 1932; Schochet, 1973; Lang & Le Calvez, 1982; Bubel & Thorp, 1985; Bubel et al., 1985). As a result, non-operculate specimens sometimes can be found in populations of normally operculate species (ten Hove, 1984). On the other hand, representatives of traditionally non-operculate groups such as *Protula*, *Protis*, and *Paraprotis* Uchida, 1978 have been shown occasionally to possess opercula (Hong, 1984; Kupriyanova, 1993b; Imajima, 1979, see also Remarks on *Protis arctica*). Based on preserved material only, it is difficult to determine whether animals belonging to these groups never had opercula or “operculate specimens . . . shed opercula when killed” (ten Hove & Wolf, 1984, for the question *Filograna* vs *Salmacina*).

Questionably monotypic genus.

Filograna implexa Berkeley, 1835

(Fig. 6A-H, Pl. 1E)

Filograna implexa Berkeley, 1835, p. 427; Wollebæk, 1912, p. 111-112, pl. XL, fig. 1-6, pl. LI, fig. 1; McIntosh, 1923, p. 339-346, pl. CXVI, fig. 5,8, pl. CXVII, fig. 2, pl. CXXI, fig. 8, pl. CXXXVII, fig. 20-21; Augener, 1925, p.115 ; Fauvel, 1927, p. 376; Ditlevsen, 1929, p. 54-55; Friedrich, 1940, 127-128, 131; Zatsepin, 1948, p. 165, tab. XXXIX, 17 a, gb, h, p; Wesenberg-Lund, 1950a, p. 61; 1950b, p. 136; Nelson-Smith & Gee 1966, p. 341, fig. 6D, 7 D; Hartmann-Schröder, 1971, p. 538; Kupriyanova & Jirkov, 1997, p. 209-211, fig. 3; Jirkov & Kupriyanova, 2001, p. 561-562, text figures 1-7, map.

Material examined. Table 1. # 2 (~ 400); # 3 (~ 300); # 8 (~ 100); # 20 (? 80); # 28 (~ 300); # 52 (1); # 184 (15); # 186 (~ 400); # 302 (~ 350); # 312 (~ 300); # 313 (~ 50); # 317 (~ 300); # 320 (2); # 323 (15); # 332 (20); # 335 (25);

341 (~ 200); # 342 (~ 200); # 344 (~ 300); # 349 (~ 70); # 356 (~ 400); # 377 (~ 1000); # 388 (25); # 392 (~ 3000); # 393 (25); # 398 (~ 400); # 399 (~ 500); # 410 (40); # 412 (10); # 413 (20); # 414 (? 120); # 416 (~ 70); # 417 (~ 200); # 418 (10); # 422 (~50); # 425 (~ 30); # 465(~ 50); # 524 (~ 5000); # 526 (20); # 611 (~ 150).

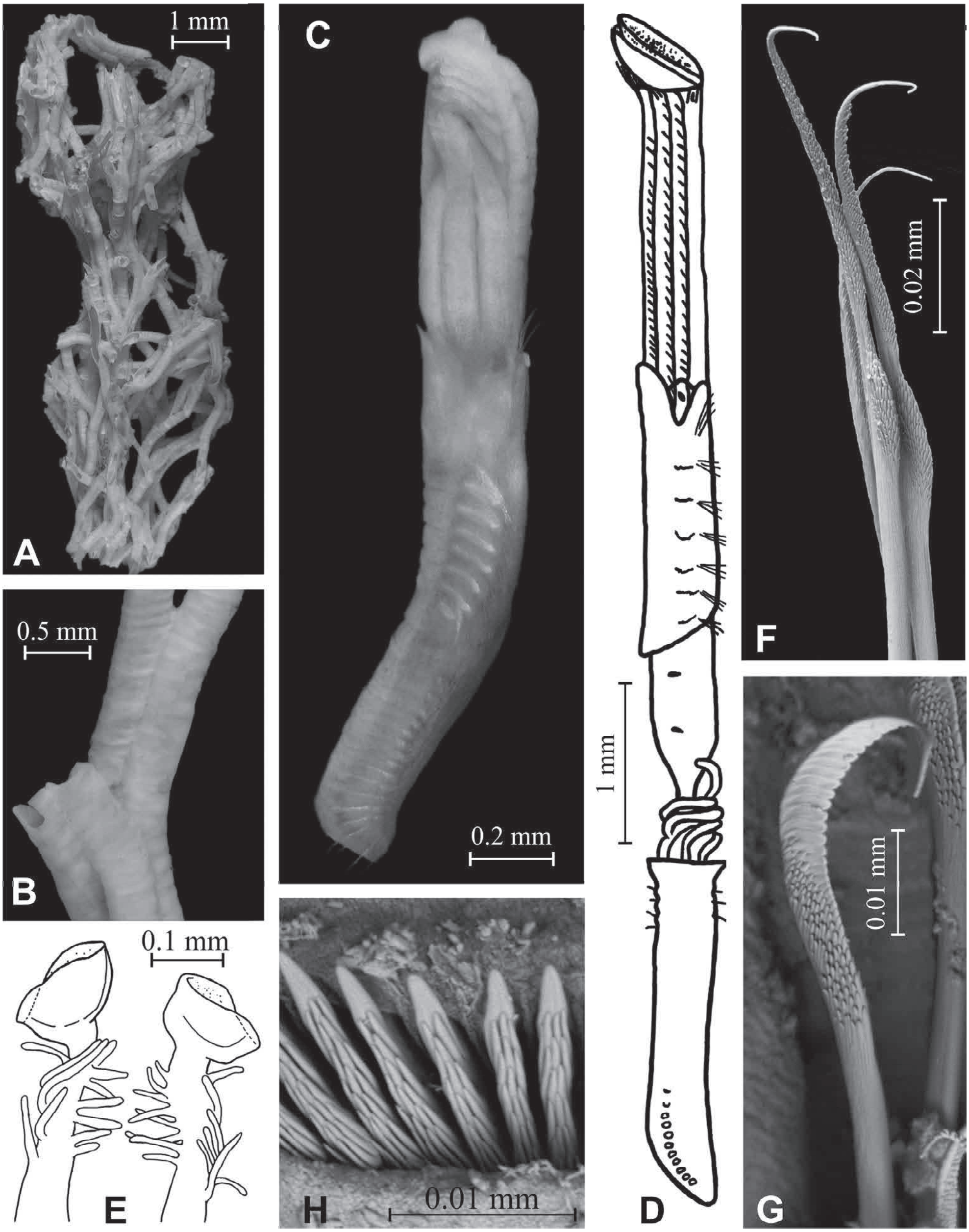

Figure 6. *Filograna implexa.* A – pseudo-colony of tubes; B – same, close-up, C – entire animal without opercula, D – lateral view of animal with 2 opercula; E – paired opercula; F – modified fin-and-blade collar chaetae; G – *Apomatus* chaetae; H – thoracic uncini. E – from Bianchi (1981), D – from Kupriyanova & Jirkov (1997). A, B, C – photo E. Wong, F, G – photo E. Kupriyanova.

Description. Tubes (Fig. 6A) form characteristic lattice-shaped pseudo-colonies consisting of numerous branching greyish/whitish tubes up to 1 mm in diameter (Fig. 6B).

Body length, without radioles, up to 6.0 mm. Live specimens red.

Three or four pairs of radioles not connected by inter-radiolar membrane. Two palps. Radiolar eyes absent.

Most dorsal pairs of radioles bearing two well-developed membranous opercula (Fig. 6E, F), but some specimens may have only one operculum or opercula may absent (Fig. 6C).

Collar covering peristomium and base of radioles. Deep lateral notches subdivide collar into two narrow, short lateral lobes, and one wide, long ventral lobe. Ventral lobe may have small median notch. Tonguelets absent. Thoracic membranes reaching end of thorax and forming a short apron ventrally. Prostomium distinct, a pair of prostomial eyes present.

Six to twelve thoracic chaetigers, including 5–11 with uncini. Thoracic neuropodia located at mid-lateral line of thorax, not shifting ventrally, not forming triangular depression. Large collar chaetae (Fig. 6F) fin-and-blade, with distal striated denticulate blade and proximal fin consisting of several rows of numerous teeth. Remaining thoracic chaetae limbate and *Apomatus* chaetae (Fig. 6G). Thoracic uncini (Fig. 6H) rasp-shaped with numerous teeth in each row.

Achaetous anterior abdominal zone short. Up to 30 abdominal chaetigers. Abdominal notopodia as short rows of uncini, approximately 3-4 times shorter than thoracic neuropodia. Abdominal chaetae small, flat narrow geniculate with rounded teeth along edge. Abdominal uncini similar to thoracic ones. Posterior glandular pad absent.

Ecology. In the Arctic recorded from depths of 84-605 m corresponding to an average temperature of 7.21ºC, found in free clusters on coarse and silty sand, on gravel, initially attached to any hard substrate, later on the pseudo-colony itself becomes a substrate for attachment of other organisms (Kupriyanova & Badyaev, 1998).

This taxon reproduces both asexually and sexually. The process of pseudo-colony formation as a result of asexual reproduction has been extensively studied in the complex *Filograna /Salmacina*. In these taxa the parental animal divides into two by transverse fission in the abdomen. Before the real separation takes place, a new cephalic region forms in the middle part of the parental specimen by transformation of abdominal segments into thoracic ones (morphallaxis). The clonal offspring gain access to the exterior of the tubes *via* escape hatches built into the tubes by the parent worms. Each escape hatch consists of a hole in the tube blocked by a calcareous disc that is kept in place by an organic membrane. After buds detach from their parents, the calcareous discs are dislodged, and buds begin to form their own tubes from the resulting openings. Repeated bouts of asexual reproduction result in the formation of aggregations of branched tubes (Pernet, 2001). Nishi & Nishihira (1994) report that in the nominal taxon *Salmacina dysteri* (Huxley, 1855) from Okinawa, Japan (might be different from the Mediterranean material), pseudo-colony formation takes place *via* a combination of asexual and sexual reproduction and this is likely to be the case for *Filograna implexa* from the Arctic as well.

Filograna and *Salmacina* are simultaneous hermaphrodites, with anterior abdominal segments usually containing male gametes, and posterior ones carrying female gametes. Distinct gonads have been described in the *Salmacina/Filograna*-complex. Eggs are 180-200 µm in diameter, which is typical for lecithotrophic development. Spermatozoa have elongated heads, characteristic of species with sperm storage in spermatheca as described for *Salmacina* by Rouse (1996). Lecithotrophic larvae are brooded inside tubes on the compressed abdomen (reviewed in Kupriyanova et al., 2001).

Remarks. Because both operculate and non-operculate specimens were found in our Arctic material, for time being we consider them as being the same taxon.

Distribution. In the Arctic, *F. implexa* has been reported from Barents, Norwegian, Greenland and North Seas, Iceland (Kupriyanova & Jirkov, 1997). Outside the Arctic it is reported world-wide, from European waters (Bellan, 2001; Muller, 2004), the East Coast of the USA (Pollock, 1998), Gulf of Mexico (Fauchald et al., 2009), South Africa (Day, 1967), Mozambique (Kalk, 1958) and New Zealand (Glasby & Read, 2009). This "cosmopolitan" species is most likely a complex of regionally distributed species.

Genus *Hyalopomatus* Marenzeller, 1878

Type species: *Hyalopomatus claparedii* Marenzeller, 1878.

Tube white, opaque, sometimes with external hyaline layer, but granular overlay absent; (semi) circular in cross-section. Exceptionally for this genus, *Hyalopomatus variorugosus* Ben-Eliahu, Fiege, 1996 is characterized by tubes with minute flap like structures, and *Hyalopomatus biformis* (Hartman, 1960) has a longitudinal keel (Bastida-Zavala, 2008). Tabulae may be present. Operculum globular, soft, without distinct endplate or consisting of proximal ampulla with slightly chitinized distal cap; well separated from peduncle by constriction; sometimes operculum absent. Peduncle very thin, cylindrical, smooth, without wings; inserted outside radiolar crown proper in front of first dorsal radiole on one side or between base of first and second radiole. Pseudoperculum absent. Arrangement of radioles short pectinate, up to 15 pairs of radioles. Inter-radiolar membrane absent. Radiolar eyes rarely present. Stylodes absent. Mouth palps present. Six thoracic chaetigerous segments. Collar trilobed, tonguelets absent. Thoracic membranes short, ending at first or second thoracic chaetiger. Large collar chaetae fin-and-blade, with or without gap between fin and blade and thus with uniform distal denticulate wing, and limbate. *Apomatus* chaetae absent. Thoracic uncini rasp-shaped with numerous small teeth, approximately 20 in profile, up to 9 teeth in a row above peg; anterior peg made of two or more rounded lobes with a shallow incision(s) in between, flat or slightly gouged in the middle. Triangular depression absent. Abdominal chaetae almost capillary ending in a long narrow tip made of pointed teeth that may be partly arranged in two rows; uncini rasp-shaped, similar to thoracic ones, but their anterior pegs crenulated with 3-6 flat rounded lobes. Achaetous anterior abdominal zone may be present. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. The recent review by ten Hove & Kupriyanova (2009) lists 12 species of *Hyalopomatus* known mainly from bathyal and abyssal depths. Sanfilippo (2009) added one more species from Mediterranean.

Kupriyanova et al. (2010) suggested that crenulated uncinal pegs (visible in SEM micrographs) is a clear synapomorphy for the genus *Hyalopomatus*. Also, SEM micrographs of abdominal chaetae in *Hyalopomatus mironovi* Kupriyanova, 1993a and *H. biformis* (see Kupriyanova et al. 2010; Kupriyanova & Nishi, 2010) show that the tips of abdominal chaetae in those species are not "flat narrow" as per ten Hove & Kupriyanova (2009), but have denticles arranged in two rows at least partly. Further SEM studies of abdominal chaetae in *Hyalopomatus* spp. are needed. Along with the distinct structure of the uncini, six thoracic chaetigers and a vesicular operculum on smooth (usually thin) peduncle make *Hyalopomatus* relatively easily distinguished from other serpulid genera, but the *Hyalopomatus* spp. are very similar morphologically. The much needed revision of this poorly known genus is currently underway (Kupriyanova & Sanfilippo in prep.).

Thirteen species, one of them known from the Arctic.

Hyalopomatus claparedii Marenzeller, 1878

(Fig. 7A-H)

Hyalopomatus claparedii Marenzeller, 1878, p. 393-394, pl. 4 fig. 2; Ehlers, 1887, p. 307; Uschakov, 1957, p. 1668-1669; McIntosh, 1879, p. 217; Knox , 1959, p. 111-112; Kupriyanova & Jirkov, 1997, p. 211-213, fig. 4A-H, map 4; Jirkov & Kupriyanova, 2001, p. 562-563, text figures 1-8, map.

Hyalopomatus claparedi: Levinsen 1884, p. 199.

Material examined. Table. 1. # 105 (1); # 106 (2); # 107 (1); # 108 (1); # 111 (3); # 123 (1); # 193 (1); # 236 (2); # 239 (2 and tubes); # 240 (10); # 241 (1); # 244 (1); # 264 (20); # 271 (1); # 282 (10); # 433 (1); # 434 (1); # 435 (2); # 437 (1); # 441 (2); # 442 (46); # 446 (2); # 447 (52); # 452 (8); # 453 (6); # 454 (9); # 497 (1).

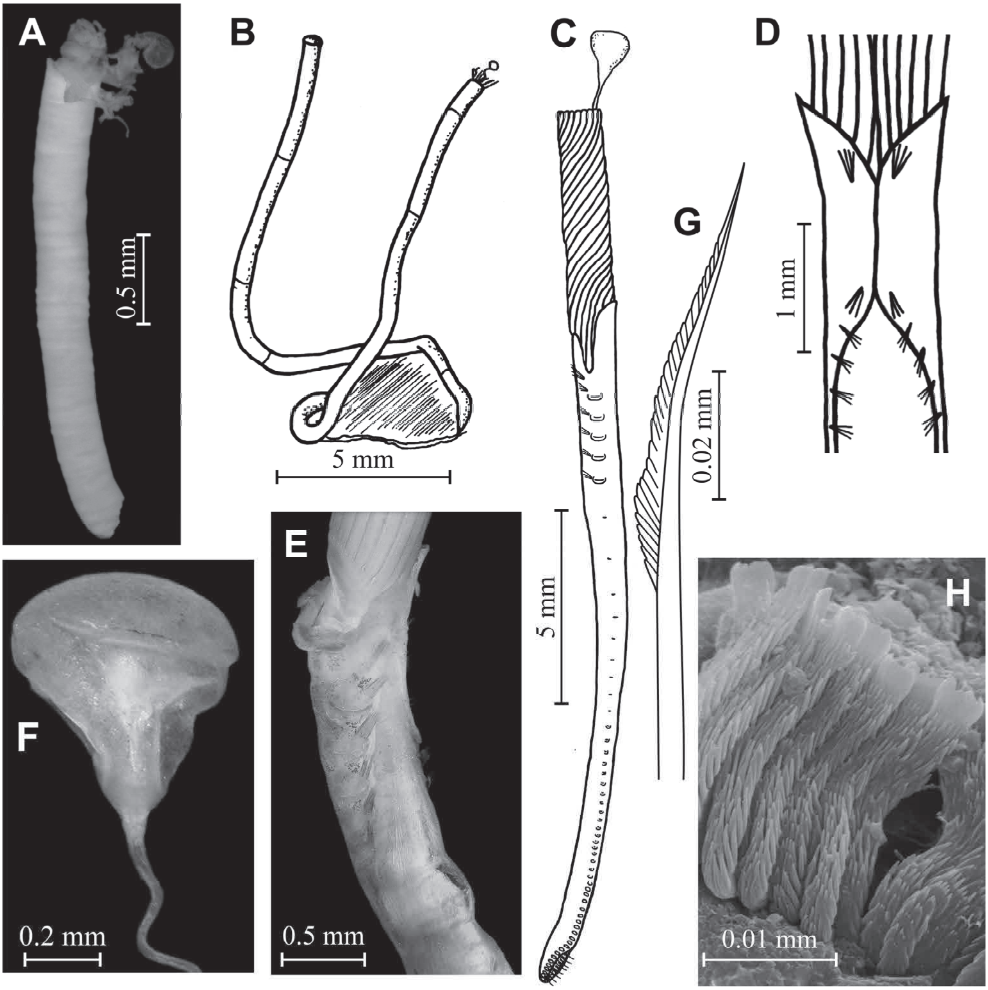

Figure 7. *Hyalopomatus claparedii*. A, B – specimens in tubes; C – entire body, lateral view; D – dorsal view of thorax; E – lateral view of thorax; F – operculum; G – collar chaeta; H – thoracic uncini. B-D, G – from Kupriyanova & Jirkov (1997). A, E, F – photo E. Wong, H – photo H.A. ten Hove.

Description. Tubes white, with smooth shiny surface, circular in cross-section, sometimes with small peristomes. Attached to substrate at proximal end only, distal end free (Fig. 7A, B).

Body length, without radioles, up to 22 mm. Colour of live animals unknown.

Three to nine pairs of radioles not connected by inter-radiolar membrane. Radiolar eyes not observed in preserved material.

Peduncle thinner than or the same as normal radioles, inserted as first dorsal radiole on one side. Operculum small, pear-shaped, membranous ampulla without distal plate (Fig. 7C, F). Pseudoperculum absent.

Collar trilobed, lateral notches deep. Dorsal and lateral lobes of same length, dorsal lobe twice as wide as lateral lobes (Fig. 7C). Collar covers radiolar lobes and very proximal part of radioles. Collar edge smooth. Tonguelets absent. Thoracic membranes (Fig. 7D) ending at 3rd thoracic chaetiger, gradually narrowing at 2nd chaetiger. No distinct prostomium.

Six thoracic chaetigers, including five with uncini (Fig. 7C, E). Thoracic neuropodia at mid-lateral line of thorax, triangular depression absent. Large collar chaetae (Fig. 7G) with denticulate blade, distal and proximal parts separated by shallow notch, thus, intermediate between limbate and modified fin-and-blade chaetae. Thoracic chaetae limbate. Thoracic uncini (Fig. 7H) rasp-shaped, about 20 teeth per row in profile view, 7-8 teeth per row, anterior peg flat crenulated.

Achaetous anterior abdominal zone absent. Up to 50 abdominal chaetigers. Abdominal chaetae with proximal blade made of two rows of denticles on anterior abdominal segments; long capillaries on far posterior chaetigers. Abdominal uncini rasp-shaped, about 20 teeth per row in profile view, 8-9 teeth per row, anterior peg flat crenulated. Posterior glandular pad absent.

Remarks. *H. claparedii* is a deep-water species known exclusively from the Arctic basin. Zibrowius (1969) gave a detailed overview of previous records of the species. However, his description is based on literature accounts only. More recently Kupriyanova & Jirkov (1997) provided a re-description and new records of the species.

Because of its membranous vesicular operculum, the species is superficially similar to the Arctic *Protis arctica* and *Apomatus globifer*; however, it clearly differs by its smooth and very thin peduncle and by having only 6 thoracic chaetigers. *H. claparedii* is most similar to *H. mironovi* Kupriyanova, 1993a, poorly known *H. langerhansi* Ehlers, 1887, and *H. sombrerianus* (McIntosh, 1885) in having a soft (semi)transparent membranous pear-shaped operculum, without a differentiated distal cap. *H. claparedii* differs from other species of the genus by large collar chaetae that are intermediate between limbate and fin-and-blade chaetae.

Ecology. In the Arctic found at depths of 142–3622 m corresponding to an average temperature of 2.01ºC, attached to shells and gravel in fine silts, rarely on sandy silt (Kupriyanova & Badyaev, 1998). Reproduction unknown.

Distribution. Central part of the Arctic. Recently one specimen was found from the Norwegian Sea off Norway (Table 1, # 497).

Genus *Hydroides* Gunnerus, 1768

Type species: *Hydroides norvegicus* Gunnerus, 1768

Tube white (sometimes bluish), more or less circular to trapezoidal (with flattened upper surface) in cross-section, peristomes and shallow keels may be present, no distinct keels. A granular overlay may be present. Operculum two-tiered, composed of basal funnel of fused radii and distal verticil (crown) of chitinized spines. Peduncle cylindrical, smooth, without wings, may or may not be separated from opercular funnel by a constriction; formed from second dorsal radiole on one side. Pseudoperculum present. Arrangement of radioles in semi-circles, up to 33 per lobe. Radiolar eyes absent. Inter-radiolar membrane generally absent, rarely present (Bastida-Zavala & ten Hove, 2002 mention only one species where it is present). Stylodes absent. Mouth palps absent. 7 thoracic chaetigerous segments, exceptionally more (9 in *Hydroides bisectus* Imajima, ten Hove, 1989 and *Hydroides* sp. 2 (Bastida-Zavala & ten Hove, 2002); 7–9 in *Hydroides bannerorum* Bailey-Brock, 1991). Collar trilobed, tonguelets absent. Thoracic membranes long, forming ventral apron. Large collar chaetae bayonet-type and limbate. *Apomatus* chaetae absent. All uncini saw-shaped with relatively few (up to 7) teeth; anterior fang pointed. Triangular depression present. Abdominal chaetae flat trumpet-shaped with denticulate edge. Achaetous anterior abdominal zone absent. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. *Hydroides* is the largest serpulid genus (in number of species) with a mainly tropical to sub-tropical distribution. Species in the genus are distinguished by well-differentiated opercula and differences in chaetal and tube structure. Ten Hove (1990) gave a standardised terminology for the structures of the operculum, and ten Hove & Jansen-Jacobs (1984) discussed the terminology describing the collar chaetae. Later, Bastida-Zavala & ten Hove (2002) standardized terminology further. Although a complete worldwide revision of the genus is yet to be completed, Bastida-Zavala & ten Hove (2002; 2003) published revisions of the *Hydroides* species from the Western Atlantic region, respectively Eastern Pacific region and Hawaii.

Ninety-two species (ten Hove & Kupriyanova 2009; Pillai 2009b), one from the Arctic.

Hydroides norvegicus Gunnerus, 1768

(Fig. 8A-I, Pl. 1B)

Hydroides norvegica Gunnerus, 1768, p. 51, fig. 11-13; Wollebæk, 1912, p. 115-116, pl. XLIII, fig. 1-6, pl. XLIV fig. 1-4, pl. LI, fig. 5; Derjugin, 1915, p. 357; McIntosh, 1923, p. 346-351, pl. CXVI, fig. 3; Augener, 1925, p. 115; Fauvel, 1927, p. 356-357, fig. 122i-o; Ditlevsen, 1929, p. 53; Zatsepin, 1948, p. 167, tab. XXXIX, 28 đ, gb, ga, h; Wesenberg-Lund, 1950a, p. 60; 1950b, p. 135; Hartmann-Schröder, 1971, p. 536; Nelson-Smith & Gee, 1966, p. 334, 339-340, fig. 2, fig. 4A, fig. 5B, fig. 7B; Zibrowius, 1968a, p. 107-109, pl. 2, fig. 1 -7; 1971b, p. 717-721, fig. 48-55; Bianchi, 1981, p. 55, fig. 17; Kupriyanova & Jirkov, 1997, p. 213-215, fig. 5A-G, map 5.

Hydroides norvegicus: Jirkov & Kupriyanova, 2001, p. 563-564; Moen, 2006, p. 118-199 (a translation of the original description); ten Hove & Kupriyanova, 2009, p. 54.

Material examined. Table 1. # 8 (tubes); # 132 (tubes); # 133 (1 and tubes); # 150 (tubes); # 182 (1); # 295 (1); # 297 (1 and tubes); # 302 (17); # 303 (1); # 307 (7); # 308 (3); # 309 (1); # 310 (17 and tubes); # 312 (1); # 313 (24); # 313 (9); # 315 (1); # 316 (1 and tubes); # 317 (6); # 321 (3 and tubes); # 323 (2); # 340 (6 and tubes); # 342 (2); # 343 (tubes); # 345 (? 100); # 346 (tubes); # 348 (9); # 349 (6); # 350 (7); # 351 (7); # 352 (2); # 353 (2); # 354 (1); # 357 (tubes); # 367 (1); # 387 (1); # 388 (20); # 389 (16); # 390 (9); # 391 (18); # 392 (31 and tubes); # 393 (2 spec.); # 395 (1); # 397 (25); # 398 (1); # 399 (79); # 400 (17); # 404 (1); # 406 (15); # 407 (17); # 408 (tubes); # 409 (1); # 410 (64); # 411 (tubes); # 413 (5); # 414 (tubes); # 415 (9); # 416 (7); # 417 (2); # 418 (57); # 419 (1); # 420 (13 and tubes); # 422 (12); # 423(2); # 424 (72); # 462 (7 and tubes); # 464 (4); # 466 (7); # 468 (2); # 469 (3); # 480 (2 and tubes).

Description. Tubes (Fig. 8A) up to 3 mm in diameter, white opaque, circular in cross-section; attached to substrate throughout entire length, distal end sometimes free. Can cover sizable parts of substrate due to gregarious settlement. Surface of tube with characteristic wavy growth rings (Fig. 8A, B). Tube peristomes or ring-shaped thickening absent.

Body length, without radioles, up to 29 mm. Colour of radioles of live specimens white with brown bands, body red.

About ten pairs of radioles connected by short inter-radiolar membrane. Radiolar eyes absent.

Peduncle cylindrical, thicker than normal radioles, inserted as second dorsal radiole on one side. Operculum (Fig. 8D) consists of distal verticil inserted at center of proximal funnel. Verticil formed of spines of chitin-like material, each spine bearing 2–4 pairs lateral spinules. Opercular radiole opposite to peduncle short, underdeveloped, bearing rounded pseudoperculum. Some specimens with two equally developed opercula.

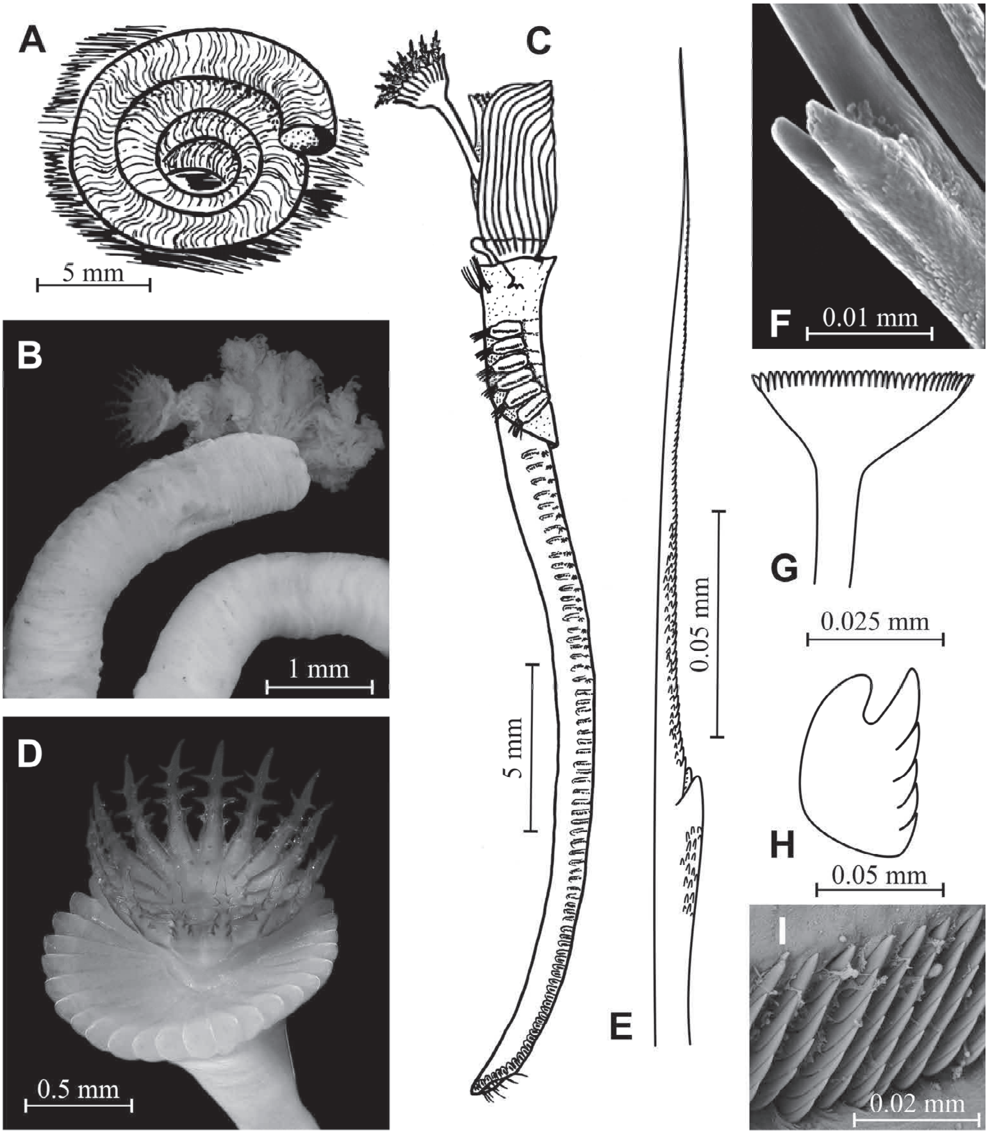

Figure 8. *Hydroides norvegicus*. A – tube; B – anterior tube part; C – entire body, lateral view; D – operculum; E – bayonet collar chaeta; F – details of bayonet collar chaeta; G – flat trumpet-shaped abdominal chaeta; H – thoracic uncinus, lateral view; I – thoracic uncini, profile view. A, C, E, G, H – from Kupriyanova & Jirkov (1997). B, D – photo E. Wong, F, I – photo H.A. ten Hove.

Collar trilobed with deep lateral notches and small, wart-like protuberances at base of junction of lateral and ventral lobes present. Tonguelets absent. Collar with smooth edge, not covering radiolar lobes. Thoracic membranes wide, well developed, continuing to end of thorax and forming a long ventral apron covering 2–4 anterior abdominal chaetigers. No distinct prostomium.

Seven thoracic chaetigers, including 6 with uncini (Fig. 8C). Rows of thoracic neuropodia located almost at mid-lateral line of thorax or shifting slightly ventrally, no triangular depression. Large collar chaetae limbate and bayonet with finely denticulate zone proximal to double basal bosses (Fig. 8E, F). Distal blade of bayonet chaetae finely denticulate. Other thoracic chaetae limbate, *Apomatus* chaetae absent. Thoracic uncini (Fig. 8H, I) saw-shaped with 5–6 teeth, anterior fang pointed.

Achaetous anterior abdominal zone absent. Up to 60 abdominal chaetigers. Abdominal notopodia shifted dorsally where touching each other. Abdominal chaetae of anterior and middle chaetigers (Fig. 8G) very small, asymmetrical flat trumpet-shaped, denticulate distally, replaced by long capillary chaetae on posterior chaetigers. Abdominal uncini saw-shaped with 5–6 teeth, anterior fang pointed, similar to thoracic uncini, but smaller. Posterior glandular pad absent.

Remarks. The operculum of *H. norvegicus* with 2–4 pairs of lateral spinules is very similar (practically indistinguishable) to that of *Hydroides elegans* (Haswell, 1883), described from Sydney Harbour*,* and a widely distributed (sub)tropical port-fouling invasive species. These two species have been confused on numerous occasions, but they differ by the structure of modified collar chaetae that are bayonet, with two large bosses in the former, but with a proximal rasp made of numerous small teeth in the latter. *H. elegans* (as well as *H. norvegicus*) can also easily be confused in tropical Indo-Pacific regions with *Hydroides centrospina* Wu & Chen, 1981, *Hydroides longispinosus* Imajima, 1976, *Hydroides multispinosus* Marenzeller, 1885, and *Hydroides nanhaiensis* Wu & Chen, 1981, species that also have verticils with lateral spinules. The nominal species *H. longispinosus* and *H. centrospina* have verticils with single, relatively long, central spines, either smooth in the former or with additional small denticles in the latter, whereas *H. multispinosus* and *H. nanhaiensis* have numerous (more than 4) pairs of lateral spinules. Whether these four nominal species are distinct is unknown.

Ecology. In the Arctic recorded from depths of 23–650 m corresponding to an average temperature of 7.7º C attached to rocks and gravel in various softer substrates excluding silty clay (Kupriyanova & Badyaev, 1998). Available literature data on reproduction and development of *H. norvegicus* mostly belong to *H. elegans* (see below and Kupriyanova et al., 2001), but it is a free spawner with planktotrophic larvae as described for all up to date studied *Hydroides* species.

Distribution. According to Kupriyanova & Jirkov (1997) the species is reported in the Arctic from Barents, Norwegian, North Seas, and Iceland. According to Moen (2006), the distribution of *H. norvegicus* extends in the Arctic from Spitsbergen, the east coast of Greenland, Iceland and along the Norwegian coastline. In boreal waters it continues along the European west coast to Gibraltar and into the Mediterranean. *H. norvegicus* is a strictly boreal/Mediterranean (in somewhat deeper water) species; all records under this name from port-fouling and/or (sub)tropical areas should be checked, but mostly belong to *H. elegans*.

Genus *Metavermilia* Bush, 1905

Type-species: *Vermilia multicristata* Philippi, 1844

Tube white, opaque, peristomes may be present, as well as several keels, sometimes denticulate. Granular overlay generally absent. Operculum with chitinous, non-calcified endplate, sometimes quite complex multi-tiered structures, or endplate may be absent. Peduncle flattened, ribbon-like, without distal wings; formed from second dorsal radiole on one side. Constriction may be present. Pseudoperculum may be present. Radioles arranged in semi-circles to short pectinate, up to 18 per lobe. Inter-radiolar membrane and stylodes absent. Radiolar eyes may be present. Mouth palps absent. 7 thoracic chaetigerous segments. Collar trilobed, tonguelets between ventral and lateral collar parts absent. Length of thoracic membranes variable, ending at thoracic segments 3–7, sometimes forming ventral apron on anterior abdominal segments. Large collar chaetae limbate. *Apomatus* chaetae present. Thoracic uncini saw-shaped with up to 15 teeth, anterior tooth blunt, rounded. Triangular depression absent. Abdominal chaetae with flat narrow geniculate blade with rounded teeth; uncini saw- or rasp-shaped. Achaetous anterior abdominal zone absent. Posterior capillary chaetae and glandular pad present.

Remarks. The genus *Metavermilia* was revised and emended by Zibrowius (1971a) for four species; since that revision, 10 more species have been added (see Nishi et al., 2007 for history and literature review). Ten Hove & Kupriyanova (2009) reported 14 species in their review. Most recently the new species *Metavermilia zibrowii* Bailey-Brock & Magalhaes, 2012 was described from Cross Seamount, southwest of Hawaii.

Fifteen species, one from the Arctic.

Metavermilia arctica Kupriyanova, 1993

(Fig. 9A-F)

Metavermilia arctica Kupriyanova, 1993, p. 155-157, fig. 1A; Kupriyanova & Jirkov, 1997, p. 215; Jirkov & Kupriyanova, 2001, p. 564-565, text figures 1-9; Nishi et al., 2007, p. 49, 54-55, fig. 4G; ten Hove & Kupriyanova, 2009, p. 10, 62.

Material examined. Table 1. # 331 (1); # 379 (4); # 426 (1); # 461 (1).

Description. Tube white, opaque, up to 1.5 mm in diameter, circular in cross-section and irregularly coiled; attached to substrate throughout entire length. Surface of tube pitted by numerous shallow oblong alveoli, each bounded laterally by inconspicuous ridges arranged somewhat irregularly, not forming keels (Fig. 9A).

Body length, without radioles, up to 16 mm. Colour of live specimens unknown.

Branchiae with 8–11 pairs of radioles not connected by inter-radiolar membrane. Length of branchial lobes approximately equal to or slightly shorter than length of collar. Radiolar eyes unknown.

Second dorsal radiole large flat ribbon-like peduncle with regular annulations (Fig. 9C). Operculum inverted cone covered with yellowish distal plate, which may be flat or slightly concave in centre (Fig. 9C). Pseudoperculum absent.

Collar trilobed with wide dorsal lobe and two narrow lateral ones. Tonguelets absent. Spotty pigmented thoracic membrane short, reaching to border between 2nd and 3rd chaetiger (Fig. 9B). No distinct prostomium.

Seven thoracic chaetigerous segments, including 6 with uncini (Fig. 9C). Thoracic neuropodia not shifted to the mid-ventral line of thorax, no triangular depression. Large collar chaetae (Fig. 9D) same as other thoracic chaetae. *Apomatus chaetae* present in posterior thoracic segments. Thoracic tori several times (6-8) longer than abdominal ones. Thoracic uncini saw-shaped with 10 teeth, anterior fang blunt rounded (Fig. 9E, F).

Achaetous anterior abdominal zone absent. Up to 80 abdominal chaetigers. Abdominal chaetae flat geniculate, with triangular denticulate blade, replaced by long capillary chaetae in posterior segments. All abdominal uncini rasp-shaped with about 12-15 teeth in profile, 2–3 teeth per row. Posterior glandular pad present.

Remarks. The simple operculum of *M. arctica* is also typical for some other species of the genus such as *Metavermilia annobonensis* Zibrowius, 1971a, *Metavermilia multicristata* (Philippi, 1844), *Metavermilia ogasawaraensis* Nishi, Kupriyanova & Tachikawa, 2007*, Metavermilia taenia* Zibrowius, 1971a, *Metavermilia nanshaensis* Sun, 1998*, Metavermilia gravitesta* Imajima, 1978*, Metavermilia inflata* Imajima, 1977, *Metavermilia ovata* Imajima, 1978 and *M. zibrowii* Bailey-Brock, Magalhaes, 2012. Out of those species, *M. inflata* stands out because of its soft globular operculum without any sign of distal plate, while the operculum of *M. ovata* is unusual in carrying a distinctive ovoid process terminating with two hooks on thick concave distal plate. The remaining species of the genus (*Metavermilia nates* Zibrowius, 1971a*, Metavermilia acanthophora* (Augener, 1914)*, Metavermilia spicata* Imajima, 1977*,* and *Metavermilia yamazotoi* Imajima & ten Hove, 1989) have easily recognizable complex multi-tiered opercula. The inverted conical operculum of *M. arctica* with flat endplate resembles the opercula of *M.*

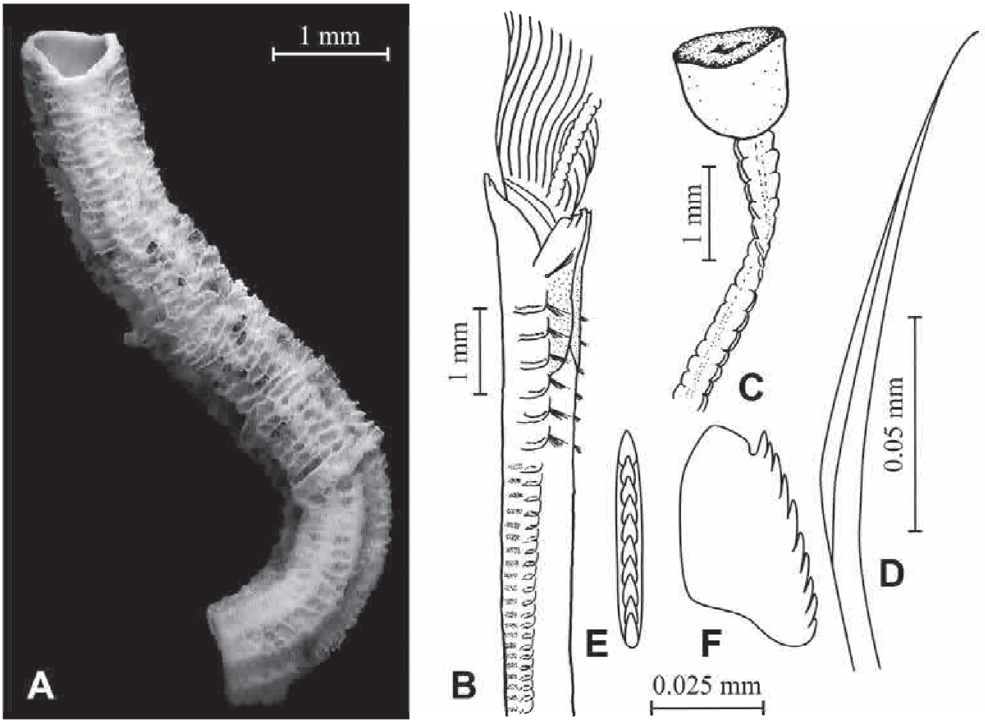

Figure 9. *Metavermilia arctica*. A – tube fragment; B – body, lateral view; C – operculum and peduncle; D – large collar chaeta; E – thoracic uncinus, profile view; F – thoracic uncinus, lateral view. B-F – from Kupriyanova (1993). A – photo A.V. Rzhavsky.

annobonensis, *M. multicristata*, *M. nanshaensis* and *M. ogasawarae* that also have a conical tubercle in the centre. *M. arctica* is has poorly developed thoracic membranes reaching thoracic chaetiger 4 as have *M. annobonensis, M. ogasawarae,* and *M. nanshaensis*. Thoracic membranes extend to thoracic chaetiger 7 in *M. acanthophora, M. multicristata, M. nates* and *M. taenia*, and chaetigers 5–6 in the other six species. *M. arctica* differs from all other species in the morphology of its tube, with its honey-comb sculptured surface made of numerous keels and transverse ridges.

Ecology. In the Arctic found at depths of 120–350 m corresponding to a temperature of 2.38º–7.27ºC, on pebble-stone grounds as well attached to stones in muddy sand (Kupriyanova, 1993). Reproduction unknown.

Distribution. Known only from the type series: South-east coast of Greenland; Norwegian Sea near Faroes; Barents Sea (Norway).

Genus *Placostegus* Philippi, 1844

Type-species: *Serpula tridentata* Fabricius, 1779

Tube triangular in cross-section, with denticulate keels, transparent or semi-transparent, often only attached to substrate at the base, collar-like rings absent. Granular overlay absent. Operculum inverse conical, with chitinous endplate, cup-shaped. Peduncle cylindrical, smooth, without wings, gradually merging into operculum, at most with shallow constriction; inserted at base of radioles on one side, between first and second normal radiole and maximally covering base of first three radioles. Pseudoperculum absent. Radioles arranged in semi-circles, up to 24 per lobe; inter-radiolar membrane, radiolar eyes and stylodes absent. Mouth palps present. Six thoracic chaetigerous segments. Collar tri- to penta-lobed, collar edge may be almost laciniate; tonguelets between ventral and lateral collar parts present. Thoracic membranes long, forming ventral apron across anterior abdominal segment. Collar chaetae absent; collar region with girdle of reddish ocelli. *Apomatus* chaetae absent. All uncini sub-rectangular, rasp-shaped with > 20 teeth in profile, and up to eight small teeth in a row; anterior peg wide, flat, bluntly truncate, almost rectangular. Thoracic triangular depression absent. Abdominal chaetae true trumpet-shaped, with distal triangular blade. Achaetous anterior abdominal zone present. Long posterior capillary chaetae may be present. Posterior glandular pad absent.

Remarks. *Placostegus* is one of several serpulid genera (including *Vitreotubus* Zibrowius, 1979, *Neomicrorbis* Rovereto, 1904 and several spirorbin taxa) with an entirely vitreous tube. It is completely transparent, glass-like in live animals, but becomes milky-white semi-transparent in old tubes and after preservation in formalin. The tube in *Placostegus incomptus* Ehlers, 1887 shows a remarkable dual appearance, proximally with closely set transverse ribs, distally smoothly triangular. Fauvel (1927, fig. 128i) and Imajima (1978, fig. 9c) mentioned a chitinous talon projecting from the endplate into the opercular ampulla.

Placostegus has one diagnostic autapomorphy, the presence of a "collar" of bright red ocelli in the region where in other genera collar-chaetae are found (e.g., Langerhans, 1884: fig. 38b, Ehlers, 1887: fig. 3, Hartman, 1969: fig. 2; ten Hove & Kupriyanova, 2009: fig. 1f, this paper Pl. 1F as vaguely visible red spots immediately behind tube mouth).

Seven species, one from the Arctic.

Placostegus tridentatus (Fabricius, 1779)

(Fig. 10A-H, Pl. 1F)

Serpula tridentata Fabricius, 1779, p. 385.

Placostegus tridentatus: Wollebæk, 1912, p. 117-118, pl. XLVII, fig. 1-8, pl. LI, fig. 2,3; McIntosh, 1923, p. 370-374, pl. CXXII, fig. 3, pl. CXXXI, fig. 8; Fauvel, 1927, p. 373, fig. 128; Ditlevsen, 1929, p. 53-54; Zatsepin, 1948, p. 167, tab. XXXIX, 26 a, t, p; Wesenberg-Lund, 1950a, p. 60; 1950b, p. 135; Hartmann-Schröder, 1971, p. 529, Addendum184; Nelson-Smith & Gee, 1966, p. 350, fig. 12A-C; Nelson-Smith, 1967, p. 38, fig. 30; Bianchi, 1981, p. 116-118, fig. 44a-f; Kupriyanova & Jirkov, 1997, p. 215-217, fig. 5A-F, map 6; Jirkov & Kupriyanova, 2001, p. 565-566, text figures 1-6, map.

Material examined. Table 1. # 10 (tubes); # 29 (1); # 53 (tubes); # 54 (1); # 55 (1 and tubes); # 56 (2); # 57 (1 and tubes); # 71 (3 and tubes); # 126 (tubes); # 128 (tubes); # 129 (tubes); # 130 (tubes); # 131 (tubes); # 133 (2); # 134 (tubes); # 135 (2 and tubes); # 136 (tubes); # 137 (tubes); # 138 (2); # 139 (2 and tubes); # 140 (1 and tubes); # 143 (tubes); # 145 (tubes); # 148 (tubes); # 149 (1 and tubes); # 150 (tubes); # 151 (2 and tubes); # 152 (tubes); # 153 (tubes); # 154 (1 and tubes); N 48 (tubes); N 49 (tubes); # 164 (1 and tubes); # 167 (tubes); # 171 (2 and tubes); # 173 (tubes); # 174 (1 and tubes); # 176 (1); # 177 (tubes); # 179 (2 and tubes); # 187 (1); # 238 (tubes); # 246 (tubes); # 296 (15); # 297 (1); # 298 (2); # 299 (4); # 302 (tubes); # 304 (15); # 305 (1); # 306 (2); # 307 (1); # 317 (9); # 320 (1); # 321 (1 and tubes); # 322 (1); # 323 (155 and tubes); # 325 (2 and tubes); # 330 (tubes); # 332 (3 and tubes); # 336 (1); # 340 (tubes); # 349 (1); # 350 (tubes); # 356(6); # 357 (2 and tubes); # 359 (tubes); # 361 (tubes); # 366 (1 and tubes); # 369 (2 and tubes); # 370 (3); # 371 (1and tubes); # 380 (tubes); # 381 (1); # 382 (2 and tubes); # 384 (1); # 390 (1); # 393 (4); # 394 (8 and tubes); # 406 (1); # 408 (tubes); # 410 (8 and tubes); # 414 (tubes); # 419 (3); # 422 (35 and tubes); # 423 (2 and tubes); # 425 (5); # 463 (tubes); # 464 (3); # 465 (1); # 466 (12); # 467 (4); # 469 (2); # 471 (tubes); # 472 (tubes); # 473 (2 and tubes); # 474 (1 and tubes); # 475 (1 and tubes); # 481 (1 and tubes).

Description. Tubes (Fig. 10A, B) triangular in cross-section, thick-walled, transparent or opalescent (semi-transparent). Keels of tube continuing into large spines at tube opening. Tubes usually attached to substrate by the proximal part only, distal part free, often spirally coiled.

Body length, without radioles, up to 23 mm. Radioles of live specimens white with red or brown bands, body red.

Up to 24 radioles not connected by an inter-radiolar membrane. Radiolar eyes absent.

Peduncle smooth, cylindrical; wider than normal radioles and slightly narrower proximally; inserted medio-dorsally at base of either radiolar lobe, covering 2–3 normal radioles. Operculum a narrow cone covered with concave (sometimes almost flat) brown endplate of chitin-like material with concentric growth rings. Pseudoperculum absent.

Collar trilobed, thin, long, covering radiolar lobes and proximal part of radioles. Lateral notches of collar deep, lobes approximately of same length, dorsal lobe wider than lateral lobes. Tonguelets present. Collar margin smooth. Thoracic membranes continuing to end of thorax forming free apron ventrally. No distinct prostomium.

Six thoracic chaetigers, all with uncini, collar chaetae absent. Thoracic notopodia close to each other, not shifting ventrally, no triangular ventral depression. Thoracic chaetae limbate, no *Apomatus* chaetae. Thoracic uncini (Fig. 10G, H) rasp-shaped, with numerous teeth per row, anterior peg rounded.

Achaetous abdominal zone present. Up to 70 abdominal chaetigers. Abdominal tori short. Chaetae in anterior and middle abdominal chaetigers (Fig. 10F) small, true trumpet-shaped, with hollow denticulate tips. Chaetae of posterior abdominal segments capillary, slightly longer than anterior chaetae. Abdominal uncini similar to thoracic uncini, but smaller. Posterior glandular pad absent.

Remarks. All the species of the genus, except for *Placostegus californicus* Hartman, 1969 from Southern California, have been described before 1900 and the genus has never been revised, therefore, morphological differences among the species and even validity of the species are unclear. The genus is badly in need of revision.

Ecology. In the Arctic found at depths of 24–715 m, corresponding to average temperature of 5.63º C on various soft substrates (excluding fine sand) with additional rocks (Kupriyanova & Badyaev, 1998).

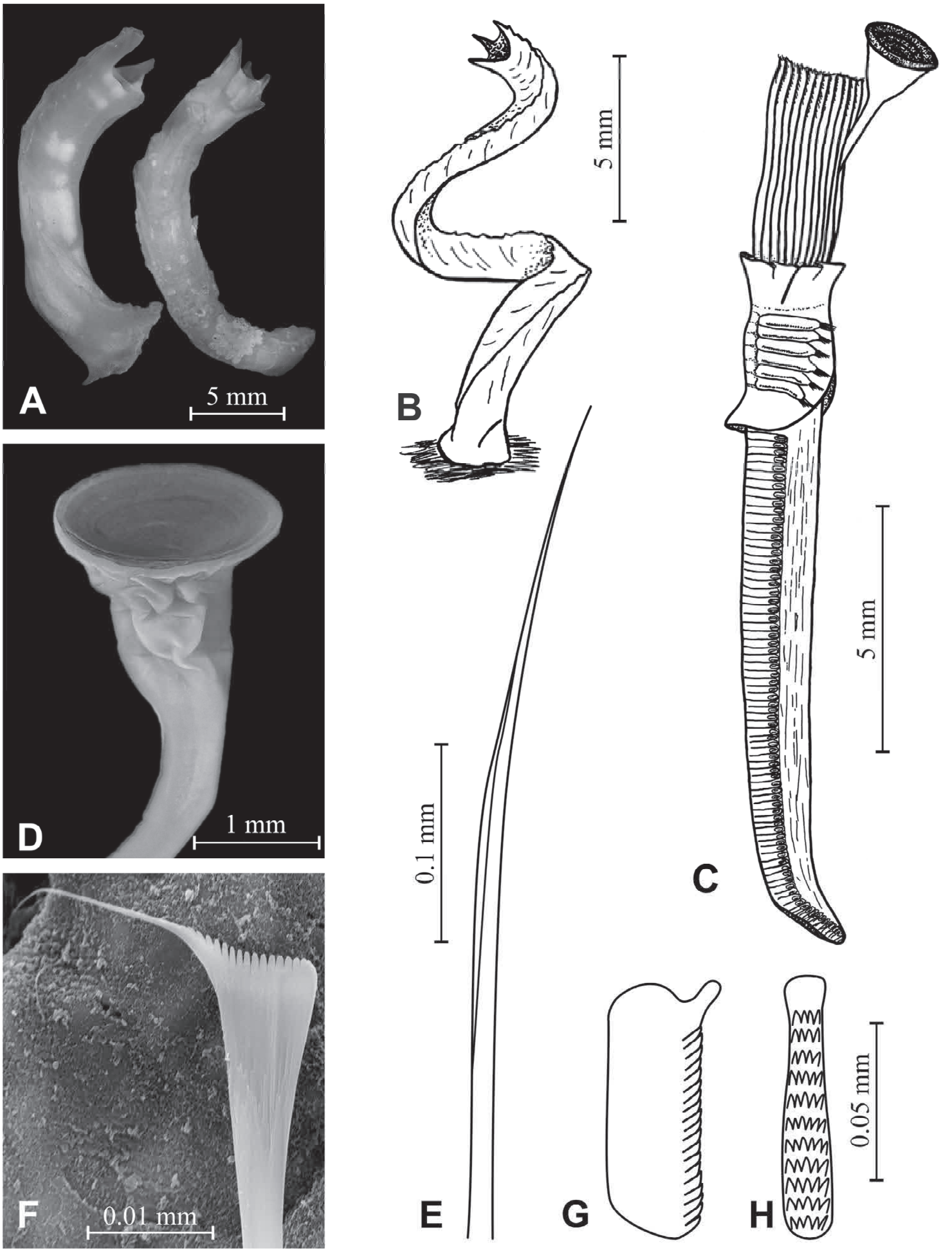

Figure 10. *Placostegus tridentatus*. A, B – tubes; C – entire body, lateral view; D – operculum; E – collar chaeta; F – abdominal chaeta; G – thoracic uncinus, lateral view; H – thoracic uncinus, profile view. B, C, E, G, H – from Kupriyanova & Jirkov (1997). A, D – photo E. Wong, F – photo E. Kupriyanova.

Spermatozoa have spherical heads, characteristic of broadcast spawning species. Egg size around 100 µm, suggesting lecithotrophic larval development (Kupriyanova, unpubl.)

Distribution. Barents, Norwegian, Greenland Seas, Iceland in the Arctic**.** Reported from the North Atlantic European waters, including UK, Greece, Portugal, Scotland, and Spain (Bellan, 2001). Records from the Indo-West Pacific are questionable (Kupriyanova, unpubl.).

Genus *Protis* Ehlers, 1887

Type species: *Protis simplex* Ehlers, 1887.

Tube white, opaque, with or without keels, flaring peristomes absent. Granular overlay absent. Operculum absent or one or more membranous globular opercula present on normal pinnulate radiole. Arrangement of radioles pectinate, up to 20 per lobe. Interradiolar membrane absent. Radiolar eyes not observed. Stylodes absent. Mouth palps absent. Seven (six in *P. akvaplani*) thoracic chaetigers. Collar trilobed with entire edge, tonguelets absent. Thoracic membranes typically to the end of thorax (mid-thorax in *P. akvaplani*) and may form ventral apron. Large collar chaetae fin-and-blade and limbate. *Apomatus* chaetae present. Thoracic uncini saw-shaped with about 6 teeth, anterior fang pointed. Triangular depression absent. Abdominal chaetae flat narrow geniculate with rounded teeth, slightly more triangular blade in *Protis hydrothermica* ten Hove & Zibrowius, 1986. Abdominal uncini rasp-shaped in all segments, with up to 6 teeth in profile, approximately 5–7 teeth in a row above fang. Achaetous anterior abdominal zone absent. Long posterior capillary chaetae present. A posterior glandular pad may be present.

Remarks. According to the original diagnosis, the lack of an operculum is a characteristic feature of *Protis* Ehlers, 1887. *Protis* was erected for the species *simplex* Ehlers, 1887. *Protula arctica* Hansen, 1878, was later referred to the genus *Protis* by Eliason (1951), followed by Zibrowius (1969) who, moreover, suggested that *Protula arctica* was a synonym of *Protis simplex*. The former species, *P. simplex* was designated the type species of the genus by Hartman (1959).

Ten Hove & Zibrowius (1986) reformulated the diagnosis and with the description of the abyssal *Protis polyoperculata* Kupriyanova, 1993b, it was further extended to include individuals with one or more opercula. Rzhavsky et al. (2013) again emended the diagnosis to include *P. akvaplani* with six thoracic chaetigers, short thoracic membranes and tubes with a high keel from the Barents Sea.

Seven species (eight if the nominal taxon *Salmacina chilensis* Gallardo, 1969 belongs to this genus), two of them known from the Arctic (ten Hove & Kupriyanova, 2009; Rzhavsky et al., 2013).

Protis akvaplani Rzhavsky, Kupriyanova & Sikorsky, 2013

(Fig. 11A-F)

Protis akvaplani Rzhavsky et al., 2013, p. 29-31, fig. 2.

Material examined. Table 1. # 491 (1); # 492 (2); # 493 (2); # 494 (1); # 497 (1); # 498 (1); # 499 (1); # 537 (1).

Description. Tube white, entirely opaque, circular in cross-section, mostly attached to substrate (although only tube fragments were present in the material), with very distinct high sharp keel (Fig. 11A), up to 1 mm in diameter.

Body length, without radioles, up to 5 mm. Colour of live specimens unknown.

Each lobe bearing five radioles with long thin pinnules, arranged pectinately, not connected by an inter-radiolar membrane. Radiolar eyes absent.

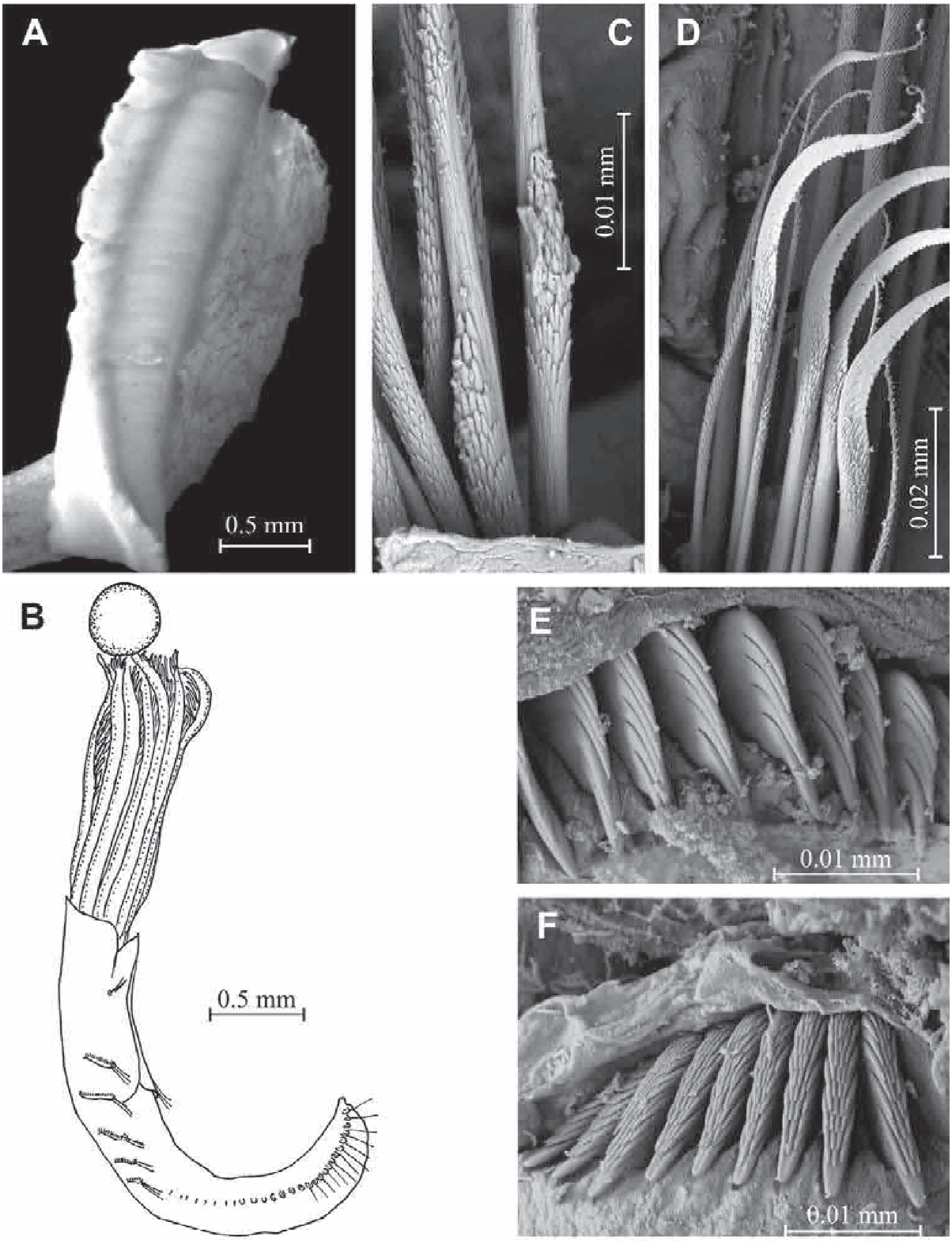

Figure 11. *Protis akvaplani.* A – tube; B – entire body, lateral view of holotype; C – modified fin-and-blade collar chaetae; D – thoracic chaetae, including *Apomatus* chaetae; E – thoracic uncini; F – abdominal uncini. A-F – from Rzhavsky et al. (2013). A, C-F – photo E. Kupriyanova.

Operculum absent or present, if present, a membranous transparent globular vesicle (Fig. 11B) on normal pinnulated second radiole. Pseudoperculum absent.

Collar with entire edge, large, covering radiolar lobes. Trilobed, medio-ventral lobe distinctly higher and wider than lateral lobes. Tonguelets absent. Collar continuous with wide thoracic membranes, ending as rounded flaps after 3rd thoracic segment, no apron (Fig. 11B). No distinct prostomium.

Thorax with six segments, five of them with uncini (Fig. 11B). Thoracic tori located more or less at mid-lateral line of thorax, not shifting ventrally, not forming triangular depression. Large collar chaetae limbate and modified fin-and-blade chaetae, with distally blade separated from proximal denticulate zone by wide gap (Fig. 11C). Subsequent chaetae limbate and capillary, *Apomatus* chaetae present in posterior thoracic segments (Fig. 11D). Uncini along entire thorax saw-shaped, with 5–6 teeth and pointed anterior fang (Fig. 11E).

Achaetous anterior abdominal zone absent. Abdomen with up to 40 chaetigers. Abdominal tori short. Abdominal chaetae flat narrow geniculate with rounded teeth and tapering tip, replaced by distinct long capillary chaetae in posterior chaetigers. Uncini rasp-shaped, with pointed fang and 7–8 teeth in profile, 3–4 teeth per row (Fig. 11F). Posterior glandular pad present.

Remarks. Although species within the genus *Protis* are difficult to distinguish, *P. akvaplani* shows very distinct characters, clearly setting it apart from *P. arctica* also known from the Arctic and all other species of the genus: it has only six thoracic chaetigerous segments, short thoracic membranes ending after the 3rd thoracic chaetiger, and a tube with a very distinct high keel.

Ecology. Found at depths of 300–317 and 586 m, on silted sediments composed mainly of sponge spicules. Reproduction unknown.

Distribution. Known only from the Barents Sea off Norway. Since the original description (Rzhavsky et al., 2013), the species was found in a location close to the type locality (Table 1, ## 497–499).

Protis arctica (Hansen, 1878)

(Fig. 12A-F)

Protis arctica: Ehlers, 1887, p. 328; Fauvel, 1909, p. 50-51; 1914, p. 325-327, pl. 30, fig. 18-25; Eliason, 1951, p. 142; Zibrowius, 1968a, p. 178; 1969, p. 15-17, fig. 6a-b; Zibrowius, 1977, p. 296; Kirkegaard, 1982, p. 257, fig. 2A-C ; Ben-Eliahu & Fiege, 1996, p. 19-24, fig. 8, 9; Kupriyanova & Jirkov, 1997, p. 220-222, fig. 8A-G, map 8; Jirkov & Kupriyanova, 2001, p. 568-569, text figures 1-7, map.

Protula arctica: Hansen, 1878, p. 13-14, pl. 10, fig. 1-10; 1882, p. 43, pl. 7, fig. 28-34; Levinsen, 1884, p. 202; Wesenberg-Lund, 1950a, p. 61; 1950b, p. 137.

Protula (?) *arctica*: Wollebæk, 1912, p. 120-122, pl. XLVIII, fig. 1-6, pl. L, fig. 7.

Material examined. Table 1. # 334 (1 and tubes); # 337 (9); # 338 (3); # 386 (1 and tubes); # 403 (6 and tubes); # 404 (56); # 438 (4).

Description. Tubes (Fig. 12A) white opaque, up to 3.5 mm in diameter, circular in cross-section, attached to substrate by proximal part only, distal end free. Tube surface rugose, with transverse growth rings.

Body length, without radioles, up to 25 mm. Colour of live specimens unknown.

Seventeen to twenty pairs of radioles not connected by inter-radiolar membrane at base. Radiolar lobes elongate, radioles arranged pectinately. Radiolar eyes not observed.

Operculum, if present, a membranous globular vesicle on a normal second radiole (Fig. 12D). Pseudoperculum on a normal radiole maybe present.

Collar trilobed, long, however not covering radiolar lobes (Fig. 12B, C). Lateral collar notches deep, with small warts at base. Dorsal lobe of collar slightly higher and distinctly wider than lateral lobes. Tonguelets absent. Thorax elongate, thoracic membranes

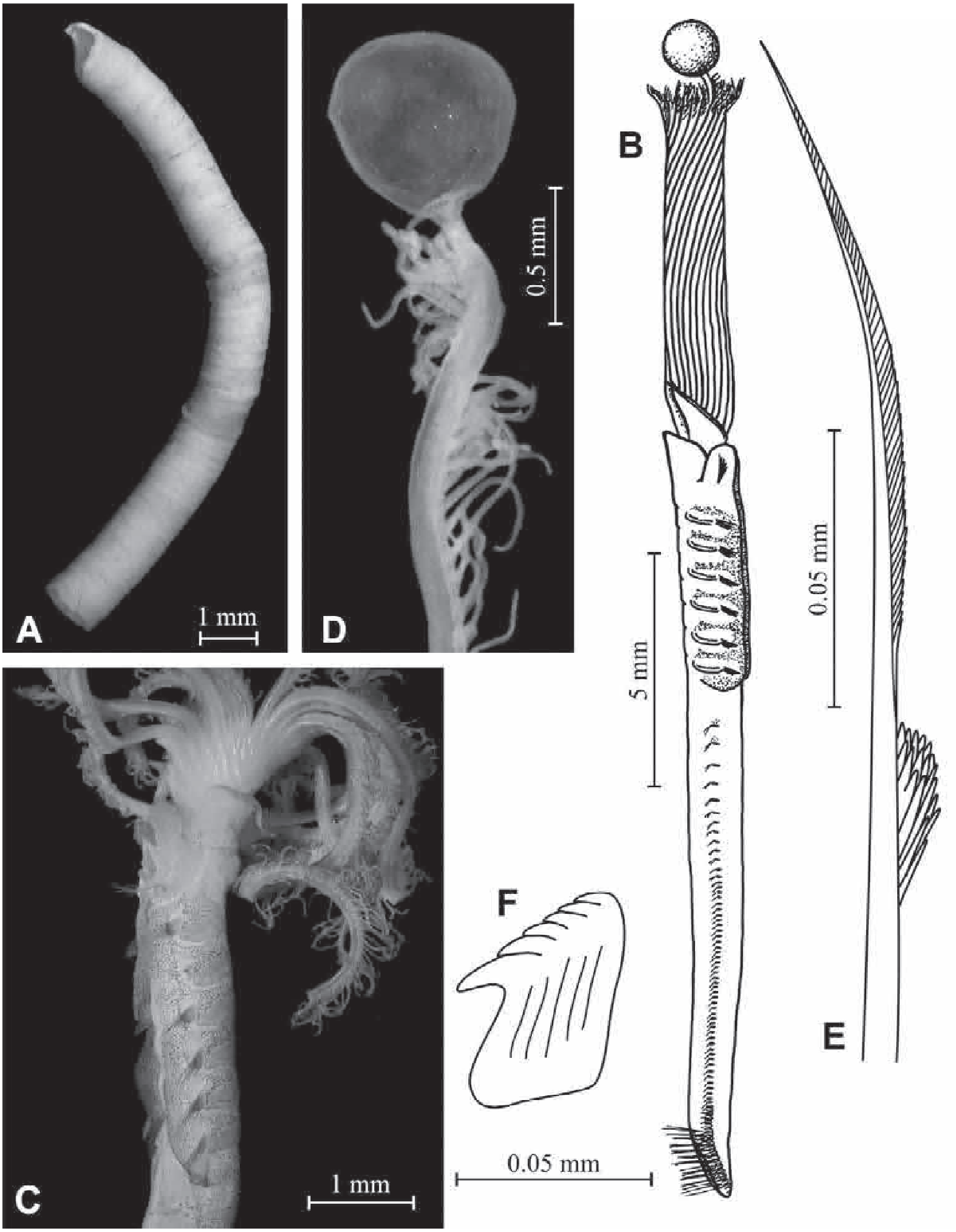

Figure 12. *Protis arctica*. A – tube; B – entire body, lateral view; C – anterior part including radiolar crown and thorax; D – operculum on pinnulated peduncle; E – collar chaeta; F – thoracic uncinus. B, E, F – from Kupriyanova & Jirkov (1997). A, C, D – photo E. Wong.

extending to last thoracic chaetiger, but not forming ventral apron (Fig. 12B, C). Surface of thoracic membranes and surface between thoracic notopodia with distinct pigment spots. No distinct prostomium.

Seven thoracic chaetigers, including 6 with uncini (Fig. 12B, C). Thoracic parapodia at mid-lateral line of thorax, not shifted ventrally, no triangular depression. Large collar chaetae (Fig. 12E) modified fin-and-blade, distal blade separated from proximal denticulate zone by wide gap. Other thoracic chaetae limbate and *Apomatus* chaetae. Thoracic uncini (Fig. 12F) saw-shaped with 5–7 teeth, anterior fang pointed.

Achaetous zone in anterior abdomen absent. Up to 100 abdominal chaetigers. Abdominal tori short. Abdominal chaetae short flat geniculate, with denticulate blade on anterior and middle chaetigers, replaced by long capillary chaetae posteriorly. Abdominal uncini similar to thoracic uncini, but smaller and rasp-shaped. Posterior glandular pad absent.

Remarks. The species was originally described (Hansen, 1878) based on two specimens from the North Atlantic (between Iceland and Norway) from 2127 m. The same specimens were re-described by Wollebæk (1912). Wesenberg-Lund (1950a) reported new specimens from the Atlantic sector of the Arctic; however, at least part of her material re-examined by Zibrowius (1969) and ten Hove (pers. comm.) turned out to be *P. tubularia*. Zibrowius (1969) suggested that the remaining specimens in Wesenberg-Lund's collection taken from depths less than 100 m also belong to *P. tubularia*. Kirkegaard (1982) reported two specimens of *P. arctica* collected from the abyssal depths of the Central Arctic. He provided an illustration of an entire specimen, but did not give a diagnosis or details of the structure of chaetae and uncini. Fauvel (1909; 1914) reported *P. arctica* from the North Atlantic (Azores, Madeira) and provided a description accompanied by illustrations of chaetae and uncini. The southernmost record of *P. arctica* is that by Eliason (1951) from the Romanche Deep in the Central Atlantic (01º N, 18º 40 W in 5250 m).

Zibrowius (1969) summarized all previous records of the species and described one specimen from the abyssal equatorial Atlantic. His specimen differs from our material by a developed apron of the thoracic membranes, a character not mentioned in the original description. However, an apron was also missing in topotypical material from the Ingolf expedition examined by Ben-Eliahu & Fiege (1996). The specimens from the Mediterranean examined by Ben-Eliahu & Fiege (1996) were also lacking aprons and the authors consider the presence of an apron to be a full expression of a size-related character in species characterized by them.

A large specimen of *P. arctica* lacking a radiolar crown from the abyssal equatorial Atlantic was reported by Eliason (1951), who compared it with the type material, but did not provide a detailed description. The report of the species from 30 m in the Gulf of Suez, Red Sea made by Amoureux et al. (1978) is rather doubtful because the location is too shallow and warm compared to all previous locations of the species. The specimen was re-examined in 1990 by ten Hove and identified as ?*Floriprotis* Uchida, 1978 (pers. comm.).

P. simplex, described from a single specimen found in the Gulf of Mexico was considered a juvenile of *P. arctica* by Eliason (1951) and Zibrowius (1969). No comparative study was performed, and the only reason for synonymizing the species was the absence of “confirmed features which allow a specific distinction between the forms” (Zibrowius 1969). Comparative studies are needed to confirm or reject this synonymy.

P. arctica clearly differs from *P. akvaplani* by the number of thoracic segments (7 in the former versus 6 in the latter), long thoracic membranes ending at the 7 thoracic chaetiger and tubes without keel. The morphological differences among other species of this poorly known deep-sea genus are unclear and revision is needed.

Kupriyanova & Jirkov (1997) report six specimens with one operculum and one with two opercula.

Ecology. In the Arctic *P. arctica* is found at the depths of 805–1820 m according corresponding to an average temperature of 0.85 ºC (Kupriyanova & Badyaev, 1998) attached to rocks or gravel in silt and silty clay. The deepest record is 5250 m (Eliason, 1951). The species broods lecithotrophic larvae inside the tube (Sanfilippo, pers. comm.).

Distribution. In the Arctic known from Norwegian, Greenland and Chukchi Seas (Kupriyanova & Jirkov, 1997). Zibrowius (1969) suggested that *P. arctica* is widespread in bathyal and abyssal depths of the Atlantic and would not penetrate into the Mediterranean because of high (around 13ºC) bottom temperature at great depths. However, Ben-Eliahu & Fiege (1996) based on their Mediterranean material stated that *P. arctica* is widespread and common in the Mediterranean from the western basin to Israel. They summarize the species distribution based on compiled records as deep-water Arctic region, Norwegian and Greenland provinces, North-South Eastern Atlantic, Caribbean-Gulf and Mediterranean provinces. According to Zibrowius (1969), the species is not found in the Indian Ocean and the record by Bellan (1964) is his erroneous quotation of Eliason (1951) that was also copied by Nelson-Smith (1967).

Genus *Protula* Risso, 1826

Type-species: *Serpula tubularia* Montagu, 1803.

Tube white, opaque, may be up to 2 cm across and 40 cm long, (semi-)circular in cross-section, keels and flaring peristomes absent. Operculum and pseudoperculum absent. Radioles arranged in two semi-circles to a spiral of up to 6 whorls, up to 320 per lobe in the largest species (e. g., *Protula superba* Moore, 1909). Inter-radiolar membrane present. Radiolar eyes may be present. Stylodes absent. Mouth palps present. 7 thoracic chaetigerous segments (however, see Remarks). Collar trilobed, tonguelets absent. Thoracic membranes long and wide, with undulating edge, forming ventral apron across anterior abdominal segments. Large collar chaetae limbate. *Apomatus* chaetae present. Thoracic and abdominal uncini rasp-shaped with approximately 30 teeth in profile, up to 6 rows of teeth above elongated rounded peg. Thoracic triangular depression absent. Abdominal chaetae with finely denticulate sickle-shaped blades or retro-geniculate. Achaetous anterior abdominal zone absent. Long posterior capillary chaetae present. Posterior glandular pad present.

Remarks. The genus *Protula* is the most problematic serpulid taxon and the phylogenetic basis for this genus is poorly defined (ten Hove, 1984). The generic characters are mainly negative characters, such as lack of operculum, lack of modified collar chaetae and lack of any characteristic ornamentation of the tubes. Because reliable species-level morphological characters are missing, species in the genus *Protula* have been described based on small differences in the shape of collar, number and arrangement of radioles, and even body and tube size, and thus, are practically indistinguishable.

Apomatus and *Protula* are separated mainly by the presence of the operculum. Hanson (1948) suggested that these genera should be fused into one because he showed that patterns of blood vessels in *P. tubularia*, *A. ampulliferus* and *A. similis* are similar to each other, but dissimilar to those of *Protula intestinum* (Lamarck, 1818). Ten Hove & Pantus (1985), also based on a study of blood vessel patterns, suggested that *Protula* and *Apomatus* are valid genera because their analysis showed consistent differences between operculate and non-operculate animals. A thorough revision of the *Protula*/*Apomatus* complex is the only way to resolve the present taxonomic confusion.

Twenty-three species according to ten Hove and Kupriyanova (2009), one species from the Arctic.

Protula tubularia **(Montagu, 1803)**

(Fig. 13A-E)

Serpula tubularia Montagu, 1803, p. 513-514.

Protula rudolphi Risso, 1826, p. 306.

Protula tubularia: McIntosh, 1923, p. 330-338, pl. CXV, fig. 6, pl. CXVI, fig. 2, pl. CXXI; fig. 5. pl. CXXX, fig. 7; Fauvel, 1927, p. 382, fig. 130a-l; Kupriyanova & Jirkov, 1997, p. 225-227, fig. 10A-H, map 10; Jirkov & Kupriyanova, 2001, p. 570-571, text figures 1-8, map.

Protula media: Zatsepin, 1948, p. 167, XXXIX, 25 a, ga, h, t.

Material examined. Table 1. # 6 (3); # 29 (1); # 30 (2); # 33 (1); # 34 (5); # 35 (1); # 36 (2); # 93 (1); # 123 (1); # 125 (1); # 127 (2); # 128 (1); # 133 (1); # 135 (1); # 141 (2); # 142 (1); # 144 (1); # 146 (2); # 148 (3); # 150 (tubes); # 154 (2); # 157 (1); # 159 (1); # 160 (1); # 161 (5); # 164 (1); # 165 (1); # 166 (1); # 167 (2); # 169 (1); # 172 (2); # 174 (1); # 175 (1); # 178 (1); # 180 (3); # 187 (2); # 193 (1); # 209 (2); # 238 (2);# 244 (2); # 245 (1); # 298 (3); # 300 (2); # 317 (1); # 319 (1); # 326 (1); # 332 (10); # 356 (tubes); # 360 (1); # 372 (3); # 373 (3); # 375 (8); # 376 (4); # 378 (2); # 382 (1); # 388 (3); # 389 (4); # 395 (3); # 401 (2); # 402 (1); # 405 (1); # 408 (1); # 431(3); # 465 (1); # 470 (1); # 508 (2 and tubes); # 522 (1); # 525 (2); # 529 (1); # 557 (6); # 576 (2).

Description. Tubes white, opaque, up to 5 mm in diameter, circular in cross-section, usually attached to substrate by proximal part only, distal part of tube free (Fig. 13A, B).

Body length, without radioles, up to 43 mm. Colour of live specimens red, crown maybe white.

Number of radioles varies from 15–50 pairs depending on size. Radioles connected by short inter-radiolar membrane. Radiolar eyes present, but observed in fresh material only. Operculum and pseudoperculum absent.

Collar trilobed, short, dorsally not covering base of radioles. Lateral collar notches shallow, one-half collar length. Lobes of equal length, dorsal lobe wider than lateral ones. Collar margin smooth. Tonguelets absent. Thoracic membranes to end of thorax forming wide apron ventrally (Fig. 13C). No distinct prostomium.

Seven thoracic chaetigers, including 6 with uncini. Thoracic neuropodial tori similar in length to abdominal notopodial tori. Thoracic tori widely separated and located more or less at mid-lateral line of thorax, not shifting ventrally, not forming triangular depression. Large collar chaetae (Fig. 13D) limbate with wide blade. Thoracic chaetae limbate and capillary in anterior thoracic chaetigers, complemented by *Apomatus* chaetae in posterior chaetigers. Thoracic uncini rasp-shaped, with numerous teeth in each row; anterior peg long, elongated rounded (Fig. 13E).

Achaetous zone in anterior abdomen short. Up to 140 abdominal chaetigers. Tori of abdominal notopodia shifted ventrally, almost touching each other on ventral side. Abdominal uncini rasp-shaped with up to 30 teeth in profile, up to 6 teeth per row above elongated rounded peg. Abdominal chaetae of anterior and middle chaetigers short, sickle-shaped, with curved distal blade; replaced by long capillary chaetae (in posterior chaetigers. Abdominal uncini similar to thoracic uncini, but smaller.

Remarks. In addition to the records given in the synonymic list, the nominal species *P. tubularia* has been recorded from all over the world; i.e., the Mediterranean (Zibrowius, 1968a), Red Sea (Amoureux et al., 1978; Vine & Bailey-Brock, 1984), South Africa

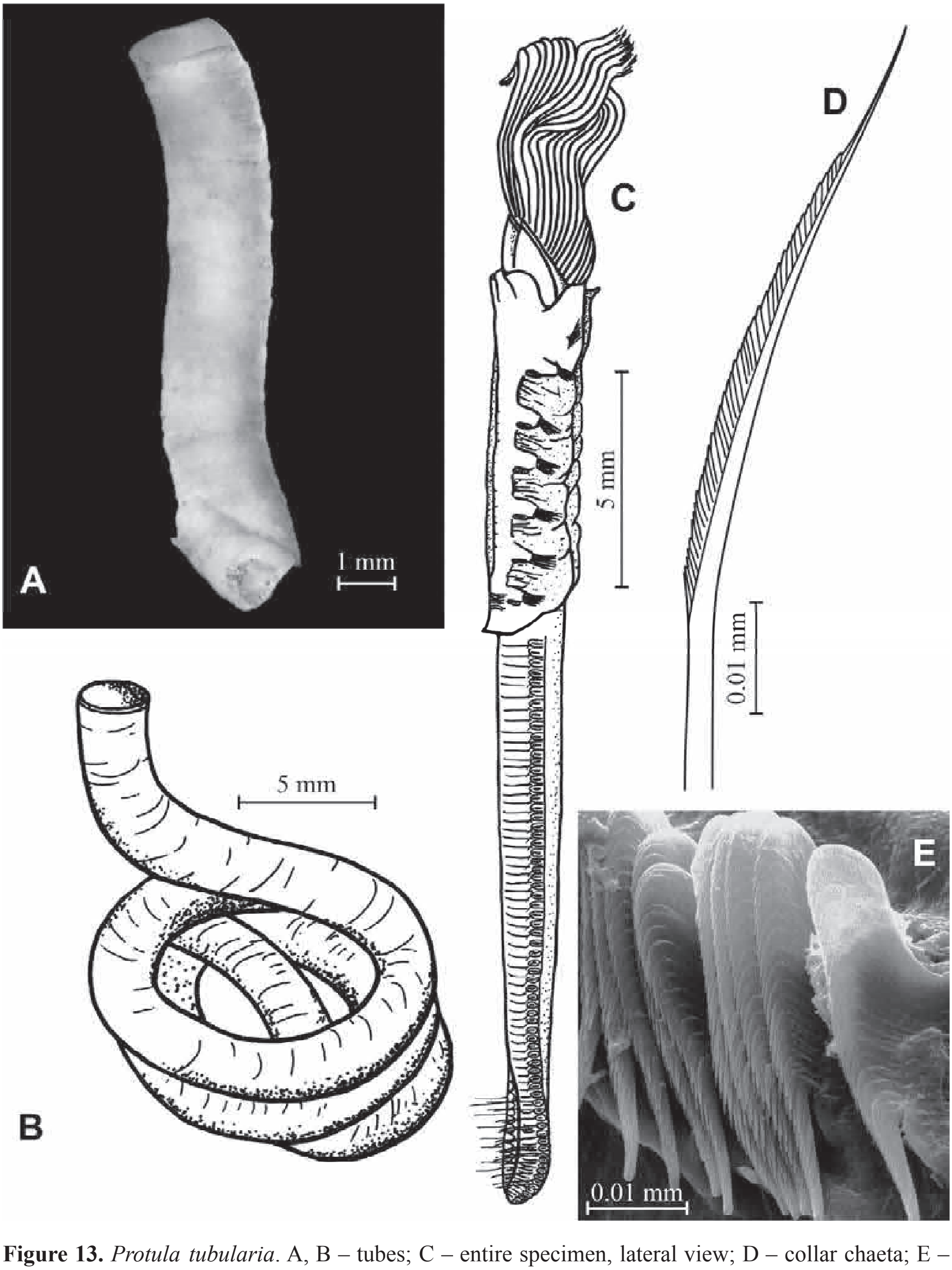

Figure 13. *Protula tubularia*. A, B – tubes; C – entire specimen, lateral view; D – collar chaeta; E – thoracic uncini. B-D – from Kupriyanova & Jirkov (1997). A – photo E. Wong, E – photo H.A. ten Hove.

(Day, 1961; 1967), India (Tampi, 1960), Australia (Day & Hutchings, 1979), Japan (Okuda, 1938; Uchida, 1978), Korea (Hong, 1984), and Ceylon (Pillai, 1971). Unfortunately, based on the literature one cannot determine whether this species indeed has such a wide distribution or, alternatively, records belong to several species. Species in the genus have been distinguished on the basis of size differences and chaetal structure without any indication of variability. The presence of radiolar ocelli is not a reliable character because pigments are not retained in preserved material. The operculum is absent according to all observations except of Hong (1984), who commented on the presence of an operculate *Protula* specimen in his material. A world-wide revision of *Protula* is the only way to resolve this taxonomic confusion.

Among arctic serpulids, *P. tubularia* is most similar to *A. globifer.* The species can be easily distinguished by the presence of opercula in the latter. If operculum is missing, they differ 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*. Because of the taxonomic problems outlined above, distinguishing the species within *Protula* is practically impossible until a world-wide revision of the genus is completed.

Ecology. In the Arctic found at depth 11–500 m corresponding to average temperature 3.81ºC attached to rocks, gravel in different soft substrates excluding fine sand (Kupriyanova & Badyaev, 1998).

Tampi (1960) reports that *P. tubularia* eggs are 85 µm in diameter and early larval development is lecithotrophic, but since his material comes from India, it is unlikely to be belong to true *P. tubularia*. Lecithotrophic larvae brooded in gelatinous masses outside tube orifice according to Kupriyanova et al. (2001).

Distribution. In the Arctic known from the Barents, Norwegian, Greenland Seas and around Iceland (Kupriyanova & Jirkov, 1997). Likely a North-Atlantic (including Mediterranean Sea) species like most shallow-water species found in the Arctic, but its true geographic distribution is unknown because the species boundaries are not understood.

Genus *Serpula* Linnaeus, 1758

Type-species: *Serpula vermicularis* Linnaeus, 1767, by subsequent designation (Heppell, 1963) under the plenary powers of the International Commission on Zoological Nomenclature (Evans & China, 1966).

Tube white, pink, orange, or yellowish, opaque; (semi)circular to trapezoidal in cross-section, rarely polygonal; keels, peristomes, a hyaline outer layer or granular overlay may be present. Operculum soft to cartilaginous, funnel shaped with crenulated edge (fused radii). Peduncle smooth, cylindrical, without wings; inserted just below and between first and second dorsal radiole on one side. In large specimens insertion outside the normal radioles, seemingly the first radiole. Radioles arranged in semi-circles, up to 50 per lobe in larger species. Pseudoperculum and inter-radiolar membrane present. Radiolar eyes may be present. Mouth palps present, though only to be observed with histological techniques (Orrhage, 1980). Stylodes absent. Seven (rarely nine) thoracic segments. Collar trilobed. Tonguelets absent, though wart-like protuberances may be present at base of cleft between ventral and latero-dorsal collar parts. Thoracic membranes long, forming ventral apron across anterior abdominal segments. Large collar chaetae bayonet-shaped and limbate. *Apomatus* chaetae absent. Uncini saw-shaped, with approximately 5 teeth, anterior fang pointed. Thoracic triangular depression present. Abdominal neurochaetae flat trumpet-shaped with denticulate edge; uncini similar to thoracic ones, smaller, anteriorly saw-shaped but becoming rasp-shaped towards the pygidium, with up to 12 teeth in profile, up to 8 teeth in a row. Achaetous anterior abdominal zone absent. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. *Serpula* is another very problematic serpulid genus. Although attribution of any given specimen to the genus *Serpula* is easy due to a very characteristic funnel-shaped operculum with rounded radii (however, see below), the number of taxonomic characters within the genus is limited and their variability is not documented enough to ensure the validity of many described species (see discussion in ten Hove & Jansen-Jacobs, 1984). Many of the original descriptions are very vague, and the characters typical for all species of the genus (such as the presence of bayonet-chaetae and a funnel-shaped operculum) have been used for specific diagnoses. Some nominal species were described based on incomplete or juvenile specimens. Moreover, juvenile *Hydroides* species, also characterized by an operculum with a single funnel-shaped operculum only, were often attributed to *Serpula* too (ten Hove & Ben-Eliahu, 2005, fig.7). The species within genus are distinguished by the shape of the opercular funnel, number of opercular radii, presence of the opercular constriction below the operculum, tube morphology and colouration, and, to a lesser degree, details of collar chaetae and thoracic membranes. The most commonly used meristic character, the number of opercular radii, shows significant population and ontogenetic variability (Kupriyanova, 1999). A much-needed revision of the genus is currently under way (Pillai et al., in prep.), and the list of "valid" species given by ten Hove & Kupriyanova (2009) is tentative only. Kupriyanova et al. (2008) demonstrated that the traditional genus *Serpula* most probably is paraphyletic and includes *Crucigera* Benedict, 1887.

Thirty-three species (according to ten Hove & Kupriyanova, 2009, see above), one from the Arctic.

Serpula vermicularis Linnaeus, 1767

(Fig. 14A-F, Pl. 1A)

Serpula vermicularis Linnaeus, 1767, p. 1267; Wollebæk, 1912, p. 116-117, pl. XLV, fig. 1-5, pl. XLVI, fig. 1-3, pl. L, fig. 1-3; Saemundsson, 1918, p. 232; Augener, 1925, p. 115; Ditlevsen, 1929, p. 52-53; Einarsson, 1941, p. 232; Wesenberg-Lund, 1950a, p. 59-60; 1950b, p. 134; 1953b, p. 4-5, fig. 1; Nelson-Smith & Gee, 1966, p. 339, fig. 5A, 7A; Nelson-Smith, 1967, p. 24, fig. 1, 2; Hartmann-Schröder, 1971, p. 528-529, Addendum186; Blake & Dean, 1973, p. 34; Kupriyanova & Jirkov, 1997, p. 227-229, fig. 11A-G, map 11; Jirkov & Kupriyanova, 2001, p. 571-572, text figures 1-7, map.

Material examined. Table 1. # 307 (1); # 310 (2); # 321 (2); # 335 (1); # 340 (1); # 345 (3); # 346 (tubes); # 349 (3 and tubes); # 350 (3 and tubes); # 352 (1 and tubes); # 356 (2); # 370 (tubes); # 385 (1); # 388 (3); # 392 (1); # 393 (2); # 395 (2); # 396 (2); # 397 (1); # 398 (19); # 399 (7); # 410 (22); # 419 (2); # 420 (tubes); # 422 (2); # 423 (1); # 424 (tubes).

Description. Tubes pink (Pl. 1 A), circular in cross-section; up to 7 mm in diameter, with wrinkled surface and with growth rings to wide collar-like peristomes. Proximal attached tube part usually with several longitudinal denticulate keels (Fig. 14A).

Body length, without radioles, up to 25 mm. Colour of live animals red, sometimes with white streaks.

Up to 38 pairs of radioles connected by short inter-radiolar membrane. Radiolar eyes absent.

Peduncle smooth, cylindrical, 1.5–2 times wider than normal pinnulated radioles, inserted as first dorsal radiole on one side. Operculum shallow funnel of approximately 40–50 fused radii with a denticulate edge; not separated from peduncle by constriction (Fig. 14C). Opercular radiole opposite to peduncle short, undeveloped, bearing rounded pseudoperculum (Fig. 14B).

Collar trilobed, with shallow lateral notches and small warts at base of notches (Fig. 14B). Tonguelets absent. Dorsal and lateral lobes similar in length and width. Collar short, not covering radiolar lobes ventrally. Thoracic membranes to end of thorax forming free apron, covering one or two abdominal chaetigers. No distinct prostomium.

Seven thoracic chaetigers, including six with uncini (Fig. 14B). Thoracic neuropodia shifting ventrally from mid-lateral line of thorax, tori of 7th thoracic segment meeting ventrally, forming triangular depression. Large collar chaetae limbate and bayonet, with

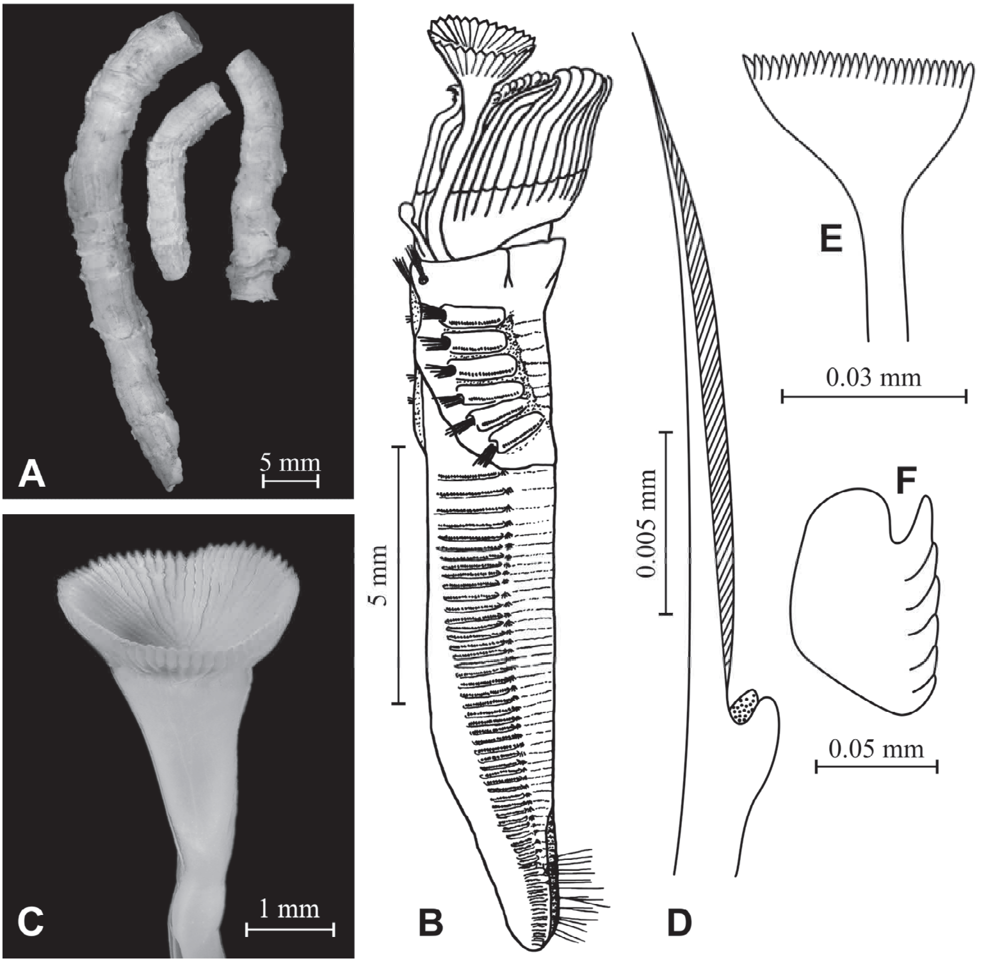

Figure 14. *Serpula vermicularis*. A – tube fragments; B – entire body, lateral view; C – operculum; D – bayonet collar chaeta; E – abdominal flat trumpet-shaped chaeta; F – thoracic uncinus. B, D-F – from Kupriyanova & Jirkov (1997). A, C – photo E. Wong.

two large proximal bosses at base of distal blade (Fig. 14D). Remaining thoracic chaetae limbate. Thoracic uncini saw-shaped, with 5–6 teeth above pointed fang.

Achaetous anterior abdominal zone absent. Up to 80 abdominal chaetigers. Chaetae of anterior and middle abdominal chaetigers asymmetrical flat trumpet-shaped, denticulate distally (Fig. 14F), replaced by long capillaries in posterior segments. Uncini similar to thoracic uncini, but smaller. Abdominal notopodial tori very long, covering entire dorsal surface of worm. Posterior glandular pad absent.

Remarks. The nominal species *S. vermicularis* has been reported from arctic to tropical conditions, neither ecologically nor biogeographically a likely distribution. *S. vermicularis* is poorly defined and its cosmopolitan status is not justified (see ten Hove & Jansen-Jacobs, 1984; Imajima & ten Hove, 1984; Kupriyanova, 1999). Most records in the literature are not accompanied by descriptions; when diagnoses are present, they are usually short and uninformative because the generic characters (such as funnel-shaped operculum or bayonet collar chaetae) are used to characterize the species. The most commonly used meristic character, the number of opercular radii, has limited taxonomic value for discriminating species because of its population and ontogenetic variability (Kupriyanova, 1999). As a result, it is impossible to compare records from different geographic locations. Earlier studies have shown that *S. vermicularis* previously recorded from the Russian Far-Eastern Seas belongs to another species (Kupriyanova & Rzhavsky, 1993), later described as *Serpula uschakovi* Kupriyanova, 1999. In this account, we report our material with some hesitation as *S. vermicularis*, mainly because the studied region is relatively close to the type locality (the UK coasts). The taxon found in the Norwegian Sea and tentatively attributed here to *S. vermicularis* is characterized by its pinkish tube with developed peristomes, a shallow opercular funnel with approximately 50–60 radii and lacking a constriction, and a well-developed apron (see Kupriyanova, 1999 for details). Until a much-needed world-wide revision of *Serpula* is completed, the specific name *S. vermicularis* should be used only with a great caution.

Ecology. In the Arctic found at depths from subtidal down to 425 m corresponding to an average temperature of 8.31ºC, attached mainly to rocks, gravel in various soft substrates excluding clay (Kupriyanova & Badyaev, 1998).

Spermatozoa have spherical heads, characteristic of broadcast spawning species (Kupriyanova et al., 2001). Because of the taxonomic confusion outlined above, it is unclear to which singular or plural species available literature data on reproduction and development of "*S. vermicularis*" (reviewed in Kupriyanova et al., 2001) should be attributed, but the described taxon from the Norwegian Sea is most likely a free-spawner with planktotrophic larvae as shown for all up to date studied *Serpula* species.

Distribution. In the Arctic known from Norwegian and North Seas and around Iceland (Kupriyanova & Jirkov, 1997). Likely a North-Atlantic and Mediterranean species, but its true geographic distribution is unclear because the species boundaries are not yet understood.

Genus *Spirobranchus* de Blainville, 1818

(including *Pomatoceros* Philippi, 1844 and *Pomatoleios* Pixell, 1913)

Type-species: *Serpula gigantea* Pallas, 1766.

Tube colour white, blue, pink or salmon, inside and/or outside. Tube typically (sub)triangular in cross-section, with median keel, rarely (sub)circular. Granular overlay absent. Operculum with inverse conical to rather shallow ampulla, covered by calcified endplate, with or without group of (non-moveable) spines, sometimes branching. Peduncle broad, with distal lateral wings; inserted at base of radiolar crown just left of medial line. Pseudoperculum absent. Operculum rarely lacking. Radioles may be arranged in a clear spiral of up to 8 whorls, but in most small species as well as in the large *Spirobranchus tetraceros* (Schmarda, 1861) arranged in a circle. Up to 50–60 pairs of radioles in larger species. Inter-radiolar membrane present. Radiolar eyes may be present; stylodes absent. Mouth palps present. 7 (rarely 6) thoracic chaetigerous segments. Collar trilobed (exceptionally penta-lobed). Tonguelets present. Thoracic membranes forming ventral apron across anterior abdominal segment. Large collar chaetae bayonet-like, with numerous hair-like processes on its basal portion (*Spirobranchus* chaetae), and limbate. *Apomatus* chaetae absent. All uncini saw-shaped (9–25 teeth), incidentally with 2 teeth above peg; anterior peg blunt, clearly gouged underneath. Ventral ends of thoracic uncinigerous tori widely separated anteriorly, gradually approaching one another towards the end of thorax, thus leaving a triangular depression. Abdominal chaetae true trumpet-shaped, i.e., distally with two rows of denticles separated by a hollow groove and forming long lateral spine. Achaetous anterior abdominal zone absent. Chaetae becoming increasingly longer posteriorly, but posterior capillary chaetae absent. Posterior glandular pad absent.

Remarks. The major difference between the nominal genera *Pomatoceros*, *Pomatoleios* and *Spirobranchus* is in the collar chaetae that are absent in *Pomatoleios*, limbate in *Pomatoceros*, and modified with a knob consisting of numerous hair-like teeth in *Spirobranchus*. However, collar chaetae are occasionally absent in *Pomatoceros* and *Spirobranchus* and present in juvenile *Pomatoleios*. Ten Hove & Kupriyanova (2009) treated the three genera as separate taxa, but stated that they likely are synonymous. Pillai (2009b) synonymized *Pomatoceros* Philippi, 1844 and *Pomatoleios* Pixell, 1913 with *Spirobranchus,* the approach followed in this account. Most of the species in the genus are found in the subtropical and tropical areas and some are obligate associates of hermatypic corals.

Twenty-six species, one from the Arctic Ocean.

***Spirobranchus triqueter* (Linnaeus, 1758) n. comb.**

(Fig. 15A-G, Pl. 1H)

Serpula triquetra Linnaeus, 1758, p. 787; 1767, p. 1265.

Pomatoceros triqueter: Wollebæk, p. 1912, p. 114-115, pl. XLII, fig. 1-6, pl. XLIX; Augener, 1925, p. 115; Fauvel, 1927, p. 370, fig. 127; Ditlevsen, 1929, p. 53; Wesenberg-Lund, 1950a, p. 60; 1950b, p. 135; Zibrowius, 1968a, p. 162-163, 164-166, pl. 8; Hartmann-Schröder, 1971, p. 529, Addendum183; Bianchi, 1981, p. 110-112, fig. 42a-i; Kupriyanova & Jirkov, 1997, p. 218-219, fig. 7A-H, map 7; Jirkov & Kupriyanova, 2001, p. 566-567, text figures 1-8, map.

Material examined. Table 1. # 133 (2); # 302 (tubes); # 307 (1); # 308 (6 and tubes); # 313 (1); # 343 (26 and tubes); # 345 (392); # 346 (3 and tubes); # 347 (tubes); # 349 (14 spec.); # 350 (tubes); # 391 (114); # 392 (25 and tubes); # 395 (tubes); # 410 (1 and tubes); # 411 (5 and tubes); # 424 (57); # 481 (tubes).

Description. Tube (Fig. 15A, B) up to 5 mm in diameter, nearly triangular in cross-section, white, without distinctive growth rings. Median keel wavy, not denticulate.

Body length, without radioles, up to 16 mm. Colour of radioles of live animals brown, blue or orange, body red.

Up to 20 radioles basally connected by an inter-radiolar membrane. Radiolar eyes absent.

Peduncle inserted medio-dorsally, at base of radioles, 2–3 times thicker than normal radioles, and roughly triangular in cross-section. Peduncle with a pair of distal wings. Operculum (Fig. 15C) oblique cone covered with endplate of calcareous material (on thin chitin-like base), normally carrying three horns. Pseudoperculum absent.

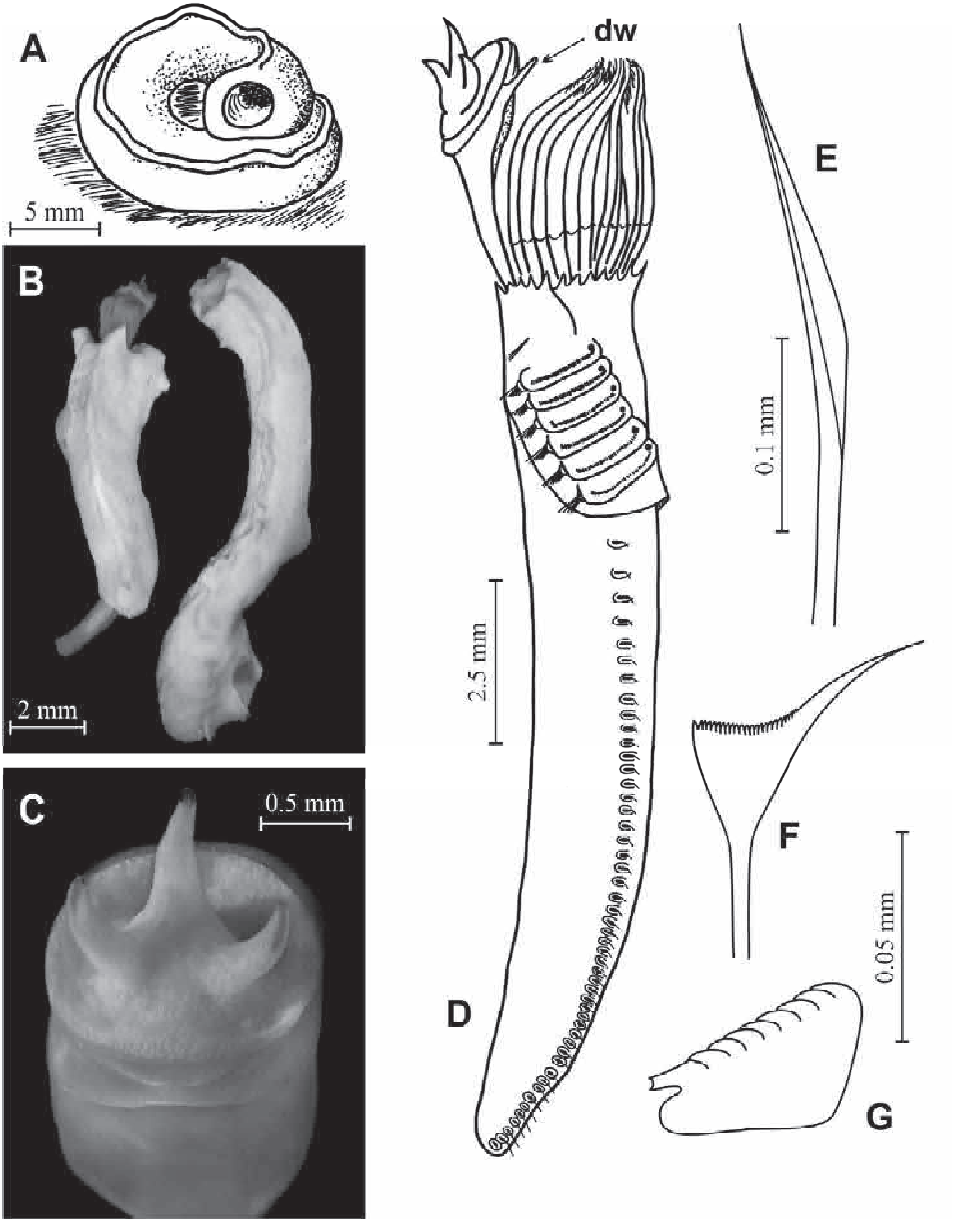

Figure 15. *Spirobranchus triqueter*. A – tube; B – tube and specimens in tube; C – operculum with three calcareous horns; D – entire body, lateral view; E – limbate collar chaetae; F – abdominal chaeta; G – thoracic uncinus, lateral view. A, D-G – from Kupriyanova & Jirkov (1997). B, C – photo E. Wong. Abbreviation: dw – one of two distal wings.

Collar thick, short, covering base of radiolar lobes only. Collar divided into three lobes of uniform length; the dorsal lobe distinctly wider than lateral lobes. Tonguelets present. Thorax with neuropodia closely spaced laterally. Thoracic tori shifted ventrally, neuropodia of 7th thoracic chaetiger meeting ventrally, forming triangular depression. Distinct black spots on ventral margins of thoracic neuropodia. Thoracic membranes to end of thorax, forming a long apron covering first 3–4 abdominal chaetigers (Fig. 15D). No distinct prostomium.

Seven thoracic chaetigers, including 6 with uncini. Collar chaetae capillary only (Fig. 15E). Remaining chaetae limbate, larger than collar chaetae. Thoracic uncini (Fig. 15G) saw-shaped with 9-10 teeth.

Achaetous anterior abdominal zone absent. Up to 70 chaetigers. Abdominal tori short. Anterior abdominal chaetae true trumpet-shaped with two denticulate edges (Fig. 15F), posterior chaetae capillary. Uncini similar to thoracic uncini, but smaller. Posterior glandular pad absent.

Remarks. Next to *Spirobranchus polytrema* (Philippi, 1844) and *Spirobranchus lima* (Grube, 1862), both easily distinguished by their ornamented tubes, Zibrowius (1968a) distinguished two similar and previously confused species inhabiting the Eastern Atlantic and Mediterranean, the intertidal *Spirobranchus lamarcki* (Quatrefages, 1866a), and the subtidal *S. triqueter*. These species can be distinguished by the shape of the operculum and the tube morphology. The tube has three longitudinal straight, not wavy keels (one median and two smaller lateral ones) in *S. lamarcki,* whereas the tube of *S. triqueter* has a single wavy keel. The operculum of *S. triqueter* is composed of small shallow basal ampulla covered with a more or less convex, sometimes elongated, but never concave, calcareous endplate, normally bearing three horns. The operculum of *P. lamarcki* has an elongated basal ampulla covered with a flat or slightly concave calcareous endplate that may bear 1–3 poorly developed projections. The status of these species was also later confirmed by enzyme electrophoresis (Ekaratne et al., 1982; Crisp & Ekaratne, 1984). All Arctic specimens are subtidal. Morphologically they all can be attributed to *S. triqueter*, which agrees with the fact that the most Northern records of *S. lamarcki* appear to be the United Kingdom (Nelson-Smith et al., 1990) and the Southern Netherlands (ten Hove & Lucas, 1996).

Ecology. In the Arctic *S. triqueter* is found from the subtidal zone to 290 m corresponding to an average temperature 8.01ºC, usually on larger rocks or smaller gravel in sand bottom, rarely on silty sand (Kupriyanova & Badyaev, 1998).

Average egg size is 60–80 μm, typical for planktotrophic larval development described in details for this species (see Kupriyanova et al., 2001).

Distribution. Barents and Norwegian Seas off Norway coast, off Iceland in the Arctic Ocean (Kupriyanova & Jirkov, 1997). The range outside the Arctic includes the Mediterranean-Atlantic and Black Sea, records from other areas are questionable according to ten Hove & Kupriyanova (2009).

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

chambers inverted cones or cup shaped with transparent non calcified lateral walls. Large collar chaetae limbate slightly bent (Fig. 21H). Sickle (*Apomatus*) chaetae present in 3rd fascicle (Fig. 21I). Abdominal chaetae (Fig. 21G) usually without projecting heel; its blades longer than those of largest collar chaetae and width of blade approximately same throughout most of their length decreasing rapidly only near tip. Abdominal uncini distributed symmetrically and present on both body sides .... ***Janua heterostropha*** (p. 92)
4b) Tube porcellaneous, unsculptured (e.g., Fig. 16A; 17A) or with median keel (very rarely up to 3 keels). Embryos stuck to each other and directly to the inside of tube wall. Opercular endplate (e.g., 16C-F; 17C-E) slightly concave, rarely flat; talon eccentric, conical or spatulate. Large collar chaetae strongly bent, blade positioned at angle of 45-90 degrees to chaetal shaft (e.g., Fig. 16G, H, 17F, G). Sickle (Apomatus) chaetae absent. Abdominal chaetae pennant-shaped (Fig. 16I), usually with projecting heel; their blades usually somewhat shorter than those of largest collar chaetae; width of blades decreasing gradually towards tip. Abdominal uncini distributed asymmetrically, on convex side of body absent or present only on last chaetigers **5**

5a) Tube (Fig. 16A, B) white, lightly porcellaneous, unsculptured or rarely with 1-3 longitudinal keels; with narrow semitransparent transverse rings. Planospiral on flat substrates; on filamentous and uneven substrates whorls overlapping, sometimes ascending over substrate or with erect anterior end. Talon (Fig. 17C-E) eccentric, small conical or somewhat flattened. Large collar chaetae modified (Fig. 16G, H) bearing vestigial cross-striation on “frontal side” of blade (not visible laterally under a dissecting microscope, under SEM only); strongly bent, with blade almost perpendicular to chaetal shaft on concave body side .... ***Circeis armoricana*** (p. 77)
5b) Tube (Fig. 17A, B; Pl. 2H) white, porcellaneous, unsculptured, semitransparent. Only initial whorls planospiral, other overlaps (Fig. 17B; Pl. 2H) or ascend over substrate like a spring, with tube height reaching 6–7 mm (Fig. 17A). Talon (Fig. 17C-E) eccentric, distinct, widely spatulate in frontal view. Large collar chaetae modified, asymmetrically cross-striated: those from concave side (Fig. 17G) strongly bent at angle of about 45 degrees and with cross-striation not visible under dissecting microscope, while chaetae from convex side (Fig. 17F) only slightly bent and bearing visible vestigial cross-striation in basal blade parts .... ***Circeis spirillum*** (p. 81)

6a) Tube white, lightly porcellaneous (e.g., Fig. 36A; 37A). Embryos in an egg string attached posteriorly by a thread to inner tube wall. Thoracic uncini narrow, rasp-shaped with 3–4 (5–6 in smallest) longitudinal rows of teeth and blunt anterior peg (Fig. 36H) that may be slightly gouged and appear bidentate (e.g., Fig. 34H) **7**
6b) Tube white, non-porcellaneous (e.g., Fig. 22A). Embryos brooded within a chamber (cup) formed by invagination of opercular ampulla and used for more than one brood (e. g., Fig. 26C; Pl. 2G). With two types of opercula, one a primary operculum being an opercular endplate with a talon (e.g., Fig. 22C; 30B, C; 31C) and another a brood chamber of various structure (e.g., Fig. 22B; 26C; 27C; 30E-H; 32 C, D). Thoracic uncini saw-to-rasp-shaped, with one row posteriorly and up to three rows of teeth near blunt anterior peg (e.g., Fig. 26H) **10**

7a) Tube thick-walled, with three massive keels, planospiral (Fig. 37A), juvenile tubes unsculptured (Fig. 37 B); last whorl widening rapidly toward tube mouth. Talon (Fig. 37

C-E) height longer than width; tooth-shaped in side view, irregular with asymmetrical lateral protuberances rounded and pointed terminally in front view. Large collar collar chaetae modified fin-and-blade on convex body side (Fig. 37F), but limbate (sometimes with a little groove in basal part of blade) on concave side (Fig. 37G) .... ***Spirorbis*** (***Spirorbis***) ***tridentatus*** (p. 146)
7b) Tube thin-walled, unsculptured, either completely planospiral or with straightened last whorls, or upward from substrate or overlapping previous whorl; last whorl widening gradually toward mouth (e.g., Fig. 33A; 34A; 35A, B). Talon width exceeding its height or approximately same (e.g., Fig. 33D; 35E). Large collar chaetae modified fin-and-blade on both body sides (e.g., Fig. 33F, G) **8**

8a) Tube rarely over 1.5 mm in coil diameter; white, but in live animals red body may be visible through very thin initial tube whorls; planospiral or whorls overlapping (Fig. 33A), but never with straight anterior end. Talon (Fig. 33C-E) approximately as long as wide; in small specimens its terminal edge bilobed in front view, but almost entire in largest. Only intertidally, usually on the red calcareous alga *Corallina officinalis* .... ***Spirorbis*** (***Spirorbis***) ***corallinae*** (p. 134)
8b) Tube up to 3–4.5 mm in coil diameter; white, coloured body never visible through initial tube whorls; planospiral (e.g., Fig. 34A) or last whorls straightened or overlapping previous whorl (Fig. 35A, B). Talon width longer than its height (often talon just a pad near periphery of opercular plate) or rarely width and length approximately same (e.g., Fig. 34D; 35E). Inhabiting intertidal or upper subtidal zone on various substrates, except for the red calcareous alga *Corallina officinalis* **9**

9a) Tube planospiral, often with a peripheral flange (Fig. 36A, B). Opercular endplate with vestigial pad-shaped talon (Fig. 36D, E). Body of live animals pale greenish-brown. Thoracic membranes very asymmetrical forming a large lateral flap on convex side (Fig. 36C). Large collar chaetae modified fin-and-blade; gap between fin and blade distinctly longer on convex side of body (Fig. 36F). Abdominal chaetae lacking heels (Fig. 36G). Generally intertidally (to 1–3 m) on fuci, rarely attached to algae such as *Laminaria, Ascophyllum,* and *Sacchorhiza* and, as an exception, to stones under button-shaped thalli of the *Himanthalia* .... ***Spirorbis*** (***Spirorbis***) ***spirorbis*** (p. 142)
9b) Tube planospiral (Pl. 2F), but last whorl may be straightened (Fig. 35B) or overlapping previous whorl (Fig. 35A); peripheral flange always absent; tube often overgrown by calcareous alga *Phymatholithon* (Fig. 35A, Pl. 2F) leaving only mouth visible. Opercular endplate with narrow pad-shaped talon (Fig. 32D, E). Abdomen and thorax of live animals orange-red (Pl. 2E). Thoracic membranes symmetrical, not forming a lateral flap on convex side (Fig. 35C). Large collar chaetae modified fin-and-blade (Fig. 35F); gaps between fin and blade approximately same on both body sides. Abdominal chaetae with distinct heels (Fig. 35G). In low intertidal zone, either clean or overgrown by *Phymatholithon*............ .... ***Spirorbis*** (***Spirorbis***) ***rupestris*** (p. 139)
9c) Tube (Fig. 34A) planospiral, sometimes whorls overlapping; peripheral flange may be present. Opercular endplate (Fig. 34C-E) of juveniles with talon approximately of same length as width, spatulate and with slightly bilobed terminal edge in frontal view; in adults talon thick in side view, usually wider than longer, with slightly bilobed or entire terminal edge and resembling a hoof, curved frontally when seen from below. Body of live animals orange, radioles colourless (Pl. 2D). Thoracic membranes asymmetrical and

form large lateral flap on convex side (Fig. 34 B). Large collar chaetae modified fin-and-blade with coarser serrated blades on convex body side (Fig. 34F), but finely serrated and almost twice as small on concave side (Fig. 34G). Abdominal chaetae with small distinct heels. Live in intertidal or low subtidal zone on various red and brown algae including fuci .... ***Spirorbis* (*Spirorbis*) *inornatus*** (p. 136)
10a) Large collar chaetae (Fig. 30I, J) modified fin-and-blade with coarsely serrated blades and distinctly cross-striated on convex body side (cross-striation on concave side may be indistinct). Endplate of primary operculum not fused with brood chamber and usually shed after chamber's development. Endplate concave, with short thick eccentric talon, knob to cone-shaped (Fig. 30B, C). Respectively brood chamber lacking talon. Brood chamber domed with helmet-shaped calcification deep on side away from radiolar crown, usually bilobed distally (Fig. 30F, G), sometimes rounded (Fig. 30D) or with lateral distal rim on side away from substrate (Fig. 30E, F). Middle-posterior part of thorax bearing a large deeply pink spot (crystalline patch) dorsally that can be scraped by needle (Pl. 2C) ....
.... ***Pileolaria* ex gr. *berkeleyana*** (p. 121)
10b) Large collar chaetae limbate (e.g., Fig. 22D) or modified fin-and-blade (Fig. 28F); blades finely serrated without cross-striation. Endplate of primary operculum either completely fused with (e.g., Fig. 28B; 29B) or attached to brood chamber (e.g., Fig. 25B; 32C) by talon (firmly or not). Respectively developed brood chamber usually keeping a talon of primary operculum. Endplates concave, flat or convex with well-developed peripheral or eccentric talons of different shapes, but never knob to cone-shaped. Distal part of brood chamber flat (e.g., Fig. 29B), concave (e.g., Fig. 32C) or domed (e.g., Fig. 27C), but never bilobed distally. Deeply pink pigmentation absent from middle-posterior part of thorax dorsally; if present, pigmented spots cannot be scraped by needle **11**

11a) Large collar chaetae modified fin-and-blade (e.g., Fig. 28F) **12**
11b) Large collar chaetae limbate (e.g., Fig. 32G) **15**

12a) Distal part of brood chamber and endplate of primary operculum (e.g., Fig. 28B-E) strongly domed; occasionally endplate of primary operculum only slightly convex or flat. Opercular endplate with talon completely fused with developed brood chamber; talon reaching at least middle of lateral wall of brood chamber; calcified zone around talon on lateral wall of brood chamber distinct and extensive **13**
12b) Distal part of brood chamber (e.g., Fig. 29B; 32C) and endplate of primary operculum flat, slightly concave or convex. Opercular endplate with talon completely fused with developed brood chamber (e.g., Fig. 29B) or firmly attached to its lateral wall by talon (e.g., Fig. 25B), leaving some space between endplate of primary operculum and distal part of brood chamber; talon not reaching middle of lateral wall of brood chamber; calcified zone around the talon on lateral wall of brood chamber distinct, indistinct, or absent **14**

13a) Tube usually planospiral, sometimes whorls overlap or last whorl may be upward from substrate. Often tube with two keels (Fig. 28A), one shifted towards the inside of last whorl and another towards periphery, giving a sub-quadrangular cross-section. However, tubes may be unsculptured or with 1 or 3 keels. Talons (Fig. 28B-E) variable, typically rhomboid (diamond-shaped), often with a distal constriction or incision on lateral side or shapeless. Length of largest thoracic uncini exceeding length of collar chaetae blades (Fig. 28F, G) .... ***Bushiella*** (***Jugaria***) ***quadrangularis*** (p. 114)

13b) Tube (Fig. 27A) initial whorls planospiral, but last whorl usually facing upward from substrate; typically 3 distinct longitudinal keels giving pentangular cross-section. Sometimes last whorls intercalated (Fig. 27B). Talon trapezoid (Fig. 27D). Largest thoracic uncini not longer than collar chaetae blades .... ***Bushiella*** (***Jugaria***) ***kofiadii*** (p. 112)

14a) Tube (Fig. 29A) planospiral or sometimes last whorls facing upward from substrate. Typically unsculptured without keels and circular in cross-section. A vestigial median keel not changing cross-section outline may be present. Endplate completely fused with developed brood chamber (Fig. 29B). Talon gradually expanding distally, usually with indistinct rounded lateral projections and small groove in median part of terminal edge. Calcified zone on lateral side of brood chamber distinct. Body of live animals may be with deep-rose pigmented spots on dorsal side of posterior thorax and achaetigerous zone. Large collar chaetae (Fig. 29C) modified with very fine teeth on both blade and fin, thus gap between fin and blade may be indistinct if not viewed in strictly lateral position ....
.... ***Bushiella*** (***Jugaria***) ***similis*** (p. 117)

14b) Tube (Fig. 25A) planospiral oval, not circular; with 3 (rarely 4) narrow high keels (rarely low or vestigial), but circular in cross-section. Endplate of primary operculum firmly attached to lateral wall of mature brood chamber only by talon, leaving space between endplate of primary operculum and distal part of developed brood chamber (Fig. 25B, C). Talon (Fig. 25C-E) gradually expanding distally, usually with distinct pointed lateral projections distally and with very narrow projection in median part of terminal edge. Calcified zone on lateral side of brood chamber present, but often poorly visible (absent in preserved material). Pigmented deeply pink spots absent. Modified collar chaetae with fine teeth on blade and larger teeth on fin ....
.... ***Bushiella*** (***Jugaria***) ***acuticostalis*** (p. 106)

14c) Tube (Fig. 26A) planospiral, unsculptured or with one keel towards inner side of whorl. Endplate of primary operculum firmly attached to lateral wall of mature brood chamber only by talon, leaving space between the plate of primary operculum and distal part of developed brood chamber (Fig. 26C); sometimes this space is very small, thus the endplate is lying very close to brood chamber, but never fused. Talon bilobed distally (Fig. 26B, C) with rounded latero-distal sides, rarely fan-shaped. Calcified zone on lateral side of brood chamber distinct. Modified collar chaetae (Fig. 26E) with very fine teeth on blade and larger teeth on fin .... ***Bushiella*** (***Jugaria***) ***granulata*** (p. 109)

15a) Primary operculum attached to distal part of brood chamber only by talon tip and easily shed after development of brood chamber (e.g., Fig. 32C). Both endplate of primary operculum and distal part of brood chamber distinctly concave (e.g., Fig. 32C-F); talon of primary operculum and distinct calcified zone of brood chamber on side opposite to radiolar crown sub-triangular or resembling a heraldic shield. Peduncle inserted outside circle of radioles, and brood chamber forms a soft-walled pouch extending posteriorly to dorsal thoracic groove. Thoracic membranes asymmetrical (e.g., Fig. 31C), on convex side of body very long and extending posteriorly at least to end of achaetigerous zone. Tubes up to 6–7 mm in coil diameter **16**

15b) Primary operculum completely (e.g., Fig. 23B) or almost completely (Fig. 22B) fused with developed brood chamber. Both endplate of primary operculum and distal part of brood chamber flat (e.g., Fig. 24B, C) or concave (Fig. 22B, C). Talon of varying shape, but not triangular or not similar to heraldic shield; calcified zone of brood chamber on side opposite to radiolar crown absent or rounded (rarely irregular) if present. Peduncle inside circle of radioles; mature brood chamber not forming a soft-walled pouch extending posteriorly in dorsal thoracic groove. Thoracic membranes reach only to end of thorax on both sides of body (Fig. 23B). Tubes no more than 3 mm in coil diameter (one species up to 5 mm) **17**

16a) Tube (Fig. 32A) unsculptured or with 1 indistinct median keel, usually planospiral, but last whorl may be upward away from substrate. Margins of thoracic membranes on convex side of body extending posteriorly, obliquely crossing long achaetigerous region, but not continuing to abdominal chaetigers (Fig. 32B). Primary operculum (Fig. 32C-E) with large eccentric sub-triangular talon comprising two pointed lateral wings which flank a central longitudinal ridge. Sometimes fine curved spines present on talon and a fan of spines tight against underside of endplate. Calcified zone of brood chamber subtriangular, longer than wide (Fig. 32C, F). Distal plate of brood chamber completely smooth or with a ring of irregular spines on periphery, but never in centre (Fig. 32C, F). Crown consisting of separate petals around distal part of brood chamber absent .... ***Protoleodora uschakovi*** (p. 130)

16b) Tube (Fig. 31A) with one vestigial keel or unsculptured; juveniles and single adults are planospiral, but in frequently formed aggregations (Fig. 32B) tubes deformed and coils may cover each other, mouth upward from substrate. Margins of thoracic membranes on convex body side, extending posteriorly and reaching 7–8th abdominal segments (Fig. 31C). Primary operculum with large eccentric triangular talon, without spines (Fig. 31D-F, H). Lateral calcareous zone of brood chamber usually looks like a heraldic shield (Fig. 31G), rarely triangular; its width and length of approximately same size, indistinct median longitudinal keel usually present. Distal part of completely developed brood chamber bearing numerous spines of different sizes, single, bifurcate, or rare trifurcate deeply (Fig. 31G). Crown around distal part of brood chamber usually subdivided into 20–30 petals (probably chitinous) (Fig. 31C, G, F). Crown delicate, often absent in poorly preserved specimens or only fragments present .. ***Protoleodora gracilis*** (p. 126)

17a) Initial whorls of tubes planospiral, last whorl evoluted and slightly curved or even straightened; unsculptured (Fig. 23A). Distance between tube mouth and opposite side of whorl up to 4–5 mm, coil diameter of planospiral part of tube being 2 mm or less. Primary operculum completely fused with developed brood chamber (Fig. 23B). Both endplate of primary operculum and distal part of brood chamber flat. Talon of median size, rhomboid and somewhat drop-shaped, its length approximately 1.5 times of maximal width; calcified zone on lateral wall of brood chamber absent. Large collar chaetae limbate (Fig. 23C) often with distinctly enlarged teeth in basal part of blade .... ***Bushiella* (*Bushiella*) *evoluta*** (p. 101)

17b) Tube (Fig. 24A) planospiral up to 2.5 mm in coil diameter; usually bearing a distinct median keel giving a subtriangular cross-section, but sometimes unsculptured. Primary operculum completely fused with developed brood chamber (Fig. 24C). Both endplate of primary operculum and distal part of brood chamber flat (Fig. 24B, C). Talon of median size, fan-shaped with even terminal edge (Fig. 24B, C); calcified zone on lateral wall of brood chamber rounded. Large collar chaetae limbate (Fig. 24D) sometimes with small basal groove .... ***Bushiella* (*Bushiella*) *verruca*** (p. 103)

17c) Tube (Fig. 22A) planospiral with two distinct keels, up to 4–5 mm in coil diameter.

Primary operculum almost completely fused with developed brood chamber (endplate of primary operculum fused with distal part of brood chamber only in central part and side close to talon, leaving space between distal plate and brood chamber on the opposite side (Fig. 22B)); free edge may be broken giving the illusion of primary operculum being completely fused with brood chamber; talon completely fused with lateral wall of brood chamber. Endplate of primary operculum (Fig. 22C) concave and retaining its shape after brood chamber formation; distal part of brood chamber slightly concave or flat. Talon large and winged laterally (Fig. 22B, C), irregularly shaped, sometimes heart- or spade-shaped. Calcified zone of brood chamber lateral wall very distinct, of irregular approximately rounded shape; its distal edge may be denticulate making its surface appear somewhat fluted. Large collar chaetae limbate without groove or enlarged teeth basally (Fig. 22D) .... ***Bushiella*** (***Bushiella***) ***barentsii*** (p. 98).

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* **Saint-Joseph, 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

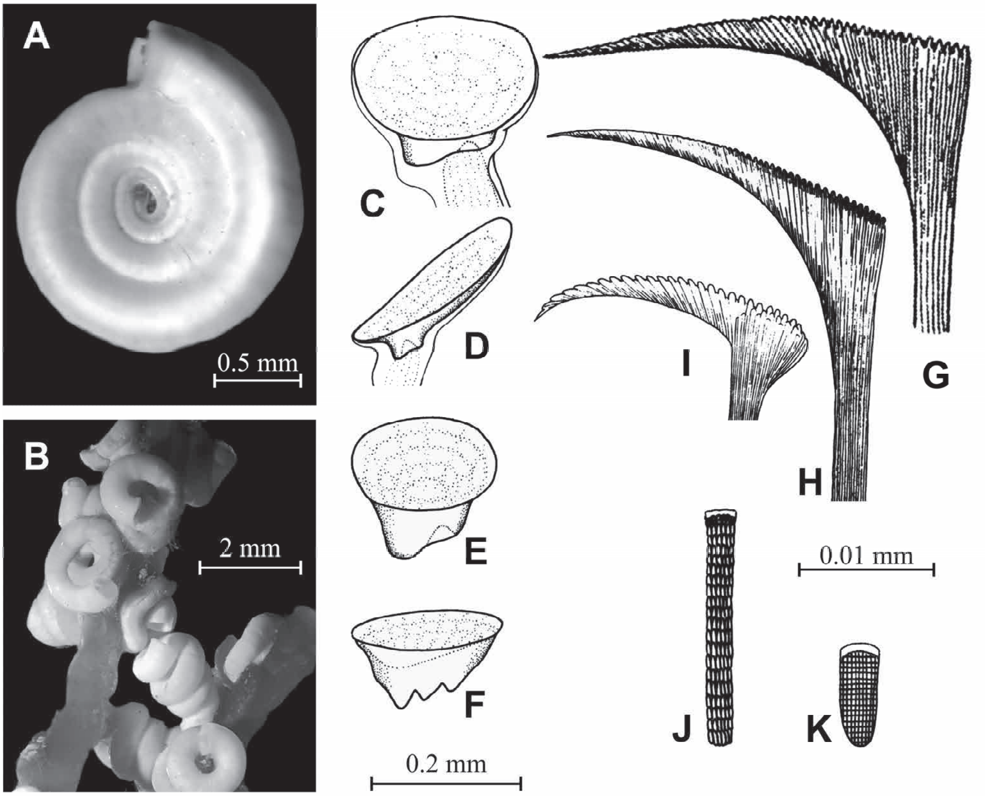

Figure 16. *Circeis armoricana*. A – planospiral tube, B – tubes with overlapping coils, C, D – typical operculum, front and lateral views; E, F – opercular variability, frontal view; G – modified collar chaeta from concave body side; H – modified collar chaeta from convex body side; I – abdominal flat 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]).

Circeis spirillum (Linnaeus, 1758)

(Fig. 17A-G, Pl. 2H)

Serpula spirillum Linnaeus, 1758, p. 786; 1767, p. 1264.

Serpula lucida Montagu, 1803, p. 515-516.

Spirorbis spirillum: Annenkova in Gorbunov, 1946, p. 39; Annenkova, 1952, p. 137 (partim?); Aleksandrov, 1981, p. 89, tab. XIII, fig. 2.

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

Circeis spirillum: Knight-Jones P. & Knight-Jones E.W., 1977, p. 471, fig. 5N-U; Knight-Jones P. et al., 1979, p. 429, fig. 3B(a-d); 1991, p. 192, fig. 2; Rzhavsky, 1989: 53, fig. 1B; 1992a, p. 8; 1992[1994], p. 100, fig. 1; 2001: 583-584, text figures 1-7, map; Jakovis, 1997, p. 41-42, fig. 4a-g; Gagaev, 2008, p. 95.

Material examined. Table 1. # 6 (3); # 16 (2); # 23 (2); # 24 (many); # 27 (6); # 44 (1); # 49 (6); # 69 (4); # 70 (7); # 75 (1); # 78 (15); # 80 (7); # 82 (many); # 87 (1); # 181 (3); # 183 (7); # 185 (~ 30); # 195 (3); # 196 (~ 15); # 198 (2); # 199 (~ 15); # 211 (1); # 215 (9); # 217 (~ 30); # 218 (many); # 219 (~ 10); # 221 (many); # 230 (15); # 233 (~ 10); # 242 (6); # 255 (1); # 269 (1); # 276 (1); # 486 (4); # 515 (~ 25); # 527 (2); # 543 (~ 50); # 554 (~ 35); # 566 (4); # 573 (3); # 574 (5); # 596 (~ 10); # 615 (many); # 617 (6);

Description. Tube dextral, but only initial whorls planospiral; other whorls overlapping (Fig. 17B, Pl. 2H) or ascend over substrate like a spring (Fig. 17A), tube length up to

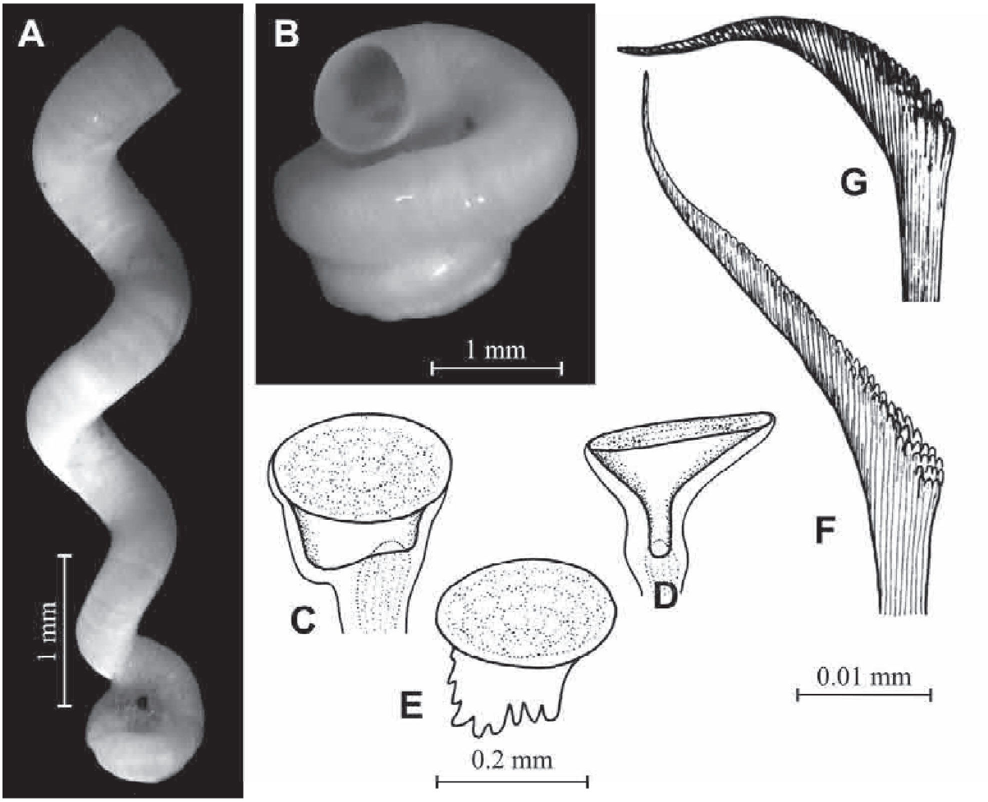

Figure 17. *Circeis spirillum*. A – typical ascending tube; B – tube with overlapping coils; C, D – typical operculum, front and lateral views; E – operculum with serrated talon, frontal view; F – modified collar chaetae with vestigial cross-striation from convex body side; G – large collar chaeta without vestigial cross-striation from concave body side. C-F – from Knight-Jones P. & Knight-Jones E.W. (1977). A, B – photo A.V. Rzhavsky.

6–7 mm; unsculptured; white, semitransparent, porcellaneous. Colour of live specimens unknown; preserved specimens colourless or flesh-coloured. Body length of adult relatively short compared to tube length.

Opercular endplate slightly concave; talon eccentric, distinct and flat, widely spatulate in frontal view; its terminal edge usually entire, but sometimes serrated (Fig. 17C-E).

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 and asymmetrically cross-striated: when a worm is observed in the recommended position, vestigial cross-striation is visible only on basal parts of blades from the convex side of body (Fig. 17F); this cannot be observed on blades from the concave body side. Chaetae from the concave body side strongly bent at angle of about 45 degrees (Fig. 17G), while chaetae from convex side are only slightly bent, their blades somewhat serrated. Capillary chaetae present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers only limbate, sickle (*Apomatus*) chaetae absent.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini rasp-shaped, 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 15 chaetigers. Usually two chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and distinctly serrated tapering blade. Blade lengths of largest abdominal chaetae shorter than those of collar chaetae. Companion capillary hooked chaetae not observed. Uncini rasp-shaped with blunt anterior pegs and numerous longi-tudinal 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. *Serpula lucida* (Montagu, 1803) is an accepted synonym of *C. spirillum,* but some other nominal taxa (as given e.g, in McIntosh, 1923) may have been synonymized erroneously or their taxonomical position remains. For a long time *C. armoricana* was considered a junior synonym of *C. spirillum*, even though these two species are clearly distinct. Unlike *C. spirillum* (Fig. 17A, B), *C. armoricana* typically has planospiral tubes (Fig. 16A), even though whorls may be ascending or overlapping (Fig. 16B) on substrates offering a small area of attachment only (e.g., algae with narrow thalli). The tubes of *C. armoricana* are not so brightly porcellaneous and not completely semitransparent as those of *C. spirillum*. Collar chaetae in *C. armoricana* are strongly bent (Fig. 16G, H), with blades positioned almost perpendicular to the chaetal shaft, and bear vestigial cross-striation on the “frontal side” of the blade only, which is not visible laterally under a dissecting microscope. In *C. spirillum* chaetae from the concave body side are less strongly bent at a maximal angle of about 45 degrees (Fig. 17G), while chaetae from the convex side are only slightly bent, their blades somewhat serrated and bearing vestigial cross-striation (Fig. 17F). Finally, the talons (Fig. 16C, D) are smaller and usually conical (rarely flattened).

These two species usually differ ecologically. *C. spirillum* almost exclusively uses hydrozoans and bryozoans as a substrate, rarely other objects (see “Ecology”), whereas larvae of *C. armoricana* are less selective and may settle on macrophytes, rocks, shells, crustaceans, although sometimes on bryozoans and hydrozoans as well. Both species live in a similar bathymetric range, although *C. spirillum* prefers depths over 50 m and is rarely found intertidally, while *C. armoricana* prefers the depths above 50 m and is common in the intertidal zone.

The species, for a long time reported as one of the most common and abundant in the Northern Hemisphere, is not rare indeed, but most of the records belong to *C. armoricana* (see e.g., Knight-Jones P. & Knight-Jones E.W., 1977; Knight-Jones et al., 1979; Rzhavsky, 1992a). Levinsen (1884) in the figure legends used the name *Spirorbis spirillum* var. *ascendentis* for specimens of "*Spirorbis spirillum*" with ascending tubes. Later some authors (Fauvel, 1927; Pettibone, 1954; Uschakov, 1955; 1965; Buzhinskaya, 1967) also used this name for specimens with such tubes, but written "var. *ascendens*". Re-examination of collections from the Russian Far-Eastern Seas demonstrated that *C. spirillum* was usually reported as "*spirillum* var. *ascendens*", whereas *C. armoricana* was mainly reported as "C. *spirillum*". Most Russian Arctic records of *C. spirillum* (material was not retained) found on the substrates other than hydrozoans and bryozoans likely belong to *C. armoricana* (see "Remarks" for *C. armoricana*). In his definition key, Zatsepin (1948) compiled data on *C. spirillum* distribution in the Arctic Ocean, but his description and illustrations correspond to those of *C. armoricana*. We agree with Knight-Jones P. & Knight-Jones E.W. (1977) that sinistral form of "*C. spirillum*" recorded by Bock (1953) belongs to *C. armoricana.*

The only other *Circeis* species with semitransparent ascendant tubes and collar chaetae not strongly bent and bearing a vestigial cross-striation is *Circeis oshurkovi* Rzhavsky, 1998 known from the Commander Islands (Rzhavsky, 1998). However, its opercular endplate is domed with a large bilaterally symmetrical spade-shape talon in frontal view.

Ecology. In the Arctic Ocean the species mainly encrusts hydrozoans and bryozoans at depths of 5–171 m. As the only known exception*, C. spirillum* was recorded from the White Sea on red algae *Ptilota* (Jakovis, 1997). Sometimes *C. spirillum* lives mixed with *B.* (*J.*) *quadrangularis* and *B.* (*J.*) *acuticostalis.* In other parts of their range, the species lives exclusively on hydrozoans and bryozoans, though juveniles sometimes are found on mussel byssus in the Sea of Japan (Rzhavsky, pers. observation) and on some red algae at the British coasts (Knight-Jones P. & Knight-Jones E.W., 1977). The animals are recorded from depths of 0–550 m, but their preferred bathymetric range is 50–100 m. Studies on reproduction and response to abiotic factors of "*spirillum*", by Polyanski (1951), Bergan (1953a), and Potswald (1967) very probably should be referred to *C. armoricana*.

Distribution. The extensive Arctic material examined here was collected from the Chukchi, Laptev, Kara, Barents, White, Greenland Seas, and the central part of the Arctic Ocean. The species is also known from the Norwegian Sea (Knight-Jones P. et al., 1991). In the North Pacific the species distribution range to Possiet Bay (Japan Sea, Russia), Japan and California, USA in the south; 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]).

Genus *Paradexiospira* Caullery & Mesnil, 1897

Type species *Spirorbis violaceus* Levinsen, 1884.

Tubes usually dextral, one species, *P.* (*S.*) *vitrea,* occasionally coiled sinistrally. Margins of collar and thoracic membrane not fused over thoracic groove. Large collar chaetae modified, bent, cross-striated or fin-and-blade cross-striated. Third thoracic chaetiger with sickle (*Apomatus*) chaetae only, 4th segment usually without chaetae. Four thoracic chaetigers in adults (juveniles rarely with only 3 chaetigers).

Two subgenera, both present in the Arctic.

Subgenus *Paradexiospira* Caullery & Mesnil, 1897

Type species *Spirorbis violaceus* Levinsen, 1884.

Large collar chaetae modified cross-striated, grooves maybe present in basal part of blades, but fins never form.

Monotypic subgenus, known from the Arctic.

Paradexiospira (*Paradexiospira*) *violacea* (Levinsen, 1884)

(Fig. 18A-F, Pl. 2B)

Spirorbis violaceus Levinsen, 1884, p. 209-210; Augener, 1928, s. 816; 1929, s. 32; Pergament, 1945, p. 131; Zatsepin, 1948, p. 166, tab. XXXIX, fig. 22; Wesenberg-Lund, 1950b, p. 140-141; 1951, p.134; 1953b: 8; Annenkova, 1952, p. 137; Denisenko & Savinov, 1984, p. 105.

Spirorbis (*Paradexiospira*) *violaceus*: Bergan, 1953b, p. 40-41, fig. 5a-b.

Paradexiospira (*Paradexiospira*) *violacea*: Knight-Jones P. et al., 1979, p. 429-430, fig. 3C(a-e); Rzhavsky, 1989, p. 53, fig. 1G, 2G; 1992f, p. 9; 1992[1994], p. 101, fig. 2; 1997b, p. 145; 2001, p. 585, text figures 1-5, map; Jakovis, 1997, p. 43-44, fig. 5a-g; Gagaev, 2008, p. 95.

Paradexiospira violacea: Knight-Jones P. et al., 1991, p. 192, fig. 2.

Material examined. Table 1. # 11 (1); # 59 (tubes); # 75 (1); # 155 (3); # 218 (1); # 460 (1); # 477 (4); # 478 (~ 10); # 538 (1); # 539 (3); # 547 (~ 150); # 590 (many); # 595 (~ 30); # 599 (~ 50); # 619 (~ 20).

Description. Tube dextral, planospiral, thick-walled, up to 3.5 mm in coil diameter; adults with three massive keels ending in three projections over aperture, juvenile tubes unsculptured; alveoli on tube periphery absent. Tube walls vitreous transparent; deep violet inner tube lining visible through tube walls, giving tubes of live animals an almost black appearance (Fig. 18A, Pl. 2B); this lining may change colour to brown in freshly preserved material and to light-brown in long-stored material. In live specimens thorax red-orange, thoracic membranes, radioles, and soft parts of operculum tinged by orange; abdomens colourless or also slightly tinged by orange; preserved specimens colourless or flesh-coloured.

Opercular endplate flat or slightly convex and usually covered by brown chitinous membrane. Talon massive and bearing two lateral oval incisions (Fig. 18B, C).

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reach end of 4th chaetiger forming apron. Four thoracic chaetigers.

Large collar chaetae modified (Fig. 18D), bent, cross-striated (sometimes indistinctly); in basal part of blade grooves mayby present, but distinct fin separated by smooth gaps from blades never form. Capillary chaetae also present in collar fascicle. Chaetae of 2nd thoracic chaetiger limbate. Chaetae of 3rd chaetiger only sickle (*Apomatus*) with serrated distal parts only about of 1/4–1/5 of blade length (Fig. 18E). Notochaetae from the 4th chaetiger not observed.

Three thoracic tori on concave and two on convex side of body (on chaetigers 2–4 and 2–3 correspondingly). Uncini rasp-shaped with up to 15 longitudinal rows of teeth throughout length of uncinus and blunt anterior pegs. Size of individual uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 20 chaetigers. Usually 1–2 chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and coarsely serrated tapering blade (Fig. 18F). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae. Companion capillary hooked chaetae not observed. Uncini 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 on concave side of body in anterior half of abdomen.

Remarks. The species is easily recognizable because of the deep violet inner tube lining visible through tube walls, so that tubes of live animals look almost black (Fig. 18A, Pl. 2B). Such colouration pattern has never been recorded for other spirorbins. Two other species of *Paradexiospir*a also differ from *P.* (*P.*) *violacea* by the presence of fin-and-blade cross-striated collar chaetae (Fig. 19D, 20F) and a long serrated distal part of sickle (*Apomatus*) chaetae (about of 1/2–1/3 (Fig. 20G) of blade length versus 1/4–1/5 (Fig. 18E)). Their opercular and talon morphology are completely different (see descriptions). Additionally, *P.* (*S.*) *cancellata* usually has alveoli in the tube periphery (Fig. 19A).

Nevertheless, re-examination of scarce, mainly unpublished material from the Arctic Seas deposited in the Russian collections showed that *P.* (*P.*) *violacea* often was misidentified as "*vitrea*". Because published records of this species from the Russian Arctic Seas were based on lost material, records were not included in the synonymy

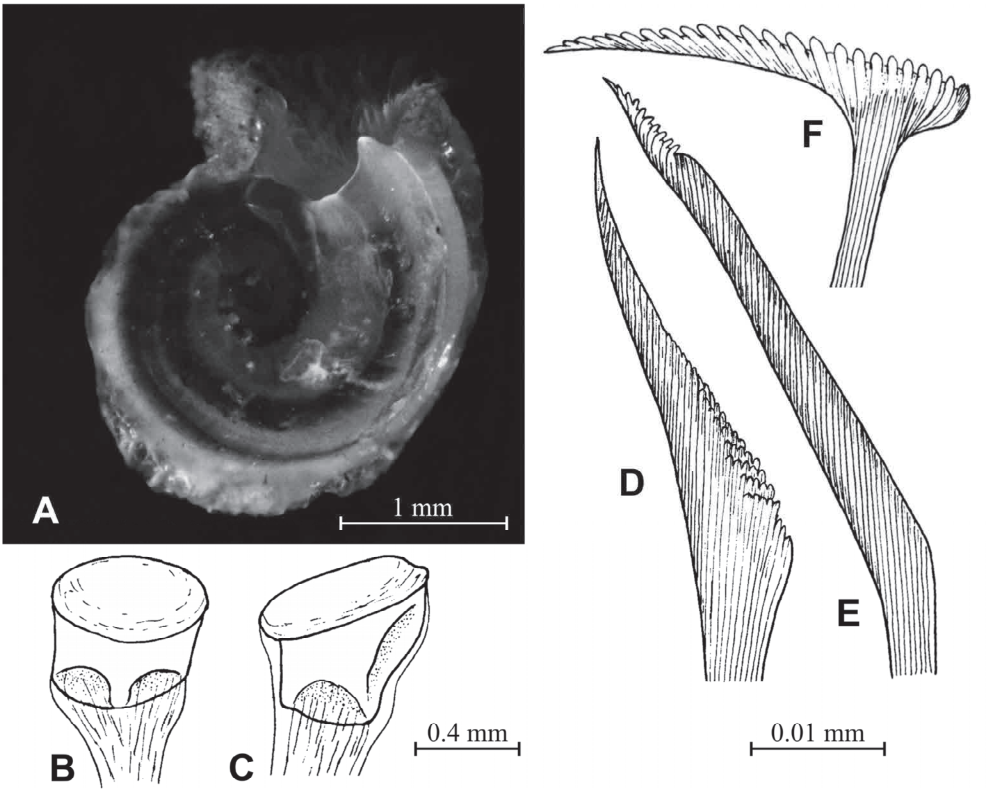

Figure 18. *Paradexiospira* (*Paradexiospira*) *violacea*. A – animal in tube; B,C – operculum, frontal and lateral views; D – modified collar chaeta; E – sickle (*Apomatus*) chaeta; F – abdominal chaeta. B-F – from Knight-Jones P. et al. (1979). A – photo A.V. Rzhavsky.

unless they were accompanied by descriptions or remarks that would confirm species identifications (Zachs, 1923; Derjugin, 1924; 1928; Gurjanova, 1924; Gurjanova & Uschakov, 1928; Gurjanova et al., 1928; Uschakov, 1948; Slastnikov, 1957; Petrovskaja, 1960; 1963; Kuznetsov, 1963; Kuderskij, 1966; Aleksandrov, 1981; Golikov et al., 1985). These excluded data do not alter conclusions about ecology and distributional limits of this species.

Although the species is quite common in the Arctic and boreal waters, it may be easily missed when attached to dark stones or shells because of its camouflage colouration.

Ecology. Our Arctic material was collected from stones, mollusc, brachiopod, and barnacle shells, serpulid tubes, and hard bryozoans at depths of 0–110 m. Animals often live mixed with *P.* (*S.*) *cancellata, P.* (*S.*) *vitrea, S.* (*S.*) *tridentatus, B.* (*J.*) *quadrangularis* and *B.* (*J.*) *similis*, sometimes with other species. This is a common and abundant species in arctic and boreal waters, attached to a variety of hard substrates at depths of 0-130 (usually 5–50) m.

Distribution. In the Arctic this species is found in the Chukchi, Kara, Barents, White, and Greenland Seas. It is also reported from the Arctic coast of West Greenland (Wesenberg-Lund, 1950b) and Iceland (Knight-Jones P. et al., 1991). In the North-Western Pacific its distribution range extends south to the North Kurile Islands, Russia (Rzhavsky, 1992a; 1992[1994]); off the American coast it is known from Alaska (Knight-Jones P. et al., 1979). In the North Atlantic the species is recorded only from Newfoundland, Canada (Knight-Jones P. et al., 1979).

Subgenus *Spirorbides* Chamberlin, 1919

Type species: *Serpula cancellata* Fabricius, 1780.

Large collar chaetae modified fin-and-blade cross-striated.

Two species, both known from the Arctic.

Paradexiospira (*Spirorbides*) *cancellata* (Fabricius, 1780)

(Fig. 19A-D)

Serpula cancellata Fabricius, 1780, p. 383.

Spirorbis cancellatus: Levinsen, 1884, p. 208-209, tab. II, fig. 8d, tab, III, fig. 17, 18; Wesenberg-Lund, 1950b, p. 139; 1951, p. 133-134; 1953a, p. 116; Aleksandrov, 1981, p. 90, tab. XIII, fig. 6.

Spirorbis (*Paradexiospira*) *cancellatus*: Bergan, 1953b, p. 38, fig. 3a-d.

Paradexiospira cancellata: Tzetlin, 1985, p. 44-45, fig. 2A, B, 3A-D; Knight-Jones P. et al., 1991, p. 192, fig. 2.

Paradexiospira (*Spirorbides*) *cancellata*: Rzhavsky, 1989, p. 55, fig. 1 Zh, 2 D, 3 D; 1992a, p. 9; 1992[1994], p. 101, fig. 2; 1997b, p. 145; 2001, p. 586, text figures 1-3, map; Jakovis, 1997, p. 45-46, fig. 7a-d.

Material examined. Table 1. # 197 (1); # 533 (1); # 535 (3); # 536 (14); # 549 (7); # 555 (3); # 559 (3); # 560 (4).

Description. Tube dextral, planospiral, thick-walled, up to 4 mm in coil diameter, usually with alveoli on tube periphery (Fig. 19A). Alveoli often absent in juveniles and rarely in adults, moreover, adult tubes detached from substrate may be broken along alveolar line. Adult tubes with 2–3 distinct keels ending as projections over aperture, juvenile tubes unsculptured or with vestigial keels. Tube walls vitreous, transparent; inner tube lining absent, tubes looking greyish-white. Body of live and preserved specimens colourless, brownish gut may be visible through body wall.

Opercular endplate deeply cup-shaped, but often covered by thin brown membranous (chitinous?) dome forming a hollow space below; membrane easily damaged, but diatoms algae often forming dome of same shape instead of membrane; talon massive, thick, shovel-shaped (Fig. 19B, C).

Large collar chaetae (Fig. 18D) modified, fin-and-blade cross-striated with coarsely serrated blades; fin distinct, but gap between fin and blade may be very small in chaetae on concave body side. Capillary chaetae present in collar fascicle. Chaetae of 2nd thoracic chaetigers limbate. Chaetae of 3rd chaetiger only sickle (*Apomatus*), serrated distal part of sickle chaetae about of 1/2 – 1/3 of blade length. Bergan (1953b) reports that notochaetae may develop on 4th chaetiger of concave side of body in adults, but says nothing about their morphology.

Three thoracic tori on concave and two on convex side of body (on chaetigers 2–4 and 2–3 correspondingly). Uncini rasp-shaped with up to about 15 longitudinal rows of teeth throughout length of uncinus and blunt anterior peg. Size of individual uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 25 chaetigers. Usually two chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and coarsely serrated tapering blade. Blade lengths of largest abdominal chaetae shorter than those of collar chaetae. Companion capillary hooked chaetae not observed. Uncini rasp-shaped with blunt anterior peg 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. Because of the short gap between fin and blade of modified collar chaetae from the concave body side in *P.* (*S.*) *cancellata* these chaetae are sometimes erroneously interpreted as “simple” (=limbate) (e.g., Tzetlin, 1985).

P. (*S.*) *cancellata* has very characteristic alveoli on the periphery of their tubes (Fig. 19A), the feature that separates this species from two other representatives of

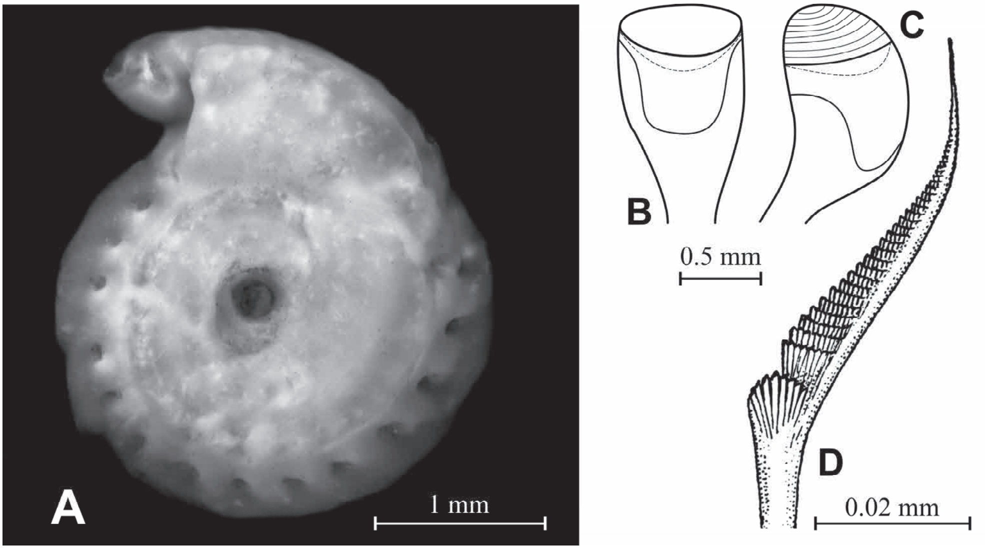

Figure 19. *Paradexiospira* (*Spirorbides*) *cancellata*. A – tube; B – operculum without domed distal part, front view; C – operculum with domed distal part, lateral view; D – modified collar chaeta. B, C – from Rzhavsky (2001); D – from Bergan (1953b). A – photo A.V. Rzhavsky.

Paradexiospira, P. (*P.*) *violacea* (Fig. 18A) and *P.* (*S.*) *vitrea* (Fig. 20A, B). In rare cases, when the alveoli are absent (usually in juveniles) or the tube is broken along the line of alveoli, the species is still easy to distinguish by the absence of any tube colouration. In comparison, tubes of live *P.* (*P.*) *violacea* look almost black, but are dark or light-brown in preserved specimens due to the inner tube lining being visible through the tube walls (Fig. 18A; Pl. 2B). In live specimens of *P.* (*S.*) *vitrea* the red body colour appears through the transparent tube walls giving them a bright pink colour (Pl. 2A), but in preserved specimens the colour is lost. All three species also have different morphologies of opercula and talons (Fig. 18B, C; Fig. 19B, C; Fig. 20C-E). Modified collar chaetae of *P.* (*S.*) *cancellata* from the concave body side have a distinct, but very short gap between fin and blade (Fig. 19D), while in *P.* (*S.*) *vitrea* the gap is well developed in chaetae from both body sides (Fig. 20F), and in *P.* (*P.*) *violacea* modified collar chaetae lack a fin (Fig. 18 D). Finally, *P.* (*P.*) *violacea* has very short serrated parts of the blade of sickle (*Apomatus*) chaetae, about 1/4–1/5 of the blade length (Fig. 18E) versus 1/2 – 1/3 (Fig. 20G) in the other two species. *Neodexiospira pseudocorrugata*, distributed in the North Sea very close to the Arctic basin proper, also has alveoli on the tube periphery, but its tubes are thin-walled, opaque, not vitreous, and do not exceed 2.5 mm in coil diameter. *P.* (*S.*) *cancellata* is that easily recognizable that we have placed all Arctic records of this species without re-examination in the synonymy, even when they are not illustrated or described.

Ecology. Our Arctic material was collected from stones and shells at depths of 20–60 m. Animals often live mixed with *P.* (*P.*) *violacea, P.* (*S.*) *vitrea, Bushiella* (*J.*) *quadrangularis,* and *B.* (*J.*) *similis*, sometimes with other species too. Within its entire distributional range the species occupies only hard substrates (stones and shells) at depths of 3–120 (usually 5–50) m.

Distribution. In the Arctic this species was found in the Kara, Barents, White, and Greenland Seas. It is also reported from the Arctic coast of West Greenland (Wesenberg-Lund, 1950b; 1953 a; Knight-Jones P. et al., 1991). In the North Pacific it is reported only off the Russian coast where its range extends south to the North Kurile Islands and northern part of Sakhalin (Rzhavsky, 1992a; 1992[1994]). In the North Atlantic it is recorded only from Newfoundland, Canada (Knight-Jones P. et al., 1991).

***Paradexiospira* (*Spirorbides*) *vitrea* (Fabricius, 1780)**

(Fig. 20A-I, Pl. 2A)

Serpula vitrea Fabricius, 1780, p. 382-383.

Spirorbis semidentatus Bush, 1905, p. 237-238, pl. XXYI, fig. 7,10, pl. XLI, fig. 13,17,23,26-30.

Spirorbis variabilis Bush, 1905, p. 238, pl. XXIX, fig. 3 a, pl. XXXIX, fig. 24,25, pl. XL, fig. 4, pl. XLIII, fig. 16, pl. XLIY, fig. 17.

Spirorbis vitreus: Bush, 1905, p. 247-248, pl. XLI, fig. 14, pl. XLII, fig. 6-7; Pergament, 1945, p.131. Zatsepin, 1948, p. 166, tab. XXXIX, fig. 23; Wesenberg-Lund, 1950b, p. 141-142; 1951, p. 132; 1953a, p. 115-116; 1953b, p. 9; Denisenko & Savinov, 1984, p. 105.

Spirorbis (*Paradexiospira*) *vitreus*: Bergan, 1953b, p. 38-39, fig. 4 a-b.

Spirorbis (*Dexiospira*) *semidentata*: Uschakov, 1955, p. 430-431, fig. 163A-E (partim); 1965, p. 405, fig. 163A-F (partim).

Spirorbis (*Paradexiospira*) *violaceus* **non** Levinsen, 1884: Streltzov, 1966, p. 90.

Paradexiospira nakamurai Uchida, 1971a, p. 629-633, fig. 1A-H, 2A-H.

Dexiospira (*Spirorbis*) *semidentata*: Tarakanova, 1974a, p. 126.

Dexiospira semidentata: Tarakanova, 1974b, p. 354; 1978a, p. 93; 1978 b, p. 161 (partim); Tarakanova in Kussakin, 1975, p. 62.

Paradexiospira vitrea: Tzetlin, 1985, p. 45-46, fig. 4, 5A-G; Knight-Jones P. et al., 1991, p. 192, fig. 2.

Paradexiospira (*Spirorbides*) *vitrea*: Knight-Jones P. & Knight-Jones E.W., 1977, p. 472-474, fig. 6 A-J; Knight-Jones P. et al., 1979, p. 430, fig. 3D (a-f); Rzhavsky, 1989, p. 53-55, fig. 1G, 2G; 1992a, p. 9-10; 1992[1994], p. 101, fig. 2; 1997b, p. 145-146; 2001, p. 587-588, text figures 1-4, map; Jakovis, 1997, p. 44-45, fig. 6a-d; Gagaev, 2008, p. 95.

Material examined. Table 1. # 11 (4); # 13 (2); # 25 (5); # 59 (tubes); # 61 (1); # 63 (1); # 64 (8); # 66 (1); # 75 (~ 15); # 218 (3); # 232 (2); # 234 (2); # 477 (2); # 486 (~ 15); # 546 (~ 100); # 553 (~ 20); # 555 (~ 25); # 559 (2); # 560 (6); # 561 (1); # 565 (~ 30); # 586 (~ 15); # 590 (~ 10); # 595 (~ 20); # 602 (10).

Description. Tube normally dextral, but sinistral specimens recorded from Pacific coast of North America (Knight-Jones P. et al., 1979; Macdonald, 2007). Up to 2–2.5 mm in coil diameter. tube walls of adults thick, hard, vitreous, with 1–3 keels (Fig. 20B); alveoli on tube periphery are absent. In live specimens red body colour visible through transparent tube walls giving bright-pink appearance to tubes (Pl. 2A). Body and as a consequence tubes of preserved specimens colourless, tubes of preserved or dead specimens may lose transparency. Whorls usually planospiral or overlapping giving a turret-like shape to tubes (Fig. 20A) when height exceeds diameter 1.5–2 times. Tubes of juveniles unsculptured and planospiral; narrow twisting (wavy) transparent zones of tube wall alternating with milky-white coloured ones. Entire body and radioles of live specimens bright red or orange-red (Pl. 2 A); preserved specimens usually colourless or flesh-coloured, but sometimes retaining reddish colour for a long time.

Opercular endplate thin walled and bowl or cup-shaped. Talon absent or vestigial cone-shaped (Fig. 20C-E).

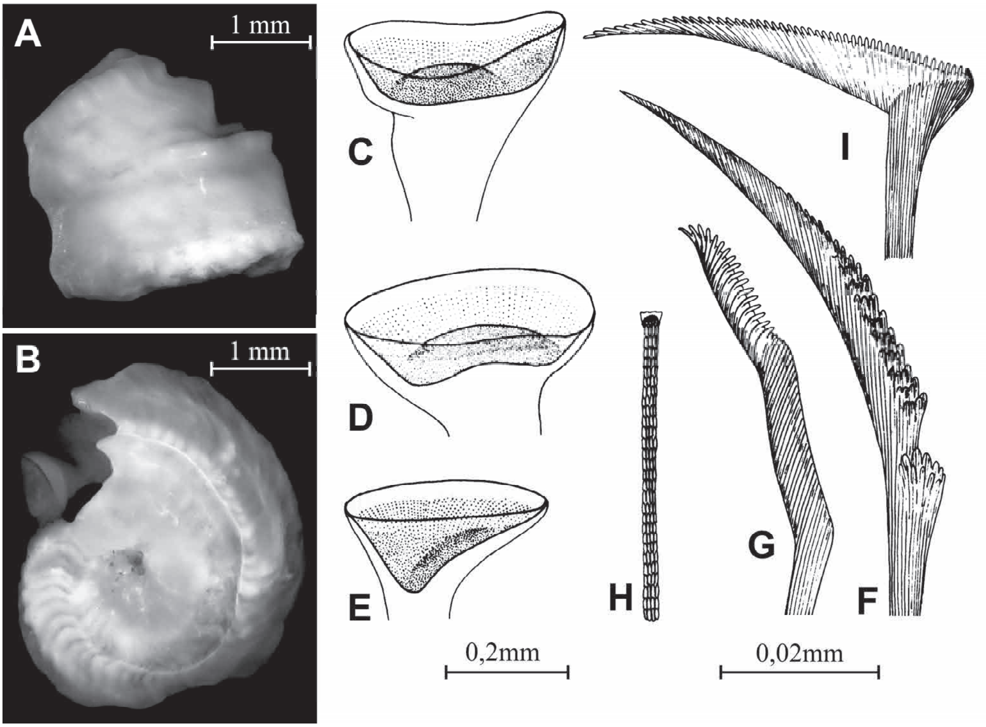

Figure 20. *Paradexiospira* (*Spirorbides*) *vitrea*. A – turret-shape tube, lateral view; B – planospiral tube with animal inside, top view; C-E – opercular variability; F – modified collar chaeta; G – sickle (*Apomatus*) chaeta; H – thoracic uncinus, profile view; I – abdominal uncinus. C-F – from Knight-Jones P. & Knight-Jones E.W. (1977). A, B – photo A.V. Rzhavsky.

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 4th chaetiger forming apron. Thorax with four chaetigers, juveniles sometimes with only three thoracic chaetigers.

Large collar chaetae (Fig. 20 F) modified, fin-and-blade cross-striated with coarsely serrated blade; fin flat and distinct in chaetae from both sides of body. Capillary chaetae also present in collar fascicle. Chaetae of 2nd thoracic chaetigers limbate. Only sickle (*Apomatus*) chaetae (Fig. 20G) present in 3rd fascicle.

Three thoracic tori on concave and two on convex side of body (on chaetigers 2–4 and 2–3 correspondingly). Juveniles sometimes with only two pairs of tori on concave side). Uncini rasp-shaped (Fig. 20H) with up to 5 longitudinal rows of teeth throughout length of uncinus and blunt anterior pegs. Size of individual uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 30 chaetigers. Usually 1–2 chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and serrated tapering blade (Fig. 20I). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae. Companion capillary hooked chaetae may be present in last chaetigers. Uncini rasp-shaped with blunt anterior peg and numerous longitudinal rows of teeth distributed quite asymmetrically; on convex body side uncini usually absent or present only on last chaetigers. Largest tori in anterior half of abdomen on concave side of body.

Remarks. We support the opinion of Knight-Jones P. et al. (1979) that *S. semidentatus* Bush, 1905 and *S. variabilis* Bush, 1905 are in fact dextral and sinistral forms of *P.* (*S.*) *vitrea* respectively. Knight-Jones et al. suggested that these were immature specimens with only three thoracic chaetigers (2 rows of thoracic uncini on the concave side of body), as indeed known for *P.* (*S.*) *vitrea*. However, because such specimens are very rare, in our opinion, Bush's (1905) report of three chaetigers is a mistake, resulting from counting chaetigers on the convex body side, more convenient for examination. Most re-examined records of "*semidentatus*" from Russian Far-Eastern seas (see synonymy) were obvious adults of *P.* (*S.*) *vitrea* with four thoracic chaetigers.

The differences between *P. nakamurai* described by Uchida (1971a) and this species are insignificant and therefore, the species names are synonyms. *P.* (*S.*) *vitrea* from Oregon (Knight-Jones P. et al., 1979) could be a new species (pers. comm. of P. Knight-Jones), but this material has not been re-examined.

All three species of *Paradexiospira* are very easy distinguishable from each other. The red body colour of live specimens of *P.* (*S.*) *vitrea* (Pl. 2 A) visible through their transparent tube walls gives a bright-pink colour to the tubes; alveoli on the tube periphery are absent (Fig. 20A, B). Tubes of *P.* (*P.*) *violacea* also lack peripheral alveoli, but have inner tube lining that is visible through transparent tube wall as dark violet in live and dark or light brown in preserved specimens (Fig. 18A; Pl. 2B). The *P.* (*S.*) *cancellata* tubes are always colourless and have very characteristic alveoli on the tube periphery (Fig. 19A). In rare cases when alveoli are absent (in juveniles) or the tube is broken along the line of alveoli, the species is easy to recognize by the absence of any tube colouration in live animals.

Although preserved specimens of *P.* (*S.*) *vitrea* usually lose their red colour after preservation, they differ from other species by the opercular and talon morphology (see descriptions). In addition, *P.* (*P.*) *violacea* has modified cross-striated collar chaetae without fin; blade of sickle (*Apomatus*) chaeta with very short serrated part (about 1/4–1/5 (Fig.

18E) of the blade length versus 1/2–1/3 (Fig. 20G) in the two other species). In *P.* (*S.*) *cancellata* modified collar chaetae from the concave body side have distinct, but very short gaps between the fins and the blades (Fig. 19D), while in *P.* (*S.*) *vitrea* the gaps (Fig. 20F) are well developed in chaetae from both sides of the body.

A re-examination of unpublished material from the Arctic Seas deposited in the Russian collections showed that specimens of *P.* (*P.*) *violacea* were often identified as "*vitrea*", but material of published records often was not retained. Therefore, we have not included published records with this species name in the synonymy unless they were accompanied by brief descriptions or remarks supporting the identification (Gurjanova & Uschakov, 1928; Uschakov, 1948; Slastnikov, 1957; Petrovskaja, 1960; 1963; Kuznetsov, 1963; Kuderskij, 1966; Aleksandrov, 1981; Golikov et al., 1985). The data thus excluded from the synonymy do not affect our conclusions about ecology and distributional limits of this species.

Absence of cross-striation of collar chaetae in as mentioned in some papers (Crisp. et al., 1967; Tzetlin, 1985) is erroneous as confirmed by re-examination of Tzetlin's material by the senior author.

Ecology. Our Arctic material was collected from stones, mollusc and barnacle shells at depths of 0–148 m. Animals often live mixed with *P.* (*P.*) *violacea, P.* (*S.*) *cancellata, B.* (*J.*) *quadrangularis, B.* (*J.*) *similis* and *C. armoricana,* sometimes with other species. *P.* (*S.*) *vitrea* is one of the most common and abundant spirorbins species in the Northern Hemisphere. It is known from depths of 0–242 (usually 3–50) m. The species inhabits only hard substrates, such as rocks, stones, mollusc, brachiopod and barnacle shells, serpulid tubes, and artificial substrates with rough surface. Juveniles are occasionally found on laminarian folds and *Abietinaria* (Hydrozoa). According to Potswald (1967) and our observations from other geographic regions, *P.* (*S.*) *vitrea* breeds throughout the year, although the proportion of specimens with embryos in winter is very low. However, Bergan (1953a) suggests that in Norway *P.* (*S.*) *vitrea* breeds only from October to April. Tubes of the species were found in stomachs of sea urchins *Strongylocentrotus* spp. off Kamchatka shores; the species appears to serve as food for asteroids (Rzhavsky, pers. obs.)

Distribution. We found this species in the Arctic from Chukchi, Kara, Barents, White, Norwegian, and Greenland Seas. It is also reported from the Arctic coasts off Greenland (Wesenberg-Lund, 1950b; 1953a) and Iceland (Knight-Jones P. et al., 1991). In the North Pacific its range reaches the Sea of Japan, Russia (Rzhavsky, 1992a; 1992[1994]) and California, USA (Knight-Jones et al., 1979; 1991). In the North Atlantic it extends to Brittany, France (Knight-Jones P. & Knight-Jones E.W., 1977) and New England, USA (Knight-Jones P. et al., 1979; 1991).

Januini Knight-Jones P., 1978

Type genus: *Janua* Saint-Joseph, 1894.

Embryos brooded in inverted opercular brood chamber formed outside of opercular ampulla; each brood chamber used only for one brood and moulting needed for embryo release; first brood chamber developing under primary endplate bearing talon; every next brood chamber developing under previous one, so that bottom of first brood chamber becoming secondary distal plate typically lacking talon. Larvae with a pair white attachment glands on thorax. Thoracic uncini narrow, rasp-shaped with 4–8 longitudinal rows of teeth throughout most length of uncinus and a pointed (rarely trifurcate) anterior peg. Abdominal uncini distributed symmetrically. Largest abdominal tori located in anterior half of abdomen. Abdominal chaetae flat geniculate, wide-bladed and coarsely serrated; projecting heel usually absent or vestigial, sometimes noticeable; blade length longer than or equal to that of collar chaetae. Abdominal companion capillary hooked chaetae absent.

Four genera *Janua, Neodexiospira, Pillaiospira* and *Leodora*, only the former is known from the Arctic.

Genus *Janua* Saint-Joseph, 1894

Type species: *Spirorbis pagenstecheri* Quatrefages, 1866b.

Tubes typically dextral, sinistral forms rare. Talon of distal plate of primary operculum small and peripheral; lateral brood chamber walls uncalcified and transparent; first brood chamber with talon on lateral wall facing away from radiolar crown, subsequent chambers lacking talons. Collar and thoracic membrane margins not fused over thoracic groove. Large collar chaetae bent, limbate, with finely serrated blades; sickle chaetae present. Always three thoracic chaetigers.

Monotypic genus.

Janua heterostropha **(Montagu, 1803)**

(Fig. 21A-K)

Serpula heterostropha Montagu, 1803, p. 503-504.

Serpula minuta Montagu, 1803, p. 505-506.

Heterodisca heterostropha: Fleming, 1825, p. 247.

Heterodisca minuta: Fleming, 1825, p. 247.

?Spirorbis ponticus Eichwald, 1830, s. 198; 1841, p. 286, tab. XXXVIII, fig. 29a, b.

? Spirorbis pusilla Rathke, 1837, s. 407 (partim?).

Spirorbis spirillum **non** Linnaeus, 1758: Pagenstecher, 1863, p. 486, tab. XXVIII, fig. 1-6, XXXIX, fig. 1-8.

Spirorbis pagenstecheri: Quatrefages, 1866b, p. 491; Wesenberg-Lund, 1953b, p. 10, fig. 2.

Mera pusilla: Saint-Joseph, 1894, p. 351, pl. XIII, fig. 388-392.

Spirorbis heterostrophus: Mörch, 1863, p. 435-436; Bush, 1905, p. 248.

Spirorbis minutus: Mörch, 1863, p. 436; Bush, 1905, p. 248.

Spirorbis pusillus: Caullery, Mesnil, 1897: 202, fig. D.

Spirorbis pusilloides: Bush, 1905, p. 250.

Spirorbis (*Dexiospira*) *pagenstecheri*: Bergan, 1953b, p. 42-43, fig. 7a, b; Zibrowius, 1968a, p. 201-203, pl. 13, fig. 6-15.

Spirorbis unicornis: Bailey & Harris M.P., 1968, p. 180, fig. 1a-h.

Spirorbis glossoeides: Harris T., 1968a, p. 593-595, 598, fig. 1A-O (partim).

Spirorbis (*Janua*) *gnomonicus*: Bailey, 1969, p. 376-377, fig. 11A-G.

Spirorbis (*Janua*) *epichysus*: Bailey, 1970, p. 73-75, fig. 148-159.

Janua (*Janua*) *pagenstecheri*: Knight-Jones P. et al., 1975a, p. 111-113, fig. 3A-H; 1979, p. 432, fig. 4A (a-d); Knight-Jones P. & Knight-Jones E.W., 1977, p. 486-488, fig. 12A-H.

Janua pagenstecheri: Knight-Jones P., 1984, p. 110; Rzhavsky, 1991b, p. 37-39; 1992 [1994], p. 103, fig. 4; 2001, p. 588-589, text figures 1-6, map.

Material examined. This species is absent from examined Arctic material and the description below is based on literature only and examined material out of Arctic.

Description. Tube (Fig. 21A) typically dextral, sinistral forms rare (Knight-Jones P. et al., 1975a; 1979); usually planospiral, up to 2 mm in coil diameter; last whorls may be overlapping or mouth may be facing away from substrate; usually with 1-3 keels, rarely unsculptured; typical for many other Januini alveoli absent; white opaque non-porcellaneous. Colour of live specimens varying from bright-orange to almost colourless, preserved specimens colourless or flesh-coloured.

Primary operculum (Fig. 21B) with flat endplate and long pin-like peripheral talon often flattened radially. Talon completely fused with first brood chamber, thus, talon attached to brood chamber lateral wall facing away from radiolar crown (Fig. 21C). Subsequent brood chambers lacking talons. All brood chambers conical or cup-shaped with transparent non-calcified lateral walls. Distal part of brood chamber calcified, flat or slightly domed, rarely slightly concave or domed with a central depression (Fig. 21D-G). Tropical populations may develop outgrowths on top of distal plates.

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 bent, limbate (Fig. 21H), sometimes vestigial groove present in basal part of blade, but fin never developed; blades finely serrated, serration more distinct

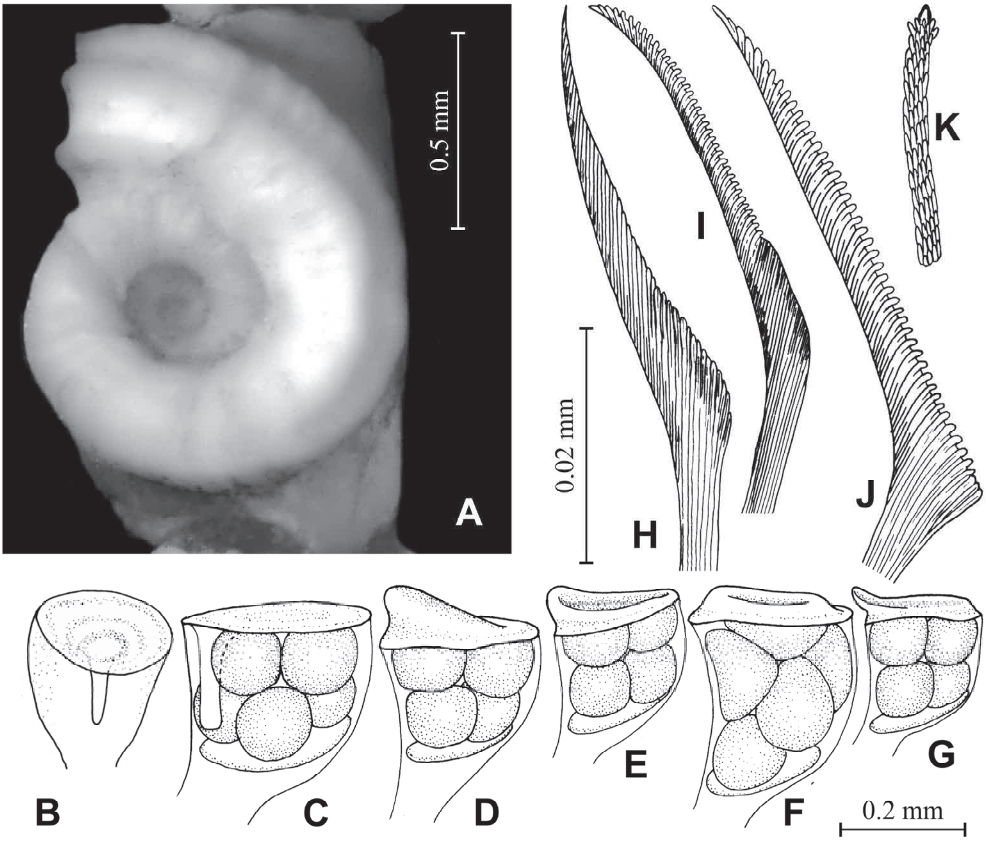

Figure 21. *Janua heterostropha*. A – tube; B – primary operculum, frontal view; B – first brood chamber with talon of primary operculum, lateral view; D-G – variability of subsequent brood chambers without primary opercular talon, lateral view; H – limbate collar chaeta; I – sickle (*Apomatus*) chaeta; J – wide-bladed abdominal chaeta; K – thoracic uncinus, profile view. B, H-K – from Knight-Jones P. & Knight-Jones E.W. (1977), C-G – from Knight-Jones P. et al. (1975). A – photo A.V. Rzhavsky.

in chaetae from convex side of body. Capillary chaetae present in collar fascicles. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae (Fig. 21I) present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini rasp-shaped with pointed anterior pegs and about 5–7 longitudinal rows of teeth throughout most length of uncinus (Fig. 21K). Size of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 12 chaetigers. One abdominal chaeta (Fig. 21J) per fascicle, flat geniculate, wide-bladed, coarsely serrated; projecting heel absent or vestigial. Blade length longer than or equal to that of collar chaetae. Companion capillary hooked chaetae absent. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncinal distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. Very extensive and complicated synonymy for this species was discussed by Knight-Jones P. et al. (1975a) and Rzhavsky (1991b). However, because Rzhavsky (1991b) was published in Russian and because here *Janua heterostropha* is suggested for the first times as a major synonym of the common species name *Janua pagenstecheri* (Quatrefages, 1866b), we summarize the main points here.

Two new spirorbin species *Spirorbis pusilla* Rathke, 1837 and monotypic *Mera pusilla* Saint-Joseph, 1894 were described from the Black Sea and off the coast of Dinard, France, correspondingly. Later, Caullery and Mesnil (1879) synonymized *Mera* Saint-Joseph, 1894 with *Spirorbis*, thus, re-establishing the single genus *Spirorbis.* This nomenclatural change resulted in potentially two "*Spirorbis pusilla*" and the species name "*pusilla*" of Saint-Joseph (1894) became unavailable. To fix this problem, Bush (1905) proposed a new species name *Spirorbis pusilloides* Bush, 1905 for the species described by Saint-Joseph.

Another new species, *Spirorbis pagenstecheri* Quatrefages, 1866b, was described on the basis of the material identified earlier as "*spirillum*" by Pagenstecher (1863). The identities of "*pusilloides*" and "*pagenstecheri*" were discussed by McIntosh (1923), who noted that attribution of some authors (Bush, 1905; Sterzinger, 1910) of modified fin-and-blade collar chaetae to both species was erroneous. Later, Zibrowius (1968a) demonstrated conspecificity of *Spirorbis pagenstecheri* Quatrefages, 1866b and *Spirorbis pusilloides* Bush, 1905 and as a result, the species name "*pagenstecheri*" was accepted in the literature as a major synonym.

McIntosh (1923) also proposed that *S. pusilla* Rathke, 1823 as well may be the same species as *Mera pusilla* (Saint-Joseph, 1894), i.e., Rathke (1823) and Saint-Joseph (1894) apparently independently and accidentally described the same species under the same name. However, Zibrowius (1968a) noted that Rathke's description is not suitable for identification. Indeed, the description is very brief and lacks illustrations. Moreover, because Rathke's diagnosis states that tubes are usually dextral, Rathke's type material likely contained specimens both with dextral and sinistral tubes. Although for some dextral species, including *J. heterostropha,* opposite direction of tube coiling is known (Knight-Jones P. et al., 1979), it is very rare and has not been reported for the population from the Black Sea. Besides, it is also strange that Mörch (1863) citing Rathke (1837) suggested that the tube of his "*pusilla*" is sinistral. Probably, Mörch determined the coiling direction from the side of substrate (as it was done in some publications of the19th century and even up to middle of the 20th century), whereas in currently accepted terms it would dextral. According to most recent data, only three spirorbins, dextral *J. heterostropha* and *Neodexiospira pseudocorrugata*, and sinistral *Pileolaria militaris* Claparède, 1870 are known in the Black Sea. *N. pseudocorrugata* is known only from a single records (Rzhavsky, 1991b), while *J. heterostropha* and *P. militaris* are common, abundant, and often occur in mixture. Therefore, we suppose that the material of Rathke (1837) probably belonged to the latter two species.

Nevertheless, *S. pusilla* Rathke, 1823 was regularly recorded from the Black, Adriatic, and Mediterranean Seas as well as from the Atlantic coast of France, while "*pusilloides*" was reported from the Black and Azov Sea (see Rzhavsky, 1991b) until Vinogradov & Losovskaja (1968) synonymized these species without any explanation. Simultaneously, Vinogradov & Losovskaja (1968) recorded both "*pusilla*" Rathke, 1823 and "*pagenstecheri*" from the Black Sea. Part of this material was either not retained (pers. comm. of G.V. Losovskaja) or no information on its deposition exists. In most cases, based on brief descriptions of these records we conclude that most of them likely belong to *J. heterostropha*. Figures given by Fauvel (1927) both for "*pusilla*" and for "*pagenstecheri*" undoubtedly illustrated *J. heterostropha*; drawings of both species in Vinogradov & Losovskaja (1968) were copied from Fauvel (1927).

Spirorbis ponticus Eichwald, 1830 from the Black Sea is also likely to be identical to *J. heterostropha*. This paper of Eichwald (1830) remained unnoticed. The former species was recorded only once by Eichwald (1941), who also suggested that *S. pusilla* Rathke might be the same as *S. ponticus.* Mörch (1863), Bush (1905), and Hartman (1959) only cited the data of Eichwald (1830; 1841). In the species diagnosis Eichwald (1830) wrote that the tube is sinistral, but later (Eichwald, 1841) he figured a dextral tube. Obviously, he determined the coiling direction looking from the substrate side. Unpublished material of Chernjavskij from the Black Sea from the eighties of 19th century labelled as "*ponticus*" and belonging to *J. heterostropha* was found in the collection of Zoological Institute RAS (St. Petersburg, Russia) by the senior author.

Spirorbis unicornis Bailey, Harris M.P., 1968, from Galapagos, *Spirorbis* (*Janua*) *gnomonicus* Bailey, 1969 from Aegean Sea and *Spirorbis* (*Janua*) *epichysus* Bailey, 1970 from West Indies were accepted as junior synonyms of "*pagenstecheri*" (Knight-Jones P. et al., 1975a). Knight-Jones P. & Knight-Jones E.W. (1977) re-examined the type material of *S. glossoeides* Harris T., 1968a from British shores and found that the paratypes described as dextral were typical juvenile sinistral *S.* (*S.*) *tridentatus,* while the only dextral specimen belonged to *Janua heterostropha* (= *pagenstecheri*).

Although the species name "*pagenstecheri*" was accepted in the literature, *Serpula heterostropha* Montagu, 1803 and *Serpula minuta* Montagu, 1803 were described earlier and both were identical to "*pagenstecheri*". Knight-Jones P. & Knight-Jones E.W. (1977) were first to publish this opinion without a suggested nomenclature change. Although deposition of the type material of "*heterostropha*" and "*minuta*" is unknown (likely it was not retained) and illustrations are absent, the descriptions given in Montagu (1803) together with the data on location and ecology support the above synonymy. Although Montagu (1803) described both *Serpula heterostropha* and *S. minuta* in the same paper, he wrote that *S. minuta* is "very minute species … and not easily distinguished from *S. heterostropha*". Indeed, this is because "*heterostropha*" specimens he described as on shells and non-calcareous algae, and the specimens from *C. officinalis* as "*minuta*", which usually smaller due to the nature of inhabited substrates. Both species name were accepted as valid by Fleming (1825) in the genus *Heterodisca* Fleming, 1825 and by Mörch (1863) and Bush (1905) in the genus *Spirorbis*. Hartman (1959) cited both species as *Heterodisca* and *Serpula* with the remark "indeterminable". Following Article 23.9 of ICZN (2000), we cannot announce these species names "*nomen oblitum*" and one of them must have a priority. Because the description of "*heterostropha*" precedes that of "*minuta*" in Montagu (1803), we use the former species name as the priority.

Sinistral forms of *J. heterostropha* are rarely recorded (Knight-Jones P. et al., 1979 as "*pagenstecheri*") and are not known from the Arctic. Because the body colour of live specimens varies from bright orange to colourless, some authors distinguish the two forms ("*aurantica*" and "*incoloris*" respectively) that are probably just a result of ecophenotypic variability (Knight-Jones P. et al., 1975a).

J. heterostropha is the only species of Januini known from the Arctic and can hardly be confused with any other spirorbins in the region. Two other widely distributed species of Januini, *Neodexiospira brasiliensis* (Grube, 1872) and *N. pseudocorrugata,* have limits of their distribution ranges close to the Arctic border in the Atlantic sector. These two species are easily distinguished from *J. heterostropha* by the absence of sickle (*Apomatus*) chaetae from 3rd fascicle, fused margins of the collar and thoracic membranes, cylindrical calcified brood chamber (generic features), as well as by fan-shaped talons of primary opercula and the structure of collar chaetae (Knight-Jones P. et al., 1975a; Knight-Jones P., 1984).

The only species of Januini slightly resembling *J. heterostropha* in having cone-shaped transparent brood chamber, free margins of collar and thoracic membranes, and pin-like talon is the tropical *Leodora knightjonesi* Silva, 1965. However, this species has sinistral tubes unusual for Januini; talon developed on every brood chamber, and lacks sickle (*Apomatus*) chaeta in the 3rd thoracic fascicle.

Ecology. The only published record of *J. heterostropha* in the Arctic (Bergan, 1953a) does not provide details on species ecology, likely the specimens were collected in shallow water localities, probably from stones. The species also occupies various algae (including calcareous corallinae), sea grasses, mollusc and barnacle shells, and rarely crustacean carapaces. Animals are usually found at depths of 0-30 m (sometimes up to 120 m) in mixture with a number of other spirorbin species (Knight-Jones P. et al., 1975a; Knight-Jones P. & Knight-Jones E.W., 1977).

Colour variability of *J. heterostropha* may be dependent on the environmental conditions. *J. heterostropha* forma *aurantica* is particularly common in high rock pools of Britain and Brittany, where it is often exposed to bright sunlight, while *J. heterostropha* forma *incoloris* is found in shaded localities and in deeper water (Knight-Jones P. et al., 1975a; Knight-Jones P. & Knight-Jones E.W., 1977).

Breeding takes place throughout the year (de Silva, 1967); cross-fertilization usually occurs, while self-fertilization is rare and self-fertilized embryos are less viable (Gee & Williams, 1965); larvae settle most readily on dark or red substrates (Neu, 1933) and tend to be gregarious (Knight-Jones E.W., 1951).

Distribution. In the Arctic the species was reported only from the Norwegian Sea (Bergan, 1953b; Knight-Jones P. et al., 1991). The species is widely distributed in both Hemispheres from southern shores of Australia, Africa, and South America (Knight-Jones et al., 1975a; Knight-Jones P. & Knight-Jones E.W., 1984) to Norway in the North-Eastern Atlantic (Knight-Jones P. et al., 1975a; Knight-Jones P. & Knight-Jones E.W., 1977) as well as Vancouver, Canada (Knight-Jones P. et al., 1979; 1991) and Sea of Japan, Russia (Rzhavsky, 1991b; 1992 [1994]) in the North Pacific.

Pileolariini Knight-Jones P., 1978

Type genus: *Pileolaria* Claparède, 1868.

Embryos brooded within chamber (or cup) formed by invagination of opercular ampulla and used for more than one brood. With two types of opercula, one only a endplate with a talon and another brooding chamber of various structures (from open cup to completely closed chamber sometimes fused with primary opercular endplate when closed). Larvae with single white attachment glands. Thoracic uncini (saw- to rasp-shaped) starting with one row of teeth posteriorly to 3 rows before blunt anterior peg. Abdominal uncini distributed symmetrically. Largest abdominal tori located in anterior or posterior half of abdomen. Abdominal chaetae flat geniculate, pennant-shaped, usually with a thick (optically dense) projecting heel. Its blade length usually somewhat shorter than that of largest collar chaetae, its width decreases gradually towards tip. Companion capillary hooked chaetae usually present on most abdominal chaetigers.

Seven genera: *Pileolaria*, *Simplaria*, *Amplicaria*, *Vinearia*, *Nidificaria*, *Protoleodora* and *Bushiella* (including subgenus *Jugaria*), three found in the Arctic.

Genus *Bushiella* Knight-Jones P., 1973

Type species: *Spirorbis evolutus* Bush, 1905.

Tubes always sinistral. Talon of opercular endplate peripheral or almost peripheral and flattened, generally large; distal plate retained and fused to brood chamber by talon and primary opercular plate (completely or partial) or only by talon; brood chamber a deeply invaginated sac totally enclosing embryos except for a pore capable of opening and closing; lining of brood chamber forming a calcified dome distally, but not calcified proximally or on the side bearing a pore; opercular peduncle inserted between 1st and 2nd radioles on left side, so that non-calcified part of chamber positioned near centre of radiolar crown. Collar and thoracic membrane margins not fused over thoracic groove; posterior edges of thoracic membranes reaching end of 3rd chaetiger. Large collar chaetae limbate or modified fin-and-blade with finely or moderately serrated blades usually lacking cross-striation; sickle (*Apomatus*) chaetae present in 3rd thoracic fascicles. Always three thoracic chaetigers.

Two subgenera *Bushiella* and *Jugaria*, both are present in the Arctic.

Remarks. Initially Knight-Jones P. (1973) erected the subgenus *Bushiella* within *Romanchella* Caullery, Mesnil, 1897, because she erroneously supposed that species of *Bushiella* incubate embryos in the tube. Later all known species of *Bushiella* at the time were transferred to the genus *Sinistrella* Chamberlin, 1919 of the tribe Pileolariini Knight-Jones P., 1978 (Knight-Jones & Fordy, 1979), while other *Romanchella* were placed in Romanchellini Knight-Jones P., 1978. Finally, *Bushiella* was restored as a valid genus within Pileolariini that also contained some species previously attributed to the genera *Sinistrella* and *Leodora* Saint-Joseph, 1894 (see Knight-Jones P., 1984).

Subgenus *Bushiella* Knight-Jones P., 1973

Type species: *Spirorbis evolutus* Bush, 1905.

Large collar chaetae limbate; groove, sometimes very distinct, may be observed in basal part of collar chaetae blade, but a distinct fin never forms.

Six species, three are known from the Arctic.

Remarks. The subgenus by default includes all species of the genus *Bushiella sensu* Knight-Jones P., 1984 and the species described by Rzhavsky (1988a; 1993) and Rzhavsky et al. (2013).

***Bushiella* (*Bushiella*) *barentsii* Rzhavsky, Kupriyanova & Sikorski, 2013**

(Fig. 22A-F)

Spirorbis verruca **non** Fabricius in Mörch, 1863: Bush, 1905, p. 247, pl. XLI, fig. 3, 12, pl. XLIV, fig. 1, 16.

Bushiella (*Bushiella*) *barentsii* Rzhavsky et al., 2013, p. 27-38, fig. 3A-E, 4A-J, 5A-F.

Material examined. Table. 1/ # 487 (40).

Description. Tube (Fig. 22A) sinistral, planospiral with 2–3 (1 in juveniles) distinct keels, up to 4–5 mm in coil diameter, white opaque non-porcellaneous. Colour of live specimens unknown. Preserved specimens dark brown, probably as a result of temporary drying.

Primary operculum (Fig. 22B) of juveniles with concave endplate which deeper in immature specimens of adult size. Talon almost lateral, large and winged laterally (Fig. 22B, C), sometimes of irregular rhomboid shape. Talon pointed or sometimes slightly bifurcated terminally. Primary operculum almost completely fused with developed brood chamber; endplate of primary operculum fused with distal part of brood chamber only in central part and side close to talon, leaving space between distal plate and brood chamber

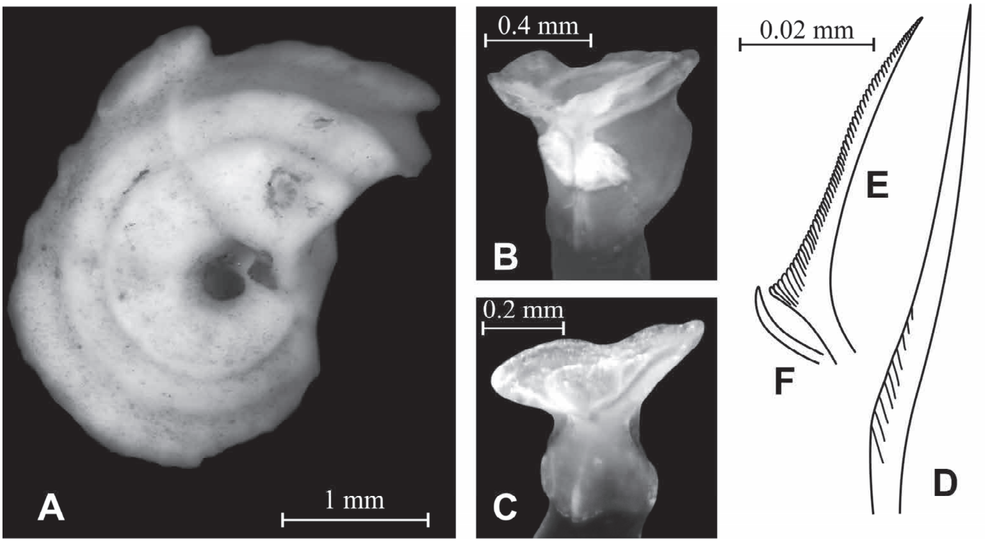

Figure 22. *Bushiella* (*Bushiella*) *barentsii*. A – tube; B – brood chamber with completely preserved primary operculum; C – juvenile primary operculum; D – limbate collar chaeta; E – abdominal chaeta; F – abdominal capillary hooked chaeta. A-F – from Rzhavsky et al. (2013). A-C – photo A.V. Rzhavsky.

on opposite side and laterally (Fig. 22B). This free edge may be broken giving an illusion that primary operculum completely fused with brood chamber, but in this case central fused part of endplate is visible as a spot on distal part of brood chamber. Talon completely fused with lateral wall of brood chamber (Fig. 22B). Distal part of brood chamber slightly convex or flat. Calcified zone of lateral wall very distinct and long on side of talon, almost reaching peduncle; distal edge of calcified zone irregular and rounded (Fig. 22B), sometimes denticulate with its surface looking somewhat fluted. Calcified zone on side opposite from talon resembling a narrow belt adjacent to distal part of brood chamber. Brooding specimens absent in studied material.

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 bent, limbate, with finely serrated blade (Fig. 22D). Capillary chaetae present in collar fascicles. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to-rasp-shaped, each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 20–25 chaetigers in juveniles and over 35 in adults. Two abdominal chaetae per fascicle throughout length of abdomen, but some anterior abdominal chaetigers bearing three chaetae and posterior only one. Chaetae flat geniculate, pennant-shaped, with heel and distinctly serrated tapering blade (Fig. 22E). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. One companion capillary hooked chaetae (Fig. 22F) present in most fascicles. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both sides of body. Largest tori in middle-anterior part of abdomen.

Remarks. Knight-Jones P. et al., 1979 wrote “there is no reason why Bush’s (1905) figured record of Greenland material should not be regarded as *Sinistrella verruca*”. However, Bush’s figures of opercula (Bush, 1905, pl. XLIV, fig. 1, 16) distinctly differs from the re-description of “*verruca*” given by Knight-Jones P. et al. (1979), which mentions a primary operculum completely fused with brood chamber and fan-shaped talon. In our opinion, Bush (1905) depicted typical brood chambers of *B.* (*B.*) *barentsii* with free margins of the primary operculum fused with the brood chamber partially, extensive calcareous zone of the lateral wall of the brood chamber from the talon side, and large winged talon.

B. (*B.*) *barentsii* differs from all *Bushiella* spp. by an unusual structure of its mature brood chamber with the primary operculum plate being only partially fused with the developed brood chamber (Fig. 22B). In all other *Bushiella* species the primary operculum is fused with the brood chamber completely (including *B.* (*B.*) *evoluta* (Fig. 23A) and *B.* (*B.*) *verruca* (Fig. 24A) also known from the Arctic) or firmly attached to the lateral wall of mature brood chamber by talon only, leaving some space between the plate of the primary operculum and distal part of the brood chamber (e.g., Fig. 25B, C). However, very careful observations are needed because the free edge of the primary operculum of *B.* (*B.*) *barentsii* may be broken giving an illusion that the primary operculum is completely fused with brood chamber; when this is the case, the central fused part of endplate is visible as a spot on the distal part of the brood chamber. Another characteristic feature that distinguishes this species from other *Bushiella* spp. is the calcified zone of the lateral wall of the brood chamber. This zone is very extensive and almost reaches peduncle on the talon side; distinct and of irregular, approximately rounded shape; its distal edge sometimes denticulate and the surface looks somewhat fluted (see Rzhavsky et al., 2013). Other species lack the lateral calcified zone (like one found in *B* (*B.*) *evoluta* (Fig. 23B)), but if the zone is present, it is with smooth distal edge reaching approximately edge of talon on lateral wall of brood chamber from the talon side.

Immature specimens of *B* (*B.*) *barentsii* lack brood chambers and may be distinguished by talon morphology. The talon is large and winged laterally, of irregular shape (Fig. 22C, see also Rzhavsky et al., 2013), while in *B.* (*B.*) *evoluta* it is rhomboid and somewhat drop-shaped (Fig. 23B), and in *B.* (*B.*) *verruca* it is fan-shaped (Fig. 24B, C). Some juvenile specimens have rhomboid (diamond-shaped) talons similar to those of *B.* (*J.*) *quadrangularis* (Fig. 28 E), but the latter species has domed opercular endplate and belongs to the subgenus *Jugaria* characterized by distinct fin-and-blade collar chaeta (Fig. 28F).

In addition, tubes of adult *B* (*B.*) *barentsii* are almost twice as large in coil diameter as other Arctic *Bushiella* spp. and bear two distinct keels (Fig. 22A), while *B.* (*B.*) *evoluta* have unsculptured tubes with evoluted and straightened last whorls (Fig. 22A), while tubes of *B.* (*B.*) *verruca* also may be unsculptured or may bear a distinct median keel giving the tube a sub-triangular cross-section (Fig. 24A).

Among *Bushiella* spp. not recorded in the Arctic, *B* (*B.*) *barentsii* is especially similar to *Bushiella* (*Bushiella*) *valida* (Verrill in Smith & Harger, 1874) recorded from the North Atlantic only. Talon of *B* (*B.*) *barentsii* sometimes may resemble the heart-shaped talon of *B.* (*B.*) *valida* (see fig. 2A in Knight-Jones P., 1984). Also these are the only two *Bushiella* species usually reaching 4-5 mm in coil diameter mm in coil diameter, whereas all others do not exceeding 3 mm. But *B.* (*B.*) *valida* has tubes without any keels, while tubes of *B.* (*B.*) *barentsii* bear 1–2 distinct keels. Primary operculum of *B.* (*B.*) *valida* attaches to the brood chamber only by the talon, leaving a space between the plate of the primary operculum and the distal part of brood chamber.

Large tubes and limbate collar chaetae are also typical for Pileolariini of the genus *Protoleodora*. Currently two of them, *P. uschakovi* and *P. gracilis* are known in the Pacific sector of Arctic, although one could be expected in the Atlantic sector of the Arctic (see “Distribution” of *P. uschakovi*). However, their tubes are unsculptured or with only vestigial keels (Fig. 31A; 32A), primary opercula attach to the brood chambers distally by talon’s tip only and often are shed (Fig. 31E, F; 32C, D), and posterior edges of the thoracic membranes on the convex body side extend posteriorly, crossing a long achaetigerous region and reaching the abdomen or continuing to abdominal chaetigers (Fig. 31C; 32B).

Ecology. The species was found at 56 m. The attachment substrate is unknown, although two specimens were attached to small shell fragments. Based on tube morphology (Rzhavsky, 1994), the new species most likely occupies hard substrates, such as shells and stones and, probably, carapaces of large decapods. Bush (1905)’s material was attached to a shell of *Chlamys islandica* (O.F. Müller, 1776), depth unknown.

Distribution. Spitsbergen Bank, Barents Sea (76^{o}7’N, 23^{o}51’48"E) and Greenland (Bush, 1905).

***Bushiella* (*Bushiella*) *evoluta* (Bush, 1905)**

(Fig. 23A-D)

Spirorbis evolutus: Bush, 1905, p. 251, pl. XLII, fig. 20-22.

Romanchella (*Bushiella*) *evoluta*: Knight-Jones P., 1973, p. 242.

Sinistrella evoluta: Knight-Jones P. & Fordy, 1979, p. 121.

Bushiella evoluta: Knight-Jones P., 1984, p. 112-114, fig. 1A-G; Knight-Jones P. et al., 1991, p. 193, fig. 3.

Bushiella (*Bushiella*) *evoluta*: Rzhavsky, 1991a, p. 7; 1993: p. 91; 2001: 591-592, text figures 1-3, map.

Material examined. Table 1. # 495 (3); # 600 (22).

Description. Tube sinistral, planospiral, unsculptured, white opaque non-porcellaneous. Initial tube whorls planospiral, but last whorl usually evoluted and only slightly curved or even straight (Fig. 23A) making coil diameter measurements difficult, but distance between tube mouth and opposite whorl side up to 4-5 mm, while coil diameter of the planospiral part of tube not exceeding 2 mm. Colour of live specimens unknown. Preserved specimens flesh-coloured, dorsal pigmented spots absent.

Juveniles with only primary operculum unknown. Primary operculum with flat endplate and completely fused with developed brood chamber. Distal part of brood chamber also flat and calcified. Lateral walls of brood chamber soft and transparent, calcified zone around talon absent. Talon rhomboid and somewhat drop-shaped, its length approximately 1.5 times exceeding maximal width, terminally it is usually slightly bifurcated (Fig. 23B).

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

Large collar chaetae limbate, often with distinctly enlarged teeth in basal part of blade (Fig. 23C); capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae present in 3rd fascicle; their teeth wider (Fig. 23D) in comparison with those of other *Bushiella* spp.

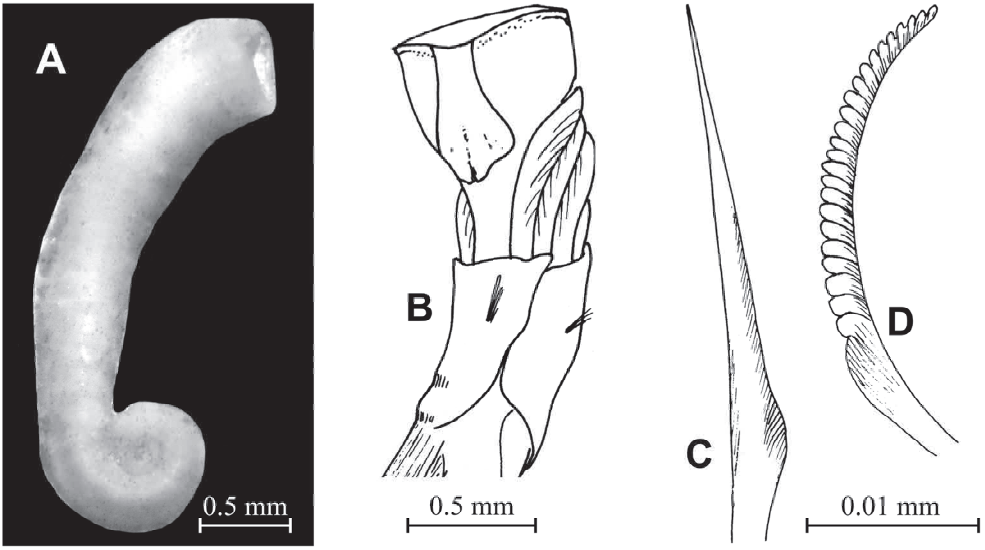

Figure 23. *Bushiella* (*Bushiella*) *evoluta*. A – tube; B – thoracic region with empty brood chamber; C – limbate collar chaeta; D – sickle (*Apomatus*) chaeta. B-C – from Knight-Jones P., 1984. A – photo A.V. Rzhavsky.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to- rasp-shaped, each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 15 chaetigers. 1–2 abdominal chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with poorly developed heel and distinctly serrated tapering blade. Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex body side. One companion capillary hooked chaetae in most abdominal chaetigers. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. This species is easily distinguishable from other *Bushiella* spp. because of its evoluted, slightly curved, or straightened last whorl of the tube (hence the species name) and the absence of calcified zone around the talon on the lateral brood chamber wall.

In comparison with other species of the subgenus *Bushiella* known in the Arctic, tubes of *B.* (*B.*) *barentsii* bear 1–2 distinct keels (Fig. 22A) and those of *B.* (*B.*) *verruca* are usually with one distinct median keel giving a sub-triangular cross-section (Fig. 24A) *versus* unsculptured tubes of *B.* (*B.*) *evoluta. B.* (*B.*) *verruca* and *B.* (*B.*) *evoluta* both have primary opercula completely fused with brood chambers (Fig. 23B, 24C), but talon of the former species is fan-shaped, while that of the latter is rhomboid and somewhat drop-shaped. *B.* (*B.*) *barentsii* have primary opercula only partially fused with brood chambers (see “Description” of *B.* (*B.*) *barentsii*) and large talon winged laterally, sometimes of irregular, somewhat rhomboid shape (Fig. 22B, C).

In *B.* (*J.*) *acuticostalis* calcified zone around the operculum is present, but is often poorly developed and may be absent in preserved material (Fig. 25B, C). This species is easy to distinguish from others by the tube usually bearing three high sharp keels (Fig. 25A), primary operculum attached to brood chamber by the talon only, and fan-shaped talon gradually expanding distally, usually with distinct pointed lateral projections (Fig. 25B-E), and by fin-and-blade collar characteristic for all species of the subgenus *Jugaria*.

Among the Arctic spirorbins, the tubes with evoluted last whorls similar to those of *B.* (*B.*) *evoluta* are found in sinistral *S* (*S.*) *rupestris* (Fig. 35B), the species that is otherwise distinct in many other morphological and ecological features (see “Description” of *S* (*S.*) *rupestris*). Similar (but dextral) tubes are also found in *C. armoricana* living in the same habitats (see below) and in mixture with *B.* (*B.*) *evoluta*.

Ecology. The animals attach only to the inner side of gastropod shells occupied by hermit-crabs, so probably are often overlooked when the material is collected. In the Arctic the species is known at depths of 5–20 m (up to 120–170 m in other parts of the distribution range). The worms are found in mixture with *C. armoricana, B.* (*J.*) *quadrangularis,* and *B.* (*J.*) *similis.* Brooding specimens in Arctic waters were recorded in September.

Distribution. Isfjord, Greenland Sea (West Spitsbergen). Outside the Arctic the species is reported from New Hampshire, USA, Newfoundland, Canada (Knight-Jones P., 1984) and Pacific coast of Kamchatka, Russia (Rzhavsky, 1991a; 1993). Limits of the distribution range are unclear because the species living in very specific habitats (see above) is easily overlooked.

Bushiella (*Bushiella*) *verruca* (Fabricius in Mörch, 1863)

(Fig. 24A-F)

Serpula glomerata **non** Linnaeus, 1767: Fabricius, 1780: 381-382.

Spirorbis verruca: Mörch, 1863, p. 431.

Spirorbis validus **non** Verrill, 1874: Pixell, 1912, p. 800, pl. LXXXIX, fig. 13.

Sinistrella verruca: Knight-Jones P. et al., 1979, p. 446, fig. 6C (a-e).

Bushiella verruca: Knight-Jones P., 1984, p. 113; Rzhavsky, 1989, p. 56, fig. 2Z.

Bushiella (*Bushiella*) *verruca*: Rzhavsky, 1992[1994], p. 103, fig. 5; 2001: 592-593, text figures 1-3, map.

Material examined. Table 1. # 244 (6); # 495 (3).

Description. Tube (Fig. 24A) sinistral, planospiral, up to 2.5 mm in coil diameter, white opaque non-porcellaneous; may be unsculptured, but frequently bearing a median keel giving a sub-triangular cross-section to tube. Colour of live specimens unknown. Preserved animals colourless with almost transparent bodies.

Primary operculum (Fig. 24B) with flat endplate and a peripheral fan-shaped talon of median size, with entire terminal edge. Primary operculum completely fused with developed brood chamber (Fig. 24C). Distal part of brood chamber also flat or slightly concave and calcified. Calcified zone of lateral wall distinct with rounded edge and projecting beyond talons terminal edge on side of talon location. On side opposite to talon, calcified zone absent or as a narrow belt adjacent to distal part of brood chamber (Fig. 24C).

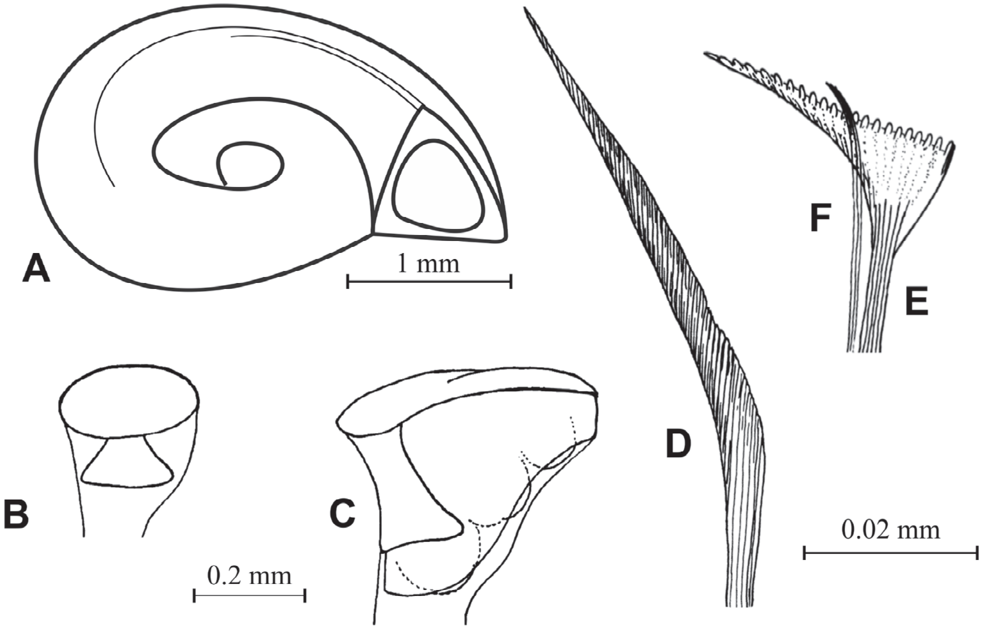

Figure 24. *Bushiella* (*Bushiella*) *verruca*. A – tube; B – primary operculum; C – brood chamber with embryos, lateral view; D – limbate collar chaeta; E – abdominal flat geniculate chaeta; F – abdominal companion capillary hooked chaeta. A-F – from Knight-Jones P. et al., 1979.

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 (Fig. 24D) bent, limbate, with almost smooth blade; sometimes small groove may be present basally on blade, but fin never forming; capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to rasp-shaped, each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 15 chaetigers. 1–2 abdominal chaetae per fascicle, flat geniculate, pennant-shaped, with slight heel and serrated tapering blade (Fig. 24E). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. One Companion capillary hooked chaeta (Fig. 24F) present in most abdominal fascicles. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncinal distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. There was some controversy regarding the year of description for this species. It is now generally accepted that the species was described by Fabricius (1780), even though the species name is absent from that paper. This mistake was apparently introduced by Fauvel (1914) and later was spread widely by Hartman (1959) and Knight-Jones P. et al. (1979). Originally, the species name "*verruca*" appeared in Mörch (1863), who used it referring to some of Fabricius's unpublished manuscript(s) and/or catalogue(s). Mörch (1863) also includes *Serpula glomerata* from Fabricius (1780) into "*verruca*" and unequivocally indicated Fabricius (no year of publication was given though) as the author of "*verruca*". Bush (1905) wrote that Fabricius had described "*verruca*" in 1822, a mistake that probably came from Mörch (1863), who in the synonymy referred to a catalogue "Cat. 1822. n. 1094".

Knight-Jones P. et al. (1979) stated that *B.* (*B.*) *verruca* has been frequently synonymized with *Bushiella* (*Bushiella*) *valida* (Verrill, 1874), even though both species show obvious differences. Our examination of literature revealed that these two species had been synonymized probably only by Uschakov (1950), though others (e.g., Bush, 1905; Pixell, 1912) included several records of "*verruca*" in the synonymy of "*validus*". However, most of the "*verruca*" and "*validus*" records could not be correctly interpreted without examining material (see Knight-Jones P. et al., 1979 for details). As to the records of "*validus*" (= "*verruca*") from the Russian Far-Eastern Seas, Knight-Jones P. et al., (1979) suggested that Annenkova's (1938) and Uschakov's (1955; 1965) material could well have been *B.* (*B.*) *verruca* because this species has been found among unidentified spirorbins from Kurile Islands deposited in the collections of Zoological Institute RAS (St. Petersburg). However, a revision of the material of Zachs (1933), Annenkova (1937; 1938) and Uschakov (1950; 1955; 1965) demonstrated that these animals belong mainly to *Protoleodora uschakovi* (Knight-Jones P., 1984) and sometimes to other *Protoleodora* spp. (Rzhavsky, 1989; 1992b).

Knight-Jones P. et al. (1979) wrote that "there is no reason why Bush's (1905) figured record of Greenland material should not be regarded as *Sinistrella verruca*". However Bush's figures of opercula (Bush, 1905, pl. XLIV, fig. 1, 16) distinctly differs from re-description of "*verruca*" given by Knight-Jones P. et al. (1979) who mentions primary operculum completely fused with brood chamber and fan-shaped talon. In our opinion, Bush (1905) depicted typical *B.* (*B.*) *barentsii* having brood chambers with free margins of primary operculum fused with brood chamber, extensive calcareous zone of the lateral wall of brood chamber from the side of talon, and large winged talon. Fauvel (1914) and Hartman (1959) incorrectly synonymized *B.* (*B.*) *evoluta,* another species known from the Arctic, with B. (*B*) *verruca*.

B. (*B.*) *verruca* differs from two other Arctic species of the subgenus *Bushiella* in many features. It has planospiral tube usually with a distinct median keel giving the tube a sub-triangular cross-section (Fig. 24A), whereas tubes are always unsculptured with evoluted distal whorls in *B.* (*B.*) *evoluta* (Fig. 23A) and almost twice as large and bearing two (less often one) blunt keels in *B.* (*B.*) *barentsii* (Fig. 22A). Both *B.* (*B.*) *verruca* (Fig. 24C) and *B.* (*B.*) *evoluta* have (Fig. 23B) flat distal parts of their brood chambers completely fused with primary opercula, but the former species has fan-shaped talon surrounded by calcified zone (talon is rhomboid, somewhat drop-shaped and without calcified zone in *B.* (*B.*) *evoluta*)). Primary operculum of *B.* (*B.*) *barentsii* (Fig. 22B) is fused with brood chamber only centrally, talon large and laterally winged, calcified zone of lateral wall is very extensive and almost reaching the peduncle on the side of the talon.

Distinguishing *B.* (*B.*) *verruca* from *B.* (*J.*) *similis* (the species with almost identical fan-shaded talons) is more problematic. The talon of *B.* (*J.*) *similis* (Fig. 29B; Pl. 2G) bears two vestigial lateral projections distally, while that of *B.* (*B.*) *verruca* (Fig. 24B, C) is triangular with flattened lateral sides. Although the former species belongs to the subgenus *Jugaria* with collar fin-and-blade chaetae, they have very delicate serration of both the blade and the fin (Fig. 29C). Therefore, under a compound microscope a modified collar chaeta not in strictly lateral position may look like a limbate chaeta with a small basal groove. Although it should be examined very accurately, structure of collar chaeta is the most reliable feature distinguishing these two species. In addition, *B.* (*J.*) *similis* usually has unsculptured tubes (Fig. 29A) and even when a median keel is present, it is vestigial and does not change the tube cross-section from circular to triangular. There is no data on colour of live *B.* (*B.*) *verruca,* but few examined fixed specimens were colourless and almost transparent. Thorax and abdomen of live *B.* (*J.*) *similis* are colourless with reddish-brown gut translucent through the body wall, while in preserved material gut is brownish and not so bright. Collar and thoracic membranes of live specimens of *B.* (*J.*) *similis* may be light brownish-yellow and bodies of live animals may bear large deep-pink pigmented spots on the dorsal side of posterior thoraxes and in the achaetigerous zone. Such spots turn brown or disappear in preserved material.

Two more species of the subgenus *Jugaria, B.* (*J.*) *acuticostalis* and *B.* (*J.*) *granulata,* known from the Arctic also have similar talon morphology (Fig. 25C; 26C). Luckily, interpretation of their fin-and-blade collar chaetae is not problematic, in these two species fin-and-blade chaetae (e.g., Fig. 26E) cannot be confused with limbate ones of *B.* (*B.*) *verruca* (Fig. 24D). Additionally, both of them have primary opercula attached to the brood chamber only by the talon leaving some space between the plate of primary operculum and the distal part of the brood chamber (Fig. 25B, C; 26C). Tubes of *B.* (*J.*) *acuticostalis* usually bear three high sharp keels (Fig. 25A). Tubes of *B.* (*J.*) *granulata* are typically unsculptured or may bear only one indistinct keel (Fig. 26A) shifted toward the inner whorl side (not median). Two remaining species of *Jugaria* known from the Arctic, *B.* (*J.*) *kofiadii* and *B.* (*J.*) *quadrangularis*, clearly differ from *B.* (*B.*) *verruca* in having fin-and-blade collar chaeta, as well as in morphology of their tubes, talons, and brood chambers (see descriptions).

B. (*B.*) *valida* that is listed in the synonymy here and is often confused with *B.* (*B.*) *verruca* is indisputably known from the northwest Atlantic only (Knight-Jones P. et al., 1979). It is distinct in having a large unsculptured tube up to 5 mm in whorl diameter, large winged or heart-shaped talon, and primary operculum that does not fuse completely with brood chamber (see Knight-Jones P. et al., 1979; Knight-Jones P., 1984).

Among non-Arctic species, only tubes of *Bushiella* (*Jugaria*) *beatlesi* Rzhavsky, 1993 (known from the Kurile Islands only) bear distinct sharp median keels similar to those found in *B.* (*B.*) *verruca*, but the former species has fin-and-blade collar chaetae, domed distal part of brood chamber, and long narrow talons, usually slightly widening towards distally bifid ends (Rzhavsky, 1993).

Ecology. The Arctic specimens were collected at depths of 67 and 445 m, in other parts of the distribution range the species is known from depths of 14-100 m. Animals attach to stones and shells, and occur as solitary organisms among *P.* (*P.*) *violacea, P.* (*S.*) *vitrea, P.* (*S.*) *cancellata, B.* (*J.*) *quadrangularis,* and *C. armoricana*.

Distribution. Our Arctic material was collected from Morsvikbotn Fjord, the Norwegian Sea and Central Arctic on the border with the Barents Sea near Spitsbergen (80° 45’6” N, 29° 57’ E). From literature the species is known from Greenland (type locality, Mörch (1863), non Bush (1905)). It is also reported in the North Pacific from Hokkaido (Japan), East Kamchatka shores and Kurile Islands, Russia and off Vancouver Island and Canoe Bay, Canada (Knight-Jones P. et al., 1979).

Subgenus *Jugaria* Knight-Jones P., 1978

Type species: *Spirorbis quadrangularis* Stimpson, 1854.

Large collar chaetae modified fin-and blade; cross-striation usually absent, although some species with vestigial cross-striation in basal part of blade.

Eight species, including the doubtful *Bushiella* (*Jugaria*) *stimpsoni* (Verrill, 1880), five known from the Arctic.

Remarks. Knight-Jones P. (1978) had erected *Jugaria* as a subgenus of *Pileolaria* and later (Knight-Jones P., 1984) changed it to the generic rank inside Pileolariini together with genera *Pileolaria, Bushiella* and others. Rzhavsky (1991a) for the purpose of spirorbin classification unification placed *Jugaria* into *Bushiella* as a valid subgenus. Currently the subgenus includes all species of *Jugaria sensu* Knight-Jones P. (1978) and three new species described by Rzhavsky (1988b, 1991a, 1993).

***Bushiella* (*Jugaria*) *acuticostalis* Rzhavsky, 1991a**

(Fig. 25A-E)

Bushiella (*Jugaria*) *acuticostalis* Rzhavsky, 1991a, p. 7-10, fig. 2A-O; 1993, p. 94; 1997b: 147.

? *Pileolaria* (*Jugaria*) *stimpsoni* **non** Verrill, 1880: Knight-Jones P., 1978, p. 229.

? *Jugaria stimpsoni*: Knight-Jones P. et al., 1991, p. 195, fig. 4g.

Material examined. Table 1. # 482 (10); # 486 (3).

Description. Tube (Fig. 25A) sinistral, planospiral, but often oval (not circular), up to 2.5 mm in coil diameter, white opaque, non-porcellaneous. Typically with three (rarely four) narrow, very high keels (in juveniles and sometimes in adults keels low or even vestigial), but tube remaining circular in cross-section. Colour of live specimens unknown. Preserved animals colourless or flesh-coloured.

Primary operculum (Fig. 25B-E) with slightly concave endplate and a peripheral talon of median size, fan-shaped, gradually expanding distally, usually with distinct pointed lateral projections and often with very narrow pointed projection in centre of distal edge. Primary operculum firmly attached by talon only to lateral wall of developed brood chamber, leaving some space between plate of primary operculum and distal part of brood chamber (Fig. 25 B, C). Distal part of brood chamber flat or slightly convex; calcified zone on lateral side of brood chamber present, but often poorly visible or absent in preserved material (Fig. 25 B, C).

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 bent, modified fin-and-blade, with very fine teeth on blade and larger teeth on flattened or slightly rounded fin; capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to-rasp-shaped, each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae. Length of largest uncini less than that of collar chaetae blades.

Abdomen with about 10–15 chaetigers. Usually one abdominal chaeta per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and serrated tapering blade. Blade length of largest abdominal chaetae shorter than those of collar chaetae from convex side. One companion capillary hooked chaeta in most ab-

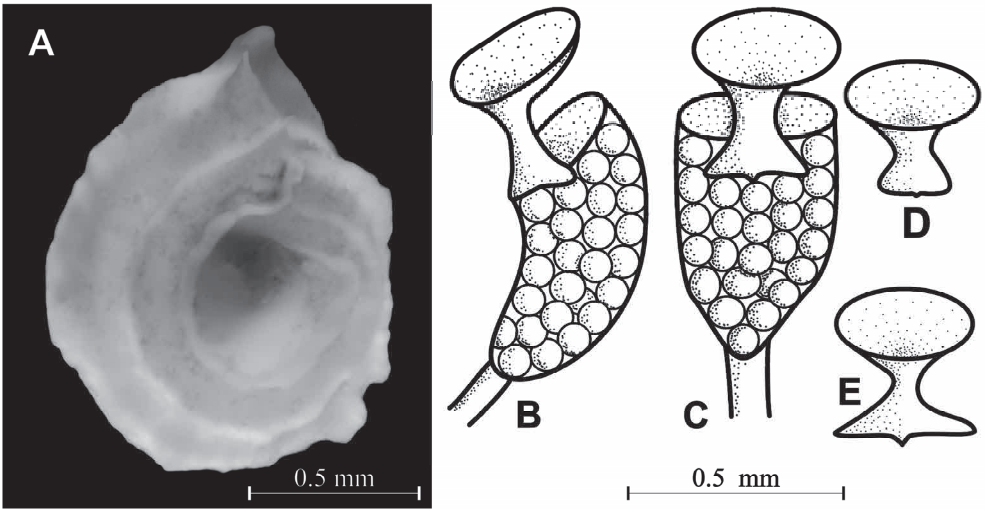

Figure 25. *Bushiella* (*Jugaria*) *acuticostalis*. A – tube; B, C – brood chamber with embryos, lateral and frontal views; D, E – variability of primary opercula. B-E – from Rzhavsky, 1991a. A – photo A.V. Rzhavsky.

dominal fascicles. Abdominal uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncinal distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. Among Arctic *Jugaria,* only *Bushiella* (*J.*) *acuticostalis* and *B.* (*J.*) *granulata* have primary opercula attached to brood chamber by talon only, leaving some space between plate of the primary operculum and the distal part of the brood chamber (Fig. 25B, C; 26C). Talons of these two species are also similar and fan-shaped, although in *B.* (*J.*) *acuticostalis* the talon is usually with distinct pointed lateral projections and often with a very narrow pointed projection in the central part of the terminal edge, while in *B.* (*J.*) *granulata* the talon is slightly bilobed distally with rounded edges. Another Arctic *Bushiella* species having a similar talon is *B.* (*J.*) *similis,* but its primary operculum is completely fused with the brood chamber (Fig. 29B). Also, *B.* (*J.*) *acuticostalis* tubes bear three distinct keels, usually high and sharp (Fig. 25A), while tubes of *B.* (*J.*) *granulata* and *B.* (*J.*) *similis* are unsculptured or with only one indistinct keel (Fig. 26A; 29A).

Three distinct keels are also typical for tubes of Arctic *B.* (*J.*) *kofiadii*, but their keels are not so high and narrow, junctions between the keels and the tube surface are gradual and the tubes are pentangular in cross-sections (Fig. 27A, B). *B.* (*J.*) *kofiadii* also has domed distal part of brood chamber completely fused with primary operculum and a large trapezoid talon (Fig. 27C, D).

Bushiella (*Jugaria*) *stimpsoni* (Verrill, 1880), very briefly described from the Atlantic coast of North America according to some reports (Knight-Jones P., 1978; Knight-Jones P. et al., 1991), also has a space between the plate of the primary operculum and the distal part of the brood chamber. Taxonomic position of this species is unclear and it is similar to *B.* (*J.*) *granulata* or *B.* (*J.*) *similis* (see “Remarks” for *B.* (*J.*) *granulata* and *B.* (*J.*) *similis*). But the Newfoundland specimens of Knight-Jones P. (1978) and Knight-Jones P. et al., (1991) re-examined by Rzhavsky were obviously different from the worms identified by Verrill (see “Remarks” to *B.* (*J.*) *similis*). They are large for spirorbins (more than 5 mm in whorl diameter) and in our opinion resemble “giant” specimens of *B.* (*J.*) *acuticostalis* rather than *B.* (*J.*) *granulata.* Unfortunately, because Knight-Jones’s material is represented by 3 poorly preserved specimens only, we cannot conclude whether it is really a “giant” *B.* (*J.*) *acuticostalis* previously known only from the north-western Pacific and currently found in the Arctic or a separate valid species. Interestingly the “gigantism” phenomenon was also observed for other spirorbins from the Newfoundland region (see Remarks for *Pileolaria* ex gr. *berkeleyana*).

Mature brood chamber of the same structure as found in *Bushiella* (*Jugaria*) *acuticostalis* are also typical for the North Atlantic *B.* (*B.*) *valida*, but the latter species has limbate collar chaetae, large (up to 5 mm) unsculptured tubes and heart-shaped talons.

Primary operculum attached to the brood chamber by a talon only is also known for some species of the genus *Protoleodora*, two of which (*P. uschakovi* and *P. gracilis*) are reported from the Arctic. However, talon in each of these species is infirmly attached to the distal part of the brood chamber (not to its lateral wall) only by the talon’s tip and is often shed (see below).

Ecology. Arctic specimens were collected at depths of 59 and 170–179 m, in other parts of the distribution range the species is reported from depths of 10–40 m. Animals usually are attached to hydrozoans and bryozoans, occasionally are found on shells of bivalves, stones, and serpulid tubes incrusted by bryozoans; live in mixture with *C. spirillum, C. armoricana*, *B.* (*J.*) *quadrangularis*, *B.* (*J.*) *similis,* and some other species.

Distribution. This is a new record for the Arctic, where *Bushiella* (*J.*) *acuticostalis* was found in the Barents Sea from Spitsbergen Bank (76º7'N, 23º51'48"E) and Kola Bay (69º19' N, 33º52' E). It is also known in the North Pacific from the Northern Kurile Islands, Sea of Okhotsk, and Commander Islands, Russia (Rzhavsky, 1991a; 1993). The species probably lives around Newfoundland (Knight-Jones P., 1978; Knight-Jones P. et al., 1991 as "*stimpsoni*").

***Bushiella* (*Jugaria*) *granulata* (Linnaeus, 1767)**

(Fig. 26A-H)

Serpula granulata Linnaeus, 1767, p. 1266.

Spirorbis granulatus: Zenkevich, 1925, p. 5; Aleksandrov, 1981, p. 90, tab. XIII, fig. 4.

?*Spirorbis* (*Laeospira*) *granulata*: Bergan, 1953b, p. 35-38, fig. 2a-c (partim?).

Pileolaria granulata: Knight-Jones P. & Knight-Jones E.W., 1977, p. 484-485, fig. 11 A-J.

Jugaria granulata: Knight-Jones P. et al., 1991, p. 193, fig. 3.

Bushiella (*Jugaria*) *granulata*: Rzhavsky, 1991a, p. 10; 1992[1994], p. 104, fig. 5; 2001, p. 593-594, text figures 1-3, map; Jakovis, 1997, p. 52-53, fig. 12a-v.

Material examined. Table 1. # 506 (~ 50); # 510 (some); # 565 (1); # 625 (some).

Description. Tube (Fig. 26A) sinistral, planospiral, up to 2.5 mm in coil diameter, white opaque non-porcellaneous; unsculptured or with one low keel shifted towards inner whorl side. Live animals almost colourless, thorax may be yellowish. Yellow-brown gut translucent through the body wall. Preserved specimens colourless.

Primary operculum (Fig. 26B) with slightly concave endplate and a peripheral talon of intermediate size, usually slightly bilobed distally, rarely fan-shaped. Primary operculum firmly attached by talon only to lateral wall of developed brood chamber, leaving some space between plate of primary operculum and distal part of brood chamber (Fig. 26C). This space sometimes very small and endplate very close to brood chamber, but never fused. Very rarely primary operculum may be shed at mature brood chamber stage (Fig. 26 D). Distal part of brood chamber flat or slightly convex, with a distal rim; calcified zone on lateral walls of brood chamber very light with poorly defined proximal limits, somewhat longer on side of talon attachment (Fig. 26 C, D).

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 (Fig. 26E) bent, modified fin-and-blade with very fine teeth on blade and large teeth on flat fin; capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae (Fig. 26F) also present in 3rd fascicle, their distal serrated part very long, occupying most of blade length.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Thoracic uncini saw-to-rasp-shaped (Fig. 26H), each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth near blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae. Length of largest uncini less than that of collar chaetae blades.

Abdomen with about up to 17 chaetigers. Usually two abdominal chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with coarsely serrated tapering blades; heel vestigial or absent (Fig. 26G). Blades length of largest abdominal chaetae shorter than those of collar chaetae from convex side. Companion capillary hooked chaetae not recorded. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both sides of body. Largest tori in mid-posterior half of abdomen.

Remarks. The relationships of the species names "*granulatus*" and "*tridentatus*" have been discussed in detail (Bergan, 1953b; Gee, 1964; Knight-Jones P. & Knight-Jones E.W., 1977) and the species name "*granulatus*" was fixed for the opercula-incubating specimens. "*Spirorbis granulatus*" is regularly recorded from the arctic-boreal waters as common and abundant. In fact, however, this species is very rare and most of its records mainly belong to *B.* (*J.*) *quadrangularis*, and also often to *B.*(*J.*) *kofiadii*, *B.*(*J.*) *similis,* and *P. uschakovi* (Knight-Jones P. & Knight-Jones E.W., 1977; Knight-Jones P. et al., 1979; Rzhavsky, 1989; 1992b; 2001). Knight-Jones P. & Knight-Jones E.W. (1977) confirmed that Bergan (1953a, b) correctly identified this species. Although we did not examine Bergan's material, Bergan's (1953b) drawing of the brood chamber in our opinion rather illustrates that of *B.* (*J.*) *similis.* Zatsepin (1948) compiled data available at the time on distribution of "*granulatus"* in the Arctic Ocean, but his drawings correspond to *B.* (*J.*) *quadrangularis*.

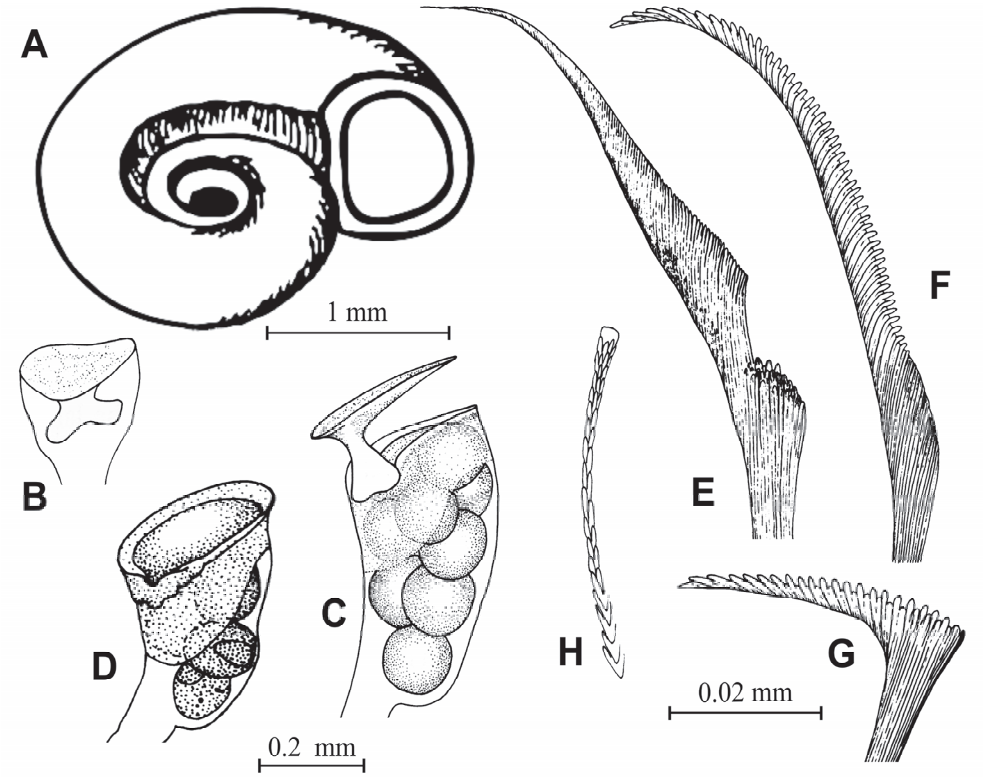

Figure 26. *Bushiella* (*Jugaria*) *granulata.* A – tube; B – primary operculum; C – brood chamber with embryos and attached primary operculum; D – brood chamber with embryos, primary is operculum shed; E – modified collar chaeta; F – sickle (*Apomatus)* chaeta; G – abdominal flat geniculate chaeta. H – thoracic uncinus. A – from Aleksandrov (1981), B-G – from Knight-Jones P. & Knight-Jones E.W. (1977).

Among the Arctic *Jugaria,* only *B.* (*J.*) *acuticostalis* and *B.* (*J.*) *granulata* have primary opercula attached to brood chambers by the talons only, leaving some space between the plate of the primary operculum and the distal part of the brood chamber (Fig. 25B, C; 26 C). Talons of these two species are also similar and fan-shaped, though in *B.* (*J.*) *granulata* the talon is slightly bilobed distally with rounded edges, while in *B.* (*J.*) *acuticostalis* the talon is usually with distinct pointed lateral projections and often with a very narrow pointed projection in the centre of the distal edge.

Another Arctic *Bushiella* species having a talon similar to *B.* (*J.*) *granulata* is *B.* (*J.*) *similis,* but its primary operculum is completely fused with the brood chamber (Fig. 29B). Tubes of both species are also similar in being unsculptured (e.g., Fig. 29A), but tubes of *B.* (*J.*) *granulata* often bear one low keel shifted towards the inner whorl side (Fig. 26A), whereas those of *B.* (*J.*) *similis* may have one vestigial median keel. Both species, including immature specimens, can by reliably distinguished by the collar chaetae that have very fine teeth on the blade and large teeth on the flat fin in *B.* (*J.*) *granulata* (Fig. 26E), while in *B.* (*J.*) *similis* both the blade and the fin are very finely serrated (Fig. 29C).

Specimens of *B.* (*J.*) *quadrangularis* (widely distributed in the Arctic and commonly misidentified as *B.* (*J.*) *granulata*) fairly often also have one low keel shifted towards the inner whorl side, but typically their tubes bear two keels, one of which is shifted towards the inner whorl and another is towards the periphery (Fig. 28A). However, *B.* (*J.*) *quadrangularis* distinctly differs from *B.* (*J.*) *granulata* by having the primary operculum completely fused with the brood chamber, domed distal part of the brood chamber and even domed endplate of the juvenile primary operculum (not flat, slightly convex or concave), and large rhomboid (diamond-shaped) talon (Fig. 2 B-E).

An unsculptured tube similar to that of *B.* (*J.*) *granulata* is also typical for *B.* (*B.*) *evoluta,* but last tube whorls in the latter species are usually evoluted and are only slightly curved or even straightened (Fig. 23A). Besides, *B.* (*B.*) *evoluta* has limbate collar chaetae (Fig. 23C), its primary operculum fuses completely with the brood chamber, it lacks calcified zone of lateral walls of brood chamber and has rhomboid or somewhat drop-shaped talon (Fig. 23B).

In addition, *B.* (*J.*) *granulata* differs from all other species of the genus by having a quite unusual distribution of the abdominal tori where the largest are located in med-posterior half of the abdomen, while in other species they are positioned anteriorly. However, this feature is not suitable for identification.

B. (*J.*) *stimpsoni* very briefly described from the Atlantic coast of North America probably resembles "*granulatus*" in having a space between the plate of the primary operculum and the distal part of the brood chamber. The taxonomic position of *B.* (*J.*) *stimpsoni* is unclear. Verrill (1874) figured "*Spirorbis nautiloides* ?" and later (Verrill 1880) included its material in synonymy with his newly described species *B.* (*J.*) *stimpsoni.* Subsequent records of "*stimpsoni*" are quite rare (Bush, 1905; Hartman, 1944; Knight-Jones P., Knight-Jones E.W., 1977; Knight-Jones, 1978; Knight-Jones, Fordy, 1979; Knight-Jones P. et al., 1991) and existing information is very incomplete and contradictory. For example, Verrill (1874) figured a small and conical breeding operculum without any talon and calcified zone; Bush (1905) provided very unclear illustrations of two opercula of *"stimpsoni"*, a small empty conical primary operculum lacking calcification of the lateral wall, but bearing a strongly bilobed talon, and another operculum "filled with embryos, with secondary calcareous plate". Knight-Jones P. (1974) stated that the primary operculum of *B.* (*J.*) *stimpsoni* was “like that of *P. granulata,* attached to the brood chamber by a short fan-shaped talon. The brood chamber is elongated with a shallower area of opaque calcification”. Later (Knight-Jones P. et al., 1991) she drew an operculum of a specimen that she referred to “*stimpsoni*” with the remark that it is “rather like *J. granulata,* but larger”. In our opinion, brief descriptions of *B.* (*J.*) *stimpsoni* by Verrill (1874; 1880) and Bush (1905) rather belong to *B.* (*J.*) *similis,* while the specimens examined of Knight-Jones P. (1978) and Knight-Jones P. et al. (1991) may belong to *B.* (*J.*) *acuticostalis* (see “Remarks” to *B.* (*J.*) *similis* and *B.* (*J.*) *acuticostalis*).

A primary operculum attached to the brood chamber by a talon *only* is also characteristic for some species of the genus *Protoleodora*, two of which (*P. uschakovi* and *P. gracilis*) are known from the Arctic. However, the opercular talons of those species are is infirmly attached to the distal parts of brood chambers (not to the lateral wall like in “*granulatus*”) only by the talon tip and are often shed (see below).

Ecology. In the Arctic the species is found at depths of 12–90 m attached to algae and stones. In other parts of the distribution range it is reported from depths of 2–70 m. Animals occupy algae (fuci and laminarians), stones, and shells. They may live in mixture with *C. armoricana, B.* (*J.*) *quadrangularis,* and *S.* (*S.*) *spirorbis.*

Distribution. In the Arctic *B.* (*J.*) *granulata is* known only from the Kara and the White Seas. All other records of this species from the Arctic are either erroneous or doubtful. The species is also recorded by Rzhavsky (2001) from the Baltic Sea near Kiel and the North Sea. It is well known off the British and Irish shores (Knight-Jones P. & Knight-Jones, E.W., 1977). Although this species is reported in many papers, its distribution is unclear because of numerous misidentifications. According to Knight-Jones P. & Knight-Jones E.W. (1977), it is distributed in the North-West Europe (excluding Iceland) as far south as Roscoff. It is certainly absent from the Pacific.

***Bushiella* (*Jugaria*) *kofiadii* Rzhavsky, 1988**

(Fig. 27A-D)

Spirorbis granulatus **non** Linnaeus, 1767: Pergament, 1945, p. 131 (partim); Annenkova, 1932, p. 190; Annenkova in Gorbunov, 1946, p. 39 (partim); Chlebovitsch, 1964, p. 179 (partim?).

Jugaria kofiadii: Rzhavsky, 1988b, p. 933-935, fig. A-M; Knight-Jones P. et al., 1991a, p. 193, fig. 3.

Bushiella (*Jugaria*) *kofiadii*: Rzhavsky, 1992[1994], p. 104; 2001, p. 594-595, text figures 1-3, map.

Material examined. Table 1. # 4 (21); # 5 (2); # 7 (1); # 11 (5); # 12 (1); # 14 (3); # 15 (? 30); # 18 (2); # 58 (2); # 62 (2); # 77 (8); # 86 (1); # 89 (3); # 124 (3); # 147 (1); # 168 (1); # 189 (5); # 192 (2); # 205 (5); # 252 (1); # 256 (6); # 257 (1); # 275 (~ 10); # 278 (3); # 284 (12); # 440 91); # 447 (1); # 449 (2); # 450 (1); # 462 (31); # 520 (1); # 528 (1); # 532 (1); # 604 (7).

Description. Tube (Fig. 27A, B) sinistral, initial whorls planospiral, but last usually facing upward from substrate; coil diameter of planospiral part up to 2.5 mm; white opaque non-porcellaneous; typically with three distinct keels giving tubes pentangular cross-sections. Sometimes last whorls resembling intercalated segments (Fig. 27B). Colour of live specimens unknown. Preserved animals colourless or flesh-coloured.

Primary operculum with a flat peripheral talon and a domed or slightly convex endplate. Talon large, trapezoid, gradually widening towards flat or slightly pointed distal end with smooth or slightly scalloped edge (Fig. 26D). Primary operculum firmly and completely fused with developed brood chamber. Distal part of brood chamber strongly domed, sometimes only slightly convex, but never flat. Calcified zone of lateral wall distinct; long on side of talon and extending beyond its distal edge, but not reaching peduncle; distal edge of calcified zone rounded. On side opposite from talon calcified zone as a narrow belt adjacent to distal part of brood chamber (Fig. 27C, D).

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

Large collar chaetae bent, modified fin-and-blade with a streamlined fin of small teeth and a finely serrated distal blade; capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to rasp-shaped, each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae. Length of largest uncini less than that of collar chaetae blades.

Abdomen with 20–30 chaetigers. Usually one abdominal chaeta per fascicle throughout length of abdomen (two in some first abdominal chaetigers), flat geniculate, pennant-shaped, with distinct heel and coarsely serrated tapering blade. Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. One companion capillary hooked chaeta in most fascicles. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. Annenkova, Pergament and Chlebovitsch identified a part of the materials examined by the senior author mainly as "*granulatus*", Vagin identified some specimens as "*violaceus*", and Annenkova labelled one specimen as "*spirillum*". In the original species description Rzhavsky (1988b) considered these records unpublished, but most of the records were published in the papers cited in the synonymy here.

Among Arctic species, *B.* (*J.*) *kofiadii* is most similar to *B.* (*J.*) *quadrangularis* in having a large talon and a strongly domed distal part of the brood chamber, which is completely fused with the primary operculum (Fig. 27C, D; 28B-E). The two species are easily distinguished by the tubes that typically have three distinct keels giving pentangular

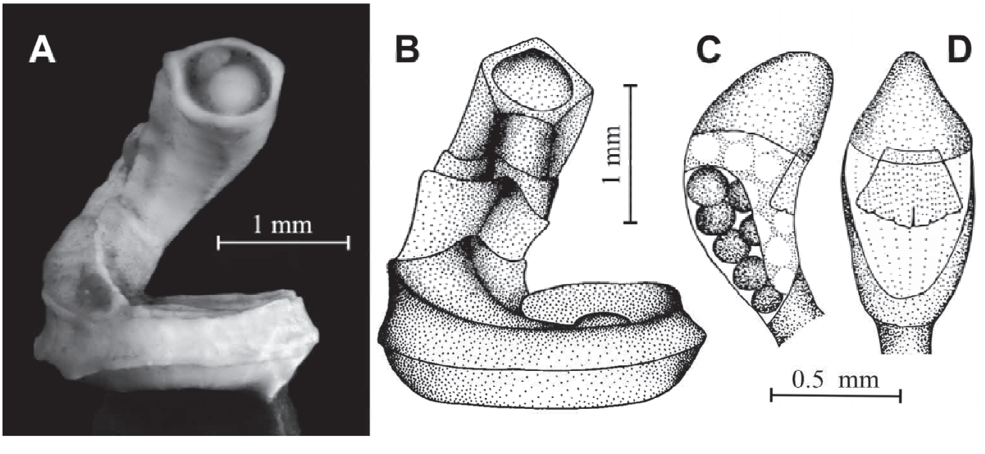

Figure 27. *Bushiella* (*Jugaria*) *kofiadii*. A, B – tube; C, D – brood chamber, lateral and frontal views. B-D – from Rzhavsky (1988b). A – photo A.V. Rzhavsky.

cross-section to tubes of *B.* (*J.*) *kofiadii* (Fig. 27A, B). Tubes of *B.* (*J.*) *quadrangularis* usually have one keel shifted towards the inside of the last whorl and another towards the periphery, giving the tube a characteristic sub-quadrangular cross-section (Fig. 28A); sometimes tubes bear a third median keel, but in such cases the keels are positioned close to each other and do not change the tube cross-section to pentangular. Also, adult specimens of *B.* (*J.*) *quadrangularis* never have intercalation of the last tube whorls, which is common in *B.* (*J.*) *kofiadii*. The two species also have different talon shapes: trapezoid, gradually widening to the terminal end in *B.* (*J.*) *kofiadii* (Fig. 27D) and rhomboid/diamond-shaped in *B.* (*J.*) *quadrangularis* (Fig. 28B, E). All other Arctic species have flat or only slightly convex distal parts of their brood chambers, different talon morphologies, and other distinguishing characters.

Among non-Arctic species, only *B.* (*J.*) *beatlesi* (known exclusively from the Kurile Islands) has a domed distal part of brood chamber completely fused with the primary operculum, similar to that observed in *B.* (*J.*) *kofiadii*, but the former species has the tube with one sharp median keel and a long narrow talon usually slightly widening toward distally bifid end (Rzhavsky, 1993).

Ecology. Tubes of polychaete of genus *Nothria* composed of flattened shell fragments is a very characteristic substrate for *B* (*J.*) *kofiadii*, which also occupies bivalves and bryozoans. The species is known from depths of 58-550 m, usually over 250 m, and may live in mixture with *B.* (*J.*) *similis*.

Distribution. Our Arctic material was collected from the East-Siberian, Laptev, Kara, Barents Seas, and the Central Arctic Basin. Knight-Jones P. also recorded it from the Greenland (Knight-Jones P. et al., 1991) and Iceland (Knight-Jones P., pers. comm.) shores. Outside the Arctic Basin the species was reported only from the North Atlantic near Newfoundland and Labrador, Canada (Rzhavsky, 2001).

***Bushiella* (*Jugaria*) *quadrangularis* (Stimpson, 1854)**

(Fig. 28A-G)

Spirorbis quadrangularis: Stimpson, 1854, p. 29; Bush, 1905, p. 2416 pl. XXXII, fig. 37, pl. XL, fig. 10-12, 23, 26 30, pl. XLII, fig. 23-29, pl. XLIII, fig. 14-15.

Spirorbis carinatus **non** Montagu, 1803: Levinsen, 1884, p. 206-207, tab. III, fig. 8.

? *Spirorbis affinis* Levinsen, 1884, p. 207, tab. III, fig. 7.

? *Spirorbis lineatus* Bush, 1905, p. 242, pl. XXXIX, fig. 29.

Spirorbis granulatus **non** Linnaeus, 1767: Borg, 1917, p. 28-31, fig. 14a,b; 15a, b (partim, non *S. granulatus* var. *similis*, fig. 16); Zachs, 1933, p. 135 (partim); Annenkova, 1937, p. 198 (partim); Annenkova in Gorbunov, 1946, p. 39 (partim); Zatsepin, 1948, p. 166, tab. XXXIX, 19, 20 (partim?); Uschakov, 1950, p. 230 (partim).

Spirorbis (*Laeospira*) *granulatus* **non** Linnaeus, 1767: Annenkova, 1938, p. 219 (partim); Pettibone, 1954, p. 343-344 Uschakov, 1955, p. 431 (partim); 1965, p. 406 (partim); Chlebovitsch, 1961, p. 235; Buzhinskaja, 1967, p. 120.

Laeospira pacifica: Uchida, 1971a, p. 646-649, fig. 7A-I, 8A-P.

Pileolaria (*Jugaria*) *quadrangularis*: Knight-Jones P. et al., 1979, p. 443, fig. 6A (a-d).

Jugaria quadriangularis [sic!]: Rzhavsky, 1989, p. 56, 2 B, 3 A.

Bushiella (*Jugaria*) *quadriangularis* [sic!]: Rzhavsky, 1992 [1994], p. 104, fig. 6; Jakovis, 1997, p. 49-51, fig. 10a-zh.

Bushiella (*Jugaria*) *quadrangularis*: Rzhavsky, 1993, p. 95-96, fig. 4A-D; 1997b, p. 147; 2001, p. 595-596, text figures 1-9, map.

Material examined. Table 1. # 3 (2); # 4 (2); # 9 (5); # 11 (4); # 13 (2); # 38 (1); # 41 (3); # 43 (? 10); # 46 (2); # 50 (2); # 51 (15); # 60 (2); # 61 (3); # 65 (1); # 66 (2); # 67 (2); # 68 (1); # 81 (1); # 88 (1); # 156 (1); # 170 (1); # 178 (2); # 197 (1); # 200 (? 20); # 202 (3); # 203 (5); # 204 (5); # 206 (1); # 211 (1); # 212 (1); # 214 (1); # 215 (2); # 216 (1); # 217 (1); # 220 (9); # 222 (2); # 224 (14); # 225(2); # 226 (14); # 227 (7); # 229 (~ 40); # 232 (3); # 243 (2); # 247 (many); # 249 (4); # 277 (15); # 427 (3); # 428 (1); # 429 (1); # 457 (~ 15); # 476 (~ 50); # 478 (1); # 483 (6); # 484 (7); # 486 (14); # 488 (2); # 489 (1); # 490 (3); # 501 (9); # 509 (some); # 511 (2); # 516 (1); # 518 (1); #

520 (3); # 530 (2); # 538 (5); # 544 (35); # 559 (4); # 560 (2); # 562 (1); # 563 (many); # 567 (~ 25); # 569 (1); # 571 (1); # 586 (5); # 587 (3); # 588 (6); # 594 (5); # 601 (43); # 621 (7); # 623 (2).

Description. Tube (Fig. 28A) sinistral, planospiral, up to 2.5 mm in coil diameter, often with last whorl upward from substrate; white opaque, non-porcellaneous. Typically tube with two keels, one shifted towards inside of last whorl and another towards periphery, giving tube sub-quadrangular cross-section. However, tubes may be unsculptured or bearing 1 or 3 distinct or vestigial keels. Live specimens colourless with red-brownish gut translucent through body wall, in preserved material gut brownish and not so bright.

Primary operculum (Fig. 28E) with a flat peripheral talon and a domed endplate that in juveniles often only slightly convex or even flat. Talons large, of variable shapes, but typically rhomboid (diamond-shaped) (Fig. 28B, E). Often talon shapeless (Fig. 28C) or bearing a constriction or incision distally on lateral sides (Fig. 28D). Primary operculum firmly and completely fused with developed brood chamber (Fig. 28B-D). Distal part of brood chamber strongly domed, sometimes only slightly convex, but never flat (Fig. 28B-D). Calcified zone of lateral wall distinct, long on side of talon and projecting beyond its terminal edge, but not reaching peduncle; distal edge of calcified zone rounded.

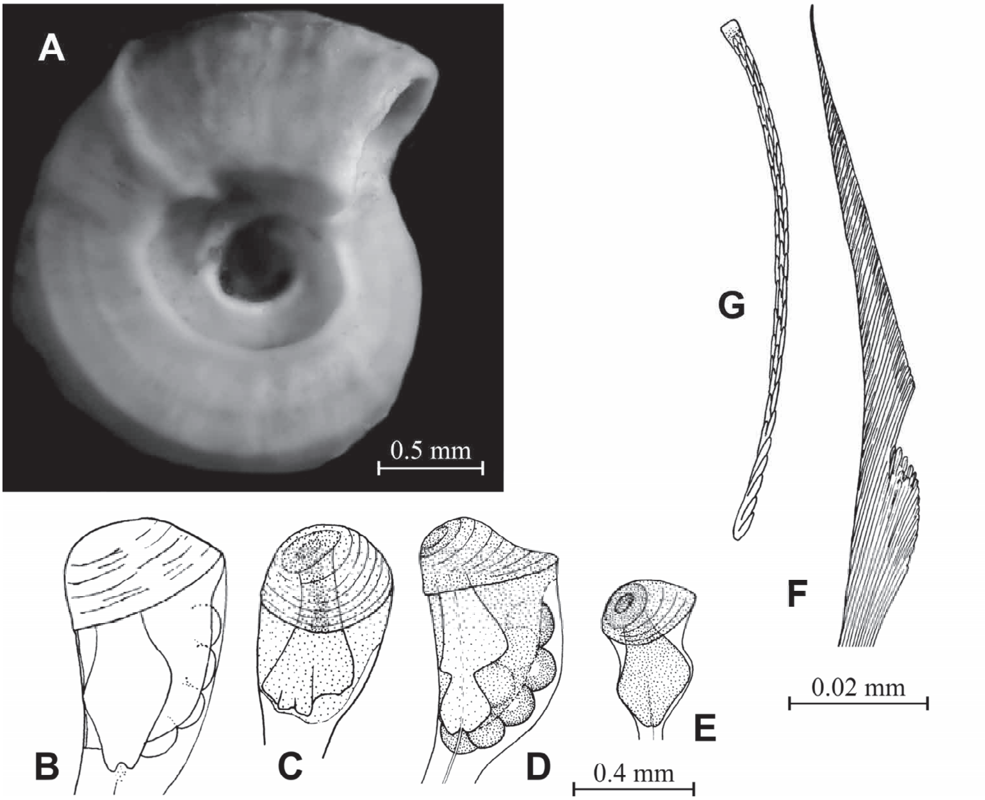

Figure 28. *Bushiella* (*Jugaria*) *quadrangularis*. A – tube; B-D – mature brood chambers, variability of talon; E – juvenile primary operculum; F – modified collar chaeta; G – largest thoracic uncinus, profile view. B, F ,G – from Knight-Jones P. et al. (1979), C-E – from Knight-Jones et al. (1991). A – photo A.V. Rzhavsky.

(Fig. 28B-D). On side opposite to talon calcified zone as a narrow belt adjacent to distal part of brood chamber. Knight-Jones P. et al. (1979) describes a glistening longitudinal fibre associated with talon. Proximally fibre running down side of peduncle to thorax, where it fanning out and connecting with uncinigerous tori. Distally it embedded in talon, and runs towards opercular plate. This structure not observed in our material.

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 (Fig. 28F) bent, modified fin-and-blade with a streamlined fin bearing small teeth and a finely serrated distal blade; capillary chaetae present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to-rasp-shaped (Fig. 28G), each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae. Largest thoracic uncini unusually long, their length exceeding that of collar chaetae blades (Fig. 28F, G).

Abdomen with about 20 chaetigers. Usually one abdominal chaeta per fascicle throughout length of abdomen, (two or three in first chaetigers), flat geniculate, pennant-shaped, with distinct heel and coarsely serrated tapering blade. Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. One capillary hooked chaeta per fascicle present, but often only in posterior chaetigers. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, distribution of unini fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. Re-examination of Levinsen's (1884) material of "*affinis*" and "*carinatus*" by Knight-Jones P. & Knight-Jones E.W.,(1977) and Knight-Jones P. et al. (1979) demonstrated that these specimens belong to *B.* (*J.*) *quadrangularis*. However, which species could have been described by Montagu (1803) under the name "*carinatus*" is unclear. True identity of the "*carinatus*" records from the Barents Sea also cannot be determined because the corresponding material (Zachs, 1923; Gurjanova, 1924; Uschakov, 1927; 1931; Gurjanova & Uschakov, 1928; Derjugin, 1928; Gurjanova et al., 1930) was neither described/ illustrated, nor deposited in any collection. We agree with Knight-Jones P. et al. (1979) who suggested that "*lineatus*" of Bush (1905), type material lost, is probably a juvenile of *B.* (*J.*) *quadrangularis*.

P. (J.) quadrangularis has been also confused with *B.* (*J.*) *granulata* in European waters and off the Pacific coast of North America (Knight-Jones P. & Knight-Jones E.W., 1977; Knight-Jones P. et al., 1979). Rzhavsky (1989; 1991a; 2001) found the same for the material from the Russian Arctic and Far Eastern Seas. Spelling of the species name "*quadriangularis*" in some papers (e.g., Rzhavsky, 1989; 1991a; 1992 [1994]; Jakovis (1997) is due to a misprint. Zatsepin (1948) compiled data on distribution of "*granulatus*" in the Arctic Sea, but drawings in his work are re-drawn from Borg (1917) or Fauvel (1927) and correspond to *B.* (*J.*) *quadrangularis*. *B.* (*J.*) *quadrangularis* and *B.* (*J.*) *granulata* differ in many features. *B.* (*J.*) *granulata* has a flat or slightly convex endplate of the primary operculum fused with the brood chamber only laterally by a talon, leaving a space between the plate of the primary operculum and the distal part of the brood chamber. The talon in "*granulata*" is smaller than that in *"quadrangularis"*, fan-shaped, and slightly bilobed distally.

Among Arctic species, *B.* (*J.*) *quadrangularis* (Fig. 28B-D) is especially similar to *B.* (*J.*) *kofiadii* (Fig. 27C, D) in having a large talon and a strongly domed distal part of the brood chamber completely fused with the primary operculum. But these two species are easy to distinguish by their tubes. Tubes of *B.* (*J.*) *quadrangularis* usually bear two keels, one shifted towards the inside of last whorl and another close to the periphery, giving the tube a sub-quadrangular cross-section (Fig. 28A); often tubes bear the third median keel, but in such cases all three keels positioned close to each other do not change the tube cross-section to pentangular. Tubes of *B.* (*J.*) *kofiadii* typically have three distinct keels giving pentangular cross-section to the tubes (Fig. 27A). Also, in adults of *B.* (*J.*) *kofiadii* the last tube whorls are intercalated, something that is never observed in *B.* (*J.*) *quadrangularis*. Finally, the two species have different talon shapes, usually rhomboid/diamond-shaped in *B.* (*J.*) *quadrangularis* (Fig. 28B-E) and trapezoid, gradually widening to the distal end in *B.* (*J.*) *kofiadii* (Fig. 27D). All other Arctic species have flat or only slightly convex distal parts of their brood chambers, different talon morphologies, and many other distinguishing characters.

Among non-Arctic species only *B.* (*J.*) *beatlesi* (known exclusively from the Kurile Islands) resembles *B.* (*J.*) *quadrangularis* in having domed distal parts of the brood chambers completely fused with the primary opercula. But the former species has tubes with one sharp median keel and long narrow talons, usually slightly widening toward the distally bifid ends; sometimes talons look somewhat rhomboid, but their lengths significantly exceed their widths (Rzhavsky, 1993).

Finally, *B.* (*J.*) *quadrangularis* differs from all other *Bushiella* species in having the largest thoracic uncini unusually long, their length exceeds that of collar chaetae blades. However, this feature is not very suitable for routine identification.

Ecology. In the Arctic *B.* (*J.*) *quadrangularis* occupies stones, shells, tubes of other serpulids, algae, decapods, barnacles, hydrozoans, bryozoans, and artificial substrates at depths of 0–280 (usually 5–100) m. Animals live in mixture with *B.* (*J.*) *similis, P.* (*S.*) *vitrea, P.*(*S.*) *cancellata, C. armoricana, C. spirillum,* and *P.* ex gr. *berkeleyana.*

Distribution. Our Arctic material was collected from the Chukchi, East-Siberian, Laptev, Kara, Barents, White, Norwegian Seas, and the Central Arctic Basin. It was also reported from the Greenland Sea and Barrow Point, Alaska (Knight-Jones P. et al., 1979). The species is widely distributed in the Northern Hemisphere. In the North Pacific its range extends to the south to Possiet Bay, Sea of Japan, Russia (Rzhavsky, 1992 [1994]), Japan (Uchida, 1971a) and Acapulco, Mexico (Knight-Jones P. et al., 1979); in the North Atlantic it extends to New England, USA.

***Bushiella* (*Jugaria*) *similis* (Bush, 1905)**

(Fig. 29A-E, Pl. 2G)

? Spirorbis nautiloides **non** Lamarck, 1801: Stimpson, 1854, p. 29; Verrill, 1874, p. 45-46, pl. IV, fig. 4

? *Spirorbis stimpsoni*: Verrill, 1880, p. 181-182; Bush, 1905, p. 250, pl. XXXIX, fig. 38, pl. XL, fig. 29, pl. XLIII, fig. 20, 21, 22 (non Knight-Jones P., 1978; Knight-Jones P. et al., 1991).

Spirorbis similis: Bush, 1905, p. 242, pl. XXXIX, fig. 16, 31, pl. XL, fig. 9, 17, 18, pl. XLIII, fig. 27, 31.

Spirorbis granulatus var. *similis*: Borg, 1917, p. 30, fig. 16.

Spirorbis granulatus: Zachs, 1933, p. 135 (partim); Annenkova, 1937, p. 198 (partim); Uschakov, 1950, p. 230 (partim).

Spirorbis (*Laeospira*) *granulatus* **non** Linnaeus, 1767: Annenkova, 1938, p. 219 (partim); Uschakov, 1955, p. 431 (partim); 1965, p. 406 (partim)

? *Spirorbis* (*Laeospira*) *granulatus* **non** Linnaeus, 1767: Bergan, 1953b: 35-38, fig. 2a-c (partim?);

Pileolaria (*Jugaria*) *similis*: Knight-Jones P. et al., 1979, p. 445, fig. 6B(a-d).

Jugaria similis: Rzhavsky, 1989, p. 56, fig. 2V; Knight-Jones et al., 1991, p. 193, fig. 3.

Bushiella (*Jugaria*) *similis*: Rzhavsky, 1991a, p. 10; 1993, p. 94-95; 1992[1994], p. 104, fig. 6; 1997b, p. 147; 2001: 596-597, text figures 1-2, map; Jakovis, 1997, p. 51-52, fig. 11a-b.

Material examined. Table 1. # 1 (3); # 11 (5); # 16 (1); # 37 (11); # 76 (1); # 85 (many); # 202 (1); # 218 (3); # 477 (~ 10); # 545 (? 60); # 551 (1); # 552 (1); # 560 (2); # 569 (2); # 588 (2); # 598 (4).

Description. Tube (Fig. 29A) sinistral, usually planospiral, up to 2.5 mm in coil diameter; sometimes last whorls facing upward from substrate; white opaque non-porcellaneous. Typically unsculptured, rounded in cross-section. A vestigial median keel not changing cross-section outline may present. Live specimens colourless with reddish-brown gut translucent through body wall, in preserved material gut brownish. Collar and thoracic membranes of live specimens light brownish-yellow. Body of live animals sometimes bearing a large pigmented spot (crystalline patch?) on dorsal side of end of thorax and achaetigerous zone, spot deep pink in live specimens and dark brown in preserved material, sometime disappearing in long-preserved specimens.

Primary operculum with a slightly concave, flat or slightly convex endplate. Talon flat peripheral, of median size, typically fan-shaped, and gradually expanding distally; usually with indistinct rounded lateral projections distally and small grooves in median part of distal edge; sometimes talon asymmetrical or with pointed lateral projections. Primary operculum firmly and completely fused with developed brood chamber (Fig. 29B; Pl. 2G). Distal part of brood chamber flat or slightly concave, but never convex (Fig. 29B; Pl. 2G). Calcified zone (Fig. 29B) of lateral wall usually distinct, but may be very light, especially in preserved specimens; rounded on side of talon and beyond only

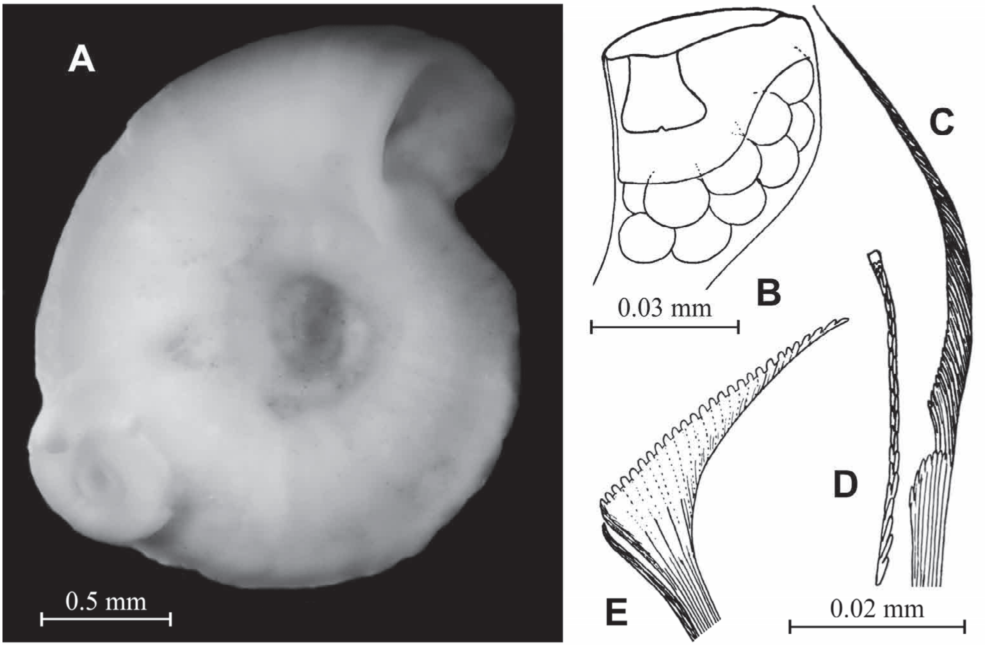

Figure 29. *Bushiella* (*Jugaria*) *similis*. A – tube; B – mature brood chamber; C – modified collar chaeta; D – largest thoracic uncinus, profile view; E – flat geniculate abdominal chaeta with companion capillary hooked chaeta. B-E – from Knight-Jones P. & Knight-Jones E.W. (1977). A – photo A.V. Rzhavsky.

up to middle part of brood chamber; distal edge of calcified zone rounded. Calcified zone on opposite side of talon as a narrow belt adjacent to distal part of brood chamber or absent.

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

Large collar chaetae (Fig. 29C) bent, modified fin-and-blade with rounded fins bearing very small teeth, only slightly coarser than those of blade; gaps between fins and blades distinct, but small; capillary chaetae present in collar fascicles. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to-rasp-shaped (Fig. 29D), each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae. Length of the largest thoracic uncini less than that of collar chaetae blades (Fig. 29C, D).

Abdomen with about 15 chaetigers. Up to three abdominal chaetae per fascicle on anterior abdominal chaetigers and only one on posterior. Chaetae flat geniculate, pennant-shaped, with distinct heel and serrated tapering blade (Fig. 29F). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. One or two capillary hooked chaetae (Fig. 29E) per fascicle on most chaetigers (may be absent on anterior chaetigerous segments). Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncinal distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. According to the brief descriptions of Verrill (1874; 1880) and Bush (1905), *B.* (*J.*) *similis* is very similar to *B.* (*J.*) *stimpsoni* (Verrill, 1880) described from the Atlantic coast of North America, however, the drawing of a brood chamber given by Verrill (1874) rather resembles a secondary brood chamber of *J. heterostropha*. Hartman (1944) synonymized "*stimpsoni*" with "*Spirorbis borealis*" without any explanation and stated that the type material of "*stimpsoni*" was deposited in Peabody Museum, USA. Knight-Jones P. (1978) and Knight-Jones P. et al. (1991) suggested that "*stimpsoni*" is a valid species that is "rather like *J. granulata,* but larger". They also gave a brief description based on their own specimens from Newfoundland, but had not studied the type material. The specimens from Peabody Museum were re-examined by the senior author (Rzhavsky, 2001). He found that these specimens were identified (at least labelled) by Verrill years after the publication of the original species descriptions, therefore, they could not belong to the type material. All specimens from Peabody Museum were identical to the worms here called *B.* (*J.*) *similis.* The Newfoundland material of Knight-Jones P. (1978) and Knight-Jones P. et al. (1991) also was briefly re-examined by the senior author and these specimens were obviously different from the worms defined (and, probably, not published) by Verrill. They were in fact large for spirorbins (more than 5 mm in whorl diameter) and in our opinion resembled "giant" specimens of *B.* (*J.*) *acuticostalis* rather than *B.* (*J.*) *granulata*. Most likely "*stimpsoni*" and "*similis*" are synonyms, but we cannot be sure because the type material of *"stimpsoni"* has not been found. Because the Knight-Joneses material is represented by 3 poorly preserved specimens only, we cannot conclude whether it is really a "giant" *B.* (*J.*) *acuticostalis* known from the north-western Pacific and Arctic or a separate valid species. Interestingly, the "gigantism" phenomenon was also observed for other spirorbins from the Newfoundland region (see Remarks for *Pileolaria* ex gr. *berkeleyana*).

Like *B.* (*J.*) *quadrangularis*, *B.* (*J.*) *similis* was for a long time confused with *B.* (*J.*) *granulata* or suggested as subspecies of *B.* (*J.*) *granulata* (see synonymy). *B.* (*J.*) *similis* is especially similar to another Arctic species, *B.* (*B.*) *verruca,* in the brood chamber and talon morphology (Fig. 24B, C, 29B). Although these two species have different type of collar chaetae (modified fin-and-blade (Fig. 29C) and limbate (Fig. 24D) respectively), fin-and-blade collar chaetae of *B.* (*J.*) *similis* have very fine serration both on the blade and on the fin (Fig. 29C). Therefore, the gap between fin and the blade may be not visible if the chaetae are observed not in strictly lateral position. On the other hand, limbate collar chaetae of *B.* (*B.*) *verruca* (and other species of subgenus *Bushiella*) may have vestigial grooves in the basal parts of the chaetal blades, although distinct gaps between the fin and the blade are never observed (Fig. 24D).

The talon morphology of *B.* (*J.*) *similis* (Fig. 29 B) also resembles that of *B.* (*J.*) *granulata* (Fig. 26C) and *B.* (*J.*) *acuticostalis* (Fig. 25C-E). Mature specimens of the two latter species may be easily distinguished by their primary opercula attached to the brood chamber by talons only, leaving some space between the plate of the primary operculum and the distal part of the brood chamber (Fig. 26C; 25B-C). Besides, the talon morphology of these species although is similar, but not identical. The talon of *B.* (*J.*) *similis* is typically fan-shaped and gradually expanding distally, with indistinct rounded lateral projections distally and small grooves in the median parts of the terminal edge (Fig. 29B; Pl. 2G). The talon of *B.* (*J.*) *granulata* is slightly bilobed distally, rarely fan-shaped (Fig. 26C). Finally, the talon of *B.* (*J.*) *acuticostalis* is fan-shaped, gradually expanding distally, usually with distinct pointed lateral projections and often with very narrow pointed projections in the central part of the distal end (Fig. 25C-E). Also, *B.* (*J.*) *similis* is distinguished from these two species in the structure of modified collar chaetae that have very fine serrations both on the blade and the fin (Fig. 29C), while *B.* (*J.*) *granulata* (Fig. 26E) and *B.* (*J.*) *acuticostalis*, as well as all *Jugaria* spp. have the fin serration obviously coarser. Additionally, *B.* (*J.*) *granulata* have an unusual distribution of the abdominal uncini, where the largest tori are located mid-posteriorly (not anteriorly). Tubes of *B.* (*J.*) *acuticostalis* bear three distinct keels (Fig. 25A), whereas tubes of *B.* (*J.*) *similis* (Fig. 29A) and *B.* (*J.*) *granulata* (Fig. 26A) are unsculptured or with only vestigial keels respective.

Two other Arctic species of the subgenus *Jugaria,* (*B.* (*J.*) *kofiadii* and *B.* (*J.*) *quadrangularis,* have domed (not flat or slightly convex) parts of the brood chambers (Fig. 27C, D; 28B-D) and usually of juvenile primary opercula (Fig. 28E) and differ from *B.* (*J.*) *similis* in many other features (see respective species descriptions).

The remaining two Arctic species of the genus, *B.* (*B.*) *evoluta* and *B.* (*B.*) *barentsii*, belong to genus having limbate collar chaetae (Fig. 22D, 23C). Although fin-and-blade collar chaetae of *B.* (*J.*) *similis* may be confused with limbate chaetae, both species have many other differences in the tube, brood chamber, and talon morphology as detailed in their descriptions. There are no species similar to *B.* (*J.*) *similis* among non-Arctic representatives of the genus *Bushiella.*

An unusual characteristic feature of *B.* (*J.*) *similis,* which probably brings it close to the genus *Pileolaria* and is unknown for other *Bushiella* spp.*,* is the presence of large dark-pompadour spots (crystalline patches?) located dorsally on the border of the thorax and the achaetigerous zone. But this character is not always found even in live worms and the spots probably disappear in preserved specimens of *B.* (*J.*) *similis*, while such spots are present even in preserved specimens of *Pileolaria* spp., thus they are, likely to have another origin.

Ecology. In the Arctic *Bushiella* (*J.*) *similis* is found attached to stones, serpulid tubes, bryozoans and shells of both live molluscs and those occupied by hermit crabs at depths of 0–313 m. They live in mixture with *P.* (*P.*) *violacea*, *P.* (*S.*) *vitrea*, *B.* (*J.*) *quadrangularis*, *B.* (*J.*) *kofiadii, P. uschakovi* and some other species. Outside the Arctic they sometimes also occupy seagrasses, but not algae, and are recorded from depths up to 636 m.

Distribution. In the Arctic *B.* (*J.*) *similis* is found in the Kara, Barents, White, Greenland Seas, and the Central Arctic Basin. In the North Atlantic the species was reported from Newfoundland, Canada (Bush, 1905) and probably from the Norwegian Sea (Bergan, 1953b). In the North Pacific the species is well known off the Russian coasts from Commander Islands and Shelikhov Gulf to Possiet Bay in the Sea of Japan (Rzhavsky, 1992[1994]). On the North American Pacific Coast it was found in Prince William Sound, Alaska and San Francisco area, USA (Knight-Jones P. et al., 1979).

Genus *Pileolaria* Claparède, 1868

Type species: *Pileolaria militaris* Claparède, 1868.

Tubes always sinistral. Talon of endplate generally small and slightly eccentric, but not peripheral; distal plate of primary operculum not fused with brood chamber and usually shed after chamber development; brood chamber a deeply invaginated sac totally enclosing embryos except for a pore capable of opening and closing; lining of brood chamber forming a calcified dome distally, but not calcified proximally or on pore bearing side; opercular peduncle inserted between 1st and 2nd radioles on left side, so that non-calcified part of chamber near centre of radiolar crown. Collar and thoracic membrane margins not fused over thoracic groove. Large collar chaetae bent, modified fin-and-blade and usually cross-striated, with coarse blade margin serration; sickle (*Apomatus*) chaetae present in 3rd thoracic fascicles. Always three thoracic chaetigers.

Nineteen species, including *Pileolaria* ex gr. *berkeleyana* (may be a species complex) the only representative of the genus *Pileolaria* in the Arctic.

Pileolaria ex gr. *berkeleyana*

(Fig. 30A-M, Pl. 2C)

? *Spirorbis moerchi*: Levinsen, 1884, s. 205 pl. II, fig. 8 a, g, pl. III, fig. 1.

Spirorbis (*Pileolaria*) *berkeleyana*: Rioja, 1942, p. 144-147, fig. 53-67.

Spirorbis tuberculatus: Bailey & Harris M.P., 1968, p. 174-175, fig. 4, 12a-h.

Spirorbis berkeleyana: Bailey & Harris M.P., 1968, p. 170-172, fig. 3e, 10a-h; Bianchi, 1981, p. 158-160, fig. 59a-k.

Laeospira rosepigmentata: Uchida, 1971b, p. 212-218, fig. 9A-F, 10A-S.

Pileolaria rosepigmentata: Knight-Jones P. et al., 1975b, p. 146, fig. 2m-u; Knight-Jones P. & Knight-Jones E.W., 1977, p. 483, fig. 10A-I; 1984, fig. 2,3; Uchida, 1978, p. 50; Rzhavsky, 1989, p. 55, fig. 2A.

Pileolaria daijonesi **non** Knight-Jones P., 1972: Knight-Jones P. & Knight-Jones E.W., 1974, p. 253.

Pileolaria (*Pileolaria*) *rosepigmentata*: Knight-Jones et al., 1979, p. 439-440, fig. 5E (a-d).

Pileolaria (*Pileolaria*) *berkeleyana*: Knight-Jones et al., 1979, p.437, fig. 5F(a-g).

Pileolaria berkeleyana: Knight-Jones E.W. & Knight-Jones P., 1980, p. 461-462; Thorp et al., 1986, p. 885-886, fig. 4A-D; Knight-Jones P. & Knight-Jones E.W., 1991, p. 581; Rzhavsky, 1992b, p. 12; 1997b, p. 146.

Pileolaria ex gr. *berkeleyana*: Rzhavsky, 2001, p. 590-591, text figures 1-10, map.

Material examined. Table 1. # 486 (2); # 489 (1); # 602 (4).

Description. Tube (Fig. 30A) sinistral, planospiral or with 1–2 indistinct keels and rough/wrinkled surface; adults usually about 2 mm in coil diameter, although reaching over 5 mm; white opaque non-porcellaneous.

Body of live animals orange-brownish and flesh-coloured when preserved. Dorsally on middle-posterior part of thorax and anterior part of achaetigerous zone a large deep-rose spot (crystalline patch) usually retaining its colour after preservation (Pl. 2C), but easily scraped by needle or scalpel.

Primary operculum (Fig. 30B, C) with concave endplate, usually with short thick eccentric talon, knob, pin or cone-shaped. Distal plate of primary operculum not fused with brood chamber and usually shed after chamber development. Brood chamber topped with deep helmet-shaped calcification on side away from radiolar crown, usually bilobed distally (Fig. 30F, G), sometimes rounded (Fig. 30D) or with lateral distal rim on side away from substrate; rim may be continuous (Fig. 3E) or as a row of tubercles (Fig. 30H). Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 3rd chaetiger forming apron. Thorax with three chaetigers.

Large collar chaetae (Fig. 30I, J) bent, modified with coarsely serrated and cross-striated blades, and distinct toothed fins. Blade lengths of chaetae from convex side (Fig. 30I) of body about 1.5 times longer than those from concave side (Fig. 30J) and more coarsely serrated. Cross-striation on concave side may be indistinct. Capillary chaetae present in collar fascicles. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae (Fig. 30K) also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw- to rasp-shaped (Fig. 30M) starting with one row of teeth posteriorly to 3 rows above blunt anterior peg. Sizes of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 15 chaetigers in specimens with coil diameter up to 20 mm (number of abdominal chaetigers at large specimens of "*moerchi*" *sensu stricto* is not recorded). 1–2 abdominal chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and serrated tapering blade (Fig. 30L). Blade lengths approximately of same length as blades of largest collar chaetae from convex side of the body, lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. One or two companion capillary hooked chaetae per fascicle in most fascicles. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both sides of body. Largest tori in middle-anterior part of abdomen.

Remarks. Specimens with a primary operculum attached to brood chamber with a pointed eccentric talon and a secondary replacing of brood chamber by a "primary" operculum were observed at the seawater header tank at the Portsmouth Polytechnic Marine Laboratory, Hayling Island, UK (Thorp, 1989), which is unusual for *Pileolaria.*

Under this species name we combined all authentic records of *P. berkeleyana*, *P. rosepigmentata* and, tentatively, *Pileolaria moerchi* (Levinsen, 1884). The group may either be a single morphologically variable species or a complex of valid species. In the former case, the species name *P. moerchi* would have a priority.

Pileolaria berkeleyana Rioja, 1942 was described from western Mexico (Rioja, 1942 as *Spirorbis*, subgenus *Pileolaria*) and was subsequently recorded from the Galapagos Islands (Bailey & Harris M.P., 1968). Now the species appears circum-global in the Northern Hemisphere. When first recorded from the Canary Islands (Knight-Jones E.W. & Knight-Jones P., 1980), Azores and the Mediterranean (Zibrowius, Bianchi, 1981), it appeared particularly abundant in harbors, as if recently introduced by shipping. A similar species, *Pileolaria rosepigmentata* (Uchida, 1971) was described from Japan (Uchida, 1971b, as *Laeospira*). It was subsequently reported from southern Britain as a recent invader on immigrant Japanese algae *Sargassum* (Knight-Jones P. et al., 1975b). Knight-Jones P. et al. (1979) recorded *P. rosepigmentata* in Monterey Harbor (USA) and *P. berkeleyana* in more southern localities of the North American West Coast, from Palos Verdes to Panama. Later *P. rosepigmentata* was recorded from Australia and south of

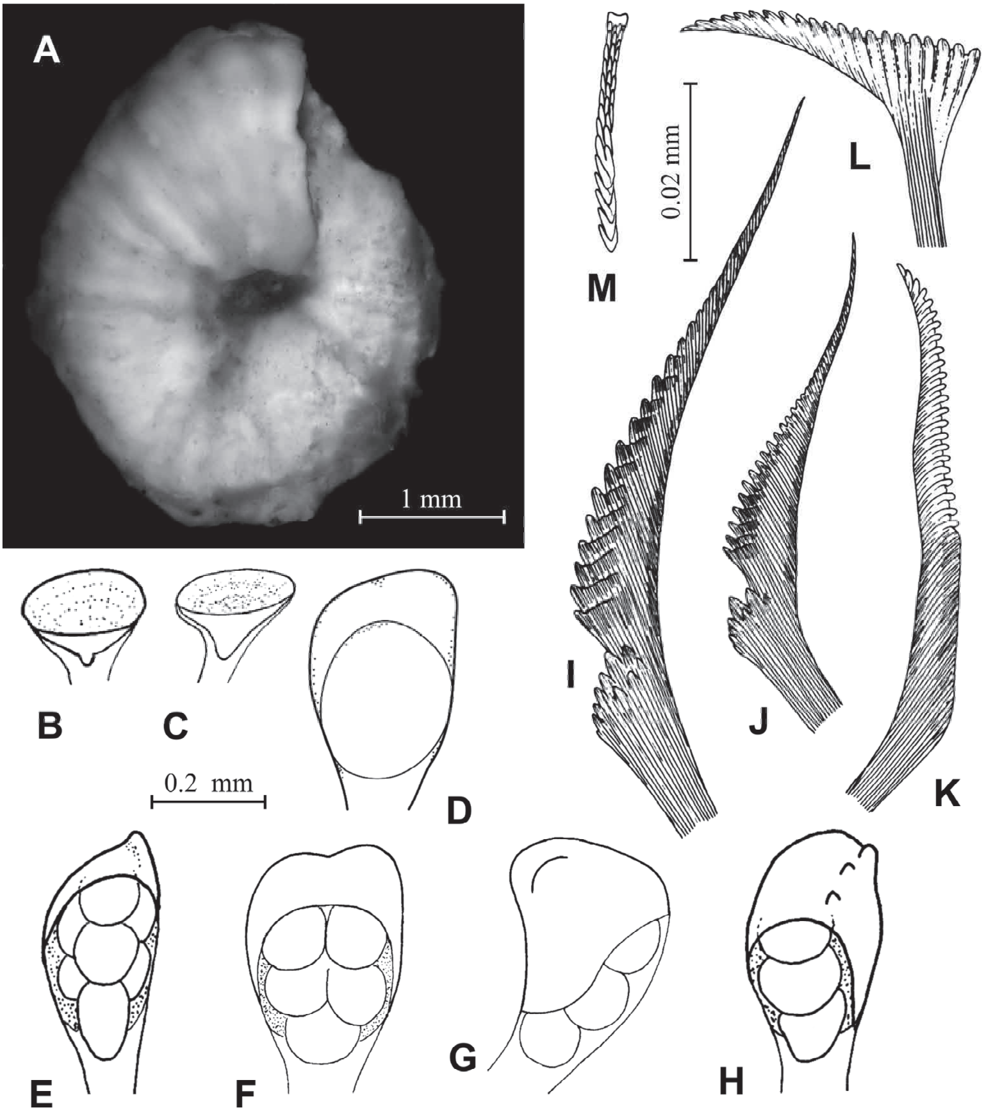

Figure 30. *Pileolaria* ex. gr. *berkeleyana*. A – tube; B, C – primary opercula; D-H – variability of brood chambers, frontal and lateral views; I – modified collar chaeta, convex body side; J – modified collar chaeta, concave body side; K – sickle (*Apomatus*) chaeta; L – abdominal chaeta; M – thoracic uncinus, front view. B, C, E-H – from Knight-Jones P. et al. (1979); D, I-M – from Knight-Jones P. & Knight-Jones E.W. (1977). A – photo A.V. Rzhavsky.

Africa (Knight-Jones P. & Knight-Jones E.W., 1984). However, Thorp et al. (1986) concluded that *P. rosepigmentata* is a junior synonym of *P. berkeleyana*, a species they recorded from harbours at Falmouth and Plymouth, UK. Similarly, Rzhavsky (1989) found *P. rosepigmentata* in Avacha Inlet of Avacha Bay, Kamchatka, but later (Rzhavsky, 1992b) based on his examination of Russian collections, changed the species attribution to the older name, *P. berkeleyana* and provided news records of the species from the Bering Sea, West Spitsbergen, Commander, and Kurile Islands.

Juveniles of *P. berkeleyana sensu lato* without mature brood chambers were described as *Spirorbis tuberculatus* Bailey & Harris M.P., 1968 from Galapagos Islands (Knight-Jones P. et al., 1979). *Spirorbis berkeleyanus* recorded from the Naples (Harris T., 1968b) is in fact *Simplaria pseudomilitaris* (Thiriot-Qiuevreux, 1965) according to Knight-Jones P. et al. (1979). *Spirorbis moerchi* was described from Greenland. Numerous records of this species from the Pacific coast of North America belong to *Simplaria potswaldi* (Knight-Jones P., 1978), which differs by the absence of sickle (*Apomatus*) chaetae from 3rd thoracic fascicles (Knight-Jones P., 1978). *P. moerchi sensu* Harris T. (1969) from the Palmer Archipelago, Antarctic Peninsula, is obviously another species, probably *Pileolaria connexa* Rzhavsky, 2010 recently described from Subantarctic waters, not *Pileolaria tegwyni* Vine, 1977 as suggested by Vine (1977). *P. moerchi sensu* Harris T. (1968b) from Naples was later re-identified by Harris T. (1969) as *P. heteropoma*. Specimens of "*Spirorbis moerchi*" from Mazatlan and Acapulco (Rioja, 1942) are *S. pseudomilitaris* according to Knight-Jones P. et al. (1979).

Material of Bush (1905) from Alaska and Queen Charlotee Island recorded as "*Spirorbis moerchi*" undoubdtly belongs to this group, but its description is not detailed enough to detect any differences between "*moerchi*" and "*berkeleyana*"–"*rosepigmentata*"; *S. moerchi* is absent in Bush's collection examined by P. Knight-Jones (1978). As a result, the only material of this species is the type specimen (holotype?) of *P. moerchi* briefly redescribed and figured by P. Knight-Jones (Knight-Jones P., 1978; Knight-Jones P. & Knight-Jones E.W., 1994) and 2 specimens from Newfoundland observed by Rzhavsky (pers. comm.) and kept in a private collection of Knight-Joneses who once mentioned it (Knight-Jones P., 1978). Most recently, three incomplete specimens with broken opercula that could belong to *P. moerchi sensu stricto,* were found in the material Akvaplan-Niva collected off Norway coast (Spitsbergen Bank). These specimens are very similar to "*berkeleyana*"-"*rosepigmentata*", only twice as large. In our opinion, the size difference alone is not sufficient for estabishing a new species especially considering that specimens of "*berkeleyana*" recorded from Isfjord, Spitsbergen earlier (Rzhavsky, 2001) were of usual size. Moreover, Rzhavsky (unpubl.) observed "giant" specimens of another spirorbin, *Bushiella* (*Jugaria*) *quadrangularis* (Stimpson, 1854), from the Newfoundland region. Additional material is needed for examination.

Pileolaria ex gr. *berkeleyana* is the only Arcitic "species" of genus *Pileolaria* that has brood chambers similar to those found in *Pileolaria tegwyni* Vine, 1977, *Pileolaria connexa* Rzhavsky, 2010 and *Pileolaria invultuosa* Rzhavsky, 2010 from Southern Hemisphere and *Pileolaria daijonesi* Knight-Jones P., 1972 off Kenya. Brood chambers of *P. connexa* and *P. invultuosa* are smooth and bilobed or domed distally (Rzhavsky, 2010). Moreover, *P. connexa* also has specimens with primary opercula attached to the brood chamber that replaces brood chambers by non-brooding opercula of "primary" type, something that was not recorded for other species of *Pileolaria*. Nevertheless, the primary operculum of *P. connexa* is fused with the brood chamber more firmly than that of *P*. ex gr. *berkeleyana* and this occurs regularly (Rzhavsky, 2010), not occasionally as claimed by Thorp (1989). Both species have distal calcified parts of brood chambers with shallow sides (not deep on the side away from the radiolar crown) and collar fin-and-blade chaetae approximately of the same size on both body sides (in *P.* ex gr. *berkeleyana* blade lengths of the collar chaetae from the convex body side are about 1.5 times longer than those from the concave side). Juveniles of *P. invultuosa* have very eccentric, long thin talons, those of *P. connexa* show more eccentric curved and pointed talon of the primary operculum, while *P.* ex gr. *berkeleyana* have somewhat eccentric short thick talons are either knob-, pin- or cone-shaped.

Both *P. tegwyni* and *P. daijonesi* have domed rounded distal parts of the brood chambers similar to those sometimes observed in *P.* ex gr. *berkeleyana.* The former species has a very extensive calcification zone of the brood chamber that always almost reach opercular peduncle on the side opposite from the radiolar crown; collar chaetae in *P. tegwyni* are of approximately the same size on both sides of body and the primary operculum is with a long straight or slightly curved massive talon (Vine, 1977). The latter species is known only off Kenya (Knight-Jones P., 1972), because the specimens reported from South Africa (Knight-Jones P. & Knight-Jones E.W., 1974) later were re-identified by Knight-Joneses as *P. rosepigmentata* (Knight-Jones P. & Knight-Jones E.W., 1984). *P. daijonesi* clearly differs from *P.* ex gr. *berkeleyana* by evoluted tube coils completely attached to the substrate, collar chaetae approximately of the same size on both sides of the body. And the primary operculum with a relatively long peg-shaped talon in a slightly eccentric position.

Specimens with smooth domed brood chambers are also known for *P. heteropoma* and have been recorded as a variety “*glabra*” (Knight-Jones P. & Knight-Jones E.W., 1977). This species from northeastern Atlantic typically bears a spine on the distal part of the brood chamber (Zibrowius, 1968a; Bianchi, 1981). When the spine is absent, the species may be distinguished by weak cross-striation of collar chaetae and absence of cristalline patches. Juveniles have the primary opercula with pin-shaped talons located almost centrally.

Somewhat similar to *P.* ex gr. *berkeleyana* is *Pileolaria aurita* Rzhavsky, Nishi, 2011 recently described from Japan (Rzhavsky & Nishi, 2011). This species has brood chambers that are also distally bilobed, but have two distinct symmetrical cone-shaped projections resembling cat ears, and two lateral seams continuing from top of the projections up to the lower border of the calcified zone. Juveniles of *P. aurita* have not been described, but adults of this species have fin-and-blade collar chaetae without cross-striations, unusual for *Pileolaria*.

Ecology. Our Arctic material was collected at depths of 2–59 m from shells or unknown substrate. Elsewhere animals may inhabit rocks, shells, other serpulid tubes, algae, artificial substrates at depths of 0–258 m. In the boreal and arctic waters the species occurs as solitary organisms mixed with *B.* (*J*) *quadrangularis*, *B.* (*J*) *similis*, and *P.* (*S.*) *vitrea*, although in other regions these species may form large aggregations. Thorp (1991) demonstrated that in the Northern Hemisphere the species broods in an aquarium throughout the year, although in winter embryos develop for several months, while in summer development takes less than two weeks.

Distribution. In the Arctic we found the species from West Spitsbergen (Norway). It is also reported from the Greenland coast as “*moerchi*” (Levinsen, 1884). The “species” is widely distributed in both Hemispheres. In the Northern Hemisphere it is reported in the North Atlantic from the Mediterranean Sea (Bianchi, 1981), south of Great Britain (Thorp et al., 1986), and off Canary Islands (Knight-Jones E.W. & Knight-Jones P., 1980). Some authors (Knight-Jones E.W. & Knight-Jones P., 1980; Zibrowius & Bianchi, 1981; Thorp et al., 1986) suggest that the species recently invaded these regions. In the North Pacific Ocean it is reported from the Bering Sea to the Sea of Japan, Russia (Rzhavsky, 1992b), Hokkaido, Japan (Uchida, 1971b) and from Monterey, USA to Panama (Knight-Jones P. et al., 1979). In the Southern Hemisphere it is recorded from Australia and South Africa (Knigh-Jones P. & Knight-Jones E.W., 1984), Brazil (Knight-Jones P. & Knight-Jones E.W., 1991) and off Galapagos Islands (Bailey & Harris M.P., 1968).

Genus *Protoleodora* Pillai, 1970

Type species: *Spirorbis asperatus* Bush, 1905.

Tubes always sinistral. Talon of primary opercular endplate sub-central or almost peripheral, flattened, large. Primary operculum attached to distal part of developed brood chamber only by talon's tip, so often shed; trace of primary operculum attachment usually present. Brood chamber a deeply invaginated sac totally enclosing embryos, except for a pore capable of opening and closing; calcified distally, but not proximally or on side bearing a pore. Forming a soft-walled pouch extending posteriorly in dorsal groove of thorax and capable of accommodating very large broods (up to 150 embryos per brood). Opercular peduncle arises outside circle of radioles. Collar and thoracic membrane margins not fused over thoracic groove; margins of thoracic membranes from convex side of body extending posteriorly and reaching at least first abdominal chaetiger. Limbate collar chaetae bent, with finely or moderately serrated blades; sickle (*Apomatus*) chaetae present in 3rd thoracic fascicles. Always three thoracic chaetigers.

Four species, two known from the Arctic.

Remarks. Bush (1905) describing the type species *S. asperatus* wrote: "strings of undeveloped eggs in some instances were found along the back of the posterior segments", i.e., the species perceived to be tube incubating. Pillai (1970) who erected the monotypic (at the time) genus *Protoleodora,* suggested that this is an operculum-incubating species without any comments. Knight-Jones P. (1984) did not examine the type material, but had suggested that Bush's (1905) description and drawings illustrated immature specimens of *P. asperata*. Most likely, Bush (1905) confused mature oocytes lying freely (released spontaneously or because of a tube damage during preparation) with embryos.

Protoleodora gracilis Rzhavsky, 1992b

(Fig. 31A-H)

Spirorbis validus **non** Verrill, 1874: Annenkova, 1952, p. 135 (partim).

? *Spirorbis* (*Laeospira*) *medius* **non** Pixell, 1912: Chlebovitsch, 1961, p. 234, fig. 14A , B.

Protoleodora asperata **non** Bush, 1905: Rzhavsky, 1989, p. 57 (non fig. 2E) (partim).

Protoleodora uschakovi **non** Knight-Jones P., 1984: Rzhavsky, 1989: 57 (partim).

Protoleodora gracilis: Rzhavsky, 1992b, p. 6-10, fig. A-T; 1997b, p. 146; 2001, p. 598-599, text figures 1-7, map.

Material examined. Table. 1. # 573 (6).

Description. Tube (Fig. 31A) sinistral, usually about 5 mm in coil diameter, up to 7–8 mm; tubes of juveniles and solitary adults planospiral, but adult tubes deforming in aggregations (Fig. 31B), coils may be covering each other, mouth facing upward from substrate; unsculptured or with one vestigial keel; white opaque, non-porcellaneous.

Colour of live specimen unknown, preserved specimens colourless or flesh-coloured.

Primary operculum (Fig. 31D, H) with large eccentric talon of triangular shape, opercular endplate slightly concave and smooth. Primary operculum attached to distal part of developed brood chamber only by talon's tip (Fig. 31E, F), so often shed (Fig. 31G); trace of primary operculum attachment visible (Fig. 31G). Development of brood chamber for *P. gracilis* was described in detail (Rzhavsky, 1992b), unlike that of other *Protoleodora* spp. Initially distal part of brood chamber smooth, convex and surrounded by small dense tubercles (Fig. 31E). During brood chamber development small spines appear on its distal part, peripheral tubercles grow, became thinner and joining to form a

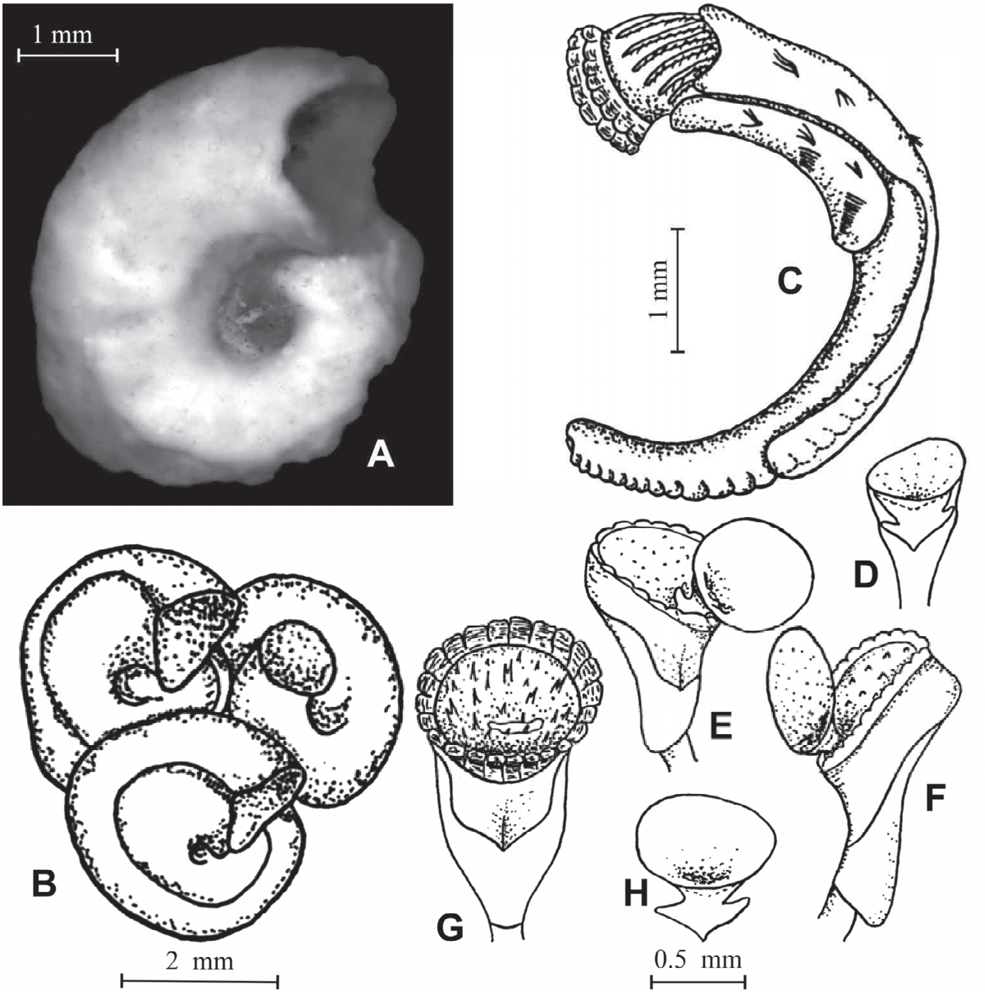

Figure 31. *Protoleodora gracilis*. A – tube; B – tube conglomerate; C – entire body with thoracic membranes covering anterior abdominal chaetigers on convex body side; D – juvenile primary operculum; E,F – developing brood chamber with primary operculum; G – fully developed brood chamber (frontal view) without embryos and with lost primary operculum; H – adult primary operculum attached to brood chamber. B-H – from Rzhavsky (1992b). A – photo A.V. Rzhavsky.

continuous low fringe with wavy edge (Fig. 31F). Completely developed brood chamber (Fig. 31G) having deeply concave distal part surrounded by delicate crown, entire or subdivided into 20–30 petals (probably chitinous) and bearing numerous spines of different sizes. Spines single, deeply bifurcate, or rarely trifurcate. Petals with lengths of same size as their widths or slightly exceeding it. Crown delicate, easily breakable, often presented only by fragments or absent in poorly preserved specimens. Lateral calcareous zone of brood chamber on concave side (looking outside of radiolar crown) usually resembling heraldic shield (Fig. 31G), rarely triangular; its width and length approximately the same, indistinct median keel usually present. No cord attached to calcareous zone apex on peduncle surface and leading to thoracic tori on concave side. On convex side of brood chamber calcified zone as a belt adjacent to distal part of brood chamber or absent. A soft-walled pouch of brood chamber extending posteriorly in thoracic dorsal groove very small or even vestigial, likely because of absence brooding specimens in examined material.

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 3rd chaetiger on concave side, on convex side of body extending posteriorly reaching 7–8th abdominal segments (Fig. 31C) though membrane may break away; apron present. Thorax with three chaetigers.

Large collar chaetae bent, limbate, on convex side with almost smooth blade; on concave side longer, more bent and with slightly serrated blades. Capillary chaetae present in collar fascicles. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to- rasp-shaped, each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae. While largest uncini only somewhat shorter than collar chaetae blades, smallest not exceeding or even shorter than abdominal uncini.

Abdomen with about 30 chaetigers. Three abdominal chaetae per fascicle on anterior abdominal chaetigers and two posteriorly. Chaetae flat geniculate, pennant-shaped, with distinct heel and serrated tapering blade. Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. One capillary hooked chaetae per fascicle on most chaetigers. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. Some specimens from the Russian Far-Eastern Seas initially identified by Rzhavsky (1989) as *P. uschakovi* or *P. asperata,* in fact, belong to *P. gracilis*. Initially material of “*abnormis*” from the littoral zone of Commander Islands (North-West Pacific) identified by Annenkova (1934) and cited by Tarakanova (1978) was tentatively synonymized with *P. gracilis* (Rzhavsky, 1992b; 1997b). The material of Annenkova is deposited in the collection of Zoological Institute Russian Academy of Sciences (St. Petersburg, Russia), but is represented mainly by empty and partly decalcified tubes and some poorly preserved specimens without opercula. The reason for the synonymy was absence of *Bushiella* (*Bushiella*) *abnormis* (Bush, 1905) in the extensive collections from Commander Islands (Rzhavsky, 1997a), while *P. gracilis* was quite common in the same habitats and it was the only species with the tube size comparable to those found in from Annenkova’s material. However, in 2011 N. Tatarenkova (Aleutian Museum of local History & Ecology, village Nikol’skoe, Commander Islands, Russia) collected three specimens of true *B.* (*B.*) *abnormis* from the same site where Annenkova's doubtful material was obtained. This new material was examined by the senior author and, as a result, Annenkova's record was excluded from the synonymy with *P. gracilis.*

Mature and well-preserved specimens of *P. gracilis* differ well from all *Protoleodora* spp. in having numerous spines all over the entire surface of the distal part of brood chamber and a delicate crown of 20–30 separate petals or entire with festoon edge (Fig. 31C, G). Another species, *P. uschakovi,* known from the Arctic, has smooth distal parts of brood chambers (rarely with a ring of irregular spines on the periphery, but never in the centre) and has no crown (Fig. 32F). Sometimes the calcareous distal part of brood chamber bearing spines may split, thus becoming smooth, but soft. Also, the crown of *P. gracilis* is delicate, easily breakable, often represented only by fragments or absent in poorly preserved specimens.

P. gracilis and *P. uschakovi* can be confused when specimens with incompletely developed brood chambers are examined. When the distal part of the brood chamber in *P. gracilis* is smooth and the brood chamber crown is incompletely developed, it may be overlooked (Fig. 31E, F). An additional distinguishing feature for these two species is the length of the posterior edges of thoracic membranes on the convex body side reaching only the beginning of abdominal chaetigers in *P. uschakovi* (Fig. 32B), but 7-8th abdominal segments in *P. gracilis* (Fig. 31C). Unfortunately, this outgrowth of thoracic membranes in *P. gracilis* is delicate and easily damaged. Also, the calcareous zone of the lateral wall of brood chambers in *P. uschakovi* (Fig. 32C, F) is somewhat more triangular and longer (almost reaching the peduncle) in comparison with that in *P. gracilis* (Fig. 31E, G). Additionally, *P. gracilis* probably has 3–2 abdominal chaetae per fascicle *versus* 1–2 chaetae in *P. uschakovi*, but this character is not suitable for reliable identification. These two species also differ ecologically: *P. uschakovi* typically occupies shells and carapaces of large decapods, but never settles on stones, while *P. gracilis* occupies mainly stones, sometimes shells, but is never found on decapods. Juveniles of both species only have primary opercula that are practically undistinguishable, so their identification is possible only when adults are present.

P. asperata known only by few reliable records from the North Pacific (Knight-Jones P. et al., 1979; Rzhavsky, 1992b) also bears spines on the distal part of the brood chamber, but the chamber lacks a crown. *Protoleodora coronata* (Zachs, 1933) known only from Asian coast of the Pacific Ocean has the crown, but its distal part of the brood chamber is deeply invaginated (funnel-shaped), without spines and bears a central projection. Some species of the genus *Bushiella* described above also have primary opercula attached to the brood chambers by talons. But in *Bushiella* spp. the talon is firmly attached to the lateral wall of the brood chamber, while in *Protoleodora* spp. the primary operculum is attached to the distal part of the brood chamber by talon's tip only, and is often shed.

Ecology. The Arctic specimens of *P. gracilis* were collected at depth of 6 m from unknown substrate. Outside the Arctic the species is recorded mainly from stones, serpulid tubes, and gastropod shells at depths of 0–10 m where it is found in mixture with *P.* (*P.*) *violacea*, *P.* (*S.*) *vitrea*, and *B.* (*J.*) *quadrangularis*.

Distribution. In the Arctic the species is recorded from the Chukchi Sea only. It is also known in the North Pacific from the Commander to South Kurile Islands, Russia (Rzhavsky, 1992b; 1992[1994]). Limits of its distribution range need to be clarified.

***Protoleodora uschakovi* Knight-Jones P., 1984**

(Fig. 32A-J)

Spirorbis validus **non** Verrill, 1874: Zachs, 1933, p. 135; Annenkova, 1937, p. 198; 1952, p. 135 (partim); Uschakov, 1950, p. 231; 1959, p. 208.

Spirorbis granulatus: Annenkova, 1937, p. 198 (partim).

Spirorbis (*Laeospira*) *validus* **non** Verrill, 1874: Annenkova, 1938, p. 219; Uschakov, 1955, p. 432, fig. 162I, 163 M1, M2 (partim?); 1965, p. 407, fig. 162I, 16 L1, L2 (partim?).

Spirorbis (*Laeospira*) *granulatus* **non** Linnaeus, 1767: Annenkova, 1938, p. 219 (partim); Uschakov, 1955, p. 431 (partim); 1965, p. 406 (partim).

Spirorbis (*Laeospira*) *medius* **non** Pixell, 1912: Annenkova, 1938, p. 211; Uschakov, 1955, p. 431, fig. 193Zh-K; 1965, p. 406, fig. G-J2.

Protoleodora uschakovi: Knight-Jones P., 1984: 115-118, fig. 3A-N; Rzhavsky, 1989, p. 57 (partim); 1992b, p. 10-11; 1992[1994], p. 102, fig. 3; 1997b, p. 146; 2001, p. 599-560, text figures 1-4, map.

Material examined. Table 1. # 74 (2); # 75 (3); # 572 (7).

Description. Tube (Fig. 32A) sinistral, usually planospiral, up to 5 mm in coil diameter; last whorl may be facing upward away from substrate; unsculptured or with one indistinct median keel; white opaque, non-porcellaneous. Colour of live specimen unknown, preserved specimens colourless or flesh-coloured.

Primary operculum with large eccentric sub-triangular talon comprising two pointed lateral wings flanking a central longitudinal keel, endplate slightly concave and smooth. Fine curved spines on talon and a fan of spines tightly pressed against underside of endplate sometimes present. Primary operculum attached to distal part of developed brood chamber only by talon's tip only, so often shed; trace of primary operculum attachment absent. Distal part of brood chamber concave, completely smooth or with a ring of irregular spines on periphery, but never in centre. Crown of separate petals surrounding distal part of brood chamber absent (Fig. 32B-D, F). Lateral calcareous zone of brood chamber on concave side (facing away from radiolar crown) subtriangular, longer than wider, usually with a vestigial median longitudinal ridge (Fig. 32B, F). Apex of calcified zone attached to a thick cord lying at surface of peduncle and leading to thoracic tori on concave side. On opposite side of brood chamber calcified zone as a belt adjacent to distal part of brood chamber present or absent. A soft-walled pouch of brood chamber extending posteriorly in dorsal thoracic groove indistinct in specimens with empty brood chambers, but well developed in specimens brooding numerous embryos (Fig. 32C, D, F).

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 3rdchaetiger on concave body side, while extending posteriorly, obliquely crossing long achaetigerous region, but not continuing to abdominal chaetigers on convex body side (Fig. 32B). Apron present. Three thoracic chaetigers.

Large collar chaetae bent, limbate with slightly serrated blade. Collar chaetae on convex body side longer than that on concave and often with small groove in basal part (Fig. 32G), but fin not forming, and distinct smooth gap between basal and distal parts of blade absent. Capillary chaetae present in collar fascicles. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini saw-to-rasp-shaped, each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth before blunt anterior peg. Size of uncini in each torus significantly decreasing in direction away from notochaetae (Fig. 32H, I). While largest uncini only somewhat shorter than collar chaetae blades, smallest not exceeding or even shorter than abdominal uncini.

Abdomen with about 20 chaetigers. One abdominal chaetae per fascicle on most abdominal chaetigers and two on some anterior chaetigers. Chaetae flat geniculate, pennant-shaped, with indistinct heel and serrated tapering blade. Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. One capillary hooked chaeta per fascicle on most abdominal chaetigers. Uncini (Fig. 32J) rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. Before the species was formally described, its specimens collected from the Pacific and Arctic were usually recorded as "*validus*" and sometimes as "*granulatus*" or "*medius*" (= "*asperatus*") (see synonymy). Knight-Jones P. et al. (1979) without examining the material erroneously presumed that "*validus*" from the Russian Far-Eastern Seas could belong to *B.* (*B.*) *verruca*. Some specimens earlier reported by Rzhavsky (1989) as *P. uschakovi* belonged to *P. gracilis,* especially those collected from stones.

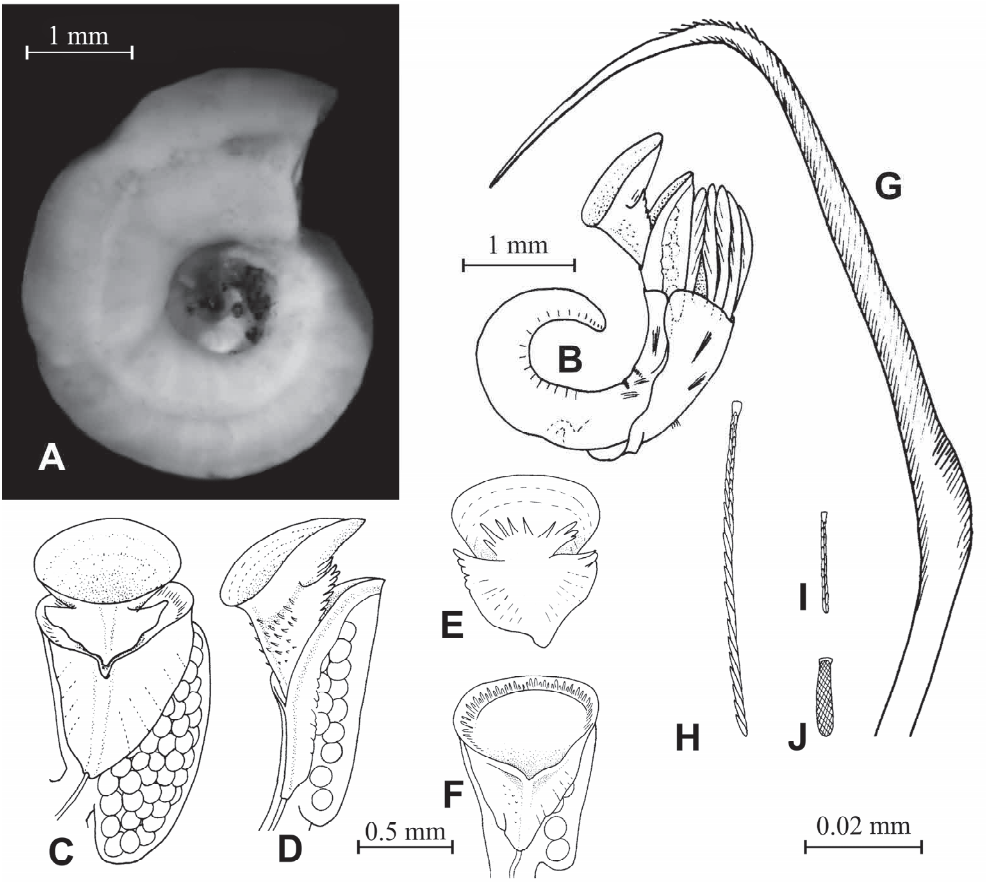

Figure 32. *Protoleodora uschakovi*. A – tube; B – entire body; C – brood chamber (frontal view) with smooth primary operculum; D – brood chamber (lateral view) with spiny primary operculum; E – primary operculum with a fan of spines underneath endplate; F – brood chamber bearing a ring of irregular spines on periphery (frontal view) without primary operculum; G – limbate collar chaeta; H – largest thoracic uncinus; I – smallest thoracic uncinus; J – abdominal uncinus. B-J – from Knight-Jones P. (1984). A – photo A.V. Rzhavsky.

In the original description of the species, Knight-Jones P. (1984) suggested that the distal plate of brood chamber was concave, completely smooth, or with a ring of irregular spines on the plate periphery, but not in the centre. However, re-examining her extensive material, Rzhavsky (1989; 1992b) found the spines only in some specimens, while most had absolutely smooth distal parts of brood chambers, including the paratypes deposited in the collection of Zoological Institute (St. Petersburg, Russia).

Mature and well-preserved specimens of *P. uschakovi* are easily distinguishable from all other *Protoleodora* spp. because of smooth distal parts of their brood chambers (rarely with a ring of irregular spines on the periphery, but never in centre) and absence a crown of petals (Fig. 32C, D, F). Another species, *P. gracilis* known from the Arctic has the entire surface of the distal part of the brood chamber covered with numerous spines; its brood chamber has a delicate crown that may be subdivided into 20–30 separate petals (Fig. 3C, E) or entire with festoon edge (Fig. 31F, G). However, sometimes spine-bearing calcareous distal parts of *P. gracilis* brood chambers may break off, thus becoming smooth, but soft. Because the crown of *P. gracilis* brood chamber is delicate and easily breakable, it is often represented only by fragments or absent altogether in poorly preserved specimens.

Identification of specimens with incompletely developed brood chambers may be problematic when distal parts of their brood chambers are smooth in both *P. uschakovi* (Fig. 32F) and *P. gracilis,* and the crown of *P. gracilis* incompletely developed and is easily missed (Fig. 31E, F). An additional distinguishing feature is the length of the posterior edges of thoracic membranes on the convex body side reaching 7-8th abdominal segments in *P. gracilis* (Fig. 31C) and extending only to the beginning of abdominal chaetigers in *P. uschakovi* (Fig. 32B); unfortunately, this outgrowth of the membrane edge in *P. gracilis* is very delicate and breaks away easily. Also, the calcareous zone of the brood chamber lateral wall resembles a heraldic shield and is rarely triangular in *P. gracilis* (Fig. 31 E, G)*,* while it is typically triangular and much longer (almost reaching the peduncle) in *P. uschakovi* (Fig. 32 C, F). In addition, *P. uschakovi* probably has 1–2 abdominal chaetae per fascicle *versus* 3–2 in *P. gracilis*, but because we do not have enough observations on this feature, this character is not reliable for identification purposes. The two species also differ ecologically: *P. uschakovi* occupies bivalve and gastropod shells, carapaces of large decapods, and probably never settles on stones, while *P. gracilis* occupies mainly stones, can occur on shells, but never on large decapods. Juveniles of both species only have primary opercula that are practically undistinguishable, so adult specimens are needed for their identification.

P. asperata is known only by few reliable records from the North Pacific (Knight-Jones P. et al., 1979; Rzhavsky, 1992b). Like in *P. uschakovi,* it has brood chamber lacking a crown, but bearing spines all over the entire surface of the distal part of the chamber, similar to *P. gracilis*. *P. coronata,* known only from the Asian coast of the Pacific, has a distal part of the brood chamber without spines, but deeply invaginated (funnel-shaped), bearing a central projection and a well-developed crown.

Some species of genus *Bushiella* described above also have primary opercula attached to the brood chamber by the talon. But in *Bushiella* the talon is firmly attached to the lateral wall of the brood chamber, while in *Protoleodora* spp. primary operculum attach to the distal part of the brood chamber only by talon's tip and is often shed.

Ecology. The Arctic specimens were collected at depth of about 40 m from shells. Outside the Arctic the species is recorded from depths of 0–320 m, usually from over 50 m. Animals attach to shells of live gastropods and bivalves, as well as to gastropod shells occupied by pagurids and carapaces of large decapods, including *Chionocetes opilio* (O. Fabricius, 1788) where they may live mixed with *B.* (*J*) *quadrangularis*, *C. armoricana*, and some other species.

Distribution. In the Arctic the species is recorded from Chukchi Sea only. Because of the specific habitats requirements , the species may be found in the Barents and other Arctic Seas on the snow crab *C. opilio*, a recent invader (Pavlov & Sokolov, 2003; Agnalt et al., 2011), if the latter indeed penetrated there from the Pacific sector of the Arctic. In the North Pacific the species is common from the Bering Strait to the south of Primorsky Kraj, Russia (Rzhavsky, 1992b; 1992[1994]). It is the only species of *Protoleodora* known from the North Atlantic off Newfoundland, Canada (Rzhavsky, 2001).

Spirorbini Chamberlin, 1919

Type genus: *Spirorbis* Daudin, 1800.

Embryos in a string attached posteriorly by a thread to inner tube wall. Operculum a distal plate with a talon. Larvae with a single white abdominal attachment gland. Thoracic uncini narrow, rasp-shaped, with 3–4 (5–6 in smallest uncini) longitudinal rows of teeth and blunt anterior peg. Abdominal uncini distributed symmetrically. Abdominal chaetae flat geniculate, pennant-shaped, usually with a thick projecting heel; their blade lengths not exceeding those of largest collar chaetae, width decreasing gradually towards tip. Abdominal capillary hooked chaetae usually appearing only on last abdominal chaetigers or may be absent.

Only genus *Spirorbis*.

Genus *Spirorbis* Daudin, 1800

Type species *Spirorbis borealis* (Daudin, 1800 (=*Serpula spirorbis* Linnaeus, 1758)).

Tube sinistral or dextral. Margins of collar and thoracic membranes not fused or fused over thoracic groove. Large collar chaetae bent, modified fin-and-blade or fin-and-blade cross-striated at least on the convex side of body; sickle (“*Apomatus*”) chaetae present in 3rd thoracic fascicles. Always three thoracic chaetigers.

Two subgenera *Spirorbis* and *Velorbis* (Knight-Jones P. & Knight-Jones E.W., 1995), only the former is known from the Arctic.

Remarks. *Spirorbis echinatus* Wesenberg-Land 1953b described from off Lofoten Islands, Norway, is unknown from elsewhere and obviously does not belong to the genus *Spirorbis*. Despite the detailed original description and the very characteristic tubes, its generic position is unclear. Therefore, the species is not included in the identification key and is not provided with a description.

Subgenus *Spirorbis* Daudin, 1800

Type species *Spirorbis borealis* (Daudin, 1800 (=*Serpula spirorbis* Linnaeus, 1758).

Margins of collar and thoracic membranes not fused over thoracic groove.

Thirteen species, five are known from the Arctic.

Remarks. Monotypic subgenus *Velorbis* known from Madeira only (Knight-Jones P. & Knight-Jones E.W., 1995) has margins of collar and thoracic membranes fused over thoracic groove.

Spirorbis (*Spirorbis*) *corallinae* de Silva, Knight-Jones E.W., 1962

(Fig. 33A-I)

Serpula spirillum **non** Linnaeus, 1758: Montagu, 1803, p. 499-500 (partim).

Spirorbis corallinae: de Silva & Knight-Jones E.W., 1962, p. 602, fig. 1I-L; Gee, 1964, p. 415-416; Toner, 1967, p. 325-326; Harris T., 1968a, p. 598; Ryland & Nelson-Smith, 1975, p. 253; Knight-Jones P. & Knight-Jones E.W., 1977, p. 461-463, fig. 3A-K; Knight-Jones P. et al., 1991, p. 190, fig. 1; Rzhavsky, 1992a, p. 10-11; 1992 [1994], p. 103, fig. 5.

Spirorbis (*Laeospira*) *inornatus* f. *scandens*: L'Hardy & Quievreux, 1962, p. 2175, fig. 5, 10.

Spirorbis (*Laeospira*) *corallinae* f. *scandens*: L'Hardy & Quievreux, 1964, p. 295, fig. 2.

Spirorbis (*Spirorbis*) *corallinae*: Rzhavsky, 2001, p. 601-602, text figures 1-7, map.

Material examined. Table 1. # 540 (~ 50).

Description. Tube (Fig. 33A) sinistral, unsculptured, planospiral or whorls may be overlappping, adults rarely more than 1.5 mm in coil diameter; white opaque porcellaneous, but in live animals orange body may be visible through thin tube walls of initial coils giving an impression of light pinkish colour. Body of live animals mainly orange, excluding colourless radioles; preserved material colourless.

Opercular endplate usually flat, but may be concave in juveniles or slightly convex in largest specimens (Fig. 33 C, D); length of talon approximately same as its width, talon quite thick in lateral view (Fig. 33C); its terminal edge usually bilobed in the frontal view (Fig. 33D), but may be almost spatulate in largest. Viewed from below terminal edge of talon (Fig. 33E) not markedly curved in adults.

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 3rd chaetiger, apron present. Collar somewhat asymmetrical without a lateral flap on dorso-convex margin (Fig. 33B). Three thoracic chaetigers.

Large collar chaetae (Fig. 33F) bent, modified fin-and-blade with distinctly serrated fin and finely serrated blades. Smooth gap between fin and blade in chaetae from concave side shorter than that in chaetae from convex body side (Fig. 33G). Capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae (Fig. 33H) also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini rasp-shaped with 3–5 longitudinal rows of teeth throughout most of their length and blunt gouged anterior pegs looking bifurcate when examined under a light microscope. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with up to 25 chaetigers. One (rarely two) abdominal chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and distinctly serrated tapering blade (Fig. 33I). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from the convex side. Capillary hooked chaetae not observed. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both body sides. Largest tori in anterior part of abdomen.

Remarks. Examined material from the Barents Sea identified by V.V. Chlebovitsch as "*Spirorbis borealis*" was collected in 1959 by O.G. Kussakin and G.A. Scherbakov. Nevertheless, this material was not recorded in the paper where the data on this survey were published (Kussakin, 1963).

This worm for a long time had not been distinguished from *S.* (*S.*) *spirorbis* until two groups of authors independently described it either as a new species (de Silva & Knight-Jones E.W., 1962) or as a variety of another new species (L'Hardy & Quievreux, 1962) also distinct from *S. (S.) spirorbis* (see synonymy).

Knight-Jones P. & Knight-Jones E.W. (1977) suggest without any explanation that Montagu (1803) recorded this species from Devon as a variety of "*Serpula spirillum*". At first glance it looks strange, because *C. spirillum* (and *C. armoricana* often synonymized with it) typically have dextral tubes, whereas tube of *S. (S.) corallinae* is sinistral. Montagu (1803) made notes on the specimens of "*S. spirillum*" that differ from the typical form and were very abundant on algae *Corallina officinalis* Linnaeus, 1758, but he did not describe the coiling direction of their tubes. There are only two species in this region living on *C. officinalis* – *S.* (*S.*) *corallinae* and *J. heterostropha*, whereas *Circeis* spp. were never recorded from this substrate. In the same paper Montagu (1803) described specimens of *J. heterostropha* (attached to *C. officinalis*) as "*Serpula minuta*" also without indication of a coiling direction. Its tube is really dextral, but it has a dirty-white rough surface and bears 2–3 distinct keels, while both forms of "*Serpula spirillum*" *sensu* Montagu (1803) are "sub-pellucid, glossy and white", which suggest that they may in fact belong to "*Serpula spirillum*" *sensu* Montagu (1803) "sub-pellucid, glossy and white" that correspond to *S. (S.) corallinae*. Therefore, the suggestion of Knight-Jones P. & Knight-Jones E.W. (1977) is likely right, because Montagu did not pay attention on the tube coiling direction and never described it for any spirorbins.

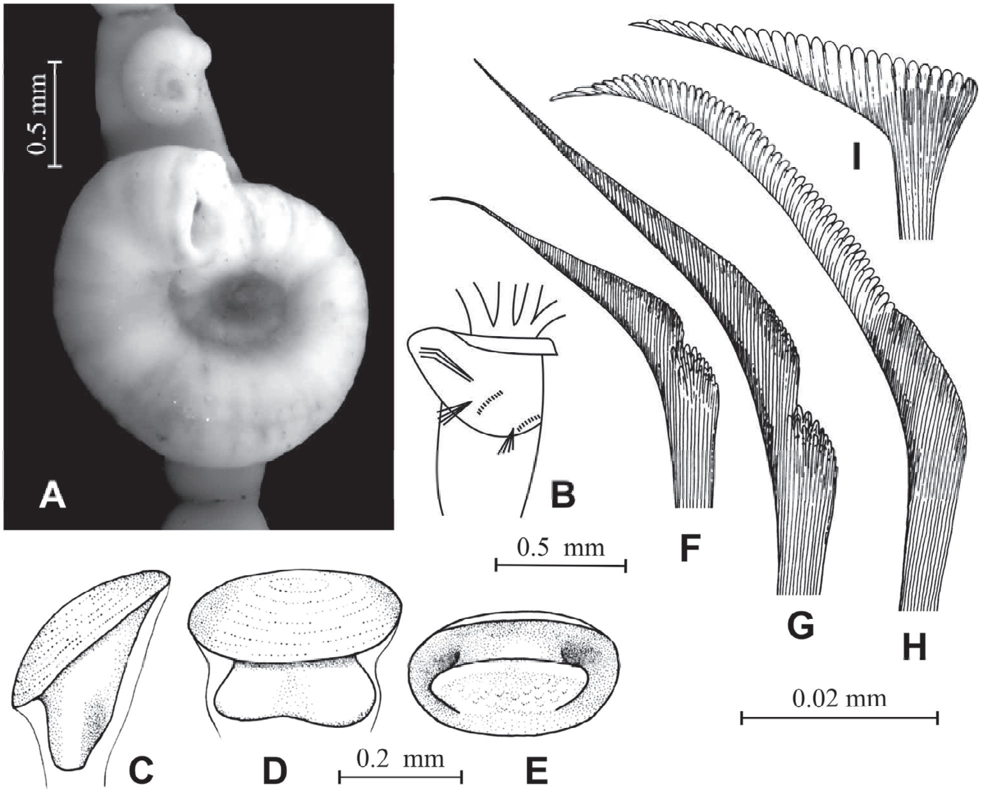

Figure 33. *Spirorbis* (*Spirorbis*) *corallinae*. A – tubes; B – thorax, convex body side; C-E – operculum (lateral, top, and below views); F – modified collar chaeta, concave body side; G – modified collar chaeta, convex side; H – thoracic sickle (*Apomatus*) chaeta; I – flat geniculate abdominal chaeta. B-I – from Knight-Jones P. & Knight-Jones E.W. (1977). A – photo A.V. Rzhavsky.

The species is similar to *S.* (*S.*) *inornatus* in the talon morphology and initially was regarded as its form by L'Hardy & Quievreux, 1962 (see synonymy). Their talon's length is approximately the same as width and its terminal edge often slightly bilobed (Fig. 33D, 34D), though in adult *S.* (*S.*) *inornatus* talon is wider than longer and resembling a horse hoof, curved frontally when seen from below (Fig. 34E).

Nevertheless, *S.* (*S.*) *corallinae* is easy to distinguish by small adult tube size (rarely more than 1.5 mm in coil diameter), semitransparent tube wall of initial whorls and absence of lateral collar flap (Fig. 33B). *S.* (*S.*) *inornatus* have adult tubes up to 3 mm in coil diameter and never semitransparent and its collar bears a distinct lateral flap (Fig. 34B). The species is also easily distinguished ecologically. *S.* (*S.*) *corallinae* live on *C. officinalis* and rarely on red algae *Chondrus*, while *S.* (*S.*) *inornatus* occupies different red (excluding calcareous) and brown algae.

Other *Spirorbis* spp. known from the Arctic also have larger adult tubes without any semitransparent zones, one of them (*S.* (*S.*) *tridentatus* bearing three distinct keels when adult (Fig. 37A). Talons of *S.* (*S.*) *rupestris* and *S.* (*S.*) *spirorbis* are wider than longer, very narrow and indistinct as edge thickens near periphery of opercular endplate on the side away from radiolar crown (Fig. 35E; 36E). Talon of *S.* (*S.*) *tridentatus* is very large, tooth-shaped in side view; it is irregular with an asymmetrical lateral boss and rounded or pointed terminally in front view (Fig. 37C-E). Some differences in the chaetal structures are also present (see descriptions).

Outside the Arctic Basin there are no *Spirorbis* species similar to *S.* (*S.*) *corallinae*.

Ecology. Our Arctic material was collected from calcareous alga *C. officinalis* in the low littoral zone. It is an intertidal species usually living in tidal pools on *C. officinalis*, in the areas exposed to strong sand abrasive action that are unsuitable for *S.* (*S.*) *inornatus*, specimens of *S.* (*S.*) *corallinae* may occupy red algae of the genus *Chondrus* (Knight-Jones P. & Knight-Jones E.W., 1977). Sometimes the species is found in mixture with *J. heterostropha*. At the British coasts breeding takes place from May to August, no synchrony in reproduction was observed (de Silva, 1967). Larvae often settle without a pelagic stage (Gee, 1963). Under laboratory conditions larvae settle exclusively on *C. officinalis* (de Silva, 1962).

Distribution. In the Arctic the species is known from the Barents Sea (our data) and Norwegian Sea (Knight-Jones P. et al., 1991). It is common in the North-East Atlantic, from the North of Scotland (UK) to south Brittany (France) (Knight-Jones P. & Knight-Jones E.W., 1977), Ireland (Toner, 1967), and Scilly Islands (Harris T., 1968a).

***Spirorbis* (*Spirorbis*) *inornatus* L'Hardy, Quievreux, 1962**

(Fig. 34A-H, Pl. 2D)

Spirorbis (*Laeospira*) *inornatus* f. *procumbens*: L'Hardy & Quievreux, 1962, p. 2175, fig. 5, 10.

Spirorbis (*Laeospira*) *corallinae f .reptans*: L'Hardy & Quievreux, 1964, p. 292, fig. 3.

Spirorbis (*Laeospira*) *inornatus*: L'Hardy & Quievreux, 1964, p. 292, fig. 1, 4-6.

Spirorbis inornatus: Gee, 1964, p. 416; Knight-Jones P. & Knight-Jones E.W., 1977, p. 463-464, fig. 3L-T; Knight-Jones P. et al., 1991, p. 190, fig. 1.

Spirorbis spirorbis **non** Linnaeus, 1758: ? Rzhavsky, 1992a, p. 10 (partim?); 1992[1994], p. 103, fig. 5 (partim?); 2001, p. 604-605, text figures 1-7, map (partim?).

Spirorbis (*Spirorbis*) *inornatus*: Rzhavsky, 2001, p. 602, text figures 1-5, map.

Material examined. Table 1. # 507 (~ 30); # 531 (1 + tubes); # 582 (~ 100); # 595 (? 100).

Description. Tube (Fig. 34A) sinistral, unsculptured, usually planospiral, rarely whorls overlapping; peripheral flange present or absent; rarely more than 3 mm in coil diameter;

white opaque somewhat porcellaneous. Body of live animals light orange, excluding colourless radioles (Pl. 2D), preserved material colourless.

Opercular endplate flat or slightly concave (Fig. 34C, D). Talon thick in lateral view (Fig. 34C); in juveniles talon approximately of same length as width and with slightly bilobed terminal edge in front view; in adults talon usually wider than longer, with slightly bilobed (Fig. 34D) or unilobed (even) terminal edge and resembling a hoof, curved frontally when seen from below (Fig. 34E).

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching the end of 3rd chaetiger forming apron. Collar asymmetrical, its dorso-convex margin forming a lateral flap (Fig. 34B). Three thoracic chaetigers.

Modified collar chaetae bent, fin-and-blade or fin-and-blade cross-striated, with distinctly serrated protuberant fin; their blades significantly wider and more bent in comparison with other *Spirorbi*s spp.; chaetae from convex body side (Fig. 34F) of with coarse serrated blades and sometimes with vestigial cross-striation, those from the concave side (Fig. 34G) finely serrated and almost twice as small, always without cross-striation. Smooth gap between fin and blade of approximately same length in chaetae from both body sides. Capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in the 3rd fascicle.

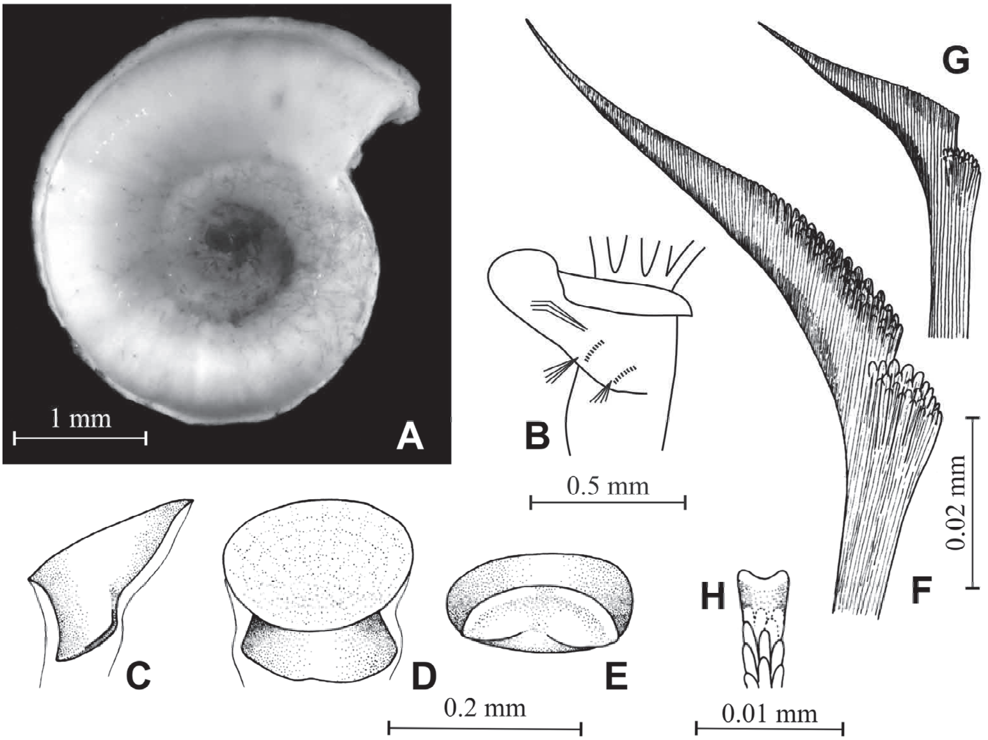

Figure 34. *Spirorbis* (*Spirorbis*) *inornatus*. A – tube with peripheral flange; B – thorax, convex body side; C-E – operculum (lateral, top and bottom views); F – special collar chaeta, convex body side; G – special collar chaeta, concave body side; H – anterior peg of thoracic uncinus. B-H – from Knight-Jones P., Knight-Jones E.W. (1977). A – photo A.V. Rzhavsky.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini rasp-shaped with 3–5 longitudinal rows of teeth throughout most length of uncinus and anterior pegs blunt and slightly gouged (Fig. 34H), looking bifurcate under a light microscope. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with up to 30 chaetigers. One (rarely two) abdominal chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and distinctly serrated tapering blade. Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. Capillary hooked chaetae not observed. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both body sides. Largest tori in anterior part of abdomen.

Remarks. This species had not been distinguished from *S.* (*S.*) *spirorbis* until L'Hardy & Quievreux (1962) described it as a separate valid species with the forms f. *procumbens* and f. *scandens*. In the same year, but earlier de Silva & Knight-Jones E.W. (1962) described *S.* (*S.*) *corallinae.* L'Hardy & Quievreux (1964) synonymized *"inornatus* f. *scandens*" living on red alga *C. officinalis* with *S.* (*S.*) *corallinae* and proposed another form, "*corallinae* f. *reptans*", living on a number of other red algae. Simultaneously they proposed "*inornatus*" as a species associated with laminarians only. Finally, Knight-Jones P. & Knight-Jones E.W. (1977) suggested that "*corallinae* f. *reptans*" is identical to *S.* (*S.*) *inornatus* (see synonymy for *S.* (*S.*) *inornatus* and *S.* (*S.*) *corallinae*).

Another serious problem is the interpretation of the material identified earlier as *S.* (*S.*) *spirorbis*. *S.* (*S.*) *inornatus* and *S.* (*S.*) *spirorbis* differ very well, especially when alive (see below). Knight-Jones P. & Knight-Jones E.W. (1977) suggested that *S.* (*S.*) *spirorbis* typically lives intertidally on fuci, while *S.* (*S.*) *inornatus* occupies a narrow bathymetric range between the lower intertidal and the 2 m depth mark where abrasive sand is absent, where it occupies various brown and red (but not calcareous) algae. Knight-Jones P. & Knight-Jones E.W. (1977) suggested that fuci is not a characteristic substrate for *S.* (*S.*) *inornatus*, though in some locations it may replace *S.* (*S.*) *spirorbis* on fuci. Because *S.* (*S.*) *spirorbis* was considered so typical on fuci in the intertidal zone of North-East Atlantic, most of such Atlantic and Arctic records of "*spirorbis*" were attributed to this species without examination (e.g., Rzhavsky, 1992a; 1992 [1994]; 2001). However, our extensive material collected in 2011 from the same habitats in the Norway, Barents Sea (our data), and White Sea (photos by Kolbasova, pers. comm.) belonged to *S.* (*S.*) *inornatus*, while *S.* (*S.*) *spirorbis* was not found at all. Therefore, most data on distribution and biology of *S.* (*S.*) *spirorbis* (see below) previously considered one of the most characteristic and abundant species in the studied area became doubtful and the records may belong to either of these two species.

As obvious from the above, *S.* (*S.*) *inornatus* is especially similar to *S.* (*S.*) *corallinae* that is also known from the Arctic. Both species have talon's length approximately the same as width and talon's terminal apical edge is often slightly bilobed (Fig. 33C; 33D), whereas in adult *S.* (*S.*) *inornatus* the talon becomes wider than long and resembles a horse hoof (Fig. 34E), curved frontally (when seen from below) and almost even terminally. *S.* (*S.*) *inornatus* is also easy to distinguish from *S.* (*S.*) *corallinae* by large (up to 3 mm in coil diameter) and completely non-transparent tubes and the collar bearing distinct lateral flaps. *S.* (*S.*) *corallinae* have tubes that are very small (rarely over1.5 mm in coil diameter) and with semitransparent walls of initial whorls; lateral collar flaps (Fig. 33B) are always absent. These species are also distinct ecologically: *S.* (*S.*) *inornatus* lives on red (excluding calcareous) and brown algae, while *S.* (*S.*) *corallinae* commonly occupies red alga *C. officinalis* and rarely of the genus *Chondrus*.

Tubes of *S.* (*S.*) *inornatus* are approximately of the same size as those in three remaining Arctic species of the genus *Spirorbis* that also have white, somewhat porcellaneous tubes. The tubes of *S.* (*S.*) *spirorbis* and *S.* (*S.*) *rupestris,* as well as juvenile tubes of *S.* (*S.*) *tridentatus* are unsculptured, like those of *S.* (*S.*) *inornatus*, but adult tubes of *S.* (*S.*) *tridentatus* bear three distinct keels (Fig. 37A).

Talons of *S.* (*S.*) *spirorbis* and *S.* (*S.*) *rupestris* are wider than longer, as a narrow indistinct edge thickening near periphery of opercular endplate on the side away from the radiolar crown (35E, 36E). On the contrary, the talon of *S. (S.) tridentatus* is very large, tooth-shaped in side view and irregularly shaped with two asymmetrical lateral bosses and rounded or pointed terminally in frontal view (Fig. 37C-E). The body of live *S.* (*S.*) *spirorbis* is pale greenish-brown, and of *S.* (*S.*) *rupestris* is bright orange-red, whereas live specimens of *S.* (*S.*) *inornatus* are light orange. Some differences in the chaetal structures are also present (see descriptions).

Outside the Arctic Basin there are no *Spirorbis* species similar to *S.* (*S.*) *inornatus*.

Ecology. Examined specimens found in the Arctic intertidally on fuci and red algae were probably floating on the surface (one sample was labelled as collected by trawl from depth of about 95 m). According to Knight-Jones P. & Knight-Jones E.W. (1977), *S.* (*S.*) *inornatus* lives strictly in a narrow bathymetric range between the lower intertidal and the 2 m depth mark and occupies brown and red (but not calcareous) algae. Knight-Jones P. & Knight-Jones E.W. (1977) also suggested that fuci is not a characteristic substrate for this species, though in some locations *S.* (*S.*) *inornatus* may replace *S.* (*S.*) *spirorbis* that is also typically found on fuci. However, our new data indicate that *S.* (*S.*) *inornatus* may be common on fuci in the White, Barents, and Norwegian Seas. The species may live in mixture with *C. armoricana*. Larval settlement behaviour has been studied in an aquarium (Knight-Jones E.W. et al., 1975; Al-Ogily, 1985). Some data on biology of *S.* (*S.*) *spirorbis* (see below) may belong to *S* (*S.*) *inornatus*.

Distribution. Our Arctic material was collected from the White, Barents, and Norwegian Seas. The species is also well known from the British and Irish coasts and Brittany, France (Knight-Jones P. & Knight-Jones E.W., 1977). Rzhavsky (unpubl.) found this species in the material from the Danish coast of Oresund.

***Spirorbis* (*Spirorbis*) *rupestris* Gee & Knight-Jones E.W., 1962**

(Fig. 35A-F, Pl. 2E, F)

? *Serpula corrugata* Montagu, 1803, p. 502-503.

Spirorbis rupestris Gee & Knight-Jones E.W., 1962, p. 642-643, fig. 1A-G; Gee, 1964, p. 416-417; Toner, 1967, p. 325-326; Harris T., 1968a, p. 601; Knight-Jones P. & Knight-Jones E.W., 1977, p. 460-461, fig. 2 K-P; Knight-Jones P. et al., 1991, p. 190, fig. 1; Rzhavsky, 2001, p. 603, text figures 1-4, map.

Spirorbis (*Laeospira*) *umbilicatus* L'Hardy & Quievreux, 1962, p. 2174-2175, fig. 3,8.

Spirorbis (*Laeospira*) *rupestris*: L'Hardy & Quievreux 1964, p. 292.

Material examined. Table 1. # 595 (~ 100).

Description. Tube sinistral, unsculptured, usually planospiral, but last whorl may be straightened (Fig. 35B); peripheral flange always absent; tube often covered with calcareous algae (Fig. 35A; Pl. 2F) *Phymatolithon purpureum* (P.L. Crouan & H.M. Crouan) Woelkerling & L.M. Irvine, 1986, leaving only mouth visible; coil diameter of planospiral tube part up to 4.5 mm. Tube white opaque, somewhat porcellaneous when not covered by algae. Abdomen and thorax of live animals bright orange-red (Pl. 2E), preserved material colourless or flesh-coloured.

Operculum oblique and slightly concave (Fig. 35D). Talon vestigial, pad-shaped, as narrow indistinct edge thickening near periphery of opercular endplate on side away from radiolar crown (Fig. 35E).

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 3rd chaetiger forming apron ventrally. Collar only slightly asymmetrical, without a lateral flap of its dorsal-convex margin (Fig. 35C). Three thoracic chaetigers.

Large collar chaetae (Fig. 35F) bent, modified fin-and-blade with distinctly serrated streamlined fin and finely serrated blades on both body sides. Smooth gap between fin and blade of approximately same length in chaetae from both body sides. Capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini rasp-shaped with 3–6 longitudinal rows of teeth throughout most length of uncinus and blunt anterior pegs. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

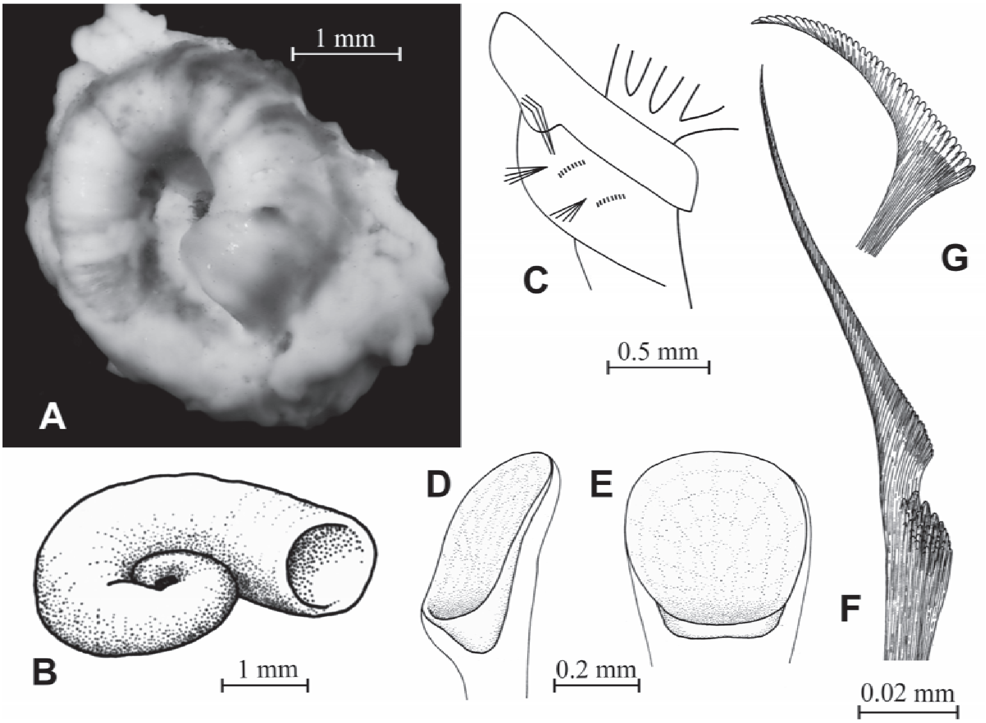

Figure 35. *Spirorbis* (*Spirorbis*) *rupestris*. A – tube associated with a calcareous alga; B – tube with evoluted last whorl, not covered with calcareous algae; C – thorax, convex body side; D-E – operculum (lateral and frontal views); F – modified collar chaeta, convex body side; G – abdominal flat geniculate chaeta. B-F – from Knight-Jones P. & Knight-Jones E.W. (1977). A – photo A.V. Rzhavsky.

Abdomen with about 25 chaetigers. Usually two abdominal chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with distinct heel and distinctly serrated tapering blade (Fig. 35G). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex side. Companion capillary hooked chaetae not observed. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both body sides. Largest tori in anterior part of abdomen.

Remarks. According to Knight-Jones P. & Knight-Jones E.W. (1977), *Serpula corrugata* Montagu, 1803 (non *Spirorbis corrugatus* (Montagu) *sensu* Caullery & Mesnil, (1879) and others) probably is the same species as *S.* (*S.*) *rupestris*, but because the type material of Montagu has not been retained and the original description is incomplete, it is hard to be certain. Bush (1905) on the basis of Caullery & Mesnil (1987)'s description of *S. corrugatus* established a new species *N. pseudocorrugata* (as *Spirorbis pseudocorrugatus*) which distinctly differs from Montagu (1803) original description. Nevertheless, many authors continued using the combination *Spirorbis corrugatus* for specimens that fitted the description of Caullery & Mesnil (1879) (see for details Knight-Jones P. et al., 1975a; Rzhavsky, 1991b).

S. (*S.*) *rupestris* is another species that had not been not distinguished from *S.* (*S.*) *spirorbis* until Gee & Knight-Jones E.W., (1962) and L'Hardy & Quievreux, 1962) almost simultaneously designated "*rupestris*" and "*umbilicatus*" within *S. spirorbis*. According to L'Hardy & Quievreux (1964), the name "*rupestris*" has a priority.

The talon morphology of *S.* (*S.*) *rupestris* is especially similar to that of *S.* (*S.*) *spirorbis*. Both species have a pad-shaped talon as a narrow thickening near periphery of opercular endplate on the side away from the radiolar crown, although in *S.* (*S.*) *rupestris* talon is somewhat thicker (Fig. 35E; Fig. 36E). Both species also have large (over 3 mm in coil diameter), white, somewhat porcellaneous unsculptured tubes. But the tube of *S.* (*S.*) *rupestris* (Fig. 36A, B) lacks a peripheral flange very typical for the tubes of *S.* (*S.*) *spirorbis* (Fig. 36A, B). The last whorl of the *S.* (*S.*) *rupestris* may be evoluted and straightened (Fig. 35B), whereas the tube of *S.* (*S.*) *spirorbis* is always planospiral (Fig. 36A, B). Live specimens are easily distinguished by the body colour that is bright orange-red in *S.* (*S.*) *rupestris* (Pl. 2E) and pale greenish-brown in *S.* (*S.*) *spirorbis.* Additional distinctive features are morphology of collar and abdominal notochaetae. The collar of *S.* (*S.*) *spirorbis* have a distinct lateral flap (Fig. 36C) on the dorso-convex body side, whereas such a flap is absent in *S.* (*S.*) *rupestris* (Fig. 35C). Abdominal chaetae of *S.* (*S.*) *spirorbis* lack distinct heels (Fig. 36G), the structure that is present in *S.* (*S.*) *rupestris* (Fig. 35G) and in most spirorbins.

S. (*S.*) *inornatus* may be another species that is difficult to distinguish from *S.* (*S.*) *rupestris.* Though the talon length in juvenile *S.* (*S.*) *inornatus* is approximately the same as its width, *S.* (*S.*) *inornatus* adults usually have talons wider than long (Fig. 34D) and thus, may be confused with vestigial talons of *S.* (*S.*) *rupestris*. Tubes of *S.* (*S.*) *inornatus* are also large, unsculptured with somewhat porcellaneous surface and bodies of live specimens are light orange (Pl. 2D). The distinguishing features of tube morphology and collar structure in *S.* (*S.*) *rupestris* and *S.* (*S.*) *inornatus* are the same as those separating *S.* (*S.*) *rupestris* and *S.* (*S.*) *spirorbis.* Bodies of both species have more or less the same colour patterns, but the body of *S.* (*S.*) *rupestris* is completely bright orange-red (Pl. 2E) and that of *S.* (*S.*) *inornatus* is mainly light orange (Pl. 2D), except for colourless branchia.

S. (*S.*) *corallinae* differs from *S.* (*S.*) *rupestris* in having the talon of the same length as width (Fig. 33C, D), small adult tubes (not over1.5 mm in coil diameter) and semitransparent tube wall of their initial whorls. *S.* (*S.*) *tridentatus* has a massive tooth-shaped talon in side view, irregularly shaped with asymmetrical lateral bosses and rounded or terminally pointed in frontal view (Fig. 37C-E). The tubes of adults bear three distinct keels (Fig. 37A); juvenile tubes are unsculptured, but their last whorls tend to cover previous ones and to widen rapidly towards aperture (Fig. 37B).

In additional to the outlined morphological differences, *S.* (*S.*) *rupestris* is distinct ecologically. It is found only intertidally on rocks and stones, where it is usually closely associated with calcareous algae *P. purpureum.* Among other *Spirorbis* species, only *S.* (*S.*) *tridentatus* also occupies hard substrates, but this species lacks any association with this alga and its morphology is very different.

Among Arctic spirorbins, the only other species that has sinistral tubes with evoluted last whorls and thus, can be potentially confused with *S.* (*S.*) *rupestris*, is *B.* (*B.*) *evoluta* (Fig. 23A). The latter differs from *S.* (*S.*) *rupestris* both morphologically and ecologically (see "Description" of *B.* (*B.*) *evoluta*). Similar tubes, but dextral, may belong to *C. armoricana* when they share the same habitats with *B.* (*B.*) *evoluta*.

Outside the Arctic Basin there are no *Spirorbis* species similar to *S.* (*S.*) *rupestris*.

Ecology. Our material was collected in the low intertidal zone from rocks that were either clean or overgrown by *P. purpureum*. According to Knight-Jones P. & Knight-Jones E.W. (1977), the species prefers fairly well illuminated stones and rocks in the lower intertidal zone, particularly where siltation rate is low. The species is susceptible to sand abrasion, but is tolerant of reduced salinity. The species is well-known to be closely associated with calcareous algae *P. purpureum* (= *polymorphum*) (Knight-Jones P. & Knight-Jones E.W., 1977) and, unlike many other *Spirorbis* spp., does not live in mixture with any other spirorbins. Populations off the British coasts breed from March to October (Gee, 1967) showing no tidal periodicity. The larvae are epibenthic, mostly lacking a pelagic stage (Gee, 1963); extracts of the alga *P. polymorphum* tend to induce larval settlement (Gee, 1965).

Distribution. Our material was collected from the Norwegian Sea (off Tromsø). Previously the species was recorded from the Arctic off Norway coast without an indication of the exact locality (Knight-Jones P. et al., 1991). The species is well known from off the British and Irish shores and Brittany, France (Knight-Jones P. & Knight-Jones E.W., 1977).

***Spirorbis* (*Spirorbis*) *spirorbis* (Linnaeus, 1758)**

(Fig. 36A-H)

Serpula spirorbis: Linnaeus, 1758, p. 786; 1767, p. 1264.

Spirorbis borealis: Daudin, 1800, p. 38; Borg, 1917, p. 22-26, fig. 5a, b, 8, 9 (partim, non var. *tridentatus*, non fig. 6, 7, 10,11); L'Hardy, Quievreux, 1962, p. 2173-2174, fig. 2, 7; Gee, 1964, p. 415; Toner, 1967, p. 326-327.

Spirorbis nautiloides: Lamarck, 1801, p. 326.

Spirorbis (*Laeospira*) *borealis*: Bergan, 1953b, p. 33-35, fig. 1 a ,c, d (partim, non var. *tridentatus*, fig 1 b, e, f); de Silva & Knight-Jones E.W., 1962, p. 602-603, fig. 1 A-D; Nelson-Smith & Gee, 1966, p. 346, fig. 8B, 10 A1-A2.

Spirorbis spirorbis: Ryland & Nelson-Smith, 1975, p. 252, fig. 2, 3; Knight-Jones P. & Knight-Jones E.W., 1977, p. 457-460, fig. 2 A-J; Knight-Jones P. et al., 1991, p. 190, fig. 1; Rzhavsky, 1992a, p. 10 (partim?); 1992[1994], p. 103 (partim?); 2001. p. 604-605, text figures 1-7, map (partim?).

Material examined. Table 1. # 19 (10); # 542 (many); # 558 (many); # 584 (~ 50); # 592 (~ 30); # 603 (many); # 605 (many); # 608 (many); # 609 (many); # 610 (many); # 618 (many); # 620 (32); # 624 (many).

Description. Tube (Fig. 36A, B) sinistral, unsculptured, planospiral, usually with peripheral flange increasing area of attachment to substrate; coil diameter up to 3 (rarely 4) mm; white opaque slightly porcellaneous. Body of live animals pale greenish-brown, sometimes tinged with orange in abdomen and thorax. Blood green, clearly visible in tentacles and dorsal blood vessel. Preserved specimens colourless or brownish.

Operculum oblique, flat or slightly concave (Fig. 36D). Talon very narrow and indistinct, pad-shaped, as edge thickens near periphery of opercular endplate on side away from radiolar crown (Fig. 36E).

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 3rd chaetiger forming apron. Collar strongly asymmetrical, its dorso-convex margin forming a lateral flap (Fig. 36C). Three thoracic chaetigers.

Large collar chaetae bent, modified fin-and-blade with distinctly serrated angular fins and finely serrated blades on both body sides. Smooth gap between fin and blade longer in chaetae from convex body side (Fig. 37F). Capillary chaetae also present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini rasp-shaped, usually with four longitudinal rows of teeth throughout most length of uncinus and blunt anterior pegs (Fig. 36H). Smaller uncini with 5–6 rows of teeth. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

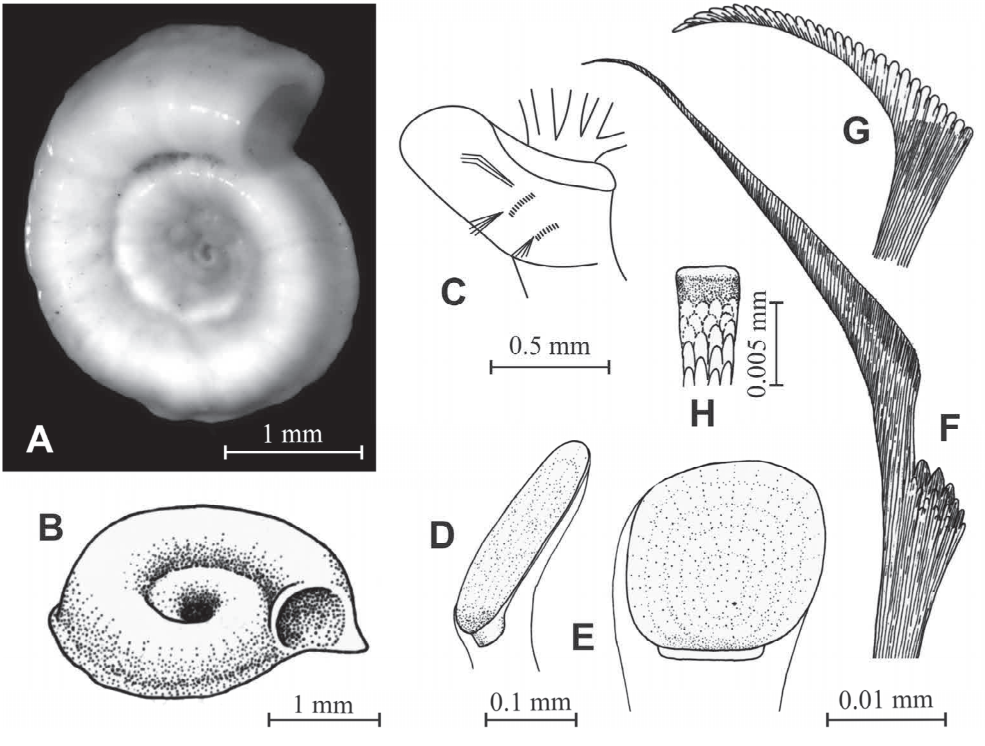

Figure 36. *Spirorbis* (*Spirorbis*) *spirorbis*. A, B – tube with peripheral flange; C – thorax, convex body side); D-E – operculum (lateral and frontal views); F – special collar chaeta, convex body side; G – abdominal flat geniculate chaeta; H – anterior peg of thoracic uncinus. B-H – from Knight-Jones P., Knight-Jones E.W. (1977). A – photo A.V. Rzhavsky.

Abdomen with about 25 chaetigers. Usually one, rarely two chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, lacking heel and with distinctly serrated tapering blade (Fig. 36G). Blade lengths of largest abdominal chaetae shorter than those of collar chaetae from convex body side. Companion capillary hooked chaetae not observed. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncini distribution fairly symmetrical on both sides of body. Largest tori in median-anterior part of abdomen.

Remarks. This is the first described spirorbin species. As Knight-Jones P. & Knight-Jones E.W. (1977) wrote, "it so typical of *Fucus* in north-west Europe that the brief description by Linnaeus (1758) must be regarded as adequate". Although the species name "*spirorbis*" has a priority, this name for a long time was synonymized with *Spirorbis borealis* Daudin, 1800. *Spirorbis nautiloides* Lamarck, 1801 is an accepted synonym of *S.* (*S.*) *spirorbis* (=*borealis*), but taxonomical position of some other proposed conspecifics (see McIntosh, 1923) remains uncertain.

This species was regarded as polymorphic until L'Hardy & Quievreux (1962), de Silva & Knight-Jones (1962) and Gee & Knight-Jones E.W., (1962) independently divided it into several, eventually five species (Knight-Jones P. & Knight-Jones E.W., 1977): *S.* (*S.*) *spirorbis, S.* (*S.*) *corallinae*, *S.* (*S.*) *inornatus*, *S.* (*S.*) *rupestris* and *S.* (*S.*) *tridentatus*. In addition, *Spirorbis* (*Spirorbis*) *cuneatus* Gee, 1964 not found in the Arctic also could have been earlier confused with *S.* (*S.*) *spirorbis.*

Whereas *S. (S.) spirorbis* is often reported as numerous and abundant without detailed descriptions, validity of those records is questionable. The information about the habitat and geographic location of these finds can provide significant guidance. First, the species range is restricted to the North Atlantic and Atlantic sector of the Arctic Ocean, therefore, all records from other regions (e.g., Hartman, 1961; 1966; 1969) are wrong. Second, the species is found almost exclusively intertidally on fuci, although some specimens may be attached to algae such as *Laminaria, Ascophyllum,* and *Sacchorhiza* and, as an exception, to stones under buttons of brown alga *Hirnanthalia*. Therefore, all records from sublittoral depths, as well as from any substrates, other than algae, are almost certainly also erroneous.

Unfortunately, there is another species, *S.* (*S.*) *inornatus,* that could live in the same habitats. Initially Knight-Jones P. & Knight-Jones (1977) suggested that *S.* (*S.*) *inornatus* occupies a narrow bathymetric range between the lower intertidal and the 2 m depth mark where abrasive sand is absent, and where it occupies various brown and red (not calcareous) algae*;* fuci is not characteristic substrate for *S.* (*S.*) *inornatus*, though in some locations it may replace *S.* (*S.*) *spirorbis* on fuci. Because *S.* (*S.*) *spirorbis* was considered very typical for intertidal fuci populations from North-East Atlantic, most records of "*spirorbis*" from this region as well as from North-West Atlantic and Arctic were attributed to this species without examination of the material (e.g., Rzhavsky, 1992a; 1992 [1994]; 2001). However, extensive material collected in 2011 intertidally from fuci in the Norway and Barents Sea (our data) and White Sea (photos by Kolbasova, pers. comm.) belonged to *S.* (*S.*) *inornatus*, while *S.* (*S.*) *spirorbis* was not found at all. Therefore, most data on the distribution and biology of *S.* (*S.*) *spirorbis* became doubtful and may belong to either of these two species.

Five of the six species from the ex -"*Spirorbis spirorbis*" complex are known from the Arctic. *S.* (*S.*) *spirorbis* differs from all of them in the abdominal notochaetae lacking a heel (Fig. 36G), while all other species have such a heel (e.g., Fig. 35G). Live *S.* (*S.*)

spirorbis is pale greenish-brown in colour, sometimes tinged with orange in the abdomen and thorax; green blood clearly visible in radioles and dorsal blood vessel. Live specimens of other species are coloured in different tints of orange and red (Pl. 2D, E) or partially uncoloured; their blood is not markedly pigmented or red.

S. (*S.*) *rupestris* that is almost identical to *S.* (*S.*) *spirorbis* in talon morphology (Fig. 35E, 36E), but differs from the latter in the absence of peripheral tube flange, often evoluted straight last whorl attached to the substrate (Fig. 35A, B), and the absence of a lateral flap formed by the collar dorso-convex margin (Fig. 35C). Besides, *S.* (*S.*) *rupestris* lives only on rocks and stones in association with calcareous alga *P. purpureum,* which often overgrows the spirorbin tubes, leaving only their mouths visible.

S. (*S.*) *inornatus* resembles S. (*S.*) *spirorbis* in having planospiral tubes with distinct peripheral flanges (Fig. 34A, 36A, B) and lateral flaps formed by collar's dorso-convex margin (Fig. 34B, 36C). Its adult talon is wider than long (Fig. 34D) and may be easily confused with a vestigial talon of *S.* (*S.*) *spirorbis* (Fig. 36E). Our data show that *S.* (*S.*) *inornatus* also often lives in the low intertidal zone on fuci. So, although live animals of the two species may be easily distinguished by their respective colouration, distinguishing preserved material might be difficult. In addition to morphology of abdominal notochaetae (see above), the species have different collar chaetae. In *S.* (*S.*) *spirorbis* modified collar chaetae (Fig. 36F) are with broad angular basal fins composed of large and medium sized teeth, and slender distal blades with very fine marginal serrations; they are similar in both collar fascicles, except that the gap between the fin and the blade is longer on the convex body side. In *S.* (*S.*) *inornatus* the blades of the collar chaetae (Fig. 34F, G) are broader relative to their lengths and basally more angular. Blade marginal serrations are much coarser on the chaetae from the convex body side, but equally fine on the concave side. Chaetae from the convex body side are almost twice as large as the chaetae from the concave side of the body.

S. (*S.*) *tridentatus* was for a long time considered as forma "*tridentatus*" of *S.* (*S.*) *spirorbis*, (e.g., Borg, 1917; Bergan, 1953b as "*borealis* forma *tridentatus*"). Adult tube of this species bears three distinct keels (Fig. 37A); has a massive talon tooth-shaped in side view, irregularly shaped with asymmetrical lateral bosses and rounded or terminally pointed in frontal view (Fig. 37C-E), collar chaetae morphology differs from that of *S. (S.) spirorbis* (see description). It lives on hard substrates only, never on fuci.

S. (*S.*) *corallinae* have small (rarely exceeding 1.5 mm in coil diameter when adult) and unsculptured planospiral tubes, in live animals orange body may be visible through the thin tube walls of initial tube coils; length of talon is approximately the same as width, its terminal edge bilobed in frontal view (Fig. 34D) in small specimens, but almost spatulate in the largest. Worms almost exclusively occupy calcareous alga *C. officinalis* and, as an exception, red algae of the genus *Chondrus,* but are never found on fuci.

The sixth species that could be a part of the ex-"*Spirorbis spirorbis*"-complex is *S.* (*S.*) *cuneatus* not reported from the Arctic and known only in the North Atlantic from Ireland and Scotland to the Mediterranean (Knight-Jones P. & Knight-Jones E.W., 1977). Its tube, although has a peripheral flange, usually bears three rounded keels; talon longer than wide, wedge-shaped in side view and often arrow-headed in frontal view.

Outside the Arctic Basin there are no *Spirorbis* species similar to *S.* (*S.*) *spirorbis*.

Ecology. Species is found almost exclusively intertidally on fuci. Sometimes *S.* (*S.*) *spirorbis* is found attached to algae such as *Laminaria, Ascophyllum,* and *Sacchorhiza*; as an exception, it is occasionally found on stones and under *Himanthalia* buttons. It may live in mixture with *C. armoricana*.

Biology of this species is well-studied, although data are often contradictory. Animals breed from May to October-November; overwintering specimens begin to reproduce after reaching 1.5 mm in coil diameter (Daly, 1978b). Most authors (Garbarini, 1933; 1936; Knight-Jones E.W., 1951; de Silva, 1967; Gee, 1967) suggested that synchrony and fortnightly periodicity in larval development and release are correlated with lunar tidal cycles. Daly (1978a) for population from Northumberland recorded a 20–23 day periodicity in breeding of *S.* (*S.*) *spirorbis* that does not suggest a correlation of breeding with tidal cycles. Bergan (1953a) did not find breeding synchrony at all in a population from Oslofjord, even though specimens from the same fuci thallus bred at the same time. Fecundity varies significantly, it does not correlate with worm size and somewhat decreases in autumn (Daly, 1978a). Facultative capability for self-fertilization is reported (Gee & Williams, 1963), but embryos resulting from self-fertilization develop longer and are less viable. Growth rates, larval behaviour and taxis were studied by some scientists (Knight-Jones E.W., 1951; 1953; Knight-Jones E.W. et. al., 1971; Gee, 1963; de Silva, 1967; Doyle, 1974). Polyanski (1950; 1951) studied response to temperature and other abiotic factors, but his species identification could be incorrect. Given our new data (see Remarks), it is not always clear which data belong indeed to *S.* (*S.*) *spirorbis*, part of it may be attributed to *S.* (*S.*) *inornatus*. Reported differences in species biology and ecology may also be simply a result of misidentification.

Distribution. Our Arctic material was collected from the White and Barents Seas. Although the species is suggested as common and aggregations of spirorbins on fuci in the Atlantic sector of Arctica are really abundant, the collection holdings are fragmental and need re-examination in view of our new data (see Remarks); the limits of the species distribution range in the Arctic need to be clarified. According to reliable literature data, the species is known from Iceland (Knight-Jones P. et al., 1991) and Norwegian Sea (Bergan, 1953b). In the North Atlantic it is certainly distributed around Britain, Ireland, west Sweden, and Brittany, France (Knight-Jones P. & Knight-Jones E.W., 1977). The report of this species from Nova Scotia, Canada (Doyle, 1974; Knight-Jones P. & Knight-Jones E.W., 1977) needs be checked.

Spirorbis (Spirorbis) tridentatus **Levinsen, 1884**

(Fig. 37A-G, Pl. 2B)

Spirorbis granulatus var. *tridentatus*: Levinsen, 1884, p. 209-210, tab. 3, fig. 9, 10.

Spirorbis granulatus **non** Linnaeus, 1767: McIntosh, 1923, p. 400-408.

Spirorbis (*Laeospira*) *borealis* var. *tridentatus*: Borg, 1917, p. 22-26, fig. 10-11; Bergan, 1953b, p. 33-35, fig. 1 b, e, f.

Spirorbis (*Laeospira*) *tridentatus*: L'Hardy & Quievreux, 1962, p. 2173, fig. 1, 6; 1964, p. 292; Gee & Knight-Jones E.W., 1962, p. 650-651.

Spirorbis tridentatus: Gee, 1964, p. 417; Toner, 1967, p. 325-326; Knight-Jones P. & Knight-Jones E.W., 1977, p. 464-466, fig. 4A-K; Aleksandrov, 1981, p. 89, tab. XIII, fig. 3; Rzhavsky, 1992a, p. 11; 1992[1994], p. 103, fig. 5; 2001, p. 605-606, text figures 1-5, map; Jakovis, 1997, p. 48-49, fig. 9a-e.

Spirorbis glossoeides: Harris T., 1968a, p. 593-595, 598, fig. 1 A-O (partim).

Spirorbis inaequalis: Harris T., 1968a, p. 595-598, fig. 2A-P.

Material examined. Table 1. # 548 (1); # 590 (many); # 595 (~ 20).

Description. Tube (Fig. 37A, B, Pl. 2B) sinistral, planospiral, thick-walled; peripheral flange always absent; coil diameter up to 3.5 mm; white opaque porcellaneous. Adult tubes with three distinct and massive keels ending in three projections at aperture (Fig. 37 A); juvenile tubes unsculptured (Fig. 37B). Last tube whorl tending to cover previous whorls and to widen rapidly towards aperture. Body of live animals mainly colourless, thorax and anterior part of abdomen may be tinged with orange; preserved specimens colourless or flesh-coloured.

Distal opercular plate slightly concave (Fig. 37C). Talon large and tooth-shaped in side view (Fig. 37C) and irregularly shaped with asymmetrical lateral bosses and rounded or pointed (usually in juveniles) distally in frontal view (Fig. 37C, D).

Collar and thoracic membranes with free dorsal margins, posterior edges of thoracic membranes reaching end of 3rd chaetiger forming apron. Collar only somewhat asymmetrical without a lateral flap on dorso-convex margin. Three thoracic chaetigers.

Large collar chaetae bent, modified fin-and-blade on convex side (Fig. 37F), but limbate (often with little groove in basal part of blades) on concave body side (Fig. 37G); fin finely serrated; blades finely serrated on both body sides. Capillary chaetae present in collar fascicle. Chaetae of 2nd and 3rd thoracic chaetigers limbate. Sickle (*Apomatus*) chaetae also present in 3rd fascicle.

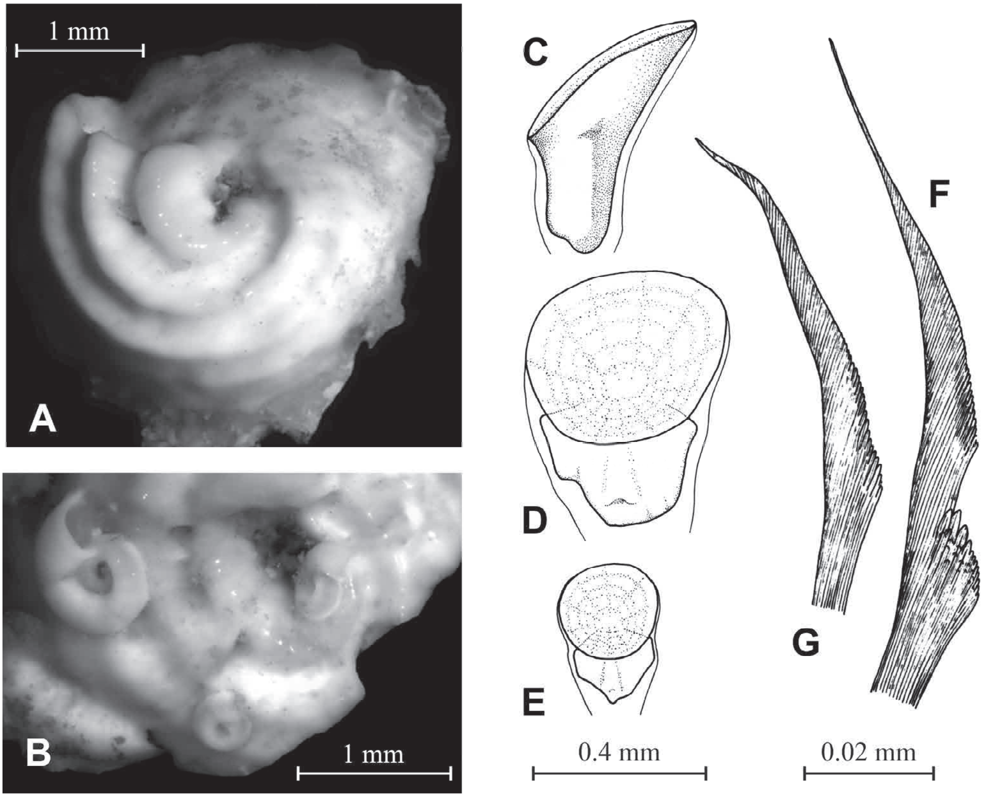

Figure 37. *Spirorbis* (*Spirorbis*) *tridentatus*. A – tube of adult; B – juveniles attached to an adult tube; C-D – operculum of adult (frontal and lateral view); E – operculum of juvenile, frontal view; F – modified collar chaeta, convex body side; G – limbate collar chaeta, concave body side. C-G – from Knight-Jones P., Knight-Jones E.W. (1977). A, B – photo A.V. Rzhavsky.

Two thoracic tori on each side of body (on chaetigers 2 and 3). Uncini rasp-shaped with 4-6 longitudinal rows of teeth throughout most length of uncinus and blunt or blunt gouged anterior pegs looking bifurcate when examined under a light microscope. Size of uncini in each torus significantly decreasing in direction away from notochaetae.

Abdomen with about 25 chaetigers. Usually one (rarely two) chaetae per fascicle throughout length of abdomen, flat geniculate, pennant-shaped, with small, but distinct heel and distinctly serrated tapering blade. Abdominal chaetae with blades as long as or longer than blades of collar chaetae from convex side of body. Companion capillary hooked chaetae not observed. Uncini rasp-shaped with blunt anterior pegs and numerous longitudinal rows of teeth, uncinal distribution fairly symmetrical on both sides of body. Largest tori in anterior part of abdomen.

Remarks. The species for a long time was considered as a variety "*S. borealis var. tridentatus*" distinct from *S. borealis* (*=spirorbis*) *sensu lato,* but there was some confusion with the assignment of "*tridentatus*" to the operculum brooding subspecies of "*Spirorbis granulatus*". The combination "*S. granulatus* var. *tridentatus*" was introduced by Levinsen (1884). Although "*granulatus*" was originally described by Linnaeus (1767), in the first adequate re-description (Caullery & Mesnil, 1897) the name was applied to an opercular-brooding species. The authors also stated that Levinsen's "var. *tridentatus*" from Greenland deposited in the Copenhagen Museum appeared to be S. *borealis* (= *spirorbis*). Later, under the name *S. granulatus* McIntosh (1923) described a common British spirorbin incubating its embryos in a characteristically ridged tube. He referred such tubes to Levinsen's "var. *tridentatus*" and suggested that *S. granulatus* of Caullery & Mesnil (1897) is yet another species. Some authors (e.g., Borg, 1917; Bergan, 1953b) considered "var. *tridentatus* Levinsen" an "ecological form" of a tube incubating "*S. borealis* (= "*spirorbis*"), whereas "*granulatus*" was assumed to be an operculum-incubating species. Thorson (1946) described "*granulatus*" as having tube incubation and suggested that the method of brood protection probably may vary. Finally a valid tube incubating species *Spirorbis tridentatus* Levinsen, 1884 was established by L'Hardy & Quievreux (1962). This confusion was discussed in details by de Silva & Knight-Jones E.W. (1962), Gee (1964) and Knight-Jones P. & Knight-Jones E.W. (1977).

Knight-Jones P. & Knight-Jones E.W. (1977) re-examined the type material of *S. inaequalis* and *S. glossoeides* described by Harris T. (1968a) and found that the former species is identical to *S.* (*S.*) *tridentatus*. Paratypes of the latter species described as dextral-coiled were typical juvenile sinistral *S.* (*S.*) *tridentatus* and the only dextral specimen belonged to *Janua heterostropha* (= *pagenstecheri*).

S. (*S.*) *tridentatus* is easily distinguished from all other Arctic *Spirorbis* spp. in many features. Their adult tube bears three distinct keels (Fig. 37A), while tubes of other species are unsculptured (e.g., Fig. 36A, B). Juveniles of *S.* (*S.*) *tridentatus* also have unsculptured tubes, but their last whorls tend to cover previous ones and to widen rapidly (not gradually) towards the aperture (Fig. 37B). Talon is large and tooth-shaped in side view and irregularly shaped with asymmetrical lateral bosses and rounded or pointed in frontal view (Fig. 37C-E) (not spatulate or vestigial (e.g., 34C-E, 36D, E)). Modified collar chaetae are fin-and-blade (Fig. 37F) on the convex body side only, but are limbate often with little grooves in the basal parts of the blades (Fig. 37G) on the concave body side (they are distinctly fin-and-blade on both body sides in other species). Among *Spirorbis* spp.*,* only *S.* (*S.*) *rupestris* also inhabit hard substrates, but it is usually associated with calcareous algae *P. purpureum* and distinctly differs morphologically as outlined above.

Some Arctic species of sinistral genus *Bushiella* (see below) also may bear three keels, but they are opercula-incubated and have other shapes of opercular talons.

Among *Spirorbis* species known only from outside the Arctic, *S.* (*S.*) *tridentatus* is somewhat similar to *S.* (*S.*) *cuneatus* distributed in the North Atlantic from Ireland and Scotland to the Mediterranean. The latter species also has tubes with three keels and large talons that are longer than wide. However, the talons of this species are arrow-headed in frontal view (not of irregular shape with asymmetrical lateral bosses); its collar chaetae fin-and-blade on both body sides and with coarsely serrated blades.

Ecology. Our Arctic material was collected in the low intertidal zone from stones, rocks, and gastropod shells. Generally, the species was found under stones and in rock crevices at depths of up to 30 m. Juveniles occasionally may be also found on algae. The animals live in mixture with *P.* (*P.*) *violacea, P.* (*S.*) *vitrea,* and *J. heterostropha*. Larvae have a short pelagic stage, are photonegative, geopositive, and under laboratory conditions may occasionally settle on alga (de Silva, 1958; 1962; Gee, 1963). De Silva (1967) studied growth rate of this species.

Distribution. In our Arctic material this species was found from the Barents and Norwegian Seas. It is reported also from the White Sea (Aleksandrov, 1981; Jakovis, 1997) and is common in the north-eastern Atlantic where it was reported from Norway (Bergan, 1953b), Sweden (Borg, 1917), Ireland (Toner, 1967), Britain (Gee & Knight-Jones E.W., 1962; Knight-Jones P. & Knight-Jones E.W., 1977), Brittany, France (L'Hardy & Quievreux, 1964), and north-western Spain (Rioja, 1923).

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	74°14'N, 19°20'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

22	“Andrei Pervozvannyj”	trawl 167, 168	1899	Barents	70º39'N, 44º53'E	no data	ZISP
23	“Andrei Pervozvannyj”	st. 221	20.06.1900	Barents	69º23'N, 33º04'E	35-59	ZISP
24	“Andrei Pervozvannyj”	st. 245	05.07.1900	Barents	70º39'N, 44º53'E	75	ZISP
25	“Andrei Pervozvannyj”	no data	07.07.1900	Barents	72°00'N, 48°10'E	95	ZISP
26	“Andrei Pervozvannyj”	no data	08.07.1900	Barents	Malyje Karmakuly, South Island, N.Z.	9-17.5	ZISP
27	“Andrei Pervozvannyj”	st. 262	15.07.1900	Barents	70º00'N, 33º32'E	171	ZISP
28	“Andrei Pervozvannyj”	330	10.09.1900	Barents	69°35'N, 33°23'E	240	ZISP
29	“Andrei Pervozvannyj”	trawl 363	1900	Barents	70°12'N, 31°50'E	303-310	ZISP
30	“Andrei Pervozvannyj”	dredge 625	1900	Barents	67°55'N, 47°25'E	53	ZISP
31	“Andrei Pervozvannyj”	no data	1900	Barents	no data	no data	ZISP
32	“Andrei Pervozvannyj”	no data	26.05.1901	Barents	69º23'N, 32º55'E	271*	ZISP
33	“Andrei Pervozvannyj”	dredge 705	03.06.1901	Barents	69°47'N, 30°57'E	127	ZISP
34	“Andrei Pervozvannyj”	trawl 957	12.06.1901	Barents	70°00'N, 34°06'E	218-246	ZISP
35	“Andrei Pervozvannyj”	dredge 909	1901	Barents	69°27'N, 32°23'E	9-31	ZISP
36	“Andrei Pervozvannyj”	trawl 853	1901	Barents	69°23'N, 32°47'E	27-104	ZISP
37	“Andrei Pervozvannyj”	no data	1901	Barents	no data	no data	ZISP
38	“Andrei Pervozvannyj”	no data	1906	Barents	no data	no data	ZISP
39	“Andrei Pervozvannyj”	no data	no data	Barents	Kazarinova Bay	9-17	ZISP
40	“Andromeda”	no data	no data	Barents	no data	no data	IEE
41	“Arctic”	no data	14.08.1933	Kara	Gulf Brandt, N.Z.	no data	ZISP
42	“Arctic”	no data	14 and 16.08.1933	Kara	Gulf Brandt, N.Z.	1.5-5	ZISP
43	“Arctic”	no data	31.08.1933	Kara	Tyulenij Bay, N.Z.	8-9	ZISP
44	“Arctic”	no data	04.09.1933	Kara	Chekina Bay, N.Z.	37-40	ZISP
45	“Arctic”	no data	06 and 14.09.1933	Kara	Chekina Bay, N.Z.	20	ZISP
46	“Arctic”	no data	09.09.1933	Kara	Tyulenij Bay, N.Z.	18	ZISP
47	“Arctic”	no data	04.06.1934	Kara	Gulf Brandt, N.Z.	24-30	ZISP
48	“Arctic”	st. 17	15.09.1934	Kara	Medvezhyj Bay, N.Z.	64-70	ZISP
49	“Arctic”	st. 4	1934	Kara	72º56'N, 56º00'E	12-19	ZISP
50	“Arctic”	no data	1934	Kara	Kankrin Bay, N.Z.	8-9	ZISP
51	“Arctic”	no data	1934	Barents or Kara	Novaya Zemlya	no data	ZISP
52	“Atlantida”	st. 1384	30.04.1972	Norwegian	70°22'N, 17°50'E	148	DHMSU
53	“Atlantida”	st. 1386	30.04.1972	Norwegian	70°12'N, 17°16'E	220	DHMSU
54	“Atlantida”	st. 1395	02.05.1972	Norwegian	69°41'N, 16°24'E	80	DHMSU
55	“Atlantida”	st. 1396	02.05.1972	Norwegian	69°40'N, 16°02'E	200	DHMSU

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
56	“Atlantida”	st. 1398	03.05.1972	Norwegian	69°00'N, 13°50'E	108	DHMSU
57	“Atlantida”	st. 1403	03.05.1972	Norwegian	68°15'N, 12°12'E	165	DHMSU
58	“Dalnie Zelentsy ”	st. 12	15.06.1993	Barents	72°30'N, 41°28'E	340	ZISP
59	“Dalnie Zelentsy ”	st. 29	13.08.1988	Barents	72°51’N, 51º54'E	no data	ZISP
60	“Delfin”	trawl 33	27.08.1920	Barents	no data	85	ZISP
61	“Derjugin”	st. 132	20.10.1957	Barents	68°55'N, 37°58'E	167	MMBI
62	“Derjugin”	st. 12	27.06.1958	Barents	72°30'N, 33°30'E	287	MMBI
63	“Derjugin”	st. 795	25.08.1959	Barents	70°16'N, 48°09'E	no data	MMBI
64	“Derjugin”	st. 809	05.09.1959	Barents	no data	no data	MMBI
65	“Derjugin”	st. 810	05.09.1959	Barents	70°47'N, 47°15'E	150	MMBI
66	“Derjugin”	st. 822	11.09.1959	Barents	71°06'N, 42°20'E	125-130	MMBI
67	“Derjugin”	st. 158	09.10.1959	Barents	70°07'N, 37°12'E	172	MMBI
68	“Diana”	st. 42	12.05.1953	Barents	69°12'N, 36°10’E	114	MMBI
69	“Diana”	st. 51	24.07.1953	Barents	68º32'N, 38º44’E	99	MMBI
70	“Diana”	st. A	13.08.1953	Barents	67º16'N, 35º01’E	126	MMBI
71	“Ermak”	3-5	05.06.1899	C. Arctic?	Spitsbergen	no data	ZISP
72	“Ermak”	st. 25	02.08.1899	C. Arctic	Spitsbergen	145	ZISP
73	“Ermak”	st. 82	03.08.1901	C. Arctic/Barents	80°26'N, 64°14'E	204	ZISP
74	“Krasin”	st. 25	23.08.1935	Chukchi	between Gerold & Wrangel Isls.	42	ZISP
75	“Krasin”	st. 59	18.09.1935	Chukchi	65º51'N, 169º14'W	48	ZISP
76	“Lieutenant Skuratov”	no data	14.08.1908	White	65°20'N, 34°36'E	no data	ZISP
77	“Lena”	st. 89	13.08.1948	Kara	77°58'N, 71°43'E	365	ZISP, IEE
78	“Lena”	st. 103	17.08.1948	Kara	75º56'N, 78º38’E	55	ZISP
79	“Lena”	st. 140	01.09.1948	Laptev	78º34'N, 105º34'E	140	ZISP
80	“Lena”	st. 156	03.09.1948	Laptev	77º35'N, 110º55'E	74	ZISP
81	“Lena”	st. 162	06.09.1948	Laptev	no data	44	ZISP
82	“Lena”	st. 164	06.09.1948	Laptev	76º27'N, 115º56'E	49	ZISP
83	“Lena”	st. 173	09.09.1948	Laptev	78º13'N, 106º00'E	170	ZISP
84	“Lena”	st. 175	09.09.1948	Laptev	78º17'N, 104º52'E	44.5	ZISP
85	“Lena”	no data	30.09.1948	Kara	80°26'N, 85°36'E	313	ZISP
86	“Lena”	st. 144	01.10.1948	Laptev	78°34'N, 10°09'E	364	ZISP
87	“Lena”	st. 190	04.10.1948	Kara	80º23'N, 78º36'E	114	ZISP
88	“Lena”	st. 192	05.10.1948	Kara	80°41'N, 78°37'E	32	ZISP
89	“Lena”	st. 18(2)	1957	Greenland	80°N, 10°E	550	ZISP
90	“Lena”	st. 1a	11.03.1958	Greenland	76°30'N, 15°02'E	608	ZISP
91	“Lena”	st. 7	14.03.1958	Greenland	76°30'N, 10°34'W	294	ZISP

92	“Lena”	st. 28	25.03.1958	Greenland	77°54'N, 5°59'W	388	ZISP
93	“Litke”	st. 37	18.07.1948	Barents	79°28'N, 57°21'E	170	ZISP
94	“Litke”	st. 73	08.08.1948	Barents	79°38'N, 60°45'E	124	ZISP
95	“Litke”	st. 75	10.08.1948	C. Arctic/Barents	79°58'N, 65°34'E	458	ZISP
96	“Litke”	st. 83	12.08.1948	Barents/Kara	79°04'N, 69°56'E	509	ZISP
97	“Litke”	st. 92	14.08.1948	Barents	77°26'N, 67°20'E	314	ZISP
98	“Litke”	st. 109	26.08.1948	Kara	77°52'N, 99°23'E	51	ZISP
99	“Litke”	st. 113	26.08.1948	Kara	78°32'N, 97°55'E	112	ZISP
100	“Litke”	st. 114	26.08.1948	Kara	78°43'N, 97°55'E	78	ZISP
101	“Litke”	st. 117	26.08.1948	Kara	78°35'N, 99°33'E	132	ZISP
102	“Litke”	st. 119	27.08.1948	Kara/Laptev	78°49'N, 100°30'E	257	ZISP
103	“Litke”	st. 127	27.08.1948	Laptev	79°35'N, 101°17'E	252	ZISP
104	“Litke”	st. 129	28.08.1948	C. Arctic	80°04'N, 99°48'E	121	ZISP
105	“Litke”	st. 132	29.08.1948	C. Arctic/Laptev	79°55'N, 103°32'E	348	ZISP
106	“Litke”	st. 145	29.08.1948	Laptev	78°31'N, 113°03'E	1367	ZISP
107	“Litke”	st. 133	30.08.1948	C. Arctic/Laptev	79°45'N, 104°52'E	432	ZISP
108	“Litke”	st. 137	30.08.1948	C. Arctic/Laptev	79°26'N, 107°48'E	1073	ZISP
109	“Litke”	st. 135	30.08.1948	C. Arctic/Laptev	79°28'N, 103°20'E	116	ZISP
110	“Litke”	st. 136	30.08.1948	C. Arctic/Laptev	79°28'N, 105°12'E	120	ZISP
111	“Litke”	st. 138	31.08.1948	C. Arctic/Laptev	79°02'N, 107°01'E	371	ZISP
112	“Litke”	st. 139	31.08.1948	Laptev	78°39'N, 106°06'E	226	ZISP
113	“Litke”	st. 144	01.09.1948	C. Arctic	78°34'N, 110°09'E	96	ZISP
114	“Litke”	st. 175	09.09.1948	Laptev	78°17'N, 104°52'E	44	ZISP
115	“Litke”	st. 185	30.09.1948	Kara	80°26'N, 85°36'E	313	ZISP
116	“Litke”	st. 189	03.10.1948	C. Arctic/Barents	80°14'N, 80°12'E	64	ZISP
117	“Litke”	st. 195	05.10.1948	Kara	no data	580	ZISP
118	“Litke”	st. 9	14.09.1955	C. Arctic	82°20'N, 47°17'E	384	ZISP
119	“Litke”	st. 11	14.09.1955	C. Arctic	82°23'N, 54°14'E	318	ZISP
120	“Litke”	st. 12	14.09.1955	C. Arctic	82°24'N, 58°25'E	276	ZISP
121	“Litke”	st. 13	15.09.1955	C. Arctic	82°11'N, 60°57'E	323	ZISP
122	“Litke”	st. 26	18.09.1955	C. Arctic	82°00'N, 42°00'E	415	ZISP
123	“Litke”	st. 41	06.10.1955	C. Arctic	82°02'N, 34°58'E	1747	ZISP
124	“Lomonosov”	st. 12	1931	Kara	78°08'N, 73°47'E	426	ZISP,IEE
125	“Maslov”	st. 183	29.11.1968	Barents	70°45'N, 33°30'E	260	DHMSU
126	“Maslov”	st. 186	29.11.1968	Barents	70°00'N, 33°30'E	190	DHMSU
127	“Maslov”	st. 187	29.11.1968	Barents	69°45'N, 33°30'E	240	DHMSU
128	“Maslov”	st. 169	16.08.1969	Barents	71°00'N, 22°15'E	260	DHMSU

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
129	“Maslov”	st. 170	16.08.1969	Norwegian	70°40'N, 19°45'E	175	DHMSU
130	“Maslov”	st. 171	17.08.1969	Norwegian	70°40'N, 19°00'E	300	DHMSU
131	“Maslov”	st. 172	17.08.1969	Norwegian	70°30'N, 18°30'E	180	DHMSU
132	“Maslov”	st. 173	17.08.1969	Norwegian	70°01'N, 17°20'E	100	DHMSU
133	“Maslov”	st. 175	17.08.1969	Norwegian	69°40'N, 16°30'E	75	DHMSU
134	“Maslov”	st. 177	18.08.1969	Norwegian	69°42'N, 16°10'E	715	DHMSU
135	“Maslov”	st. 178	18.08.1969	Norwegian	69°50'N, 16°30'E	270	DHMSU
136	“Maslov”	st. 179	18.08.1969	Norwegian	70°13'N, 17°04'E	560	DHMSU
137	“Maslov”	st. 180	19.08.1969	Norwegian	70°40'N, 17°27'E	510	DHMSU
138	“Maslov”	st. 182	19.08.1969	Norwegian	71°30'N, 16°46'E	300	DHMSU
139	“Maslov”	st. 183	19.08.1969	Norwegian	72°02'N, 17°02'E	360	DHMSU
140	“Maslov”	st. 184	20.08.1969	Norwegian	72°28'N, 17°00'E	370	DHMSU
141	“Maslov”	st. 189	20.08.1969	Norwegian	73°30'N, 15°30'E	500	DHMSU
142	“Maslov”	st. 187	20.08.1969	Norwegian/ Barents	73°20'N, 17°00'E	500	DHMSU
143	“Maslov”	st. 189	21.08.1969	Norwegian	73°40'N, 16°15'E	440	DHMSU
144	“Maslov”	st. 193	21.08.1969	Norwegian/ Barents	74°10'N, 18°00'E	160	DHMSU
145	“Maslov”	st. 198	22.08.1969	Norwegian	74°34'N, 16°00'E	525	DHMSU
146	“Maslov”	st. 203	23.08.1969	Barents	74°00'N, 21°30'E	290	DHMSU
147	“Maslov”	st. 200	23.08.1969	Barents	74°50'N, 17°30'E	230	DHMSU
148	“Maslov”	st. 208	25.08.1969	Barents	72°30'N, 19°00'E	365	DHMSU
149	“Maslov”	st. 209	25.08.1969	Barents	72°00'N, 19°00'E	320	DHMSU
150	“Maslov”	st. 210	25.08.1969	Barents	71°00'N, 19°00'E	190-210	DHMSU
151	“Maslov”	st. 212	25.08.1969	Barents	71°01'N, 21°30'E	155	DHMSU
152	“Maslov”	st. 213	26.08.1969	Barents	71°30'N, 21°30'E	325	DHMSU
153	“Maslov”	st. 215	26.08.1969	Barents	72°30'N, 21°30'E	350	DHMSU
154	“Maslov”	st. 221	27.08.1969	Barents	74°14'N, 23°28'E	265	DHMSU
155	“Maslov”	st. 225	28.08.1969	Barents	72°26'N, 25°30'E	110	DHMSU
156	“Maslov”	st. 229	29.08.1969	Barents	77°10’N, 25°30'E	no data	DHMSU
157	“Maslov”	st. 232	29.08.1969	Barents	76°40'N, 25°47'E	30	DHMSU
158	“Maslov”	st. 234	30.08.1969	Barents	76°26'N, 25°30'E	110	DHMSU
159	“Maslov”	st. 237	30.08.1969	Barents	74°30'N, 25°30'E	300	DHMSU
160	“Maslov”	st. 239	31.08.1969	Barents	75°00'N, 27°30'E	310	DHMSU
161	“Maslov”	st. 269	07.09.1969	Barents	75°11'N, 15°56'E	250	DHMSU
162	“Maslov”	st. 270	07.09.1969	Barents/ Greenland	75°10'N, 15°18'E	310	DHMSU
163	“Maslov”	st. 271	08.09.1969	Greenland	78°00'N, 10°00'E	160	DHMSU

164	“Maslov”	st. 279	09.09.1969	Greenland	77°38’N, 11°10’E	300	DHMSU
165	“Maslov”	st. 280	09.09.1969	Greenland	77°25’N, 11°30’E	230	DHMSU
166	“Maslov”	st. 282	10.09.1969	Greenland	77°36’N, 12°49’E	70	DHMSU
167	“Maslov”	st. 283	10.09.1969	Greenland	76°57’N, 12°50’E	215	DHMSU
168	“Maslov”	st. 284	10.06.1969	Greenland	77°03’N, 13°24’ E	420	ZISP
169	“Maslov”	st. 285	11.09.1969	Greenland	77°04’N, 13°30’E	300	DHMSU
170	“Maslov”	st. 286	11.09.1969	Greenland	77°07’N, 13°37’E	200	DHMSU
171	“Maslov”	st. 288	11.09.1969	Greenland	77°10’N, 14°10’E	55	DHMSU
172	“Maslov”	st. 295	12.09.1969	Barents/ Greenland	76°08’N, 16°00’E	290	DHMSU
173	“Maslov”	st. 299	13.09.1969	Barents	75°45’N, 17°33E	210	DHMSU
174	“Maslov”	st. 306	16.09.1969	Barents	75°30’N, 16°30’E	210	DHMSU
175	“Maslov”	st. 311	16.09.1969	Barents/ Greenland	76°01’N, 15°00’E	350	DHMSU
176	“Maslov”	st. 312	17.09.1969	Greenland	76°12’N, 15°00’E	505	DHMSU
177	“Maslov”	st. 313	17.09.1969	Greenland	76°20’N, 15°00’E	240	DHMSU
178	“Maslov”	st. 329	24.09.1969	Barents	78°30’N, 50°00’E	230	DHMSU
179	“Maslov”	st. 334	25.09.1969	Barents	77°10’N, 50°00’E	335	DHMSU
180	“Maslov”	st. 396	09.10.1969	Barents	78°00’N, 33°30’E	165	DHMSU
181	“Maslov”	st. 10/14	12.08.1970	Kara	67°45’N, 47°04’E	46	DHMSU
182	“Maslov”	st. 350	16.08.1970	Barents	69°29’N, 59°35’E	23	DHMSU
183	“Maslov”	st. 100/42	16.08.1970	Kara	69°50’N, 57°15’E	47	DHMSU
184	“Molchanov”	st. 801	no data	Barents	68°51’N, 37°20’E	96	DHMSU
185	“Molchanov”	st. 9105	18.04.1986	Barents	70°24’N, 04°31’E	80	IEE
186	“Murman”	st. 16	30.05.1898	Barents	Volokova Inlet, Kola Bay	220	ZISP
187	“Ob’”	st. 1	16.08.1956	Greenland	78°05’N, 09°48’E	214	ZISP
188	“Ob’”	st. 9	19.08.1956	Greenland	78°04’N, 08°34’W	207	ZISP
189	“Ob’”	st. 11	1956	Greenland	78°01’N, 13°07’W	136	ZISP, IEE
190	“Ob’”	st. 13	20.08.1956	Greenland	77°58’N, 17°43’W	368	ZISP
191	“Ob’”	st. 14	22.08.1956	Greenland	78°34’N, 15°34’W	56	ZISP
192	“Ob’”	st. 15	1956	Greenland	78°15’N, 15°51’W	165	ZISP
193	“Ob’”	st. 17	23.08.1956	Greenland	79°31’N, 13°31’W	212	ZISP
194	“Ob’”	st. 40	30.08.1956	Greenland	79°56’N, 05°17’W	1135	ZISP
195	“Onega”	st. 76(2)	24.08.1961	White	no data	no data	ZISP
196	“Onega”	st. 77/1	24.08.1961	White	no data	no data	ZISP
197	“Onega”	st. 6	06.10.1962	White	no data	42	ZISP
198	“Onega”	st. 12	08.10.1962	White	no data	28,5	ZISP

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
199	“Onega”	st. 12/330	25.06.1964	White	no data	8-10	ZISP
200	“Onega”	st. 1/343	06.07.1964	White	no data	7	ZISP
201	“Onega”	data incomplete	06-12.07.1964	White	Levaja Bay of Chupa Inlet, Kandalaksha Gulf	2-8	ZISP
202	“Onega”	st. 4/346	09.07.1964	White	no data	7-8	ZISP
203	“Onega”	st. 7/351	12.07.1964	White	Levaja Bay of Chupa Inlet, Kandalaksha Gulf	no data	ZISP
204	“Onega”	no data	24.10.1964	White	no data	no data	ZISP
205	“Pahtusov”	st. 6	19.07.1909	Barents	69°20'N, 33°32'E	280	ZISP
206	“Pahtusov”	st. 11	17.08.1909	Barents	69°34'N, 32°12'E	70	ZISP
207	“Polarstern”	st. 3-42I GKG	17.09.1991	C. Arctic	85°25' N, 12°07' E	1350	SNHM
208	“Polarstern”	st. 3-45II GKG	18.09.1991	C. Arctic	85° 06' N, 14° 25' E	1350	SNHM
209	“Pomor”	trawl 41	28.06.1898	Barents	69°18'N, 33°42'E	72	ZISP
210	“Pomor”	st. 11	24.09.1992	C. Arctic	Scott-Keltie Isl., F.J.L.	4-5	ZISP
211	“Pomor”	st. 12	24.08.1992	C. Arctic	80°22'N, 52°17'E	73	ZISP
212	“Pomor”	st. 13	24.08.1992	C. Arctic	80°25'N, 52°34'E	101	ZISP
213	“Pomor”	st. 30	28.08.1992	C. Arctic	Kuhn Isl., F.J.L.	10	ZISP
214	“Pomor”	st. 31	29.08.1992	C. Arctic	Kuhn Isl., F.J.L.	25-40	ZISP
215	“Pomor”	st. 36	29.08.1992	C. Arctic	Stoliczka Isl., F.J.L.	9	ZISP
216	“Professor Mesjatsev”	st. 823(1)	16.10.1961	White	Onega Bay	no data	ZISP
217	“Professor Mesjatsev”	st. 831	21.10.1961	White	no data	10	ZISP
218	“Professor Mesjatsev”	st. 973	12.08.1962	White	no data	38-39	ZISP
219	“Professor Mesjatsev”	st. 980(II)	13.08.1962	White	no data	32-35	ZISP
220	“Professor Mesjatsev”	st. 1143/11	14.09.1963	White	no data	no data	ZISP
221	“Professor Mesjatsev”	st. 1168/1	16.08.1964	White	no data	38-39	ZISP
222	“Rusanov”	no data	07.08.1931	Kara	74°35'N, 75°26'E	32	ZISP
223	“Rusanov”	no data	15.08.1931	Kara	79°27'N, 76°40'E	34	ZISP
224	“Rusanov”	st. 21	20.08.1931	Kara	70°23'N, 64°00'E	158	ZISP
225	“Rusanov”	st. 52(22)	25.08.1931	Kara	79°24'N, 91°13'E	24	ZISP
226	“Rusanov”	no data	29.08.1931	Barents	Varneka Bay, Vaygach Isl.	7	ZISP
227	“Rusanov”	st. 43	20.09.1931	Kara	69°46'N, 60°35'E	20	ZISP
228	“Rusanov”	no data	1931	Kara	Dikson Isl.	no data	ZISP
229	“Rusanov”	no data	1933	Kara	no data	no data	ZISP
230	“Sadko”	no data	29.07.1929	C. Arctic	F.J.L.	23,5	ZISP

231	“Sadko”	no data	06.08.1929	C. Arctic	Tihaja Bay, Hooker Isl., F.J.L.	7	ZISP
232	“Sadko”	no data	09.09.1929	Barents	73°77' N, 53° 00'E	145	ZISP
233	“Sadko”	no data	16.07.1930	C. Arctic	Tihaja Bay, Hooker Isl., F.J.L.	5	ZISP
234	“Sadko”	st. 53(23)	25.08.1930	C. Arctic	79°24'N, 91°13'E	24	ZISP
235	“Sadko”	st. 1/12	17.07.1935	Greenland	76°18'N, 16°24'E	99-136	ZISP
236	“Sadko”	st. 6/24	21.07.1935	Greenland	78°04'N, 03°51'E	2460	ZISP
237	“Sadko”	st. 7/26	22.07.1935	Greenland	78°02'N, 09°12'E	820	ZISP
238	“Sadko”	st. 8/28	30.07.1935	Greenland	78°08'N, 09°40'E	225	ZISP
239	“Sadko”	st. 9/30	31.07.1935	Greenland	78°37'N, 03°52'E	2300	ZISP
240	“Sadko”	st. 10/2	01.08.1935	Greenland	80°02'N, 08°19'E	2380	ZISP
241	“Sadko”	st. 11/34	01.08.1935	Greenland	80°02'N, 09°17'E	500	ZISP
242	“Sadko”	st. 15/47	07.08.1935	Barents	80º10'N, 29º12'E	340	ZISP
243	“Sadko”	st. 16/49	08.08.1935	Barents	80°19'N, 34°34'E	115	ZISP
244	“Sadko”	st. 18/50	08.08.1935	Barents	80°46' N, 29°57'E	445	ZISP
245	“Sadko”	st. 20/52	12.08.1935	C. Arctic	81°09'N, 26°40'E	160	ZISP
256	“Sadko”	22/53	15.08.1935	Greenland	81°10'N, 30°01'E	157	ZISP
247	“Sadko”	st. 24/55	16.08.1935	Barents	between F.J.L. & N.Z.	280	ZISP
248	“Sadko”	st. 29/64	25.08.1935	Kara	78°33'N, 73°21'E	410	ZISP
249	“Sadko”	st. 31/66	26.08.1935	Kara	79º12'N, 76º08’’E	153	ZISP
250	“Sadko”	st. 32/68	26.08.1935	Kara	80°19'N, 72°47'E	360	ZISP
251	“Sadko”	st. 35/71	28.08.1935	C. Arctic/Kara	81°11'N, 66°53'E	520	ZISP
252	“Sadko”	st. 40/74	30.08.1935	Kara	80°45'N, 69°46'E	560	ZISP
253	“Sadko”	st. 39/73	30.08.1935	Kara	80°44'N, 68°08'E	542	ZISP
254	“Sadko”	st. 43/77	01.09.1935	Kara	81°35'N, 75°57'E	225	ZISP
255	“Sadko”	no data	02.09.1935	Kara	81º35'N, 75º57’’E	74	ZISP
256	“Sadko”	st. 44	02.09.1935	Kara	80°38'N, 80°26'E	74	ZISP, IEE
257	“Sadko”	st. 47/82	05.09.1935	Kara	81°11'N, 75°20'E	124	ZISP
258	“Sadko”	st. 49/84	06.09.1935	Kara	79°57'N, 79°11'E	140	ZISP
259	“Sadko”	st. 50/87	07.09.1935	Kara	79°47'N, 84°32'E	200	ZISP
260	“Sadko”	st. 51/88	07.09.1935	Kara	80°11'N, 86°24'E	250	ZISP
261	“Sadko”	st. 52/91	08.09.1935	Kara	80°27'N, 88°15'E	279	ZISP
262	“Sadko”	st. 53/92	08.09.1935	Kara	80°30'N, 85°09'E	297	ZISP
263	“Sadko”	st. 55/95	09.09.1935	Kara	81°32'N, 83°06'E	300	ZISP
264	“Sadko”	st. 59/99	13.09.1935	Kara	82°42'N, 87°03'E	2365	ZISP
265	“Sadko”	st. 61/102	14.09.1935	Kara	80°21'N, 81°19'E	115	ZISP
266	“Sadko”	st. 62/108	15.09.1935	Kara	80°33'N, 77°48'E	105	ZISP

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
267	“Sadko”	st. 63/104	16.09.1935	Kara	70°57'N, 65°21'E	283	ZISP
268	“Sadko”	st. 9	09.09.1936	Kara	80°58'N, 73°32’E	444	ZISP
269	“Sadko”	no data	19.09.1936	C. Arctic	81º05'N, 53º54'E	225	ZISP
270	“Sadko”	st. 20	19.09.1936	C. Arctic	80º10'N, 58º04'E	31	ZISP
271	“Sadko”	st. 24	25.09.1936	Barents	78°27'N, 39°01'E	142	ZISP
272	“Sadko”	st. 2	11.08.1937	Kara	77°16'N, 96°54'E	75	ZISP
273	“Sadko”	st. 4	13.08.1937	Kara	77°43'N, 102°58'E	40	ZISP
274	“Sadko”	st. 5	13.08.1937	Kara	77°50'N, 104°07'E	203	ZISP
275	“Sadko”	st. 10	16.08.1937	Laptev	77°25'N, 118,17' E	869	ZISP
276	“Sadko”	st. 18	16.09.1939	C. Arctic	81°05'N, 53°32'E	422	ZISP
277	“Sadko”	st. 32	21.08.1937	E. Siberian	74°07'N, 156°37' E	20-40	ZISP
278	“Sadko”	st. 89	20.01.1938	C. Arctic	78°05'N, 149°36'E	58	ZISP
279	“Sadko”	st. 92	01.04.1938	E. Siberian	79°05'N, 151°45'E	81	ZISP
280	“Sadko”	st. 93	12.04.1938	E. Siberian	79°3'0N, 150°10'E	89-91	ZISP
281	“Sadko”	st. 94	16.04.1938	C. Arctic	79°38'N, 150°00'E	153-162	ZISP
282	“Sadko”	st. 99	14-19.06.1938	C. Arctic	81°15'N, 140°35'E	1630-1900	ZISP
283	“Sadko”	st. 129	24.08.1938	E. Siberian	77°07'N, 151°33'E	38	ZISP
284	“Sadko”	st. 18	16.09.1939	C. Arctic	81°05'N, 53°32' E	422	ZISP
285	“Sedov”	st. 44/14	12.08.1930	Kara	78°58'N, 68°25'E	350	ZISP
286	“Sedov”	st. 44/19	19.08.1930	Kara	78°55'N, 79°15'E	148	ZISP
287	“Sedov”	st. 57/21	20.08.1930	Kara	77°53'N, 79°45'E	102	ZISP
288	“Sedov”	st. 57/27	31.08.1930	Kara	79°55'N, 88°58'E	185	ZISP
289	“Sedov”	st. 58/28	31.08.1930	Kara	80°26'N, 88°57'E	170	ZISP
290	“Sedov”	st. 59/29	31.08.1930	Kara	80°47'N, 89°50'E	52	ZISP
291	“Sedov”	st. 60/30	01.09.1930	Kara	79°00'N, 87°07'E	180	ZISP
292	“Sedov”	st. 61/31	02.09.1930	Kara	78°33'N, 86°20'E	119	ZISP
293	“Sedov”	st. 62/32	02.09.1930	Kara	78°02'N, 86°30'E	108	ZISP
294	“Sedov”	st. 68/38	04.10.1930	Kara	76°36'N, 74°48'E	157	ZISP
295	“Sevastopol”	st. 1046	09.07.1957	Norwegian	67°30'N, 11°26'E	115	DHMSU
296	“Sevastopol”	st. 1047	09.07.1957	Norwegian	65°45'N, 10°20'E	333	DHMSU
297	“Sevastopol”	st. 1049	09.07.1957	Norwegian	65°40'N, 08°30'E	405	DHMSU
298	“Sevastopol”	st. 1050	09.07.1957	Norwegian	65°45'N, 07°29'E	360	DHMSU
299	“Sevastopol”	st. 1052	10.07.1957	Norwegian	65°46'N, 05°58'E	435	DHMSU
300	“Sevastopol”	st. 1056	12.07.1957	Norwegian	65°47'N, 02°32'E	1590	DHMSU
301	“Sevastopol”	st. 1073	14.07.1957	Norwegian	65°27'N, 12°39'W	135	DHMSU
302	“Sevastopol”	st. 1076	15.07.1957	Norwegian	64°08'N, 14°00'W	110	DHMSU

303	“Sevastopol”	st. 1078	15.07.1957	Norwegian	63°55’N, 13°03’W	650	DHMSU
304	“Sevastopol”	st. 1081	15.07.1957	Norwegian	63°37’N, 11°37’W	385	DHMSU
305	“Sevastopol”	st. 1083	15.07.1957	Norwegian	63°20’N, 10°47’W	395	DHMSU
306	“Sevastopol”	st. 1088	16.07.1957	Norwegian	62°40’N, 08°18’W	485	DHMSU
307	“Sevastopol”	st. 1089	16.07.1957	Norwegian	62°30’N, 07°48’W	150	DHMSU
308	“Sevastopol”	st. 1090	16.07.1957	Norwegian	62°30’N, 07°10’W	90	DHMSU
309	“Sevastopol”	st. 1094	17.07.1957	Norwegian	61°42’N, 04°50’W	235	DHMSU
310	“Sevastopol”	st. 1102	18.07.1957	Norwegian	60°35’N, 0°36’W	135	DHMSU
311	“Sevastopol”	st. 1099	18.07.1957	Norwegian	61°08’N, 02°13’W	520	DHMSU
312	“Sevastopol”	st. 1100	18.07.1957	Norwegian	61°10’N, 01°36’W	140	DHMSU
313	“Sevastopol”	st. 1103	18.07.1957	Norwegian	60°35’N, 0°00’E	105	DHMSU
314	“Sevastopol”	st. 1104	18.07.1957	Norwegian	60°35’N, 0°45’E	130	DHMSU
315	“Sevastopol”	st. 1105	19.07.1957	Norwegian	60°35’N, 01°21’E	130	DHMSU
316	“Sevastopol”	st. 1108	19.07.1957	Norwegian	60°35’N, 03°27’E	295	DHMSU
317	“Sevastopol”	st. 1110	19.07.1957	Norwegian	60°36’N, 04°35’E	340	DHMSU
318	“Sevastopol”	st. 1123	22.07.1957	Norwegian	63°01’N, 03°41’W	2386	DHMSU
319	“Sevastopol”	st. 1130	23.07.1957	Norwegian	63°02’N, 09°18’W	500	DHMSU
320	“Sevastopol”	st. 1132	24.07.1957	Norwegian	62°39’N, 07°47’W	375	DHMSU
321	“Sevastopol”	st. 1157	31.07.1957	Greenland	64°56’N, 24°25’W	155	DHMSU
322	“Sevastopol”	st. 1160	31.07.1957	Greenland	65°15’N, 26°41’W	180	DHMSU
323	“Sevastopol”	st. 1161	31.07.1957	Greenland	65°23’N, 27°17’W	370	DHMSU
324	“Sevastopol”	st. 1162	31.07.1957	Greenland	65°28’N, 27°47’W	775	DHMSU
325	“Sevastopol”	st. 1163	01.08.1957	Greenland	65°37’N, 28°35’W	1035	DHMSU
326	“Sevastopol”	st. 1165	01.08.1957	Greenland	65°52’N, 29°39’W	300	DHMSU
327	“Sevastopol”	st. 1167	01.08.1957	Greenland	66°08’N, 30°56’W	438	DHMSU
328	“Sevastopol”	st. 1168	01.08.1957	Greenland	66°16’N, 31°35’W	345	DHMSU
329	“Sevastopol”	st. 1169	01.08.1957	Greenland	66°23’N, 32°14’W	330	DHMSU
330	“Sevastopol”	st. 1170	01.08.1957	Greenland	66°29’N, 32°55’W	300	DHMSU
331	“Sevastopol”	st. 1170	01.08.1957	Greenland	66°29’N, 32°55’W	300	ZMMGU
332	“Sevastopol”	st. 1172	02.08.1957	Greenland	65°28’N, 33°53’W	212	DHMSU
333	“Sevastopol”	st. 1212	07.08.1957	Greenland	67°39’N, 22°36’W	650	DHMSU
334	“Sevastopol”	st. 1235	10.08.1957	Greenland	70°04’N, 12°50’W	1690	DHMSU
335	“Sevastopol”	st. 1352	25.03.1958	Norwegian	65°18’N, 10°29’E	198	DHMSU
336	“Sevastopol”	st. 1357	25.03.1958	Norwegian	66°16’N, 06°46’E	342	DHMSU
337	“Sevastopol”	st. 1374	29.03.1958	Greenland/ Norwegian	70°05’N, 10°00’W	1820	DHMSU
338	“Sevastopol”	st. 1378	30.03.1958	Greenland	68°54’N, 15°33’W	1520	DHMSU

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339	“Sevastopol”	st. 1403	05.04.1958	Norwegian	63°26'N, 06°42'E	265	DHMSU
340	“Sevastopol”	st. 1411	06.04.1958	Norwegian	61°50'N, 01°45'E	185	DHMSU
341	“Sevastopol”	st. 1427	09.04.1958	Norwegian	64°45'N, 12°31'W	157	DHMSU
342	“Sevastopol”	st. 1428	09.04.1958	Norwegian	64°22'N, 13°29'W	160	DHMSU
343	“Sevastopol”	st. 1443	11.04.1958	Norwegian	62°30'N, 07°12'W	94	DHMSU
344	“Sevastopol”	st. 1446	11.04.1958	Norwegian	62°44'N, 06°24'W	350	DHMSU
345	“Sevastopol”	st. 1453	16.04.1958	Norwegian	62°00'N, 06°14'W	112	DHMSU
346	“Sevastopol”	st. 1462	17.04.1958	Norwegian	61°01'N, 01°38'W	175	DHMSU
347	“Sevastopol”	st. 1463	17.04.1958	Norwegian	60°56'N, 0°59'W	115	DHMSU
348	“Sevastopol”	st. 1464	17.04.1958	Norwegian	60°34'N, 0°36'W	145	DHMSU
349	“Sevastopol”	st. 1465	17.04.1958	Norwegian	60°35'N, 0°01'W	110	DHMSU
350	“Sevastopol”	st. 1466	18.04.1958	Norwegian	60°35'N, 0°47'E	128	DHMSU
351	“Sevastopol”	st. 1467	18.04.1958	Norwegian	60°35'N, 01°23E	140	DHMSU
352	“Sevastopol”	st. 1468	18.04.1958	Norwegian	60°35'N, 02°05'E	127	DHMSU
353	“Sevastopol”	st. 1469	18.04.1958	Norwegian	60°36'N, 02°52'E	107	DHMSU
354	“Sevastopol”	st. 1470	18.04.1958	Norwegian	60°36'N, 03°31'E	312	DHMSU
355	“Sevastopol”	st. 1471	18.04.1958	Norwegian	60°36'N, 04°12'E	302	DHMSU
356	“Sevastopol”	st. 1472	19.04.1958	Norwegian	60°36'N, 04°36'E	372	DHMSU
357	“Sevastopol”	st. 1485	27.04.1958	Barents	71°16'N, 25°36'E	315	DHMSU
358	“Sevastopol”	st. 1486	27.04.1958	Barents	71°33'N, 25°00'E	300	DHMSU
359	“Sevastopol”	st. 1488	28.04.1958	Barents	72°29'N, 23°07'E	335	DHMSU
360	“Sevastopol”	st. 1494	29.04.1958	Barents	74°16'N, 19°09'E	55	DHMSU
361	“Sevastopol”	st. 1555	20.06.1958	Norwegian	62°58'N, 09°01'W	420	DHMSU
362	“Sevastopol”	st. 1574	25.06.1958	Greenland	63°10'N, 23°48'W	390	DHMSU
363	“Sevastopol”	st. 1576	25.06.1958	Greenland	62°40'N, 24°55'W	560	DHMSU
364	“Sevastopol”	st. 1583	27.06.1958	Greenland	63°12'N, 24°30'W	262	DHMSU
365	“Sevastopol”	st. 1584	27.06.1958	Greenland	63°20'N, 25°18'W	320	DHMSU
366	“Sevastopol”	st. 1586	27.06.1958	Greenland	64°10'N, 24°42'W	210	DHMSU
367	“Sevastopol”	st. 1591	28.06.1958	Greenland	66°19'N, 23°54'W	125	DHMSU
368	“Sevastopol”	st. 1609	01.07.1958	Greenland	66°52'N, 29°58'W	425	DHMSU
369	“Sevastopol”	st. 1615	03.07.1958	Greenland	65°48'N, 26°47'W	490	DHMSU
370	“Sevastopol”	st. 1616	03.07.1958	Greenland	65°35'N, 27°10'W	425	DHMSU
371	“Sevastopol”	st. 1644	16.07.1958	Greenland	63°35'N, 37°33'W	230	DHMSU
372	“Sevastopol”	st. 1649	17.07.1958	Greenland	62°36'N, 40°32'W	245	DHMSU
373	“Sevastopol”	st. 1652	18.07.1958	Greenland	62°27'N, 40°20'W	300	DHMSU
374	“Sevastopol”	st. 1655	18.07.1958	Greenland	62°13'N, 40°30'W	430	DHMSU

375	“Sevastopol”	st. 1657	19.07.1958	Greenland	62°07'N, 40°53'W	184	DHMSU
376	“Sevastopol”	st. 1659	19.07.1958	Greenland	61°50'N, 40°54'W	240	DHMSU
377	“Sevastopol”	st. 1662	20.07.1958	Greenland	63°14'N, 40°04'W	215	DHMSU
378	“Sevastopol”	st. 1664	21.07.1958	Greenland	63°56'N, 38°11'W	210	DHMSU
379	“Sevastopol”	st. 1664	21.07.1958	Greenland	63°56'N, 38°11'W	210	ZMMGU
380	“Sevastopol”	st. 1669	22.07.1958	Greenland	65°27'N, 33°22'W	340	DHMSU
381	“Sevastopol”	st. 1696	26.09.1958	Norwegian	65°29'N, 09°50'E	320	DHMSU
382	“Sevastopol”	st. 1698	26.09.1958	Norwegian	65°50'N, 08°32'E	410	DHMSU
383	“Sevastopol”	st. 1699	26.09.1958	Norwegian	66°02'N, 07°52'E	370	DHMSU
384	“Sevastopol”	st. 1702	27.09.1958	Norwegian	66°38'N, 04°59'E	1125	DHMSU
385	“Sevastopol”	st. 1723	02.10.1958	Greenland	68°34'N, 14°04'W	1280	DHMSU
386	“Sevastopol”	st. 1730	04.10.1958	Norwegian	66°37'N, 9°05'W	1475	DHMSU
387	“Sevastopol”	st. 1753	12.10.1958	Norwegian	61°32'N, 02°04'E	350	DHMSU
388	“Sevastopol”	st. 1754	13.10.1958	Norwegian	61°33'N, 01°07'E	176	DHMSU
389	“Sevastopol”	st. 1774	19.10.1958	Greenland	66°51'N, 22°10'W	130	DHMSU
390	“Sevastopol”	st. 1776	21.10.1958	Norwegian	64°08'N, 13°48'W	120	DHMSU
391	“Sevastopol”	st. 1790	22.10.1958	Norwegian	62°32'N, 07°00'W	100	DHMSU
392	“Sevastopol”	st. 1792	24.10.1958	Norwegian	62°00'N, 06°14'W	115	DHMSU
393	“Sevastopol”	st. 1793	24.10.1958	Norwegian	61°55'N, 05°49'W	264	DHMSU
394	“Sevastopol”	st. 1795	24.10.1958	Norwegian	61°42'N, 04°50'W	320	DHMSU
395	“Sevastopol”	st. 1801	25.10.1958	Norwegian	60°56'N, 01°34'W	134	DHMSU
396	“Sevastopol”	st. 1802	25.10.1958	Norwegian	60°58'N, 0°52'W	115	DHMSU
397	“Sevastopol”	st. 1803	25.10.1958	Norwegian	60°35'N, 0°34'W	140	DHMSU
398	“Sevastopol”	st. 1804	26.10.1958	Norwegian	60°35'N, 0°02'E	110	DHMSU
399	“Sevastopol”	st. 1805	26.10.1958	Norwegian	60°35'N, 0°35'E	138	DHMSU
400	“Sevastopol”	st. 2419	28.10.1958	Norwegian	69°20'N, 15°30'E	160	DHMSU
401	“Sevastopol”	st. 2454	06.11.1959	Greenland	70°58'N, 12°29'W	450	DHMSU
402	“Sevastopol”	st. 2473	09.11.1959	Greenland	66°52'N, 14°00'W	220	DHMSU
403	“Sevastopol”	st. 2474	09.11.1959	Greenland	66°35'N, 14°22'W	150	DHMSU
404	“Sevastopol”	st. 2479	11.11.1959	Norwegian	67°30'N, 09°00'W	1680	DHMSU
405	“Sevastopol”	st. 2500	15.11.1959	Norwegian	67°30'N, 09°30'E	255	DHMSU
406	“Sevastopol”	st. 2502	16.11.1959	Norwegian	67°30'N, 11°30'E	125	DHMSU
407	“Sevastopol”	st. 2508	17.11.1959	Norwegian	65°45'N, 08°30'E	420	DHMSU
408	“Sevastopol”	st. 2535	27.11.1959	Norwegian	64°01'N, 13°30'W	190	DHMSU
409	“Sevastopol”	st. 2540	27.11.1959	Norwegian	63°25'N, 11°00'W	420	DHMSU
410	“Sevastopol”	st. 2547	28.11.1959	Norwegian	62°36'N, 07°40'W	185	DHMSU
411	“Sevastopol”	st. 2548	28.11.1959	Norwegian	62°30'N, 07°15'W	95	DHMSU
412	“Sevastopol”	st. 2563	08.12.1959	Norwegian	62°57'N, 04°30'E	605	DHMSU

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
413	“Sevastopol”	st. 2564	08.12.1959	Norwegian	62°56'N, 05°25'E	125	DHMSU
414	“Sevastopol”	st. 2568	09.12.1959	Norwegian	60°34'N, 04°33E	330	DHMSU
415	“Sevastopol”	st. 2571	10.12.1959	Norwegian	60°35'N, 02°50'E	95	DHMSU
416	“Sevastopol”	st. 2574	10.12.1959	Norwegian	60°36'N, 0°45'E	130	DHMSU
417	“Sevastopol”	st. 2575	10.12.1959	Norwegian	60°37'N, 0°02'E	125	DHMSU
418	“Sevastopol”	st. 2576	11.12.1959	Norwegian	60°35'N, 0°35'W	130	DHMSU
419	“Sevastopol”	st. 2577	11.12.1959	Norwegian	60°56'N, 01°00'W	103	DHMSU
420	“Sevastopol”	st. 2578	11.12.1959	Norwegian	61°01'N, 01°36'W	150	DHMSU
421	“Sevastopol”	st. 2581	11.12.1959	Norwegian	61°21'N, 03°10'W	1320	DHMSU
422	“Sevastopol”	st. 2584	12.12.1959	Norwegian	61°42'N, 04°51'W	220	DHMSU
423	“Sevastopol”	st. 2585	12.12.1959	Norwegian	61°49'N, 05°21'W	175	DHMSU
424	“Sevastopol”	st. 2586	12.12.1959	Norwegian	61°54'N, 05°45'W	290	DHMSU
425	“Sevastopol”	st. 2589	12.12.1959	Norwegian	62°47'N, 06°26'W	350	DHMSU
426	“Sevastopol”	st. 2589	12.12.1959	Norwegian	62°47'N, 06°26'W	350	ZMMU
427	“Severnyj Poljus”	no data	03.08.1946	Chukchi	71°31'N, 171°34' E	58	ZISP
428	“Severnyj Poljus”	st. 6(II)	03.08.1946	Chukchi	71°30'N, 171°54' W	58	ZISP
429	“Schmidt”	st. 2901	05.08.1986	Barents	74°03'N, 20°01' E	90	IEE
430	“SP-3”	st. 17	25-26. 09.1948	C. Arctic	88°14'N, 64°54'E,	no data	ZISP
431	“SP-3”	st. 73	08.08.1948	Barents	79°38'N, 60°45'E	124	ZISP
432	“SP-4”	st. 2	19.06.1954	C. Arctic	76°47'N, 173°17'E	no data	ZISP
433	“SP-22”	st. 21	no data	C. Arctic	81°07'N, 128°24'W	3550	DHMSU
434	“SP-22”	st. 50	no data	C. Arctic/ Beaufort	73°48'N, 125°35'W	2990	DHMSU
435	“SP-22”	st. 58	no data	Beaufort/Chukchi	73°35'N, 160°00'W	2100	DHMSU
436	“SP-22”	st. 60	no data	Chukchi	73°43'N, 161°50'W	300	DHMSU
437	“SP-22”	st. 69	no data	C. Arctic/Chukchi	74°25'N, 164°08'W	445	DHMSU
438	“SP-22”	st. 72	07.01.1979	C. Arctic/Chukchi	74°35'N, 164°00'W	795	DHMSU
439	“SP-22”	st. 74	03.01.1979	E. Siberian	74°38'N, 164°00'E	465	DHMSU
440	“SP-22”	st. 76	13.01.1979.	C. Arctic/E. Siberian	74°56'N, 166°10'E	460	DHMSU
441	“SP-22”	st. 94	no data	C. Arctic	74°55'N, 170°02'W	230	DHMSU
442	“SP-22”	st. 98	no data	C. Arctic	75°00'N, 170°20'W	260	DHMSU
443	“SP-22”	st. 77,1	no data	C. Arctic	78°37'N, 161°00'W	177	DHMSU
444	“SP-22”	st. 77,2	no data	C. Arctic	78°43'N, 160°44'W	160	DHMSU
445	“SP-22”	st. 77,3	no data	C. Arctic	78°53'N, 160°55'W	199	DHMSU
446	“SP-22”	st. 101	no data	C. Arctic	75°00'N, 170°10'W	250	DHMSU
447	“SP-22”	st. 103	24-25. 02.1979	C. Arctic	75°11'N, 170°05'W	315	DHMSU
448	“SP-22”	st. 108	no data	C. Arctic	75°13'N, 170°30'W	370	DHMSU

449	“SP-22”	st. 111	08.03.1979	C. Arctic	75°15'N, 170°45'W	390	DHMSU
450	“SP-22”	st. 112	10-11. 03.1979	C. Arctic	75°15’N, 171°15' W	450-460	DHMSU
451	“SP-22”	st. 115	no data	C. Arctic	75°02'N, 171°30'W	382	DHMSU
452	“SP-22”	st. 120	no data	C. Arctic	74°54'N, 171°37'W	330	DHMSU
453	“SP-22”	st. 122	no data	C. Arctic	74°55'N, 171°40'W	345	DHMSU
454	“SP-22”	st. 124	no data	C. Arctic	74°55'N, 171°55'W	355	DHMSU
455	“Tajmyr”	no data	03.09.1913	C. Arctic	79°16'N, 103°20'E	99	ZISP
456	“Tajmyr”	no data	09.09.1913	Kara/Laptev	Cape Chelyuskin	7	ZISP
457	“Tajmyr”	st. 65	09.09.1913	Laptev	78°40'N, 104°30'E	7	ZISP
458	“Tajmyr”	21/66	17.08.1915	Kara	76°20'N, 95°14'E	44	ZISP
459	“Tajmyr”	no data	18.08.1915	Kara	76°20'N, 95°14'E	18	ZISP
460	“Toros”	st. XIX	08.1980	Barents	Seven Islands archipelago	no data	MMBI
461	“Tunets”	st. 2	08.06.1978	Barents/ Norwegian	70°26'N, 17°56'E	120	IO
462	“Tunets”	st.2	08.06.1978	Barents/ Norwegian	70°26'N, 17°56'E	120	DHMSU
463	“Tunets”	st. 55	13.06.1978	Norwegian	67°30'N, 9°30'E	260	DHMSU
464	“Tunets”	st. 7	15.06.1978	Norwegian	67°50'N, 10°30'E	201	DHMSU
465	“Tunets”	st. 88	16.06.1978	Norwegian	68°25'N, 12°56'E	167	DHMSU
466	“Tunets”	st. 12	21.06.1978	Barents	71°10'N, 19°00'E	202	DHMSU
467	“Tunets”	st. 11	21.06.1978	Barents/ Norwegian	71°10'N, 17°00'E	356	DHMSU
468	“Tunets”	st. 13	28.06.1978	Barents	70°32'N, 18°20'E	225	DHMSU
469	“Tunets”	st. 14	28.06.1978	Barents	70°41'N, 18°56'E	328	DHMSU
470	“Tunets”	st. 19	02.07.1978	Barents	70°58'N, 21°23E	168	DHMSU
471	“Vodnik”	st. 23	06.06.1968	Barents	71°15'N, 30°00'E	325	DHMSU
472	“Vodnik”	st. 26	08.06.1968	Barents	71°21'N, 27°00'E	245	DHMSU
473	“Vodnik”	st. 39	10.06.1968	Barents	71°30'N, 25°30'E	275	DHMSU
474	“Vodnik”	st. 43	12.06.1968	Barents	72°15'N, 23°30'E	285	DHMSU
475	“Vodnik”	st. 44	12.06.1968	Barents	72°30'N, 23°30'E	300	DHMSU
476	“Vukvol”	data incomplete	10.07.-22.08.1986	E. Siberian	Chaunskaya Bay	6-8	ZISP
477	“Vychegda”	st. 8	18.07.1977	Barents	69°49'N, 31°35'E	35	IEE
478	“Vychegda”	st. 20	05.08.1977	Barents	69°12'N, 35°47'E	30	IEE
479	“Vychegda”	st. 21	07.08.1977	Barents	69º04'N, 36º25'E	35	IEE
480	“Yuksporit”	st. 3	25.08.1978	Barents	69°49'N, 31°51'E	50	DHMSU
481	“Yuksporit”	st. 4	26.08.1978	Barents	69°52'N, 31°35'E	47	DHMSU
482	“Yuksporit”	st. 17	23.09.1978	Barents	69°19'N, 33°52' E	170-179	IEE
483	“Zarja"	no data	02.09.1900	Kara	75°54'N, 92°59'E	15-17	ZISP
484	“Zarja"	no data	31.08, 18.09.1900	Kara	no data	13-18	ZISP

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
485	“Zarja"	st. 44	18.08.1901	Kara	76°59'N, 100°20'E	28	ZISP
486	Exp. Akvaplan-Niva	st. 11 - 1,3,4	08.08.1992	Barents	76°07'N, 23°51'48''E	59	IEE
487	Exp. Akvaplan-Niva	st. 11 - 1,3,4	08.08.1992	Barents	76°07'N, 23°51'48''E	59	IEE, ZISP, AMRI, ZMBN
488	Exp. Akvaplan-Niva	st. 14 – 3, 5	09.08.1992	Barents	75°22'N, 26°37'E	189	IEE
489	Exp. Akvaplan-Niva	pr. 4273	31.08.2008	C. Arctic	79°33’'N, 18°46'E	10	IEE
490	Exp. Akvaplan-Niva	st. 7, 9	04.02.2010	Norwegian	Tromsø Havn, Norway	5-6	IEE
491	Exp. Akvaplan-Niva	st. 8	23.05.2010	Barents	71°46'N, 21°10'E	317	AMRI
492	Exp. Akvaplan-Niva	st. 9	23.05.2010	Barents	71°46'N, 21°13'E	317	ZMBN, AMRI
493	Exp. Akvaplan-Niva	st. 4	24.05.2010	Barents	71°47'N, 21°08'E	317	AMRI
494	Exp. Akvaplan-Niva	st. 7	24.05.2010	Barents	71°46'N, 21°32'E	316	ZMBN
495	Exp. Akvaplan-Niva	st. 2	16.06.2010	Barents	Mørsvikbotn Havn, Norway	67	IEE
496	Exp. Akvaplan-Niva	no data	04.10.2010	Norwegian	Tromsø Havn, Norway	5	IEE
497	Exp. Akvaplan-Niva	LN-12	07.06.2012	Norwegian	64°29'N, 06°48'E	300	AN
498	Exp. Akvaplan-Niva	LN-07	08.06.2012	Norwegian	64°28'N, 06°49'E	300	AN
499	Exp. Akvaplan-Niva	ON-08	09.06.2012	Norwegian	64°25'N, 06°58'E	301	AN
500	Exp. BBS MSU	st. 344, 346, 349, 376, 377, 382, 399	08.1976	White	Shombach Point, Kochinnyj Point, Nischevskaja Bay, mouth of River Niva, Knjazhaja Bay, Rjazhkov Isl. of Kandalaksha Gulf	2-10	IEE
501	Exp. BBS MSU	st. 330, 374, 385, 364	08.1976	White	Turij Point, Kovda Bay, Rjazhkov Isl., Velikij Isl. of Kandalaksha Gulf	2-10	IEE
502	Exp. BBS MSU	st. 62	19.08.1936	Barents	Murman coast	73-76	ZISP
503	Exp. BIOICE project	st. 2862	30.08.1995	Border of Atlantic Ocean and Greenland Sea	61°10.10'N,18°00.50'W,	2399	IINH
504	Exp. FMRI	st. 2	13.08.1921	Barents	68º53'N, 43º27'E	65	ZISP
505	Exp. FMRI	st. 29	27.08.1921	Kara	72°14'N, 62°04'E	121	ZISP
506	Exp. FMRI	st.73	03-04. 07.1923	White	65°55'N, 38°15'E	90	ZMMU
507	Exp. FMRI	st.73	03-04. 07.1923	White	65°55'N, 38°15'E	90*	ZISP, IEE
508	Exp. FMRI	st. 101	01.09.1923	Barents	78°07'N, 54°17'E	250	ZISP

509	Exp. FMRI	st. 117d	28.09.1923	Barents	Belushaya Inlet, N.Z	10.5-13	ZISP, ZMMU
510	Exp. FMRI	st. 117d	28.09.1923	Barents	Belushaya Inlet, N.Z	10.5-13	ZMMU
511	Exp. FMRI	113b	09-10.1923	Barents	Belushaya Inlet, N.Z	no data	ZISP
512	Exp. FMRI	st. 185	03.09.1924	Barents	77°33'N, 40°58'E	220	ZISP
513	Exp. FMRI	st. 2136	24.09.1924	Greenland	Cole Bay, Ice-Fiord, W.S.	no data	ZISP
514	Exp. FMRI	no data	09.10.1924	Barents	69º20'N, 33º59'E	131*	ZISP
515	Exp. FMRI	no data	09.10.1924	Barents	69º20'N, 33º59’’E	131	ZISP
516	Exp. FMRI	no data	12.09.1925	Barents	Zabludyaschaja Inlet, N.Z.	18	ZISP
517	Exp. FMRI	st. 373	13-14. 09.1925	Barents	Novaya Zemlya	8.5	ZISP, ZMMU
518	Exp. FMRI	st. 373, dredge 23	14.09.1925	Barents	Novaya Zemlya	8.5	ZISP
519	Exp. FMRI	st. 547, dredge 6	19.08.1926.	Barents	Krestovaja Inlet, N.Z.	19	ZMMU
520	Exp. FMRI	st. 571	28.08.1926	Barents	79°08'N, 43°10'E	260	ZISP
521	Exp. FMRI	st. 573	29.08.1926	Barents	78°59'N, 40°16'E	182	ZISP
522	Exp. FMRI	st. 574	29.08.1926	Barents	78°39'N, 38°40'E	190	ZISP
523	Exp. FMRI	st. 601	11.09.1926	Barents	73º32'N, 54º13'E	24	ZISP
524	Exp. FMRI	st. 989	01.07.1928	Barents	69°00'N, 38°00'E	171	ZISP
525	Exp. FMRI	no data	26.08.1928	Barents	69°18'N, 33°42'E	72	ZISP
526	Exp. FMRI	st. 1222	06.08.1929	Barents	69°28'N, 34°17'E	107	ZISP
527	Exp. FMRI	Dredge 12	1936	Barents	no data	no data	ZISP
528	Exp. FMRI	st. 96	29.08.1938	Barents	79°10'N, 40°30'E	380	ZISP
529	Exp. FMRI	st. 1239	18.08.1959	Barents	77°17'N, 35°36'E	138	ZISP
530	Exp. FMRI	st. 1136	no data	Barents	no data	no data	ZMMU
531	Exp. FMRI	no data	no data	Barents	Vardø Isl.	49*	ZISP
532	Exp. FMRI	st. 836	no data	Barents	no data	no data	ZISP
533	Exp. IEE	st.10	28.08.2002	Barents	Dalnezelenetskaja Inlet	30-32	IEE
534	Exp. IEE	tr. 4, st. 1	30.08.2002	Barents	Dalnezelenetskaja Inlet	6-7	IEE
535	Exp. IEE	st. 13	17.08.2009	Barents	69°8'N, 36° 01'E	35	IEE
536	Exp. IEE	st. 6,7	01.09.2010	Barents	Sisjayarve Lagoon, Varanger Fjord	24,5-26	IEE
537	Exp. NIMRB (MERANO)	st. 578	09.08.2010	Barents	71°38'N, 16°18'E	586	ZMBN
538	Exp. SHI	st. 247	1921	Kara	Klokov Gulf, N.Z.	no data	ZISP
539	Exp. SHI	st. 251	27.09.1921	Kara	Klokov Gulf, N.Z.	no data	ZISP
540	Exp. ZI	Tr. XXIV, st. 4	1959	Barents	Ainov Isls	Low littoral	ZISP

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
541	Exp. ZI&MMBI	data incomplete	09.06.1987-19.06.1988	Barents	Jarnyshnaja Inlet	2-21	ZISP
542	Exp. ZI&MMBI	no data	14.07-01.08.1987	Barents	Jarnyshnaja Inlet	Low littoral	ZISP
543	Exp. ZI&MMBI	data incomplete	14.07.1987 - 05.08.1987	Barents	Jarnyshnaja Inlet	4-10	ZISP
544	Exp. ZI&MMBI	data incomplete	27.07-31.07.1987, 24.05-19.06.1988	Barents	Jarnyshnaja Inlet	1-55	IEE, ZISP
545	Exp. ZI&MMBI	data incomplete	30-31.07.1987, 24.05-09.06.1988	Barents	Jarnyshnaja Inlet	3-31	IEE, ZISP
546	Exp. ZI&MMBI	data incomplete	30.07.1987-19.06. 1988	Barents	Jarnyshnaja Inlet	3-55	IEE, ZISP
547	Exp. ZI&MMBI	data incomplete	30.07.1987-19.06.1988	Barents	Jarnyshnaja Inlet	0,5-55	ZISP, MMBI, IEE
548	Exp. ZI&MMBI	transect 2, st. 1	21.08.1987	Barents	Jarnyshnaja Inlet	littoral	ZISP
549	Exp. ZI&MMBI	transect 4, st. 1	15.11.1987	Barents	Jarnyshnaja Inlet	61	IEE
550	Averintsev V.G.	data incomplete	26.09-12.12. 1981	C. Arctic	Heiss Isl., F.J.L.	3-7	MMBI
551	Averintsev V.G.	st. 12	24.08.1982	C. Arctic	80°22'N, 52°17’’E	73	ZISP
552	Averintsev V.G.	pr. 23(2)	25.08.1992	C. Arctic	Tihaja Bay, Hooker Isl., F.J.L.	120	ZISP
553	Averintsev V.G.	data incomplete	26.08.1982	C. Arctic/Barents	Etheridge Islands, F.J.L.	5-10	ZISP
554	Averintsev V.G., Kussakin O.G.	data incomplete	02.10-12.11.1981	C. Arctic	Heiss Isl., F.J.L.	1.5-6.5	MMBI, ZISP
555	B.-Birulja A.A.	dredge 42	1899	Greenland	Ice-Fjord, W.S.	no data	ZISP
556	B.-Birulja A.A.	dredge 76	1895	White	Solovetsky Isls.	no data	ZISP
557	Cheremisina V.T.	st. 548	04.03.1946	Barents	69°34'N, 32°26'E	no data	ZISP
558	Gertzenshtein S.M.	st. 51	1880	Barents	Teriberka Inlet	no data	ZISP
559	Gertzenshtein S.M.	st. 27	15.06.1887	Barents	Teriberka Inlet	100	ZISP
560	Gertzenshtein S.M.	st. 36	1887	White	no data	no data	ZISP
561	Gertzenshtein S.M.	st. 66	1887	White	no data	no data	ZISP
562	Gertzenshtein S.M.	no data	1887	White	no data	no data	ZISP
563	Gertzenshtein S.M.	no data	no data	White	Pesja Bay, Kemskie Shhery Isls.	no data	ZISP

564	Golikov A.N.	no data	30.03.1960	White	Kartesh Cape	2-3	ZISP
565	Golikov A.N.	transect II, st. 8	18.07.1967	White	Chupa Inlet	25	ZISP
566	Golikov A.N.	transect III, st. 6	21.07.1967	White	Levaja Bay of Chupa Inlet, Kandalaksha Gulf	6-8	ZISP
567	Golikov A.N.	data incomplete	06.07.1967 - 26.05.1967	White	Bays Seldyanaya, Kruglaya, Levaya of Chupa Inlet, Kandalaksha Gulf	3-20	ZISP
568	Golikov A.N.	data incomplete	15.07.1967 - 13.05.1968	White	Bays Seldyanaya, Kruglaya, Levaya of Chupa Inlet, Kandalaksha Gulf	2-18	ZISP
569	Golikov A.N.	st. 338, 63	1967-1968	White	no data	no data	ZISP
570	Golikov A.N.	no data	20.09.1970	C. Arctic	Heiss Isl., F.J.L.	3-5	ZISP
571	Golikov A.N.	no data	28.07.1976	Chukchi	Kozhevnikova Bay	13	ZISP
572	Golikov A.N.	transect IV	17.08.1976	Chukchi	Wrangel Isl.	25	ZISP
573	Golikov A.N.	no data	25.08.1976	Chukchi	Wrangel Isl.	3 - 6	ZISP
574	Golikov A.N.	transect IV	06.09.1976	Chukchi	Provideniya Bay	5	ZISP
575	Golikov A.N.	data incomplete	28.09.1983	Chukchi	Cape Serdtse-Kamen	4-5	ZISP
576	Gorbunov A.V.	st. 24	04.09.1929	Barents	78°40'N, 58°00'E	162	ZISP
577	Gorbunov A.V.	st. 25	05.09.1929	Barents	78°38'N, 63°10'E	363	ZISP
578	Gorbunov A.V.	st. 20	22.07.1929	C. Arctic	82°14'N, 52°10'E	165	ZISP
579	Gorbunov A.V.	st. 22	25.08.1929	C. Arctic?	Franz Joseph Land	300	ZISP
580	Gorbunov A.V.	st. 41	19.09.1931	Kara	73°33'N, 62°37'E	120	ZISP
581	Gorbunov A.V.	st. 42	19.09.1931	Kara	73°36'N, 59°42'E	345	ZISP
582	Gudimov A.V.	no data	10. 2011	Barents	Jarnyshnaja Bay	L. littoral	IEE
583	Gurjanova. E.F., Uschakov P.V	no data	1925	Barents	Chernaya Inlet, N.Z.	15-20	ZISP
584	Knight-Jones., P.& E.W.	no data	16-17.09. 1996	White	Kartesh Cape and Solovetsky Isls.	littoral	IEE
585	Knight-Jones., P.& E.W.	no data	16-18.09.1996	White	Kartesh Cape and Solovetsky Isls.	2 - 5	IEE
586	Knight-Jones., P.& E.W.	no data	09.1996	White	Kartesh Cape	3	IEE
587	Knipovich N.M.	Dredge 58-59	04.08.1890	Barents	Kolguyev Isl.	no data	ZISP
588	Knipovich N.M.	no data	1893	Barents	no data	no data	ZISP
589	Knipovich N.M.	no data	1893; 16.06.1894	Barents	Motovsky Bay	7,5-8,5	ZISP

№	R/V, expedition or collector	St. ident.	Date	Sea	Location	Depth (m)	Deposition
590	Libman E.P.	no data	1946	Barents	Pechenga Inlet	U. sublittoral	ZISP
591	Libman E.P.	no data	1946	Barents	Pechenga Inlet	19	ZISP
592	Libman E.P.	no data	1946	Barents	Pechenga Inlet	no data	ZISP
593	Pereladov M.V.	sample 3	25.05.2002	Barents	Ambarnaja Bay, Varanger Fjord	no data	IEE
594	Pereladov M.V.	sample 3, 5	no data	Barents	Ambarnaja Bay, Varanger Fjord	U. sublittoral	IEE
595	Rzhavsky A.V.	no data	30.09.2011	Norwegian	Telegraph Bay, Tromsø, Norway	M.&L. littoral	IEE
596	Tabachnik K.R, Mokievsky V.O	transect 5, st. 1	02.09. 1989	Greenland	Cole Bay, Ice-Fiord, W.S.	12-18	IEE
597	Tabachnik K.R, Mokievsky V.O	data incomplete	02-09. 09.1989	Greenland	Cole Bay, Ice-Fiord, W.S.	3-18	IEE
598	Tabachnik K.R, Mokievsky V.O	no data	02-17. 09.1989	Greenland	Cole Bay, Ice-Fiord, W.S.	15-25	IEE
599	Tabachnik K.R, Mokievsky V.O	no data	07-09. 09.1989	Greenland	Cole Bay, Ice-Fiord, W.S.	3-25	IEE
600	Tabachnik K.R, Mokievsky V.O	no data	22.08-07. 09.1989	Greenland	Cole Bay, Ice-Fiord, W.S.	4-25	IEE
601	Tabachnik K.R, Mokievsky V.O	data incomplete	23.08-09. 09.1989	Greenland	Cole Bay, Ice-Fiord, W.S.	2,5-35	IEE
602	Tabachnik K.R, Mokievsky V.O	no data	23.08-09. 09.1989	Greenland	Cole Bay, Ice-Fiord, W.S.	2-25	IEE
603	Tzetlin A.B.	no data	15.06.1980	White	Velikaja Salma, Kandalaksha Gulf	L. littoral	IEE
604	Uschakov P.V.	trawl 15	1927	Barents /Kara	Matochkin Shar, N.Z.	213	ZISP
605	Vasilenko S.V.	no data	30.06.1961	White	Sharapov Cape, Kandalaksha Gulf	U. subtidal	ZISP
606	Vasilenko S.V.	no data	06.07.1961	White	Seldyanaja Bay of Chupa Inlet, Kandalaksha Gulf	1.5 - 2	ZISP
607	Zevina G.B.	st. 22	04.02.1964	Barents	Kislaja Inlet	no data	MMBI
608	Zevina G.B.	no data	04.07.1964	Barents	Kislaja Inlet	no data	MMBI
609	Zevina G.B.	st. 42	1964	Barents	Kislaja Inlet	L. littoral	MMBI
610	no data	no data	03.07.1899	White	Orlovskij lighthouse (Gorlo), Russia	littoral	ZISP
611	no data	st. 109	17.08.1899	Barents	69°58'N, 32°31'E	140-174	ZISP
612	no data	no data	18.08.1911	Barents	Krestovaja Inlet, N.Z.	no data	ZISP
613	no data	st. 554	22.08.1926	Barents	Gorbovy Isls., N.Z.	no data	ZISP
614	no data	st. 596	10.09.1926	Barents	Mitjushina Inlet	3-5	ZISP

615	no data	st. 682	03.07.1927	Barents	69º10' N, 41º13'E	90	ZISP
616	no data	st. 244, 250	1927	Kara	Klokov Gulf, N.Z.	no data	ZISP
617	no data	no data	1933	Kara	Izvestiy TSIK Isls.	no data	ZISP
618	no data	no data	1946	White	Sedlovataja Luda Isl., Kandalaksha Gulf	littoral	ZISP
619	no data	no data	01.04.1949	Barents	Dal'nezelenetskaja Inlet	no data	ZISP
620	no data	no data	01.06.1949	Barents	Dal'nezelenetskaja Inlet	littoral	ZISP
621	no data	no data	04.06.1949	Barents	Dal'nezelenetskaja Inlet	no data	ZMMU
622	no data	st. 735	16.08.1960	White	no data	no data	ZISP
623	no data	no data	no data	Barents	80°19'N, 34°36'E	115	ZISP
624	no data	no data	no data	Barents	Vardø Isl., Norway	no data	ZMMU
625	no data	no data	no data	Barents	Vardø Isl., Norway	49	ZMMU

*Indicated depth is given on the label, but worms were attached to algae. More probably these caught in trawl from the surface.

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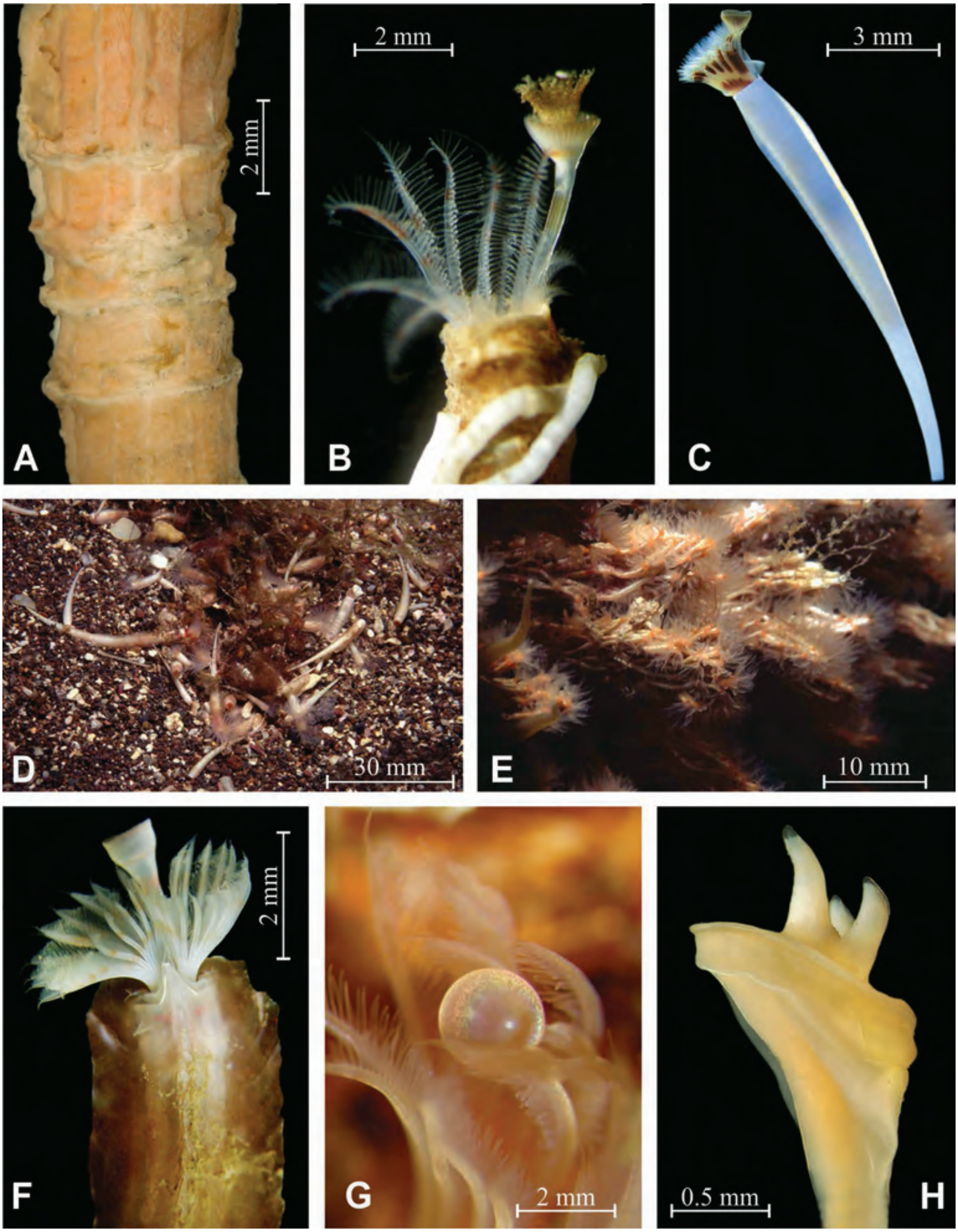

Plate 1. A – tube fragment of *Serpula vermicularis,*; B – branchial crown and operculum of *Hydroides norvegicus*; C – *Ditrupa arietina*, tube with the animal inside; D – *Ditrupa arietina*, animals *in situ*; E – *Filograna implexa*, colony of tubes *in situ*; F – *Placostegus tridentatus*, anterior 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.

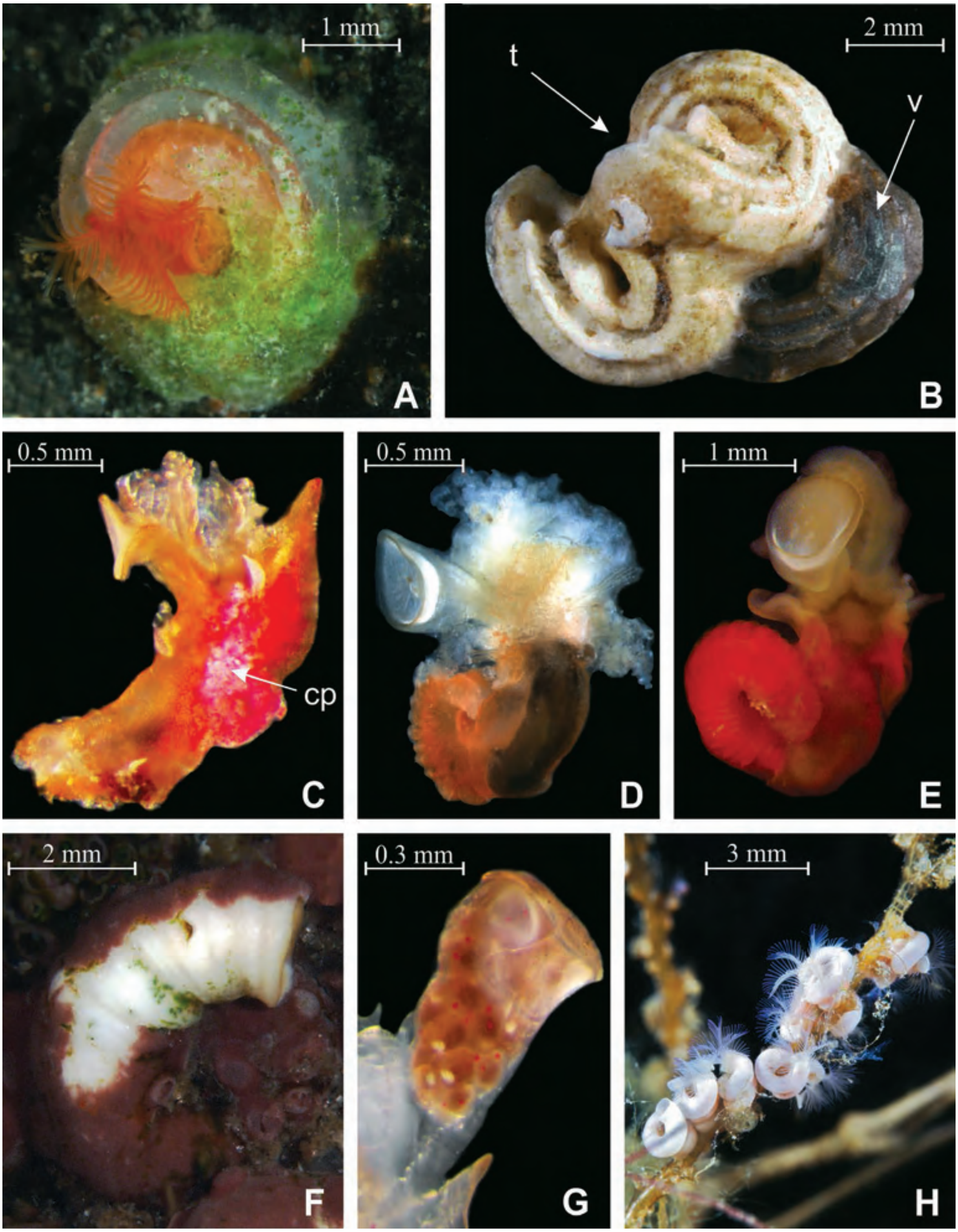

Plate 2. A – *Paradexiospira* (*Spirorbides*) *vitrea*, tube with body; B – tubes conglomerate of *Paradexiospira* (*Paradexiospira*) *violacea* (p) and *Spirorbis* (*Spirorbis*) *tridentatus* (t); C –*Pileolaria* ex gr. *berkeleyana*, entire body (cp – crystalline patches); D – *Spirorbis* (*Spirorbis*) *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.