

## **Tube morphology, ultrastructures and mineralogy in recent Spirorbinae (Annelida: Polychaeta: Serpulidae). I. General introduction. Tribe Paralaeospirini**

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**ABSTRACT:** This report is the first part of a series of papers that provide an overview of tube morphology, mineralogy, and ultrastructures within the subfamily Spirorbinae, including the discussion of taxonomic and phylogenetic significance of the tube features. This paper reviews published data on the subject and provides descriptions of ultrastructure and mineralogy for the tribe Paralaeospirini Knight-Jones, 1978. The species of the tribe have uniformly simple calcitic unilayered tubes of the same irregularly oriented prismatic (IOP) ultrastructural type, which is regarded as plesiomorphic among serpulids.

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**KEY WORDS:** Tube ultrastructures, tube morphology, tube mineralogy, scanning electron microscopy, X-ray diffraction analysis, Spirorbinae, Paralaeospirini.

## **Морфология, ультраструктуры и минералогия трубок современных Spirorbinae (Annelida: Polychaeta: Serpulidae). I. Общее введение. Материал и методы. Триба Paralaeospirini**

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**РЕЗЮМЕ:** В настоящей серии статей приводится обзор морфологического, ультраструктурного и минералогического разнообразия трубок подсемейства Spirorbinae, а также обсуждается возможное таксономическое и филогенетическое значения признаков трубок. В первой части серии мы приводим обзор опубликованных данных, а также даем описания морфологии трубок, их ультраструктур и минералогии для трибы Paralaeospirini Knight-Jones, 1978. Установлено, что виды, представляющие трибу, имеют однослойные кальцитовые трубки из хаотически ориентированных призматических кристаллов. Данный тип строения трубок интерпретируется как архаичный для серпулид.

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КЛЮЧЕВЫЕ СЛОВА: Ультраструктура трубок, морфология трубок, минералогия трубок, сканирующая электронная микроскопия, рентгенодифракционный анализ, Spirorbinae, Paralaeospirini.

## Introduction

Subfamily Spirorbinae of the family Serpulidae Rafinesque, 1815 is a widely distributed group of small marine polychaetes that inhabit calcareous tubes tightly coiled into spirals and attached to a variety of substrata. Recent spirorbins have world-wide distribution ranging from littoral to abyssal depths, but are most commonly found in the sublittoral zone.

Family Serpulidae was traditionally subdivided into subfamilies Spirorbinae Chamberlin, 1919, Serpulinae Rafinesque, 1815, and Filograninae Rioja (1923) (e.g., Rioja, 1923; Fauvel, 1927). Pillai (1970) elevated Spirorbinae to the family status, which was accepted both in Recent and fossil taxonomy (e.g., Knight-Jones P., Fordy M., 1979; Lommerzheim, 1981; Jäger, 1993, 2005; Rzhavsky, 1994). Later numerous authors (e.g., ten Hove, 1984; Smith, 1991, Kupriyanova, 2003; Kupriyanova et al., 2006; Lehrke et al., 2007), based on the results of phylogenetic analyses of morphological and molecular data, concluded that spirorbins constitute a monophyletic group nested inside the Serpulidae. Therefore, the rank of the spirorbids was lowered to the subfamily and all former subfamilies established within Spirorbidae (see Knight-Jones P., Fordy, 1979) became tribes (Rzhavsky et al., 2013). The current state of classification of Spirorbinae that includes 6 tribes, 24 genera, and 131 (135?) species is summarized in Table 1.

***Spirorbin fossil record.*** Spirorbins calcareous tubes have a good potential to fossilize, providing a basis for substantial fossil record for these polychaetes. Contrary to the long-held view (e.g., Goldfuss, 1831; Zittel, 1880; Howell, 1962; Pillai, 1970; Lommerzheim, 1979,

1981; Jäger, 1983, 1993) that spirorbins are an ancient group dating back to the Ordovician period (~445–485 Ma<sup>1</sup>), true spirorbins seem to appear from the Latest Jurassic or Earliest Cretaceous (~145 Ma: see Taylor, Vinn, 2006). Non-spirorbin nature of more ancient Paleozoic to Early Mesozoic tubes, which look undistinguishable from spirorbins by external morphology, was recognized by morphology of their internal septae (Burchette, Riding, 1977), study of tube microstructures (Burchette, Riding, 1977; Weedon, 1990, 1991) and comparison with those of Recent forms (Weedon, 1994; Taylor, Vinn, 2006). These ancient fossils are now placed not only outside Spirorbinae, but also outside the phylum Annelida (see Vinn, Taylor, 2007).

During the Cretaceous period (145–66 Ma), coiled serpulids attributed to spirorbins were represented mostly by the large-sized and peculiar genus *Neomicrorbis* Rovereto, 1903. The most ancient finds of this genus are described from the Late Barremian (~128 Ma; Jäger, 2011), but finds of somewhat similar tubes are more ancient (see Jäger, 1983, 1993, 2011). *Neomicrorbis* tubes, unlike most spirorbins, are coiled in any direction and often have characteristic sculpture of numerous rows of tiny tubercules. Information on the body morphology available from the only known Recent species *Neomicrorbis azoricus* Zibrowius, 1972 (Zibrowius, 1972; Hove, Kupriyanova, 2006) does not allow to make a certain conclusion about its phylogenetic position inside Serpulidae.

Unquestionable spirorbin species that appeared in the middle of the Early Cretaceous

<sup>1</sup> Absolute ages are provided according to official site of the International Commission of Stratigraphy ([www.stratigraphy.org/GSSP/index.html](http://www.stratigraphy.org/GSSP/index.html)), accessed 01-03-2013.

Table 1. Compiled classification of Recent spirorbins, including tribes, genera and number of valid species. Some species of uncertain generic affinity are not considered in the table.  
 Таблица 1. Классификация современных спирорбин (трибы, рода и число валидных видов).  
 Некоторые виды неясной родовой принадлежности не учтены.

Tribe	Genus	Number of species
Paralaeospirini Knight-Jones, 1978	<i>Paralaeospira</i> Caullery et Mesnil, 1897	10
<i>Incertae sedis</i> (Paralaeospirini?)	<i>Anomalorbis</i> Vine, 1972	1
	<i>Crozetospira</i> Rzhavsky, 1997	1
Spirorbini Chamberlin, 1919	<i>Spirorbis</i> Daudin, 1800	15
Circeini Knight-Jones, 1978	<i>Circeis</i> Saint-Joseph, 1894	6
	<i>Paradexiospira</i> Caullery et Mesnil, 1897	3(4?)
Romanchellini Knight-Jones, 1978	<i>Eulaeospira</i> Pillai, 1970	2
	<i>Helicosiphon</i> Gravier, 1907	1
	<i>Knightjonesia</i> Pillai, 2009	1
	<i>Metalaeospira</i> Pillai, 1970	4
	<i>Protolaeospira</i> Pixell, 1912	12
	<i>Romanchella</i> Caullery et Mesnil, 1897	8
Januini Knight-Jones, 1978	<i>Janua</i> Saint-Joseph, 1894	1
	<i>Leodora</i> Saint-Joseph, 1894	1
	<i>Neodexiospira</i> Pillai, 1970	10(11?)
	<i>Pillaiospira</i> Knight-Jones, 1973	3
Pileolariini Knight-Jones, 1978	<i>Amplicaria</i> Knight-Jones, 1984	1
	<i>Bushiella</i> Knight-Jones, 1973	13(14?)
	<i>Nidificaria</i> Knight-Jones, 1984	8
	<i>Pileolaria</i> Claparède, 1868	21(22?)
	<i>Protoleodora</i> Pillai, 1970	4
	<i>Simplaria</i> Knight-Jones, 1984	3
	<i>Vineararia</i> Knight-Jones, 1984	3
<i>Incertae sedis</i>	<i>Neomicrorbis</i> Rovereto, 1903	1

(Late Barremian; ~126 Ma; Jäger, 2011) are represented by tubes, morphologically comparable with those of extant species of genera *Pileolaria* and *Neodexiospira*. From the latest Cretaceous (Late Maastrichtian; ~66 Ma) spirorbins became a very common element of encrusting communities (e.g., Jäger, 1983, 1993). Younger Paleogene (Paleocene, 62–59 Ma; Lommerzheim, 1981) and especially Neogene (like Badenian, 16–13 Ma; Radwańska, 1994, etc.) sediments already contain highly diversified spirorbini communities similar to Recent ones.

Classification of Recent spirorbins is currently built around the methods of embryos incubation, as well as body and chaetal characters, while tubes are mostly neglected. This approach walls off paleontologists who work predominantly with tubes and rarely calcified opercula. In non-spirorbini serpulids tube mor-

phology is less uniform and better studied to allow classification of fossil species within Recent genera (see Jäger, 1993, 2005), while for spirorbini determination of generic affinity based on empty tubes remains problematic. As a result, despite existing fossil record, zoologists still have no reliable paleontological data for understanding evolutionary history of the group, while paleontologists are restricted in their geological, paleoecological, and biogeographical interpretations because no direct comparison of fossils with Recent taxa is possible. If determinations of fossil spirorbini tubes from Late Barremian (~126 Ma) are correct, this means that two of the Recent tribes characterized by complex incubation methods (Pileolariini and Januini) have already established in the middle Early Cretaceous, suggesting that the main diversification of spirorbini should take place before.

***Tube ultrastructures and mineralogy and their potential in decrypting paleontological record.*** Serpulid tube ultrastructural diversity has a good potential for decrypting their paleontological record. It became obvious as a result of the early studies (Bohnné Havas, 1981; Bubel et al., 1983; Bandel, 1986; ten Hove, Zibrowius, 1986; Zibrowius, ten Hove, 1987) that calcium carbonate crystals of the tube wall may have a variety of shapes and sizes, and may be arranged in different ways. Studies over the last two decades revealed outstanding ultrastructural diversity in serpulid tubes (e.g., Nishi, 1993; Sanfilippo, 1998a,b, 2001; Vinn, 2005, 2007, 2008; Vinn et al., 2008a), which is currently classified into 13 ultrastructural types (Vinn et al., 2008a,b).

The idea to evaluate generic affiliation of fossil serpulid species using tube ultrastructures was first proposed by Sanfilippo (1998b). In Recent forms tube transparency can be a result of certain ultrastructural characters (ten Hove, Zibrowius, 1986; Ippolitov, Rzhavsky, 2008; Vinn et al., 2008a; Vinn, Kupriyanova, 2011); in one case such tube wall ultrastructure was included into the diagnosis of species [*Placostegus tridentatus* (Fabricius, 1780), see Sanfilippo, 2003]. Vinn et al. (2008a), who have analyzed the largest set of tubes scattered among serpulid genera, concluded that ultrastructure is more likely to be a specific character rather than a generic one. This assumption devaluates ultrastructures as a tool for determining generic affinity of fossils. However, some outline of evolutionary interrelations of different ultrastructural types can be provided (e.g., Vinn et al., 2008a; Vinn, Kupriyanova, 2011; Vinn, 2013), and together with fossil record analysis, this approach can be used for decrypting the evolutionary interrelations of major clades (*sensu* Kupriyanova et al., 2009) within Serpulidae. Tube ultrastructures in some serpulids have been also shown to have adaptive significance (Vinn et al., 2008a,b; Tanur et al., 2009; Vinn, Kupriyanova, 2011), but these investigations do not provide any connections to taxonomy for the moment. The approach of a systematic analysis of ultrastructural diversity within closely related groups of species adopted in this inves-

tigation has not been previously applied to any serpulid genera, and can potentially shed light on the problem of empty tube generic affiliation.

Mineralogical investigations, in particular, estimating the calcite-aragonite ratio of serpulid tubes, received little attention. Lowenstam (1954) has shown that calcium carbonate of serpulid tubes may be represented by calcite, aragonite, or their mixture. The first comprehensive overview of serpulid tube mineralogy was presented by Bornhold and Milliman (1973) who analyzed over 100 specimens belonging to 30 species from 15 genera. Their results showed no correlations of mineralogical composition with temperature, and also no correlations were found with taxonomic groups (genera). Moreover, calcite-aragonite ratio significantly varied not only among, but also within species, and even within a single tube (Bornhold, Milliman, 1973). Vinn et al. (2008a) has demonstrated some correlations of mineralogy with ultrastructural types, but no clear correlations with taxonomy (genera) were found. The most recent comprehensive analysis (Smith et al., 2013) of both published and new data has shown that phylogenetic factor is the most important for understanding tube mineralogy. Like in case of ultrastructures, mineralogical composition of tubes shows more or less clear correlations with large clades of Serpulidae *sensu* Kupriyanova et al. (2009).

***Spirorbin tube ultrastructures and mineralogy.*** All the ultrastructural and mineralogical investigations so far covered mainly non-spirorbin Serpulidae. Spirorbin ultrastructures were not included in most extensive overview of serpulid tubes by Vinn et al. (2008a). The only paper focused on Spirorbinae was published by Ippolitov and Rzhavsky (2008). A list of spirorbin species with published and figured tube ultrastructures counts eight Recent species, which are not always correctly identified:

1. *Neodexiospira* sp., probably *Neodexiospira foraminosa* (Bush in Moore et Bush, 1904); originally determined as *Janua steueri* (Sterzinger, 1909) (see Nishi, 1993, Fig. 1F).

2. *Spirorbis* cf. *rupestris* Gee et Knight-Jones, 1962 (see Weedon, 1994, Fig. 3; in fact it is probably not a true *Spirorbis*).

3. *Spirorbis spirorbis* (Linnaeus, 1758); also fossil material (Early Pleistocene; 1.8–1 Ma) from Mediterranean region was studied (see Sanfilippo, 1998a, Pl. 2).

4. *Spirorbis* sp. (see Taylor, Vinn, 2006, Fig. 1D; can be identified only as “Spirorbinae sp.”).

5. *Spirorbis rothlisbergi* Knight-Jones, 1978 (see Ippolitov, Rzhavsky, 2008, Fig. 1a).

6. *Protolaeospira (Dextralia) stalagmia* Knight-Jones et Walker, 1972 (see Ippolitov, Rzhavsky, 2008, Fig. 1c).

7. *Protolaeospira augeneri* Vine, 1977 (see Ippolitov, Rzhavsky, 2008, Fig. 1d).

8. *Protolaeospira uschakovi* Knight-Jones, 1984 (see Ippolitov, Rzhavsky, 2008, Fig. 1b).

Nishi (1993, tab. 1) provided crystal measurements for one more species, “*Pileoralia* [sic!] *giridis*” (probably = ?*Pileolaria* sp.; name unknown in literature), but has not accompanied them with any description or figure. Five more specimens of *Spirorbis* spp., without further specification, ranging from Pliocene to Recent, have been only referred to have “fine-grained” tubes (Taylor, Vinn, 2006). Also, two species of Recent “*Spirorbis* spp.” (Weedon, 1994) and a fossil species from the Early Santonian (~86 Ma) of UK mentioned as “*Spirorbis plana* (Woodward)” [probably should be referred to *Neomicrorbis crenatostriatatus subrugosus* (Münster in Goldfuss, 1831)] were stated to have studied ultrastructures (Taylor, Vinn, 2006); however, no descriptions or figures were provided.

Most authors found spirorbins to have simple unilayered tubes consisting of ricegrain-like crystals, oriented chaotically. But it also was shown (Ippolitov, Rzhavsky, 2008) that like in serpulids inner and outer tube surfaces are often strengthened by different types of ultrastructures, providing consolidation of the tube wall — “dense layers” *sensu* Vinn and Kupriyanova (2011). The main conclusion of Ippolitov, Rzhavsky (2008) was that spirorbins tube ultrastructures are not uniform. After the diversity of Recent non-spirorbins serpulids became known

(Vinn et al., 2008a,b), it should be stated that spirorbins ultrastructural diversity is comparable with that of other serpulids. Both in non-spirorbins serpulids and spirorbins, studies of tube ultrastructures can potentially become useful for estimating generic affiliations.

Mineralogical data on spirorbins tubes are also scarce. Bornhold and Milliman (1973) mention two specimens of *Spirorbis borealis* Daudin, 1800 (junior objective synonym of *Spirorbis spirorbis* (Linnaeus, 1758)). One of them was found to be pure calcitic, while another had 10.5% aragonite content. Neither data on accuracy of the analysis, nor any morphological characteristics confirming the determinations are available.

**Objectives of study.** The aims of the present investigation are 1) to provide comprehensive descriptions of mineralogy and ultrastructures of spirorbins tubes covering as many Recent species as possible and 2) to examine potential correlations of ultrastructural and mineralogical characters with taxonomic groups, tube morphology, as well as with ecological and biogeographical patterns.

The results of our study will form a series of papers, each of them dealing with a tribe of Spirorbinae. Tribes will be presented in the order of growing complexity of their brooding methods (Paralaeospirini → Spirorbini → Circeini → Romanchellini → Januini → Pileolarini), while genera within tribes and species within genera will be arranged in alphabetical order. Conclusions on each tribe, as well as corresponding discussions, will be provided in the relevant parts, while the extended general discussion will be published in the last paper of the series.

## Tube morphology and terminology

Spirorbins live in small tubes coiled into spirals 1.5–4 (up to 8) mm in diameter, attached to substrate and containing up to 5 coils. Normally the spirals are flat, but distal parts may be uncoiled (evolute) and raising above the substrate (Fig. 1C), with overlapping coils, or

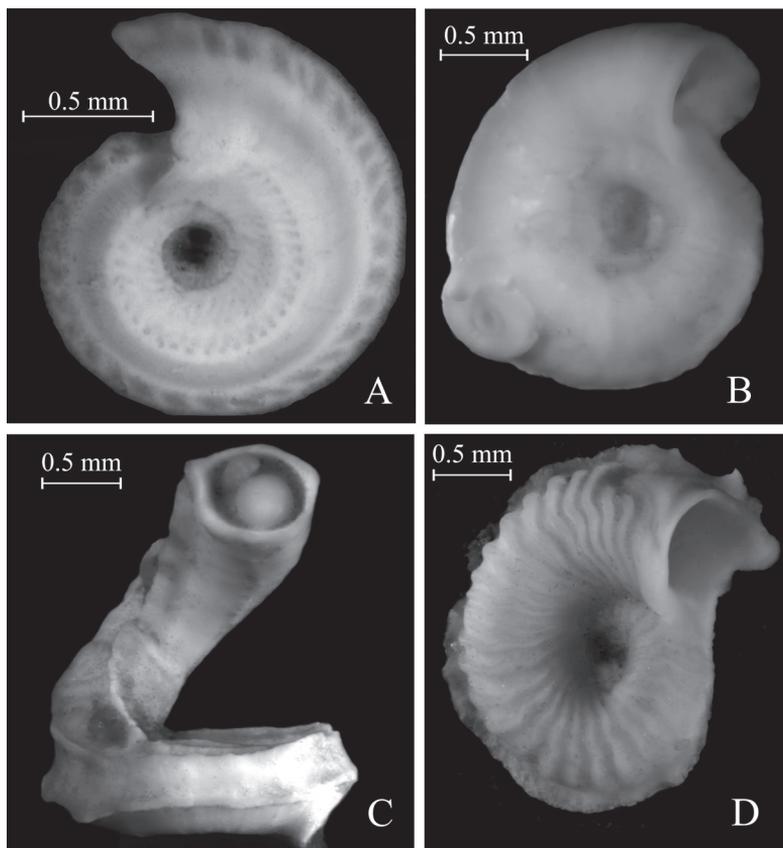


Fig. 1. External morphology of Spirorbinae tubes. A — *Neodexiospira alveolata* (Zachs, 1933): dextral (anticlockwise) tube with longitudinal keels and alveoli; B — *Bushiella (Jugaria) similis* (Bush, 1905): sinistral (clockwise) unsculptured tube; C — *Bushiella (Jugaria) kofiadii* Rzhavsky, 1988: sinistral (clockwise) tube with three longitudinal keels and tube mouth facing upward from substrate; D — *Protolaeospira eximia* (Bush, 1905): sinistral (clockwise) tube with transverse ridges.

Рис. 1. Внешняя морфология трубок спирорбин. А — *Neodexiospira alveolata* (Zachs, 1933): правозакрученная (против часовой стрелки) трубка с продольными киями и альвеолами; В — *Bushiella (Jugaria) similis* (Bush, 1905): левозакрученная (по часовой стрелке) нескульптированная трубка; С — *Bushiella (Jugaria) kofiadii* Rzhavsky, 1988: левозакрученная (по часовой стрелке) трубка с тремя продольными киями и приподнятым над субстратом устьем; D — *Protolaeospira eximia* (Bush, 1905): левозакрученная (по часовой стрелке) трубка с поперечными гребнями.

straight and attached to the substrate. Among completely attached forms, tubes may have all the coils well visible or the later coils may partly or completely cover the previous ones, resulting in hiding the entire spiral by the last coil (see Rzhavsky, 1994, Fig. 1G, J). Coiling direction can be clockwise (sinistral; Fig. 1B–D) or anticlockwise (dextral; Fig. 1A). To determine the direction of the coiling, tubes should be observed from the upper side, opposite the sub-

strate. Most species are known to have only one coiling direction, but tubes of several *Spirorbis* species may coil in either direction, and all species of *Neomicrobis* normally coil in either direction. Rarely, some Circeini and Januini (normally dextral) may have specimens with clockwise coiling, but dextral specimens have never been recorded among typically sinistral species.

Tubes may be unsculptured (Fig. 1B) or have external ornamentation (sculpture) on the

tube surface. Typically it consists of longitudinal (Fig. 1A, C) or transverse (Fig. 1B) elements. A single major prominent longitudinal keel or several parallel keels, often termed longitudinal ridges (usually 2–5, but up to 10 and even more in *Neomicrorbis*), may be present. The keels may either be sharp or obtuse, high or low, or have the appearance of longitudinal rows of larger denticles and smaller tubercles. In most cases all keels are equally developed, but often certain keels (usually the median one) can be better pronounced. Transverse tube ornamentation in spirorbins may be presented by regularly spaced transverse collar-like ridges, sometimes interpreted as growth stops. Also, in some spirorbins tube surface may be completely or partially pitted by alveoli (Fig. 1A) that sometimes completely perforate keels. Attached tube parts often produce flattened peripheral flanges that also may contain regularly spaced alveolar structures.

Tubes are usually chalky white (opaque), rarely they may be completely transparent (vitreous) or partially transparent (semitransparent) or somewhat transparent, the last state is probably caused by the low thickness of the wall. In spirorbins with vitreous tubes the coloured inner lining of the tube or the body of live specimens may be seen through tube walls. The tube surface may be rough, more or less smooth, or smooth with shining (porcellanous) outer layer.

### Terminology of ultrastructures

We follow the classification of ultrastructures and their terminology developed for Recent serpulids by Vinn et al. (2008a) and based on classification of carbonate ultrastructures by Carter et al. (1990). They distinguish 12 types of ultrastructures arranged in 1 to 4 wall layers, and one additional type was described separately (Vinn et al., 2008b). These types are usually referred to by abbreviations of their full names.

The term “parabolic structure” widely used in older paleontological literature (= “chevron” structure of Weedon (1994)) was transformed in Vinn’s papers into “parabolic growth lines” or “parabolic lamellae”. Because the configura-

tion of growth lines does not correlate with appearance of crystals, and thus, cannot be interpreted as a character related to ultrastructure, therefore, we follow Vinn’s suggestion.

The term “layer” in application to serpulid tubes needs some clarification. It is not always possible to distinguish layers within the wall based on different amount of amorphous cement, as was proposed by Vinn et al. (2008a: 643). In such case, multiple contradictive interpretations of layers number become possible, depending, for example, on the method of study. Also, crystal appearance can gradually change within a wall (Vinn et al., 2008a; and below), forming slight transitions from one “layer” to another. In the present series we use term “layer” only for well-delimited longitudinally structural elements, distinguishable by the certain shape and/or size of crystals, while in all other cases more neutral terms “outer”, “middle” and “inner part/zone” of the wall/layer are used. This terminology is consistent with that of Weedon (1994).

### Material and methods

The study is based on a collection of spirorb- in tubes made by A.V. Rzhavsky and deposited in A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow (IPEE RAS). Two specimens of *Neomicrorbis azoricus* were obtained from the collections of P.P. Shirshov Institute of Oceanology of Russian Academy of Sciences, Moscow (SIORAS). Although the tubes studied with scanning electron microscopy (SEM) and analyzed for mineralogy have been destroyed, conspecific tubes from the same samples are available in the collection. Over 750 SEM microphotographs and 70 X-ray diffraction diagrams were obtained and analyzed, and a number of photographs of tubes were taken to illustrate external tube morphology.

For the SEM dried tubes were cracked mechanically and covered with a thin layer of gold or platinum. We used longitudinal sections running along the lateral sides of the tube. This direction of sectioning allows observing para-

bolic growth lines (“parabolic lamellae”, “chevrons” *sensu* Weedon, 1994). For most species we studied both external (outside the whorl) and internal (near the centre of whorl) walls of the tube, however, descriptions are primarily based on longitudinal sections of the external wall, which are the most informative. In some species tube cross sections were also studied. No special etching techniques were used to prepare sections. Although sections are often embedded into epoxide resin with subsequent polishing and etching, both literature (Bohnné Havas, 1981; Weedon, 1994) and our comparative etching trials using four agents (hydrogen peroxide, Javel water, formic acid and acetic acid) showed that thin details of ultrastructure, such as crystal appearance, are better seen in simple fractures than in polished etched material. Sections were observed using a CamScan electron microscope in the Office of Instrumental Analytics of Paleontological Institute of Russian Academy of Sciences, Moscow (PIN RAS) and a Vega-Tescan microscope in the Electron Microscopy Laboratory of IPEE RAS (Moscow). In total, tubes of over 70 species from all 6 Spirorbinae tribes were studied with SEM, thus, covering 53% of total Recent spirorbin richness. When possible, we examined several specimens of each species to assess potential intraspecific variability of ultrastructures.

For X-RAY diffraction analysis spirorbin tubes pounded into powder were analyzed with an X-ray diffractometer DRON-3M in the laboratory of the Geological Faculty of Moscow State University (GF MSU). Signal was analyzed in the interval  $30\text{--}36^\circ 2\theta$  with step  $0.1^\circ$ , containing major peaks of both calcite ( $34.35^\circ 2\theta$ ; corresponding spacing between diffracting planes  $d=3.04$  Å) and aragonite ( $31.00^\circ$  and  $31.65^\circ 2\theta$ ; corresponding spacing between diffracting planes  $d=3.40$  Å and  $d=3.29$  Å, respectively). Calcite/aragonite ratio was calculated using Ca/Ar main peak intensity ratio, and high Mg content of calcite in several cases was estimated visually by the shift of the peak to dolomite ( $3.00\text{--}3.01$  Å), with no further calculations because of insufficient amount of the material. To demonstrate the reliability of the data, we

provide values of absolute intensity (I) of reflection peaks. If the intensities of calcite ( $I_{\text{calc}}$ ) and/or aragonite ( $I_{\text{arag}}$ ) major peaks are close to the background intensity ( $I_{\text{bgr}}=5\text{--}6$ ), the calculations of calcite/aragonite ratio for corresponding sample are unreliable.

Because most spirorbins are small, the quantity of powder obtained from a single tube often falls somewhere around the edge of the diffractometer resolution ability. To improve data reliability, in most cases we had to analyze calcite-aragonite ratios averaged over a set of specimens. Yet, for some species the quantity of available material was insufficient even for such kind of analysis, so our mineralogical study covered only about 80% of species studied with SEM. Exact quantity of powder studied in each case differed depending on material availability for each species, thus affecting reliability of analysis for each case. For several species, two independent samples were taken: one based on a single specimen, another averaged over several specimens.

For illustration of tube morphology spirorbins tubes were photographed with a digital camera DFC295 under microscope Leica MZ6 by method of sequential layers. Helicon Focus software was used for merging differently focused images.

## Results

### Tribe Paralaeospirini Knight-Jones, 1978

**Diagnosis.** The egg-string is incubated in the parent's tube, being neither attached to the tube wall, nor to the body of a parent; accordingly, the only type of operculum throughout life time is an endplate, usually with a talon. Other characteristic features are: 1) narrow saw to rasp-shaped thoracic uncini, each starting with one row of large teeth posteriorly and ending with 3 rows of large teeth in front of blunt anterior peg; 2) abdominal uncini distributed asymmetrically: they are absent from the convex side of body, or present only on last chaetigers; 3) abdominal chaetae are flat geniculate, pennant-shaped (blade width decreases gradu-

ally towards tip), usually with a thick projecting heel; the length of their blade is no longer than blade length of largest collar chaetae; 4) abdominal companion capillary hooked chaetae may be present only on last abdominal chaetigers; 5) larvae are without white attachment glands.

**Remarks.** The tribe unconditionally contains the only genus *Paralaeospira* Caullery et Mesnil, 1897. Genera *Metalaespira* Pillai, 1970 and *Eulaespira* Pillai, 1970 initially included in Paralaeospirini (Knight-Jones, Fordy, 1979; Knight-Jones P. et al., 1979) incubate embryos in the sac attached to the body, have brush-type abdominal chaetae and therefore, belong to the tribe Romanchellini (Knight-Jones P., Knight-Jones E.W., 1994).

Two monotypic genera *Anomalorbis* Vine, 1972 and *Crozetospira* Rzhavsky, 1997, with yet unknown incubation method, were originally placed within Paralaeospirini provisionally. Therefore, only tubes of *Paralaeospira* are discussed here, while tube ultrastructures of *Crozetospira dufresnei* Rzhavsky, 1997 will be described in subsequent papers, among other spirorbins of uncertain tribe attribution. Material on *Anomalorbis* was not available for our study.

**Distribution.** Mostly south temperate belt and Antarctic (Knight-Jones P., Knight-Jones E.W., 1984), though *P. malaridi* is known only from boreal waters of north-eastern Atlantic (Knight-Jones P., Knight-Jones E.W., 1977; Knight-Jones P. et al., 1991).

### Genus *Paralaeospira* Caullery et Mesnil, 1897

**Type species:** *Spirorbis (Paralaeospira) aggregata* Caullery et Mesnil, 1897

**Diagnosis.** Sinistral tubes; margins of collar and thoracic membranes not fused over thoracic groove; large collar chaetae bent, with basal fins and distal serrated blades without cross-striation; simple limbate and sickle chaetae in 3<sup>rd</sup> thoracic fascicles; four thoracic chaetigers.

**Composition.** The genus includes 10 species, four of which are covered in the present study.

**Distribution.** As for the tribe.

### *Paralaeospira claparedei* Caullery et Mesnil, 1897

Fig. 2A–D.

For descriptions see Caullery, Mesnil, 1897: 204, Pl. VIII, fig. 10 (as "*Spirorbis (Paralaeospira) claparedei*"); Harris, 1969: 142–145, fig. 4 a–l (as "*Spirorbis claparedei*").

**Material examined.** Two specimens were examined with SEM in longitudinal sections (IPEE No. 3/2562, Magellan Strait, shallow water, on *Macrocystis* fronds). Mineralogy was analyzed by a single tube from the same sample. Outer tube morphology was illustrated for specimens from the same sample and from IPEE No. 1/2536 (Prince Edward Islands, depth 110 m, on bryozoans).

**Tube morphology.** Tubes are sinistral, planospiral (Fig. 2A) or with overlapping coils (Fig. 2B), tube mouths may be facing upward from substrate (Fig. 2C). Whorl diameter is up to 2.5 mm. Tube walls are thin and fragile, white opaque or somewhat transparent, non-porcellanous or slightly porcellanous. Tube surface is smooth, unsculptured; specimens attached to algae may produce peripheral flange (Fig. 2B).

**Tube ultrastructures.** Wall is unilayered, with irregularly oriented prismatic (IOP) structure. Two studied specimens have slightly different appearance of crystals in tube wall. One demonstrates isometric small crystals 0.5–0.75  $\mu\text{m}$  long mixed with some cement in inner part of the wall, gradually turning to slightly elongated angular crystals up to 1–2  $\mu\text{m}$  long and 0.7–1.2  $\mu\text{m}$  wide in the outer part; total wall width in the same section is 32–35  $\mu\text{m}$ . A section obtained for another specimen (Fig 2D) shows mostly elongated crystals of 2–3  $\mu\text{m}$  long mixed with a small amount of cement, except for innermost zone, where crystals are small and isometric; corresponding total wall width is 35–40  $\mu\text{m}$ . Crystal shapes are angular in both studied specimens. Distinct growth lamellae are absent, but at least one area with unclear orientation of elongated crystals along growth lines was observed (Fig. 2D). Inner organic lining is thin (not exceeding 1  $\mu\text{m}$ ).

**Tube mineralogy.** 100% calcite ( $I_{\text{calc.}}=32$ ) with high Mg content.

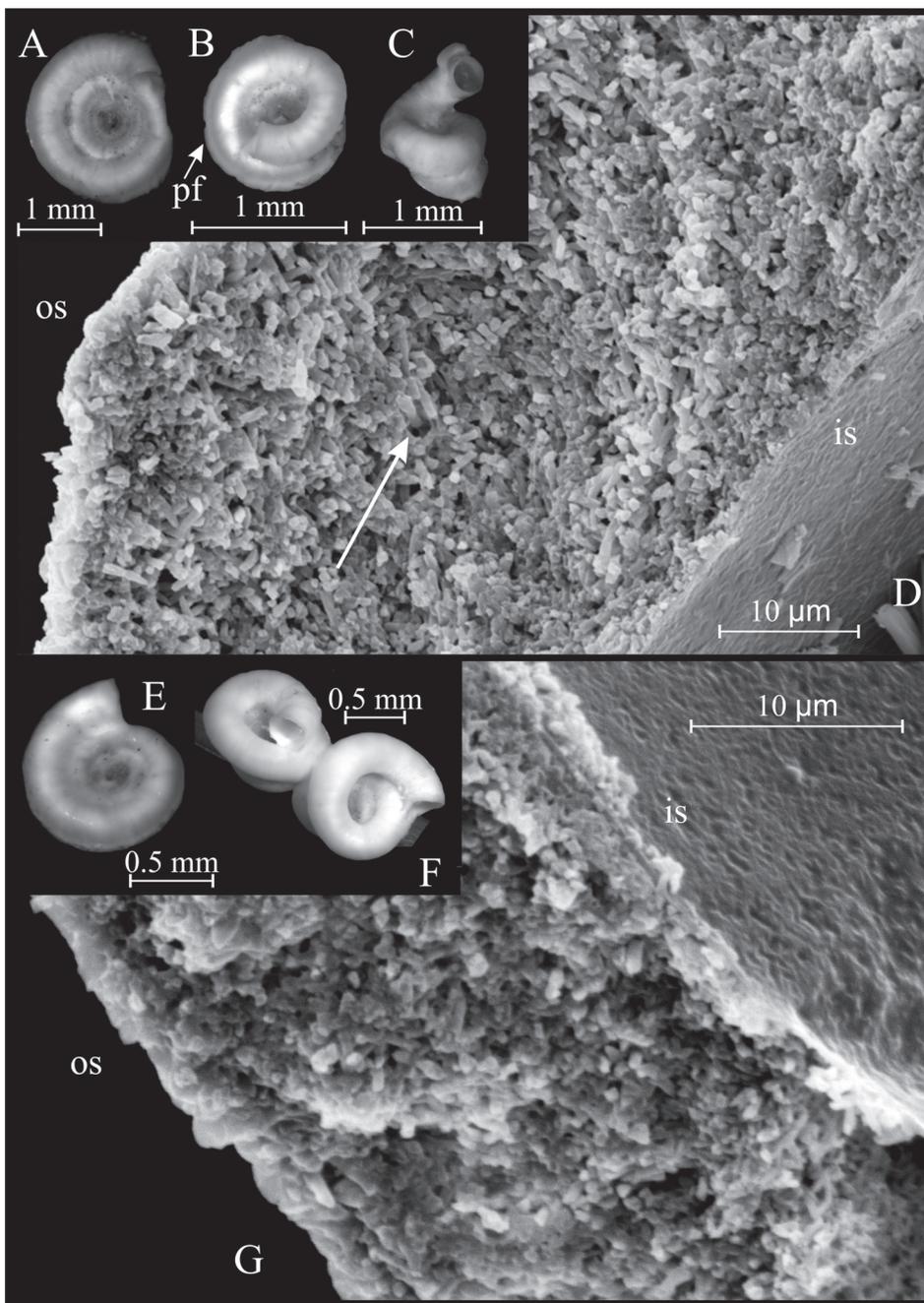


Fig. 2. A–D — *Paralaeospira claparedei*. A–C — tubes: A — planospiral tube (IPEE No. 3/2562), B — tube with overlapping coils and C — tube with mouth faced upward from substrate (IPEE No. 1/2536); D — longitudinal wall section at the external side of spiral showing IOP ultrastructure, note smaller crystals near the internal side of the wall, probably representing inner layer of oriented prismatic crystals; E–G — *Paralaeospira levinseni*. E–F — tubes: E — planospiral tube (IPEE No. 1/2398), F — tubes with overlapping coils (IPEE No. 2401); G — longitudinal wall section at the external side of the coil, showing IOP structure.

**Distribution.** Southern Atlantic and Atlantic sector of Southern Ocean: Magellan Strait (Knight-Jones P., Knight-Jones E.W., 1991) and Cape Horn (Caullery, Mesnil, 1897), probably Falkland and South Orkney Isles (Knight-Jones P., Knight-Jones E.W., 1984). Southern Indian Ocean: Kerguelen Isles (Harris, 1969); Prince Edward and Crozet Isles (Rzhavsky, 1998).

**Ecology.** The species is known from the shallow water (probably intertidally) up to 110 m deep. It lives on brown algae, seaweeds, shell fragments, and bryozoans.

**Remarks.** *P. claparedei* is known only from several records. Its tube morphology is similar to that of another rare species from the Southern Hemisphere, *P. patagonica* that may be the same species as *P. claparedei* (see Remarks for *P. patagonica*).

***Paralaeospira levinseni* Caullery et Mesnil, 1897**

Fig. 2E–G.

For descriptions see Caullery, Mesnil, 1897: 204, Pl. VIII, fig. 14 (as “*Spirorbis (Paralaeospira levinseni)*”); Knight-Jones P., Walker, 1972: 33–35, Fig. 1 a–n, 2 a, b; Vine, 1977: 17–20, Fig. 2 e, 6 c, 8 a–j.

**Material examined.** Two specimens were examined with SEM in longitudinal sections (IPEE No. 1/2398, South Georgia Island, upper sublittoral zone, on the *Macrocystis* thallus). Mineralogical composition was analyzed in one sample averaged over 3 tubes from the same sample. Outer tube morphology illustrated using specimens from IPEE No. 1/2398, and IPEE

No. 2/2401 (Bunger-Hills, Mawson Sea, depth 20–50 m, on the sea urchin spines).

**Tube morphology.** Tubes are sinistral, planospiral (Fig. 2E) either with overlapping coils (Fig. 2F) or last whorl can be evolute (Vine, 1977, Fig. 8a). Whorl diameter is up to 2.5 mm; tube walls are thin and fragile, white opaque or slightly transparent, with smooth non-porcellanous or slightly porcellanous surface; unsculptured or rarely with vestigial longitudinal keel. Dense aggregations are often formed as a result of larval gregarious settlement on adult tubes (see Knight-Jones P., Walker, 1972, Fig. 1a, 2a, b; Vine, 1977, Fig. 8a).

**Tube ultrastructures.** Wall is unilayered with irregularly oriented prismatic (IOP) structure. Crystal average size and appearance is more or less uniform throughout wall, but changes slightly from the inner to the outer zones. Crystals in the inner half of the wall are mostly isometric to slightly elongated (Fig. 2G), small (0.3–1 μm). Outer half of the wall contains relatively more elongated larger crystals ~1–1.2 μm, rarely up to 2 μm long; corresponding wall thickness is 20 μm. No distinct growth lamellae are visible. Inner organic lining is thin (0.5 μm or less).

**Tube mineralogy.** 100% calcite ( $I_{\text{calc.}}=115$ ) with high Mg content.

**Distribution.** The species is widely distributed in the Southern Hemisphere. Known throughout the South American coast from Peru in the Pacific to Uruguay in Atlantic; off many islands in Southern, South Atlantic, and South Indian Oceans; south coasts of Africa and Australia, New Zealand and Antarctica coasts (Knight-Jones P., Knight-Jones E.W., 1984).

Abbreviations: os — outer surface, is — inner surface, pf — peripheral flange. Large arrow indicates tube growth direction.

Рис. 2. А–D — *Paralaeospira claparedei*. А–С — трубки: А — планоспиральная трубка (IPEE No. 3/2562), В — трубка с налегающими оборотами, С — трубка с устьем, приподнятым над субстратом (IPEE No. 1/2536); D — продольное сечение стенки трубки с внешней стороны спирали, демонстрирующее ультраструктуру из хаотически ориентированных призматических кристаллов; заметно, что возле внутренней стороны стенки кристаллы имеют более мелкий размер, возможно, они представляют внутренний слой из призматических кристаллов, ориентированных более-менее параллельно поверхности; Е–G — *Paralaeospira levinseni*. Е–F — трубки: Е — планоспиральная трубка (IPEE No. 1/2398), F — трубки с налегающими оборотами (IPEE No. 2401); G — продольное сечение стенки на внешней стороне оборота, демонстрирующее структуру из хаотически ориентированных призматических кристаллов.

Условные обозначения: os — наружная поверхность, is — внутренняя поверхность, pf — периферийный фланг. Большая стрелка показывает направление роста трубки.

**Ecology.** The species lives from the intertidal zone up to about 50 m deep, where it occupies stones, algae, ascidians, other spirorbin tubes, and sea urchin spines.

***Paralaeospira malardi* Caullery et Mesnil, 1897**

Fig. 3A–F.

For descriptions see Caullery, Mesnil, 1897: 205, Pl. VIII, fig. 11a, b (as “*Spirorbis (Paralaeospira) malardi*”); Knight-Jones P., Knight-Jones E.W., 1977: 474–476, Fig. 7 A–H.

**Material examined.** Two specimens were examined with SEM in longitudinal sections (IPEE No. 1/2558, English Channel, depth 1–5 m, on stones). Outer tube morphology was illustrated for a specimen from the same sample.

**Tube morphology.** Tubes are sinistral, planospiral; up to 2.0 mm in whorl diameter; white opaque with distinctly porcellanous smooth surface, bearing an obtuse median keel often terminating as a tooth-like projection over tube mouth (Fig. 2A); juveniles usually lack keel. Tube aggregations are unknown.

**Tube ultrastructures.** Tube wall is visually unilayered with irregularly oriented prismatic (IOP) structure consisting of two distinct zones. Outer and middle parts of the wall are made of isometric crystals mixed with cement (Fig. 3B). Crystal size range is 0.5–3  $\mu\text{m}$ , typically about 0.5–1  $\mu\text{m}$ ; corresponding wall width is 40  $\mu\text{m}$  (Fig. 3C, D). Crystals of the innermost wall part form a thin layer, often not clearly visible in longitudinal sections and consisting of acicular crystals 3–5  $\mu\text{m}$  long and 0.5–0.8  $\mu\text{m}$  wide, lying more or less parallel to the lumen with no further orientation. A longitudinal section made near the tube base shows elongated acicular crystals similar to those of the innermost zone by shape, but sometimes slightly longer, up to 5

$\mu\text{m}$  long (Fig. 3E). Indistinct growth lamellae marked by some difference in amount of cement along smallest discernible growth lines can be observed in all sections. Inner organic lining is thick, about 5–6  $\mu\text{m}$  (Fig. 3C).

**Tube mineralogy.** Not studied due to insufficient material.

**Distribution.** This is the only *Paralaeospira* known from the Northern Hemisphere. It is recorded from north-east Atlantic off the British, Irish, French and Spanish coasts (Knight-Jones P., Knight-Jones E.W., 1977).

**Ecology.** The species lives from the lower intertidal zone to the depths of about 25 m, where it usually occupies stones, sometimes mollusk shells and decapod carapaces, rarely can be found on algae.

***Paralaeospira patagonica* Caullery et Mesnil, 1897**

Fig. 4A–I.

For descriptions see Caullery, Mesnil, 1897: 205–206, Pl. VIII, fig. 12 (as “*Spirorbis (Paralaeospira) patagonicus*”); Harris, 1969: 162, fig. 15a–l (as “*Spirorbis patagonicus*”).

**Material examined.** Two specimens were examined with SEM in longitudinal sections (IPEE No. 2/2575, Swakopmund, Namibia, low intertidal zone, on undersides of stones). Mineralogical composition was analyzed by a single tube from the same sample. Outer tube morphology was illustrated for specimens from the same sample and from IPEE No. 1/2561 (Kerguelen Island, Southern Indian Ocean, on algae, depth unknown).

**Tube morphology.** Tubes are sinistral, planospiral (Fig 4A, B) or often with overlapping coils (Fig. 4C); up to 2.5 mm in whorl diameter; thin-walled, fragile, white opaque; with smooth non-porcellanous or slightly porcellanous sur-

Рис. 3. *Paralaeospira malardi*: А — трубка с хорошо развитым срединным килем и блестящей фарфоровидной поверхностью; В–Е — ультраструктуры трубок, экземпляр № 1 [В — продольное сечение наружной стороны оборота; С — внутренняя органическая мембрана трубки, также заметны прилипшие к ней призматические кристаллы  $\text{CaCO}_3$ ; D — внутренняя поверхность трубки (органическая мембрана удалена), демонстрирующая уплощенную поверхность с удлиненными кристаллами]; Е — кристаллы непосредственно под органической мембраной]; F — экземпляр № 2, продольное сечение наружной части последнего оборота).

Условные обозначения: os — наружная поверхность, is — внутренняя поверхность, iol — внутренняя органическая мембрана.

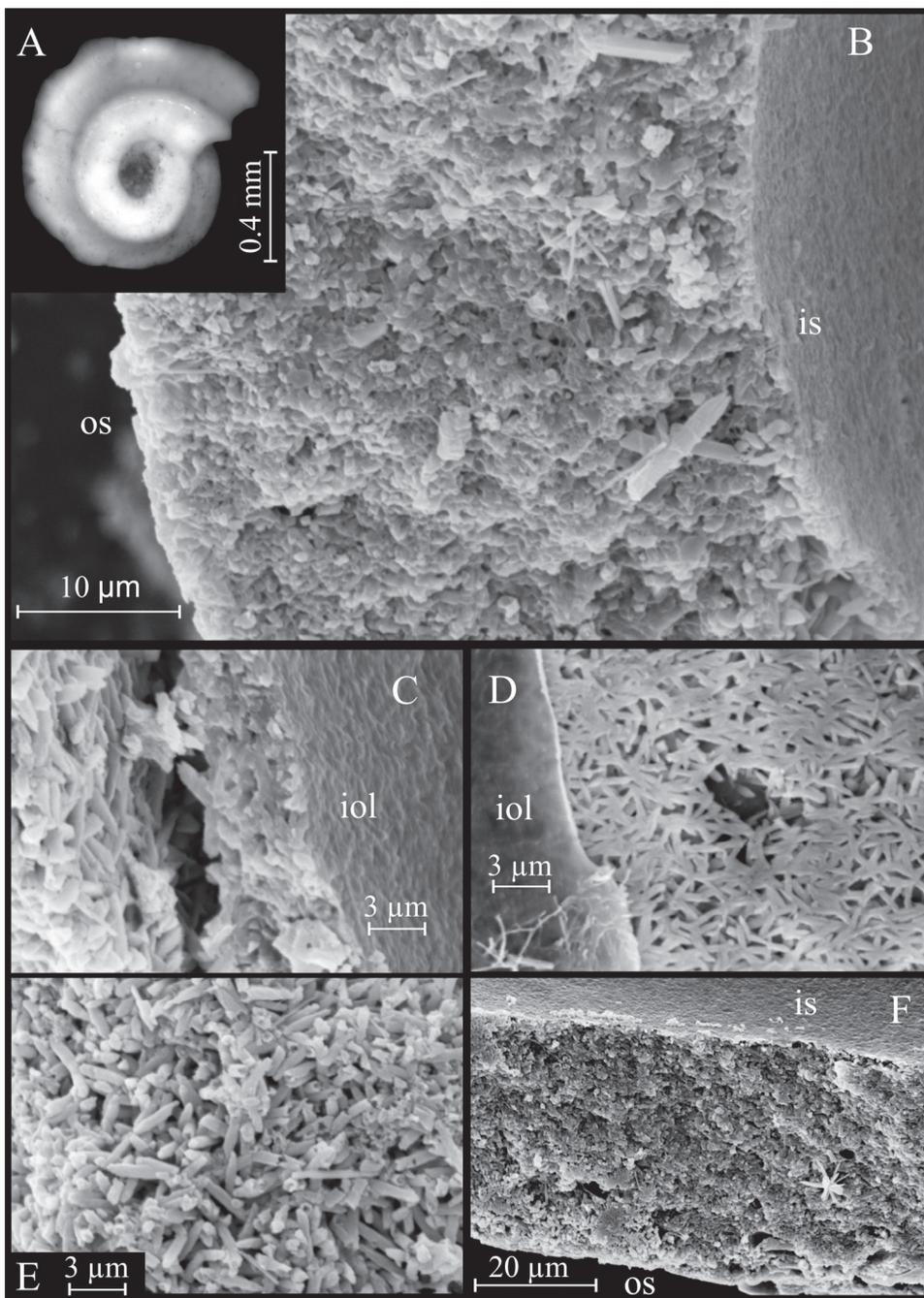


Fig. 3. *Paralaeospira malardi*: A — tube with well-developed median keel and porcellanous surface; B–E — tube ultrastructures. Specimen 1 [B — longitudinal section of the external side of the coil; C — inner organic lining, also showing embedded prismatic  $\text{CaCO}_3$  crystals; D — inner surface of the tube (organic layer removed) showing flattened surface made of elongated crystals; E — crystals near the lumen]; F — specimen 2, longitudinal section of the external side of the last whorl.

Abbreviations: os — outer surface, is — inner surface, iol — inner organic lining.

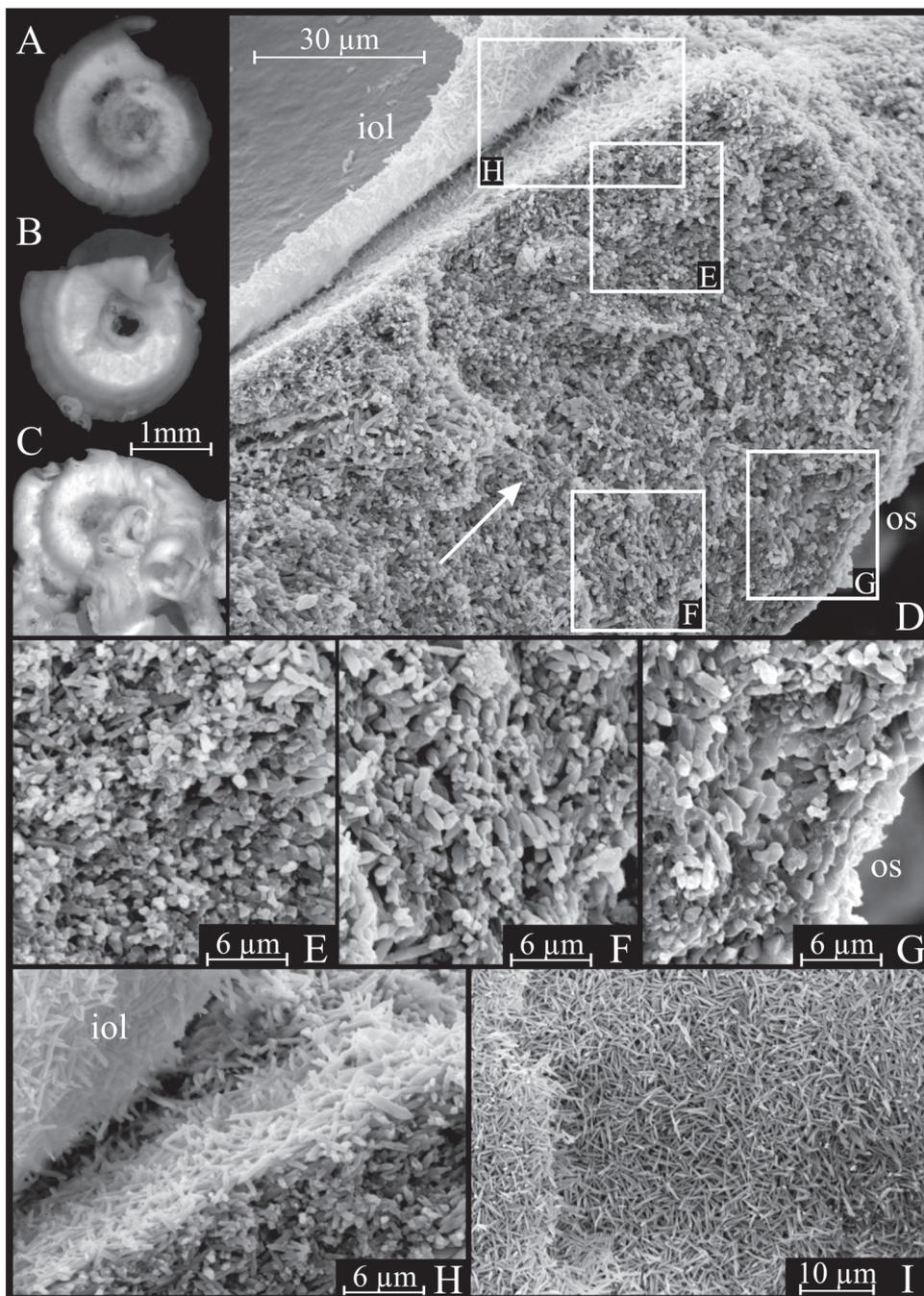


Fig. 4. *Paralaeospira patagonica*. A–C — tubes: A — planospiral tube with a single vestigial keel and pronounced growth lines, B — planospiral tube with two vestigial keels (IPEE No. 1/2561), C — aggregation of unsculptured tubes with overlapping coils (IPEE No. 2/2575); D–I — tube ultrastructures: D — general view of longitudinal section near the tube mouth, E–G — details of different parts of the wall, H — contact of the mineral wall with inner organic lining, note the adhesion of calcite crystals to the organic lining, I — tube surface just under the inner organic lining.

face (Fig. 4C), unsculptured, or bearing one or two vestigial keels (Fig. 4A, B); dense aggregations are often formed (Fig. 4C).

**Tube ultrastructures.** Wall is unilayered, with IOP ultrastructure represented by slightly elongated to distinctly elongated loosely packed crystals 1–3  $\mu\text{m}$  long; corresponding wall width is 70  $\mu\text{m}$  (Fig. 4D). Crystals are gradually becoming less elongated and more isometric (Fig. 4G) towards external tube surface. Middle part of the wall contains numerous smaller isometric crystals of uniform size and interspersed among larger elongated crystals (Fig. 4E, F). Innermost part of the wall is represented by acicular crystals (4–6  $\mu\text{m}$  long and  $\sim 0.5$   $\mu\text{m}$  wide) lying parallel to the lumen (Fig. 4H, I). Growth lamellae are distinct and marked by variations of crystal size. Parabolic lamellae symmetrical, their axes are located centrally in the wall. Inner organic lining is 3–6  $\mu\text{m}$  wide.

**Tube mineralogy.** 100% calcite ( $I_{\text{calc}}=73$ ). Calcite has high Mg content (main peak at 34.61 2 $\theta$ ).

**Distribution.** The species is known through the south coast of Africa from Namibia to Port Elisabeth, Republic of South Africa; off the south of Chile and some islands of South Atlantic and Atlantic sector of Southern Ocean (Knight-Jones P., Knight-Jones E.W., 1984); off some islands of Southern Indian Ocean (Rzhavsky, 1998).

**Ecology.** This is a shallow water species living in the intertidal and upper sublittoral zones, but exact bathymetric data are absent. It occupies bryozoans, algae, and undersides of stones.

**Remarks.** *P. patagonica* is known only by several records and is similar in external tube morphology as well as in opercular and chaetal structure to another rare species from Southern Hemisphere, *P. claparedei*, which in our opinion may be a synonym of the *P. patagonica*. General appearance of wall ultrastructures in these two species also shows high similarity, like in all studied Paralaespirini. Although in *P. claparedei* we have not observed an inner layer made of oriented elongated crystals, similar to that found in *P. patagonica*, this may be due to scarcity of studied material. Additional morphological studies are needed to clarify the relationship between these two species; here we consider them both valid.

### Tube morphology of species not covered with the SEM study

External tube morphology markedly varies among six species of *Paralaespira* not covered with SEM study. Two of these species, *P. pseudotenuis* Rzhavsky, 1997 and *P. sicula* Knight-Jones et Knight-Jones, 1994, were examined by the second author. General morphology of *P. pseudotenuis* tube is similar to those of *P. claparedei*, *P. levinseni*, and *P. patagonica* (Fig. 5A, B). Tubes of *P. sicula* are usually evolute and have quadrangular cross-section with very characteristic sharp keels (Fig. 5C, D).

Tube morphology of other species of *Paralaespira* is known from literature only. *P. monacantha* (Augener, 1923) has tubes similar to those of *P. claparedei*, *P. levinseni*, and *P. patagonica* and often produce aggregations (Fig. 5E). *P. parallela* Vine, 1977, like *P. malardi*, is

Abbreviations: os — outer surface, is — inner surface, iol — inner organic lining. Large arrow indicates the direction of tube growth.

Рис. 4. *Paralaespira patagonica*. А–С — трубки: А — планоспиральная трубка с одним зачаточным продольным килем и выраженными линиями нарастания, В — планоспиральная трубка с двумя зачаточными продольными килями (ИПЕЕ № 1/2561), С — агрегация нескульптированных трубок с налегающими оборотами (ИПЕЕ № 2/2575); D–I — ультраструктуры трубок: D — общий вид продольного сечения близ устья трубки; E–G — различные участки стенки, более крупно, H — контактовая зона стенки и внутренней органической мембраны, хорошо заметно прилипание кристаллов кальцита к мембране, I — внутренняя поверхность трубки и облик кристаллов непосредственно под мембраной.

Условные обозначения: os — наружная поверхность, is — внутренняя поверхность, iol — внутренняя органическая мембрана. Большая стрелка показывает направление роста трубки.

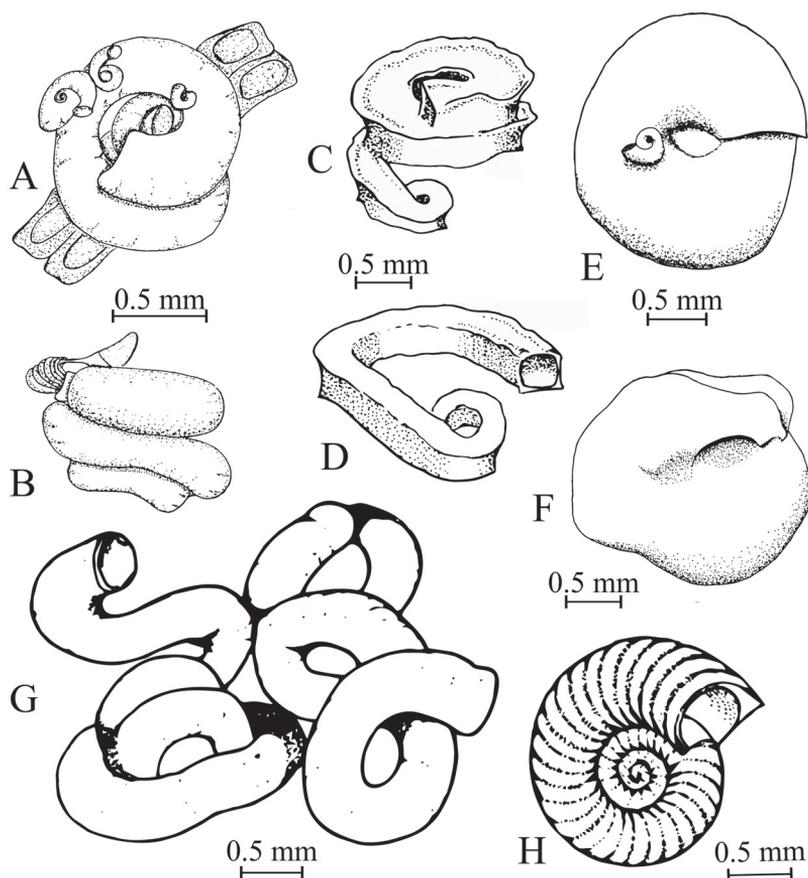


Fig. 5. Tubes of *Paralaespirini* species not covered in the present study. A, B — *Paralaespirina pseudotenius* (from Rzhavsky, 1997); C, D — *P. sicula* (from Knight-Jones, Knight-Jones, 1994); E — *P. monacantha* (from Vine, 1977); F — *P. parallela* (from Vine, 1977); G — *P. aggregata* (from Harris, 1969); H — *P. adeonella* (from Day, 1963).

Рис. 5. Морфологическое разнообразие трубок представителей *Paralaespirini*, которые не изучались авторами в ходе настоящего исследования. A, B — *Paralaespirina pseudotenius* (из Rzhavsky, 1997); C, D — *P. sicula* (из Knight-Jones, Knight-Jones, 1994); E — *P. monacantha* (из Vine, 1977); F — *P. parallela* (из Vine, 1977); G — *P. aggregata* (из Harris, 1969); H — *P. adeonella* (из Day, 1963).

always solitary and has planospiral hard tubes that are, however, non-porcellanous and lack longitudinal keel(s). The characteristic feature of the *P. parallela* tube is the mouth completely covering the preceding whorl (Fig. 5F). *P. aggregata* (Caullery et Mesnil, 1897), like *P. malardi*, has porcellanous tubes, but unlike *P. malardi*, it lacks any longitudinal sculpture. Besides, tubes of *P. aggregata* are never planospiral, coils always overlap and the last coil is usually straightened. This species always forms

dense aggregations (Fig. 5G). *P. adeonella* (Day, 1963) known only from its original description, has thick-walled, hard and vitreous tubes with well-pronounced transverse ridges (Fig. 5H). Similar tubes are not known for other *Paralaespirina* spp. and are more common in the genus *Protolaespirina* from tribe Romanchellini. Unfortunately, data on incubation method and morphology of abdominal chaetae that could have helped to clarify systematic position of *P. adeonella*, were not provided.

## Discussion

**Patterns and variations.** Although three of the four species described herein have similar tube ultrastructures, variability in tube morphology among all species of *Paralaeospira* is very high. The only stable characters are the coiling direction (always sinistral) and the absence of or small number of keels (usually one, rarely two). Mineralogical tube composition in all three studied *Paralaeospira* species was purely calcitic, and all studied species had the same ultrastructural type (IOP) composed of slightly elongated to isometric angular crystals lying loosely with no clear orientation of their long axes (Table 2).

*P. malardi* shows distinct characteristics (wall consisting mostly of isometric crystals with high content of cement, probably of organic nature), allowing its recognition among studied *Paralaeospira* spp. by ultrastructure only. Tube morphology of this species also differs from those of other studied species by being more thick-walled, always planospiral, white opaque with distinctly porcellanous surface, and bearing an obtuse median longitudinal keel that often terminates as a tooth-like projection over the mouth. Opaque tube appearance is of *P. malardi* is probably the result of high content of cement, which is more abundant, than in other studied species. Other examined species of *Paralaeospira* are characterized by relatively thin-walled tubes, sometimes even semi-transparent, with non-porcellanous or slightly porcellanous surfaces; coiling can vary from planospiral to overlapping, or last coil can even be evolute; longitudinal keel, if present, is vestigial. Additionally, all these species may form aggregations, whereas *P. malardi* is always solitary. *P. malardi* is also isolated biogeographically as it is the only species of the genus *Paralaeospira* known from the Northern Hemisphere, while others are restricted to the Southern Hemisphere. Nevertheless, general appearance of tube ultrastructures is still very similar among all studied Paralaeospirini.

Inner organic lining in *P. malardi* and *P. patagonica* is underlain by a thin layer of acic-

ular crystals (length up to 5  $\mu\text{m}$ , width 0.3–0.5  $\mu\text{m}$ ), lying parallel to the lumen with no further orientation. A similar thin layer built of acicular crystals was also observed for the non-spirorbin serpulid *Ficopomatus enigmaticus* (Fauvel, 1923) by Aliani et al. (1995). Such a layer was not mentioned for any species studied by Vinn et al. (2008a), probably due to different methods of sample preparation, which always included treating by aggressive agents. The nature of this “layer” is probably mechanical arrangement of elongated rice grain-shaped crystals near the lumen during the tube formation, and therefore, its presence is not indicative of close phylogenetic relationship. The presence of inner layer with acicular crystals still cannot be excluded for two other species of *Paralaeospira* (*P. levinseni* and *P. claparededei*), but this needs to be clarified with new material.

**Comparison with other Serpulidae.** The unilayered IOP walls found in *Paralaeospira* are very common among non-spirorbin serpulids (Vinn et al., 2008a), and therefore, ultrastructures are not diagnostic. It is easy to distinguish *Paralaeospira* from all these taxa by external morphology, in particular, clockwise tube coiling combined with small size. Detailed comparisons with other spirorbin tribes will be provided in the subsequent parts of the present series.

**Phylogenetic significance.** Unilayered tube with IOP ultrastructure of *Paralaeospira* is very similar to IOP ultrastructures described for serpulids of “clade B” *sensu* Kupriyanova et al. (2009). This clade includes genera such as *Filograna*, *Salmacina*, *Protis*, *Vermiliopsis*, *Metaveremia*, *Protula*, and *Chitinopoma*. These genera form a sister-group to monophyletic spirorbins (Kupriyanova et al., 2006, 2009). Given that in many spirorbins ultrastructures appear more derived than those of Paralaeospirini (Ippolito, Rzhavsky, 2008), the hypothesis that Paralaeospirini having simplest method of embryos incubation is the most primitive spirorbin group is well supported. Therefore, our data confirm a closer relationship of primitive spirorb-

Table 2. Main tube characters for studied Paralaospirini. Abbreviations: arag — aragonite; calc — calcite.  
Таблица 2. Основные черты строения трубок изученных видов Paralaospirini. Условные обозначения: arag — арагонит; calc — кальцит.

Species	External morphology				Mineralogy		Ultrastructures			
	Max. coil diameter (mm)	Longitudinal keels	Transparency	Surface	arag/calc content (%)	Mg content in calc	Dense outer layer	Main layer and crystal length (µm)	Dense inner layer	Cement content
<i>P. claparedei</i>	2.5	0	opaque or somewhat transparent	smooth, non-porcellanous or slightly porcellanous	0/100	high	no	IOP 1–2 (rarely 3)	no	low
<i>P. levinsoni</i>	2.5	0–1 vestigial	opaque or somewhat transparent	smooth, non-porcellanous or slightly porcellanous	0/100	high	no	IOP 1–1.2	no	low
<i>P. malardi</i>	2.0	1 distinct median	opaque	smooth, distinctly porcellanous	no data	no data	no	IOP 1–3 (5 near lumen)	no	medium
<i>P. patagonica</i>	2.5	0–2 vestigial	opaque or somewhat transparent	smooth, non-porcellanous or slightly porcellanous	0/100	high	no	IOP 1–3 (4–6 near lumen)	no	low

ins to “clade B”, rather than to other serpulids. However, tubes belonging to the listed genera of “clade B” are characterized by predominantly aragonite mineralogy with only little calcite (Bornhold, Milliman, 1973; Vinn et al., 2008a; Smith et al., 2013). The only species that may have calcitic tubes is *Filograna implexa* (Berkeley, 1835) (see discussion in Vinn et al., 2008a: 646).

Aragonitic mineralogy of serpulid tubes is interpreted as the most ancient (Vinn, Mutvei, 2009) according to the well-accepted hypothesis that seawater chemical environment of Late Carboniferous – Early Jurassic interval, when true serpulids first appeared in paleontological record, was more suitable for aragonite than for calcite precipitation. In frame of this hypothesis, first spirorbins, which appear later in the “calcitic” seas of the Late Jurassic – Early Cretaceous, should have calcitic tubes. This agrees with plesiomorphy of Paralaeospirini inferred from the simplest incubation method among Spirorbinae. However, why aragonitic serpulids should preserve their mineralogy through the “calcitic” epoch, as well as why calcitic serpulids would not switch their mineralogy to aragonite according to Recent environments, has no good explanation now.

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