A.V. Rzhavsky, E.K. Kupriyanova, A.V. Sikorski

Field guide to calcareous tubeworms (Polychaeta, Serpulidae) of the Arctic Ocean



KMK Scientific Press Moscow 2018 A.N. Severtzov Institute of Ecology and Evolution RAS Australian Museum Research Institute Akvaplan-niva



A.V. Rzhavsky, E.K. Kupriyanova, A.V. Sikorski

## FIELD GUIDE TO CALCAREOUS TUBEWORMS (POLYCHAETA, SERPULIDAE) OF THE ARCTIC OCEAN

KMK Scientific Press Moscow 2018 A.V. Rzhavsky, E.K. Kupriyanova, A.V. Sikorski. Field guide to calcareous tubeworms (Polychaeta, Serpulidae) of the Arctic Ocean. Moscow. KMK Scientific Press, 2018. 187 p.

The book is a taxonomic guide to serpulid polychaetes (including the subfamily Spirorbinae) of the Arctic Ocean. Taxonomic keys include 37 serpulid spesies described and illustrated in detail. It starts with a description of serpulid morphology and includes a comprehensive glossary. Taxonomic treatment of species includes basic synonymy, references, and brief differential diagnoses. Information is also available on species reproduction, geographical distribution, and habitats in the Arctic Basin. Species illustrations are presented as light and scanning electron microscopy micrographs, photos of live specimens and line drawings. The book is based on extensive (over 600 samples) material collected all over the Arctic Ocean and deposited in Russia, Iceland, Germany, Norway, and Australia. The guide is based on the same material as Rzhavsky et al. (2014) "Calcareous tubeworms (Polychaeta, Serpulidae) of the Arctic Ocean", but it has another concept and target user: it is a simplified and lavishly illustrated field guide for identification definition of calcareous tubeworms in the field and laboratory. Detailed synonymy and taxonomic discussions are excluded. This guide is intended for undergraduate and graduate students, educators and naturalists as well as invertebrate zoologists, marine ecologists, and environmental consultants.

> Cover photos F. Pleijel, A.V. Rzhavsky Editor:

*T.A. Britayev*, A.N. Severtsov Institute of Ecology and Evolution RAS, Moscow, Russia

**Reviewers:** 

A.B. Tzetlin, Department of Invertebrate Zoology, M.V. Lomonosov Moscow State University, Russia

N.E. Budaeva, P.P. Shirshov Institute of Oceanology Russian Academy of Sciences, Russia

© KMK Scientific Press, 2018. © Akvaplan-niva, 2018.

ISBN 978-5-6040493-7-2

#### ACKNOWLEDGEMENTS

The authors greatly appreciate efforts of numerous colleagues and expedition staff who collected the material used in preparation of this book from 1880 to 2013 (see Table 1 in Rzhavsky et al., 2014). We thank the staff of the Institutions and Museums where these collections are deposited for the opportunity to work with this material, especially G. N. Buzhinskaja and V. V. Potin (Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia), I. A. Jirkov (Department of Hydrobiology of Moscow State University, Moscow, Russia), and D. L. Ivanov (Zoological Museum of Moscow State University, Moscow, Russia). Also we are grateful to the people who provided photos: E. Wong (The University of Queensland, Brisbane, Australia), R. Sanfilippo (Dipartimento di Scienze Geologiche, Sezione di Oceanologia e Paleoecologia, Catania University, Catania, Italy), G. Rouse (Scripps Institution of Oceanography, UCSD, La Jolla, CA, USA), H. A. ten Hove (Netherlands Centre for Biodiversity Naturalis, Leiden, Netherlands), P. Wirtz (Centro de Ciencias do Mar do Algarve Campus de Gambelas, Faro, Portugal), F. Pleijel (University of Gothenburg).

Publication of this book and part of the research were supported by Akvaplan-niva (Tromsø, Norway) and a grant from the Norwegian Research Council (Project 233635/H30 "Environmental management of petroleum activities in the Barents Sea: Norwegian-Russian collaboration").

### CONTENTS

Acknowledgments	3
Contents	4
Introduction	6
General morphology	7
Methodological remarks	. 17
- Recommendations for identification of non-spirorbins	. 17
- Recommendations for identification of spirorbins	. 18
Glossary	. 20
The former subfamilies "Serpulinae" and "Filograninae"	
- Key to non-spirorbins based on tube morphology	.24
- Key to non-spirorbins based on specimen morphology	. 32
- Genus Apomatus	. 38
- Apomatus globifer	. 40
- Genus Bathyvermilia	. 42
- Bathyvermilia eliasoni	. 44
- Bathyvermilia islandica	. 46
- Genus Chitinopoma	. 48
- Chitinopoma serrula	. 50
- Genus Ditrupa	. 52
- Ditrupa arietina	. 54
- Genus Filograna	. 56
- Filograna implexa	. 58
- Genus Hyalopomatus	. 60
- Hyalopomatus claparedii	. 62
- Genus Hydroides	. 64
- Hydroides norvegica	. 66
- Genus Metavermilia	. 68
- Metavermilia arctica	. 70
- Genus Placostegus	. 72
- Placostegus tridentatus	. 74
- Genus Protis	. 76
- Protis akvaplani	. 78
- Protis arctica	. 80
- Genus Protula	. 82
- Protula tubularia	. 84
- Genus Serpula	. 86
- Serpula vermicularis	. 88
- Genus Spirobranchus	. 90
- Spirobranchus triqueter	. 92
Spirorbinae	
- Key to spirorbins	. 94
- Tribe Circeini	108
- Genus Circeis	108
- Circeis armoricana	110

- Circeis spirillum	112
- Genus Paradexiospira	114
- Subgenus Paradexiospira	114
- Paradexiospira (Paradexiospira) violacea	116
- Subgenus Spirorbides	118
- Paradexiospira (Spirorbides) cancellata	120
- Paradexiospira (Spirorbides) vitrea	122
- Tribe Januini	124
- Genus Janua	124
- Janua heterostropha	126
- Tribe Pileolariini	128
- Genus Bushiella	128
- Subgenus Bushiella	129
- Bushiella (Bushiella) barentsii	130
- Bushiella (Bushiella) evoluta	132
- Bushiella (Bushiella) verruca	134
- Subgenus Jugaria	136
- Bushiella (Jugaria) acuticostalis	138
- Bushiella (Jugaria) granulata	140
- Bushiella (Jugaria) kofiadii	142
- Bushiella (Jugaria) quadrangularis	144
- Bushiella (Jugaria) similis	146
- Genus Pileolaria	148
- Pileolaria ex.gr. berkeleyana	150
- Genus Protoleodora	152
- Protoleodora gracilis	154
- Protoleodora uschakovi	156
- Tribe Spirorbini	158
- Genus Spirorbis	158
- Subgenus Spirorbis	158
- Spirorbis (Spirorbis) corallinae	160
- Spirorbis (Spirorbis) inornatus	162
- Spirorbis (Spirorbis) rupestris	164
- Spirorbis (Spirorbis) spirorbis	166
- Spirorbis (Spirorbis) tridentatus	168
References	170
Index	181

#### 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 ventral to dorsal in the abdomen, while the chaetae switch from dorsal in the thorax to ventral 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 nested inside 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., 2007; 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 spirorbids sub-families 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.).

The Arctic Ocean, smallest of the world's oceans, centres approximately on the North Pole, covers much of the Arctic and washes upon northern North America and Eurasia. It is connected to the Pacific Ocean by the Bering Strait and to the Atlantic Ocean through the Greenland Sea and Labrador Sea, and is sometimes regarded as an estuary of the Atlantic Ocean. A number of opinions exists regarding the exact borders of the Arctic Oean. Here we accept the opinion of Makkaveev (2005) that the line separating the Atlantic and Arctic Oceans goes along the entrance to Hudson Strait and through Davis Strait along 70°N from Baffin Island to the west coast of Greenland; then through the Denmark Strait from Cape Brewster on the east coast of Greenland to the Reydinupyur Point on the west coast of Iceland and along the Icelandic northern coast to Gerpir Point on the east. From Iceland the demarcation line goes to the Faroe Islands, passes north of Shetland Islands and then along 61°N to the Norwegian coast. The border of Arctic and Pacific Oceans passes through the Bering Strait from Cape Dezhnev to Cape Prince of Wales.

#### **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 (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 the feeding position. Tubes are usually chalky (**opaque**) white with rough or more or less smooth surface or white with smooth shining (porcellaneous) surface; rarely tubes may be completely or partially semitransparent because of the thin wall. Completely transparent tubes are termed **vitreous**.

Although tubes are mostly white, they may be completely or partly pink, bluish, orange purple, mustard, or even white with dark-brown transverse stripes. In spirorbins with vitreous tubes the inner tube lining or body of live specimens may be visible through tube walls, thus making the tubes appear coloured.

Spirorbins live in small spiral (hence the name) tubes 1.5–4 (up to 8) mm in coil diameter. Normally the spirals are flat, but the distal parts may be uncoiled and raised above the substrate, whorls being positioned on top of each other or attached to the substrate, not forming a spiral. Spirorbin tubes may be coiled clockwise (**sinistral**) or counter clockwise (**dextral**). 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 dextral) have specimens with opposite coiling directions. Dextral forms have never been recorded for typically sinistral species.

In other 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. No-table exceptions are the free-living *Ditrupa* (one species is known from the Arctic) and some deep-sea taxa.

Serpulid tubes are usually circular or sub-circular in external cross-section. Longitudinal **keels** usually do not change the tube cross-section, but some species may have triangular, quadrangular, pentangular or even octangular cross-sections. Within a single tube changes may occur from trapezoidal to multiangular or from triangular respectively trapezoidal/semi-circular to circular.

The external ornamentation (**sculpture**) of the tube surface typically consists of **longitudinal** and **transverse** elements. A single major prominent **keel**  (often termed **longitudinal ridge** in spirorbins) or several identical keels may be present. 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.

Transverse tube ornamentation in spirorbins may be presented by growth lines (**transverse striations**) 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, 1993d. Sculpturing may differ between the free distal and attached proximal parts of a tube. Tube surface may also be completely or partially pitted by numerous **alveoli**, that may completely perforate tube keels in *Neodexiospira* spp. **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** and may also contain alveolar structures.

Genera such as *Salmacina* and *Filograna* (formerly Filograninae) build characteristic aggregations (often incorrectly termed **colonies**) made of numerous branching tubes. These aggregations are 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 (Fig. 1A); 2) Embryo positioned in a sac fixed to the thorax or to the abdomen by an epithelial stalk – Romanchellini (Fig. 1B); 3) Embryos adhering to each other and directly to the internal tube wall – Circeini (Fig. 1C); 4) Embryo string attached posteriorly to the internal tube wall by a filament – Spirorbini (Fig. 1D). Opercular brooding: 1) Embryos brooded in the re-usable **brood chamber** formed by invagination of the operculum – Pileolariini (Fig. 1E); 2) 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. 1F-G). Only the species of the Spirorbini, Circeini, Pileolariini and Januini are found in the Arctic.

While many non-spirorbin serpulids are free-spawners with feeding larvae, some brood embryos inside the tube (e. g., *Filograna*), in various tube ovicells (*Chitinopoma*), inside the radiolar crown, in pockets of the thoracic



**Figure 1**. Embryo incubation in Spirorbinae. A – Paralaeospirini; B – Romanchellini; C – Circeini; D – Spirorbini; E – Pileolariini; F, G – Januini. A – from Knight-Jones P., Walker (1972), B-E from Knight-Jones P., Vine (1972), F, G – from Okuda, 1934.

membranes, and in a gelatinous mass near the tube mouth (*Protula*), etc. (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., see Knight-Jones P., Fordy, 1979, fig. 1, 3). The thoracic region of spirorbins is turned to the substrate by the dorsal side (bearing notochaetae), 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 taxonomic little 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 part of thorax and achaetigerous zone on the side facing the substrate has iridescent crystalline red, pink, purple patches 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. 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**. 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.

**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*), although normally operculate genera may include non-operculate species (e.g., *Spirobranchus*) and normally non-operculate genera may include operculate species (e.g., *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*) or spoon-shaped (e.g., *Filograna*) to very elaborate. The operculum mostly consists of a basal bulbous part (**ampulla**) and a distal part often reinforced with chitinous **endplate**. The chitinous endplates may be additionally reinforced by calcareous deposits, sometimes with non-movable spines (e.g., *Spirobranchus*). 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* and *Serpula* are composed of numerous **radii** and covered with a thickened **cuticle**. While the operculum in species of *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. The talon size varies from poorly developed to very long continuing into the opercular **peduncle**; the talon shape is often species-specific. Only several spirorbins species have non-calcified endplate or lack talon.

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.

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, Protoleodora* and *Bushiella*). In *Protoleodora* the primary operculum remains attached to the distal part of the brood chamber only with the distal talon end and is easily separated. 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 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.

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. 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)). 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* and *Serpula* are characterized by a **pseudoperculum**, a club-shaped underdeveloped operculum carried on a short rudimentary radiole on the side of the opercular 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.

**Opercular peduncle.** In some genera the radiole that bears the operculum is identical to other radioles, e.g., *Filograna, Apomatus*, and *Protis*. In most

other serpulids and in all spirorbins 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 thin peduncle as wide as the normal radioles. The peduncle may gradually merge into the basal opercular ampulla or be separated from it by a **constriction**. 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.

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 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*). 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.

**Collar and 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) probably did not distinguish between the thoracic membranes and the collar, but used the term "collar" 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 in most non-spirorbins. 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*). The collar chaetage are absent e.g., in *Ditrupa*, *Placostegus*, and some *Spirobranchus*.

The latero-dorsal collar lobes continue into the **thoracic membranes** that they may be ending at the second thoracic chaetiger (e.g., *Chitinopoma serrula*), reach the mid-thorax (e.g., *Vermiliopsis*), or continue throughout the length of the thorax and end posterior to the last thoracic segment (e.g., *Protis arctica*). Thoracic membranes continuing past the end of the thorax often fuse ventrally over the first abdominal segment(s), forming the **apron**, e.g., *Serpula*, *Hydroides*, *Protula* and *Spirobranchus*. In non-spirorbin genera, margins of thoracic membranes are fused dorsally only in *Ficopomatus uschakovi*(Pillai, 1960).

In spirorbins collar and thoracic membranes are usually with free dorsal (the side facing the substrate) margins, 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 and continue to the last thoracic segment and fuse ventrally forming 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.

**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. *Neomicrorbis* is a questionable spirorbin, has up to 7 thoracic segments and probably belong any other serpulid subfamilies) All Arctic species have three or four 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 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 wide than the shaft and is gradually narrowing distally. Capillary chaetae are smaller than limbate; they are gradually narrowing 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. 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, probably, are 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, Hydroides); 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, Protis); 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); 4) The last 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 (see 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) are the same as fin-andblade chaetae of other serpulids, with a distinct basal fin clearly separated from the limbate blade; 2) with distal only modification (cross-striated chaetae) found only in spirorbins (e.g., Paradexiospira (P.) violacea); the blades of these chaetae are bent and have denticles organized into distinct long transverse rows; under a compound microscope this looks like a crossstriation; 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 and asymmetrical, when the rows are present only on the one "lateral sides" of chaetal blade (e.g., Circeis spirillum). Unusual modified strongly bent collar chaetae 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); 3) chaetae with both distal and basal modifications include fin-and-blade cross-striated chaetae having 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*, *Paradexiospira* (*Spirorbides*) *vitrea*), or vestigial (e.g., *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. *Neodexiospira pseudocorrugata* (Bush, 1905), 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. These chaetae, termed "*Apomatus*" chaetae (or sickle chaetae in spirorbins), 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 third 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 anterior tooth), 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 the structure of the anterior tooth is very variable. A pointed anterior tooth is termed **fang** in serpulid genera such as e.g., *Filograna, Hydroides, Serpula* 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.

**Abdomen.** The number of abdominal segments is very variable depending on size of the animals; 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*, and *Serpula* 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); 2) flat triangular- with a knee-like bend and with dentition on the outside of a wide triangular distal blade (e.g., Chitinopoma); 3) flat narrow geniculate - as 2), but with more elongated not so sharply bent blade (e.g., Bathyvermilia).

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

#### A.V. Rzhavsky E.K. Kupriyanova A.V. Sikorski

# FIELD GUIDE TO CALCAREOUS TUBEWORMS (POLYCHAETA, SERPULIDAE) OF THE ARCTIC OCEAN

Moscow: KMK Scientific Press, 2018. 187 p.